Flatfish and the origins of European marine fishing

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Abstract

During the Early Medieval period, most fish consumed in areas around the southern North Sea were taxa which could have been caught in freshwater habitats. From around the 11th century CE significantly more marine species appear in inland archaeological deposits — the so-called 'marine fish event horizon'. As flatfish are ecologically varied, they could have been amongst the first marine taxa exploited, but so far, their role in this economic transition has been unclear due to difficulties in identifying marine, estuarine, and riverine flatfish morphologically.

To assess the role of flatfish in the marine fish event horizon, a timeline is constructed for the frequency of six species from thirteen sites around the southern North Sea to explore how flatfish fisheries changed per region during the Medieval period (6-16th centuries CE).

Firstly, flatfish identifications are refined via morphological and molecular approaches. It is found that comparative osteology and geometric morphometrics have limited applicability on archaeological material, however, a more thorough understanding of flatfish morphology is described. ZooMS identifications (n=467) using eight newly described peptide markers, reveal a relative decrease of flounder (*Platichthys flesus*) and an increase of plaice (*Pleuronectes platessa*) throughout the Medieval period.

Secondly, multi-isotope analysis of a substantial dataset ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$; n=476) indicates an early onset of marine fishing and a continuation of freshwater fisheries of flatfish throughout the Medieval period. Changes in isotope values and species abundances could be linked to a more marine-oriented fishing practice across the southern North Sea in the High Medieval period.

This first multi-disciplinary study of flatfish remains has revealed species-specific interpretations about where and when people exploited flatfish, providing insight into economic, social and environmental changes in the North Sea area during a key period of economic transition in the Medieval period.

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“BioArCh is more than a building”, might not be our lab’s official slogan, but it couldn’t be truer. This amazing group of people make you feel at home in a foreign country separated from friends and family. And they are pretty smart too.
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"Fish are friends, not food" - Bruce, *Finding Nemo*

Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references.

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This thesis represents a compilation of chapters which include some that are in paper format. Chapter 5 is a multi-authored paper that has already been published in an international peer reviewed journal. Chapters 3, 4 and 6 are in various stages of formatting for submission for publication.

Chapter 3 is intended to be submitted imminently. The author of this thesis selected the reference specimens, completed the analysis and drafted the paper. The paper will be co-authored by Wim Wouters (Royal Belgian Institute of Natural Sciences). He helped select the skeletal elements of interest and provided museum reference material to work with. He further provided feedback on the results and the summarising texts for each element as well as the discussion. Anne-Marie Wittek (ADIA, Association pour la Diffusion de l'Information Archéologique) patiently illustrated all the bones.

Chapter 4 is intended to be submitted imminently. The author of this thesis has been responsible for making the photographs, performing the analysis and interpreting the results, making the figures, and drafting the paper. The paper will be co-authored with Antonio Profico (University of Pisa), who helped with the coding and analysis of this study. He also provided feedback on the manuscript. Samples for this study were provided by Tarek Oueslati (University of Lille) and the York Archaeological Trust.

The majority of Chapter 5 is formed of a paper recently published in Royal Society Open Science (Dierickx, K., Presslee, S., Hagan, R., Oueslati, T., Harland J., Orton, D., Alexander, M., Hendy, J., Harvey. V. (2022). Peptide mass fingerprinting of preserved collagen in archaeological fish bones for the identification of flatfish in European waters. *Royal Society Open Science*, 9(7), 220149.). It is a multi-authored paper that includes a number of individuals that played various roles in the research. The author of this thesis has been responsible for conceiving the idea for this study, sample collection, lab work, data analysis, interpretation of the zooarchaeological results and drafting the paper. Modern museum specimens were provided by the York Zooarchaeology Lab and the Royal Belgian Institute for Natural Sciences. Tarek Oueslati (University of Lille), the York Archaeological Trust and Cecily Spall (Field Archaeology Specialists) provided the archaeological samples. Lab work and analyses was done with the training by and support of Samantha Presslee (University of York), Richard Hagan (University of York), Jessica Hendy (University of York), Virginia Harvey (University of York; University of Chester), and the Bioscience Technology Facility and Chemistry Department at the University of York. Results of the archaeological analysis were analysed and discussed with the help of Tarek Oueslati and Jen Harland (University of York; University of the Highlands and Islands). Michelle Alexander (University of York) and David Orton (University of York) provided feedback on the manuscript. The general archaeological application of collagen peptide mass fingerprinting has not yet been published and it is intended to include these results in the same publication as the isotope results (Chapter 6).

Chapter 6 is further from publication in the current format. The author of this thesis is responsible for sample selection, lab work, data analysis, making figures, interpreting the zooarchaeological results, and drafting the paper. The publication will be co-authored by Michelle Alexander and David Orton, who advised on the analysis and provided feedback on the manuscript, Matt von Tersch (University of York), who assisted with the lab work, and Peter Schauer (University of York), who advised on the statistical analysis of the data. This chapter will be shortened, several paragraphs will be added as supplementary information, and parts of other chapters of this thesis (Chapters 1, 2 and 7) will be added when it will be submitted for publication.

Preface

There are plenty of fish in the sea, is what is often said. But where can you find the ones you want? Where to fish? That might be the question people throughout the Medieval period once wondered in western Europe. We don't know this for sure, but what we do know from archaeological and historical research is that those people got a taste for saltier fish from the open seas around the 11th century CE. While before they were relying mostly on locally caught fish from the rivers and ponds behind their houses or near the shore, they ventured more and more into the North Sea to capture plenty of big and wild fish. Cod, haddock, herring, and whiting all became popular for daily consumption. Pike, salmon, and cyprinids, however, became less of a fishing focus for medieval people. What the precise reason for this transition is, is not clear. There were probably many factors at play that changed the customs of fisheries. The rise of Christianity, better technology, pollution of freshwater systems, increase of human population, urbanisation, climate change, and the migration of Scandinavians have all been suggested as reasons for the marine fish event horizon.

There is one group of popular fish we haven't mentioned yet, simply because we are not sure how they fit in the story of the marine fish event horizon. Were they highly favoured during the Early Medieval period or more during the Late Medieval period? Where were they captured, in freshwater or marine environments? The reason we don't know is because this group, the flatfish, are very diverse in species, but also in ecology. Some species and early life stages can occur in freshwater environments, while adult flatfish often live in open marine habitats. People can thus catch them wherever. Previous archaeological research of flatfish has not been able to answer the questions of which fish was captured where since species look very similar osteologically and molecular techniques are needed to distinguish between different catch habitats. We do know that they were being consumed at the start of the Medieval period, were quite popular throughout the Medieval period and they remain so till this day. But to learn more about their precise exploitation and changes within we have to dive deeper into their remains and find novel ways to identify species and infer catch habitats. This is exactly what this dissertation will do.

One might wonder what the purpose of such a study is. A flatfish is only good for eating, right? Why should we study where people were fishing these fish centuries ago? There might not be a direct practical reason for this, but understanding how and why people changed fisheries, can tell us much about our history and how we coped with changes in the past, which is of course very relevant in this 21st century. We can also better understand what the situation of the flatfish and the health of the stocks were in the Medieval period. Perhaps these species have been highly affected by the millennium long exploitation, or perhaps, they are still doing as well as they always have since before humans developed a taste for them. We can only know if we start to explore their past. Without this information, modern day management of these economically and ecologically important fish and their habitats might not be as successful as we would like it to be.

Chapter 1. Research questions and literature review

Flatfish are bizarre looking fish that live on the bottom of the continental seas, such as the North Sea. Throughout history, many flatfish from this sea have been an important economic group of species as they are highly valued for consumption.

Archaeological flatfish studies have been limited in the past due to two issues: a lack of species identifications, and our previous inability to differentiate between habitats a fish has been living in and was most likely captured from. It is therefore unknown which species was being consumed and when and where flatfish were being caught. This study aims to address these issues to ultimately construct a timeline for each exploited flatfish species and explore how flatfish fisheries changed during the Medieval period around the southern North Sea, particularly in relation to the marine fish event.

The following research questions will be addressed:

1) Which flatfish species were fished throughout the Medieval period (600 – 1600 CE) and is there a difference in importance of certain species before and after the marine fish event and between regions?

   In order to address this question, the following factors need to be established: can we distinguish the main commercial and archaeologically recovered flatfish species, and if so, which methodology is the most useful for archaeological remains? In order to address this, three methodologies frequently applied in zooarchaeological studies will be evaluated to test for their ability to distinguish flatfish species:

   - Comparative osteology: some reference work exists for a few flatfish species (e.g., Wouters *et al*., 2007). However, this method will be analysed in more depth to include other common flatfish species and skeletal elements as well and to (re-)evaluate diagnostic criteria of their most common skeletal elements and species recovered in archaeological remains (chapter 3).
   - Geometric morphometrics: vertebrae of flatfish have been well-known to show limited diagnostic features to distinguish between the most common species (e.g., Watt *et al.,* 1997; Wouters *et al.,* 2007), yet are common in the archaeological record. For this reason geometric morphometric analysis will be applied as an alternative morphological and non-destructive tool to identify flatfish vertebrae as it can detect less easily visible differences between taxa (chapter 4).
   - ZooMS, or collagen peptide mass fingerprinting, is a molecular alternative that has proved to be useful to identify fish remains in the past, especially as it can be used on heavily fragmented material or elements with no diagnostic features as well (e.g., Harvey *et al.,* 2018). However, at the moment, there is no general overview of biomarkers that can be used to identify flatfish species in the North Sea area, which will have to be described after analysis (chapter 5).

Once flatfish species can be identified accurately, the following question arises: which species of flatfish do we find in archaeological sites dating from the Medieval period? This will be answered by performing a large-scale analysis of species presences in archaeological sites. For this, selected archaeological sites (chapter 2) will be re-analysed with the identification techniques developed earlier to compare sites, regions and time periods to see which species were being caught when and where throughout the Medieval period (see respective chapters).

2) Where were flatfish captured throughout the Medieval period, and is there a difference between before and after the marine fish event horizon and between regions?
For this research question, bulk stable isotope analysis of carbon, nitrogen and sulfur on archaeological samples from the selected sites is used to provide insight into the living habitat and catch environment of archaeological flatfish remains (chapter 6).

The following chapters will discuss the different aspects of the research that will answer these questions. To better understand the historic exploitation of this group of fish and the onset of marine fishing in Northwestern Europe in general, a literature review of what is currently known on flatfish biology, the North Sea geographic region and historic fish exploitation will be provided in the remainder of this chapter. A literature review of the different methodologies applied in this study will also provide a better background, which allows a better interpretation of the data of the archaeological analyses.

1.1 Flatfish biology

1.1.1 Taxonomy

Flatfish is the common name for fish belonging to the taxonomic order of Pleuronectiformes (Teleostei; Acanthopterygii). The first classification of these fish was done by Linnaeus (1758), who placed all described species in the genus *Pleuronectes*. Later authors divided species into different genera (e.g. Lacepède, 1802; Rafinesque, 1810; Cuvier, 1816; Bonaparte, 1833; Bleeker, 1862; Günther, 1862), which were assigned to several subfamilies of the Pleuronectidae placed in the suborder of Heterosomata (Jordan & Goss, 1889). It wasn't until the late 19th century that flatfish were classified into different families, with the first division made between the Pleuronectidae and Soleidae (Jordan & Everman, 1898). In the following decades authors proposed different classifications with new subfamilies or families (e.g., Regan, 1910; Jordan, 1923; Regan, 1929; Norman, 1934). The order Heterosomata, later Pleuronectiformes, was also divided into two suborders, Psettodoidae and Pleuronectoidae (Regan, 1910). These suborders are still valid today as Psettodoidei and Pleuronectoidei and the division between them is verified by phylogenetic analysis (e.g., Berendzen & Dimmick, 2002; Harrington *et al.*, 2016; Betancur-R *et al.*, 2017). After the revision by Norman (1934), flatfish consisted of two suborders and five families of which two also had subfamilies: Psettodidae, Cynoglossidae, Soleidae, Bothidae (Paralichthinae, Bothinae, Scophthalminae), and Pleuronectidae (Pleuronectinae, Poecilopsettinae, Samarinae, Paralichthodinae, Rhombosoleinae). Since the earliest classifications, these early subfamilies have been elevated to family level (Hubbs, 1945; Amaoka, 1969; Lauder & Liem, 1983; Chapleau &

Table 1.1. Overview of the taxonomic classification by Nelson *et al.* (2016) of flatfish present in the North Sea. References for the occurrences can be found in table 1.2. Only the mostly used English name is provided here. Trivial names of fish are complex and many regions use local names. These species also have common names in other relevant languages.

Order	**Suborder**	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**	**Author**	**Common name**
Pleuronectiformes	Pleuronectoidei	Citharoidea	Citharidae			*Citharus*	*linguatula*	(Linnaeus 1758)	Spotted flounder
		Pleuronectoidea	Scophthalmidae			*Lepidorhombus*	*boscii*	(Risso 1810)	Four-spot megrim
							whiffiagonis	(Walbaum 1792)	Megrim
						Scophthalmus	*maximus*	(Linnaeus 1758)	Turbot
							rhombus	(Linnaeus 1758)	Brill
						Zeugopterus	*norvegicus*	(Günther 1862)	Norwegian topknot
							punctatus	(Bloch 1787)	Topknot
							regius	(Bonnaterre 1788)	Eckström's topknot
			Pleuronectidae	Microstominae		*Glyptocephalus*	*cynoglossus*	(Linnaeus 1758)	Witch
						Microstomus	*kitt*	(Walbaum 1792)	Lemon sole
				Hippoglossinae		*Hippoglossus*	*hippoglossus*	(Linnaeus 1758)	Halibut
				Pleuronectinae	Hippoglossoidini	*Hippoglossoides*	*platessoides*	(Fabricius 1780)	Long rough dab
						Limanda	*limanda*	(Linnaeus 1758)	Dab
					Pleuronectini	*Platichthys*	*flesus*	(Linnaeus 1758)	Flounder
						Pleuronectes	*platessa*	Linnaeus 1758	Plaice
			Bothidae			*Arnoglossus*	*laterna*	(Walbaum 1792)	Mediterranean scaldfish
		Soleoidae	Soleidae			*Buglossidium*	*luteum*	(Risso 1810)	Solenette
						Microchirus	*variegatus*	(Donovan 1808)	Thickback sole
						Pegusa	*lascaris*	(Risso 1810)	Sand sole
						Solea	*solea*	(Linnaeus 1758)	Dover sole
			Cynoglossidae	Cynoglossinae		*Cynoglossus*	*browni*	Chabanaud 1949	Nigerian tonguesole

Keast, 1988) and new taxa were created (Achiropsettidae by Evseenko, 2000; Cyclopsettidae by Betancur-R *et al.*, 2017; Oncopteridae by Campbell *et al.*, 2019), resulting in the current taxonomic classification of this order, following Nelson *et al.* (2016) (table 1.1).

According to Fricke *et al.* (2022), there are currently 818 species within Pleuronectiformes divided into 15 families, with the Cyclopsettidae (see below) not accepted. Their number will probably continue to increase in the following years, as might be expected from the new species of flatfish still being discovered every year from all around the world (e.g., Fricke *et al.*, 2017; Amaoka & Ho, 2018; Tongboonkua *et al.*, 2018; Fricke, 2019; Fricke *et al.*, 2019; Naito & Endo, 2019; Voronina, 2019; Munroe, 2021).

1.1.2 Phylogeny

Understanding relationships between flatfish species is relevant for the identification methods used in this thesis. It can be hypothesised that closely related species might be more similar in their osteology and thus are more prone to error in identification using osteology or geometric morphometrics, depending on their ecomorphological adaptations. For the same reason, closely related species might have similar collagen fingerprints that can be confused with each other (figure 1.1).

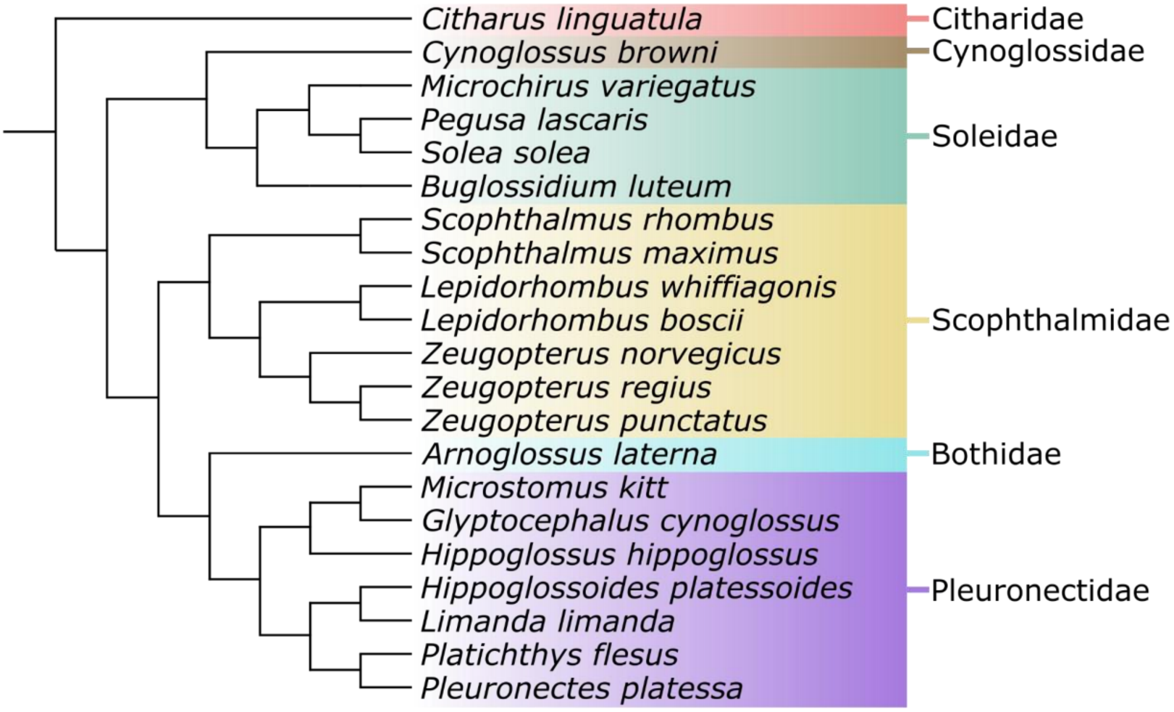

Figure 1.1. Cladogram of North Sea Pleuronectiformes based on Tinti *et al.* (2000), Chanet (2003), and Betancur-R *et al.* (2017). References for the occurrences can be found in table 1.2.

The phylogeny of flatfish has long been of interest, since there are no other groups of vertebrates that have such an asymmetrical shape and undergo such dramatic orbital migration during their life. The phylogenetically closest living species to flatfish do not share any of their peculiar morphological characters.

Based on a phylogenetic study combining nuclear and mitochondrial DNA as well as fossil calibrations, it appears that the Centropomidae are closely related to the Pleuronectiformes and both fall within the Carangimorpha containing Carangiformes, Istiophoriformes and several smaller families such as Polynemidae, Toxotidae and Sphyraenidae (Betancur-R *et al.*, 2017).

Pleuronectiformes appear to be monophyletic based on molecular and morphological studies (Cooper & Chapleau, 1998; Berendzen & Dimmick, 2002; Betancur-R *et al.*, 2013; Betancur-R & Ortí, 2014; Campbell *et al.*, 2014; Harrington *et al.,* 2016; Betancur-R *et al.*, 2017). The unique morphological adaptations of flatfish, such as the asymmetry, the extended dorsal fin and the protruding eyes thus evolved once. Different molecular studies, however, show that the relationships between genera and families is not always agreed upon (e.g., Verneau *et al.*, 1994; You *et al.*, 2005; Pardo *et al.*, 2005; Azevedo *et al.*, 2008; Roje, 2010; Sharina & Kartavsev, 2010; Campbell *et al.*, 2014; Harrington *et al.*, 2016; Ji *et al.*, 2016; Betancur-R *et al.*, 2017; Vinnikov *et al.*, 2018). Furthermore, the current taxonomic classification by Nelson *et al.* (2016) does not agree with three recent phylogenetic analyses by Harrington *et al.* (2016), Betancur-R *et al.* (2017), and Atta *et al.* (2022). The genera *Cyclopsetta, Paralichthys, Syacium, Citharichthys* and *Etropus* are more related to the genera classified in the family Bothidae than to those of Paralichthyidae (Harrington *et al.,* 2016; Betancur-R *et al.*, 2017) in which they are classified according to Nelson *et al.* (2016). Betancur-R *et al.* (2013; 2017) and Atta *et al.* (2022) therefore proposed a new family, Cyclopsettidae. According to Betancur-R *et al.* (2017), one genus classified in Rhombosoleidae, two in Achiropsettidae and the species *Oncopterus darwinii* Steindachner 1874 fall in the phylogenetic clade containing the Pleuronectoidae instead of the Soleoidae in which they are classified (Nelson *et al.*, 2016; Betancur-R *et al.*, 2017), even though the same species form a sisterclade to the Achiridae according to Harrington *et al.* (2017). *Microchirus* is not monophyletic based on an mtDNA phylogenetic analysis unless the genus *Monochirus* is included (Tinti *et al.*, 2000; Infante *et al.*, 2004). Some studies using nDNA or whole-genome analyses found that one species of Psettodidae is more related to other Perciform fish than to Pleuronectoided species, meaning that the Pleuronectiformes is a paraphyletic order (Campbell *et al.*, 2013; Lü *et al.*, 2021). However, since most phylogenetic analyses, both molecular and morphological, support the monophyly of Pleuronectiformes, it is also retained in this study.

All extant Pleuronectiformes are highly asymmetrical as adults with one orbit that has migrated over the midline of the head and usually one paler lateral side. The frontal of the blind side also migrates to the eyed side, while the ethmoid grows larger. Their eyes also protrude because of the recessus orbitalis, a muscular organ. The dorsal fin is extended anteriorly and has no spines. Precaudal vertebrae have anteriorly curved neural spines (figure 1.2). The asymmetry causes parts of the neurocranium and, depending on the taxon, also the jaws, pectoral girdle and vertebrates to be asymmetrical as well (Chapleau, 1993; Friedman, 2008). Paired elements can differ strongly from each other (see chapter 3).

1.1.3 Evolution

Besides knowing the phylogenetic relationships between species, a timing of divergence between taxa could also be of use to estimate how alike different species are in their morphology or collagen peptide mass fingerprints. The longer two species have been diverged from each other, the more differences might have appeared.

A phylogenetic analysis with fossil calibration estimates that the Pleuronectiformes diverged from the other percomorph lineages, such as the Polynemidae, during the Paleocene (Harrington *et al.*, 2016). With fossil calibration and phylogenetic analysis, it is estimated that the divergence of flatfish from the other Carangimorph taxa occurred quite fast (between 7.96 Myr and 470 kyr) and the earliest body plans of flatfish as we know them today may have appeared during the (late) Paleocene or (early) Eocene (Harrington *et al.*, 2016). The earliest known specimens of Pleuronectiform fish date from the Ypresian and Lutetian in the Lower Eocene found in Bolca (Italy) and France and include several different genera with distinct asymmetry of their orbits: *Amphistium* Agassiz 1935, *Eobothus minimus* Agassiz 1834, and one specimen of *Heteronectes* Friedman 2008 (Chanet, 1999; Friedman, 2008; 2012). Another fossil flatfish dating from the middle Eocene is *Eobuglossus eocenicus* Chanet 1994 from Egypt (Chanet, 1994). *Eobuglossus eocenicus* and *Turahbuglossus cuvilieri* Chabanaud 1937 are the oldest known representatives of the Soleidae based on several apomorphies. This indicates that the families Soleidae and Cynoglossidae were already diverged from each other and from the other Pleuronectiform families over 40 million years ago during the Eocene (Chanet, 1994). Also other families, like Citharidae, were already diverged, since *Eobothus minimus* is placed in the bothoid lineage (=Pleuronectoidea) and not Citharidae by Chanet (1999). Several other extinct taxa within Pleuronectiformes are known. Sakamoto *et al.* (2003) describe *Oligoscophthalmus weissi* Sakamoto *et al.* 2003*,* a scophthalmid specimen from the Rupelian (Oligocene), found in Germany. On Sakhalin Island near the Pacific Ocean, *Psettoraptor armatus* Nazarkin 2002 and a *Hippoglossus* sp., both Pleuronectids, were found dating from the Miocene (Nazarkin, 2002). Other specimens possibly belonging to Paralichthyidae and Pleuronectidae from the Oligocene and Neogene in Japan have been described (Uyeno *et al.*, 1990; Sakamoto & Uyeno, 1997).

Besides both *Amphistium* and *Heteronectes* having some general percomorph features that are lost in most modern flatfishes except in *Psettodes*, e.g. dorsal and anal fin spines and palatine teeth (Friedman, 2012), the former genus further shows other characters typical for flatfish, such as the first dorsal fin reaching further anteriorly, a procumbent first pterygiophore of the dorsal fin, and curved neural spines of the precaudal vertebrae (Friedman, 2008; 2012). There are also equal numbers of sinistral and dextral *Psettodes* and *Amphistium* (Friedman, 2008). Both fossil genera do not have the typical appearance of modern flatfish in which both eyes are positioned on the same lateral side. The migrated orbit is located at the dorsal side of the body, but has not crossed the midline as in Pleuronectoidei, whereas it is positioned on the orbital midline in *Psettodes* (Friedman, 2008; 2012). The fish of the genus *Psettodes* (Psettodoidei) diverged early in the evolution of flatfish (Harrington *et al.*, 2016; Betancur-R *et al.*, 2017). This indicates that some old lineages of Pleuronectiformes have intermediate characteristics, which means that the evolution of the asymmetry of flatfish might have occurred gradually, and possibly in only a few million years (Friedman, 2008; Janvier, 2008; Harrington *et al.*, 2016; Evans *et al.*, 2021).

North Sea families seem to have diverged early on sometime during the Eocene, as based on fossil calibrations of DNA analysis, while some species within families (especially Pleuronectidae) have only diverged a few million years ago (Betancur-R *et al.*, 2017).

1.1.4 Biogeography

In order to assess where people were capturing flatfish during the Medieval period, it is necessary to understand where each flatfish species is likely to occur. This could be the geographical region, but also the habitat it lives in.
Fish of the order Pleuronectiformes are found in all oceans of the world. Tropical regions are much more diverse than polar and temperate regions in terms of flatfish species, but within families, the distributions are different (Gibson *et al.*, 2015). Most families are found in more than one of the large oceans, Atlantic, Indian and Pacific, whereas others are restricted to one. The Achiropsettidae are the only flatfish species that live in the Antarctic ocean. In the Atlantic Ocean 14 families occur - all families of the order except Rhombosoleidae and Samaridae - and most families and genera are restricted to a specific region. For example, the Achiridae are only found in the western Atlantic Ocean and Eastern Pacific Ocean and do not occur in European waters. In the North Sea currently 4 families of flatfish are regularly found: Bothidae, Pleuronectidae, Scophthalmidae and Soleidae. Over 20 species of flatfish are reported from the North Sea and none of them is endemic (table 1.2).

Further, a number of species of Cynoglossidae, Soleidae and Bothidae are found in areas around the North Sea, and might occasionally enter the North Sea or might have occurred there once. *Solea senegalensis* can also be found along the Portuguese and French coasts, and *Pegusa impar* can be found in Gibraltar and the Mediterranean Sea (Whitehead, 1986). *Platichthys solemdali* is a (sub)species found in the Baltic Sea and differs from *Platichthys flesus* genetically and by its spawning style (Momigliano *et al.*, 2018).

Pleuronectiformes are regarded as being primarily marine species. Some species, however, are known to occur, at least during a part of their lives (see below), in brackish and freshwater systems. Out of those species, 34 species from Achiridae, Soleidae and Cynoglossidae complete their life cycle exclusively in fresh water and these are found in areas in South America, Oceania, Asia and Africa (Wirjoatmodjo, 1988; Gibson *et al.*, 2015; Froese & Pauly, 2021). *Platichthys flesus*, or European flounder, is also known to occur in brackish waters and in rivers (e.g., in the Thames in London, McGoran & Morritt, 2017).

The precise geographical ranges where species occur is affected by multiple abiotic variables, such as temperature, depth, and latitudinal gradients (Ryer *et al.*, 2004; Cabral *et al.*, 2007). Flatfish occurrence is highly correlated with the presence of fine sediment, which is related to their ability to bury (see below) and possibly also with the ability to change its colour to match the environment (e.g., Tyrie *et al.*, 2015). Biotic factors such as presence of vegetation, community composition, prey and predators, as well as structure of the sea bed further impacts the occurrences of species (Stoner *et al.*, 2001; Ryer *et al.*, 2004). The factors influencing the occurrences depend on the age and size of flatfishes as well (e.g., Gibson & Robb, 1992; Braber & De Groot, 1973). Climatic changes can further influence the precise distribution of flatfish populations. One study combined current species distributions with climate models to predict the future shifts of North Sea species and found that *Lepidorhombus whiffiagonis* will decline in the next 80 years, whereas *Microstomus kitt* and *Solea solea* will increase in abundance (Maltby *et al.*, 2020). Recent studies on modern flatfish have shown that with increasing temperature, *Solea solea* spawns earlier in the year and the larvae might have a higher survival rate, which may result in larger populations in the North Sea in warmer climate conditions (Teal *et al.*, 2008; Fincham *et al.*, 2013). This species also generally seems to change to a more southwestern distribution in the North Sea, while *Pleuronectes platessa* moves to more northern areas and favours deeper waters with the water becoming warmer (Engelhard *et al.*, 2011). *Platichthys flesus* is known to retreat away from estuaries and inland waters earlier to spawn in open marine environments during cooler periods (Sims *et al.*, 2004). No extensive reports on responses of other flatfish species in the North Sea on climate change were found in published literature. Given the historical climatic shifts that occurred at the start, during, and at the end of the Medieval period (see section 1.3), flatfish species distributions and abundances might have been different from what we know today, which could have had implications for medieval fisheries.

Table 1.2. Taxonomic overview of species per family reported in the North Sea. Sources of the occurrences are Nijssen (1966)[1], Nijssen and De Groot (1974)[2], Heessen *et al.* (2015)[3], and Froese and Pauly (2022)[4]. Maximum sizes (cm) were taken from Heessen *et al.* (2015) and Froese and Pauly (2022).

Species	Max. size (cm)	Occurrence
Bothidae		
Arnoglossus laterna	22	common[3]
Citharidae		
Citharus linguatula	40	very rare[4]
Cynoglossidae		
Cynoglossus browni	40	occasional[1&2]
Pleuronectidae		
Glyptocephalus cynoglossus	60	common in northern part; rare in southern part[3]
Hippoglossoides platessoides	48	common in northern part; rare in southern part[3]
Hippoglossus hippoglossus	254-400	common in northern part; absent in southern part[3]
Limanda limanda	45	very common[3]
Microstomus kitt	66	common[3]
Platichthys flesus	61	common in southern part; rare in northern part[3]
Pleuronectes platessa	91	very common; smaller more common in eastern part[3]
Scophthalmidae		
Lepidorhombus boscii	41	very rare[3]
Lepidorhombus whiffiagonis	61	rare[3]
Zeugopterus norvegicus	13	common[3]
Scophthalmus maximus	100	common[3]
Scophthalmus rhombus	61-100	common; smaller more common in eastern part[3]
Zeugopterus punctatus	25	rare[3]
Zeugopterus regius	20	rare[3]
Soleidae		
Buglossidium luteum	22	common[3]
Microchirus variegatus	33	rare[3]
Pegusa lascaris	40	rare; English Channel[3]
Solea solea	70	common[3]

Flatfish occur at a wide range in depths with some species found at only 1 m deep, while others live 2000 m under the water surface. The geographic distribution ranges from shallow estuaries and shorelines to the edge of the continental shelf and continental slope (Gibson *et al.*, 2015). The depth at which flatfish are found varies throughout their lifetime and for every species. For example, right after transformation in April in the west coast of Scotland *P.*

platessa can be found at depths around 5 m and quickly moves to shallower water of around 1 m deep until summer when they again migrate to deeper water, whereas *L. limanda* can be found on all depths between 1 m and 5 m evenly (Gibson *et al.*, 2002). People thus have to adapt their fishing techniques and know where and how they can find each species throughout the year. The deepest living species in the North Sea are *Lepidorhombus boscii,* which can be found down to depths of 1000 m (Munroe & Chanet, 2016), *Glyptocephalus cynoglossus* at 1600 m, and *Hippoglossus hippoglossus* at depths of around 2000 m deep, although these maximum depths are not recorded in the North Sea, as this shelf sea is only 700 m deep at max (Nielsen, 1986; Scot & Scot, 1988, cited by Gibson *et al.*, 2015).

1.1.5 Osteology

This section discusses the key resources available on the comparative osteology of flatfish (figure 1.2) in the published literature. The number of previous studies on flatfish osteology is limited. The most in-depth comparative osteological study on flatfish so far was carried out by Wouters *et al.* (2007), which described the differences between 34 skeletal elements of the three most common species found in the archaeological record from the North Sea area, i.e. *Pleuronectes platessa*, *Platichthys flesus* (right- and left-eyed), and *Limanda limanda*. This study showed that *L. limanda* can easily be distinguished from the other two species on the basis of many elements, but smaller specimens of *P. platessa* and *P. flesus* are more difficult to distinguish on single elements. Skeletal elements that did not appear to prove useful for identification were the supracleithrum, the second precaudal vertebra, the first caudal vertebra, the penultimate vertebra, the antepenultimate vertebra, and the left nasal bone. Of the 34 studied elements, 19 showed characters that allowed the identification of at least one species clearly and easily (Wouters *et al.*, 2007).

There is little information on comparative osteology for other flatfish species found in the North Sea. Norman (1934) described some osteological features of flatfishes in general and how they are related to other groups and each other, but does not provide skeletal character descriptions usable for species identification. Härkönen (1986) provided a detailed overview of otoliths (which are several mineral structures made of calcium carbonate in the inner ear of fish of which the largest are called sagittae) shape of different flatfish species, which was later applied by Van Neer *et al.* (2002) to identify archaeological otoliths. Some species can be easily identified, but others species, such as *P. flesus* and *P. platessa* differ less clearly (Härkönen, 1986). Using dermal denticles, Enghoff (1986) was able to identify *P. flesus* and *S. maximus* down to species level in an archaeological excavation in Denmark, but provided a single photograph of dermal denticles of only one species and gave a vague comparison with other species of the North Sea. The pteroticum and sphenoticum of *P. flesus* can easily be distinguished from other flatfish, especially *P. platessa* and *L. limanda*, by a nodose-serrated margin (Enghoff, 1989). Fuller *et al.* (2012) mention that *H. hippoglossus* has very diagnostic criteria, without providing more details. The articular, dentary, quadrate, preopercular, cleithrum, urohyal, frontal, neurocrania are also found to be useful elements to identify archaeological remains of Pleuronectids with at least one species being identified down to species level (often dab or flounder) (Rosello 1986; Heinrich, 1987; Enghoff 1989; De jong, 1994; Enghoff 1994). Brinkhuizen (1989) used the prefrontal, frontal, supraoccipital, articular, maxilla, ceratohyal, hyomandibular and cleithrum to identify archaeological bone remains. Brinkhuizen (1989) further states that morphological characteristics of os anale do not allow species identification, contrary to Lepiksaar & Heinrich (1977). An overview of osteology in terms of phylogeny of flatfish was made by Cooper (1998), but the descriptions are limited and comparisons between North Sea species sparse. Clavel (1997) identified flatfish using 18 different elements, but did not provide any osteological description, and many pleuronectids could not be identified to species level. Sakamoto (1984) compares in great detail the cranium, orbital bones, jaw apparatus, suspensorium and opercular apparatus, hyoid arch, branchial apparatus, gill rakers, fins, pectoral and pelvic girdles, urohyal, vertebrae, and caudal skeleton of Pleuronectidae, but does not provide much specific information or figures on the species relevant to the North Sea area. Most descriptions discuss articulated bones and not the characters of single skeletal elements. However, given his finds of some characters being stable within a genus, the development of the interorbital bone on the frontal of the blind side differs between *Glyptocephalus* and *Hippoglossus-Microstomus* and *Hippoglossoides-Pleuronectes-Platichthys* (Sakamoto, 1984). A similar detailed description of mostly articulated elements of Pleuronectidae is given by Cooper and Chapleau (1998). Watt *et al.* (1997) give a detailed and well illustrated identification key including most of the flatfish species found in the North Sea for the left and right premaxilla and vertebrae. Other figures of some flatfish skeletal elements can be found in Lepiksaar (1994). Illustrated osteological descriptions of Citharidae with *C. linguatula* are also available (Hubbs, 1945; Hoshino, 2001). Osteology and scale morphology of some North Sea Scophthalmidae is illustrated and described by Chanet (2003) and Voronina (2010) respectively, while Märss *et al.* (2017) provide descriptions of some Pleuronectidae and Scophthalmidae oral and pharyngeal jaws. Yazdani (2009) compared and illustrated the jaws, containing the premaxilla, maxilla, dentary and articular, for many species found in the North Sea, including most Scophthalmidae, Pleuronectidae, Soleidae and Bothidae, and related the morphology to the trophic ecology of these species. Species feeding on fish and actively hunting have curved teeth and relatively large and rather symmetrical mouths and jaws, such as *H. hippoglossus* and *Scophthalmus* species (Yazdani, 2009). Species that feed on smaller prey have smaller mouths and bottom-hunters have a more pronounced asymmetry in their jaws towards the blind side with the other side having fewer or no teeth (Yazdani, 2009). *Pleuronectes platessa* feeding on molluscs, has molariform teeth, whereas polychaete feeders, like *M. kitt, G. cynoglossus* and Soleidae, have small and slender teeth. The hunting strategy also impacts the morphology with horizontal hunters, like *G. cynoglossus*, having long jaws, whereas *M. kitt* has a short mouth since it hunts the worms from above and curves its head to catch them (Yazdani, 2009). Other publications describing, usually articulated, osteology of species found in other places than the North Sea are Amaoka (1972), Futch *et al.* (1972), Makhdoom Hussain (1981), Chapleau (1988), Chapleau and Keast (1988), Hoshino and Amaoka (1998), Guibord (2003), and Voronina and Chanet (2014).

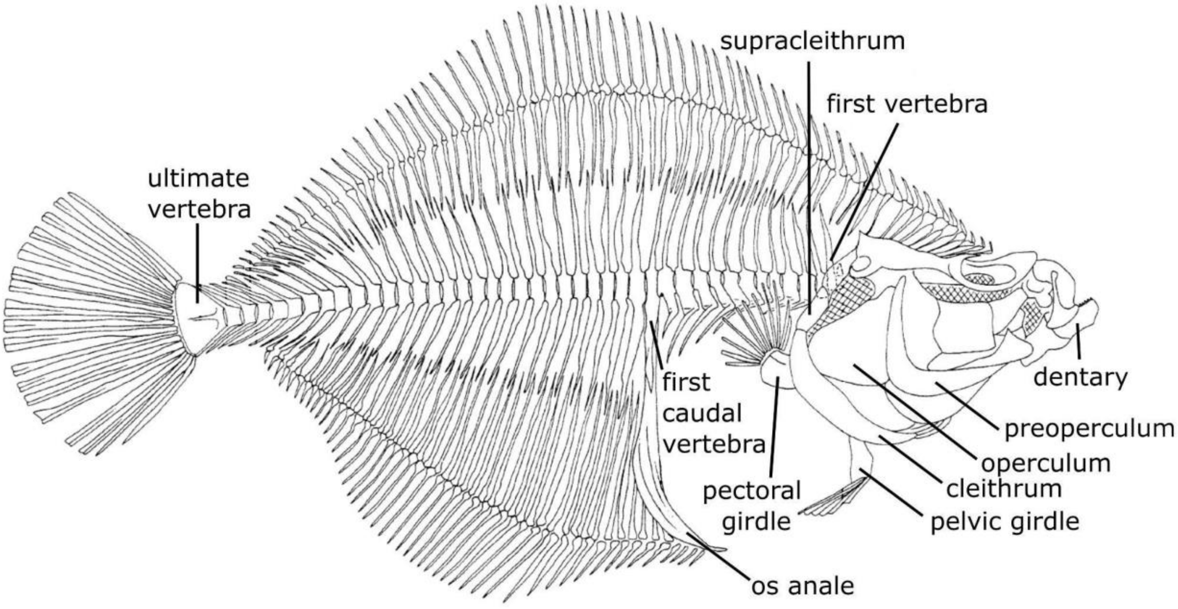

Figure 1.2. Skeleton of a plaice (adapted from van Neer & Pieters, 1997). For more details and information on osteology and illustrations of the cranial bones, including those not visible on this figure, see chapter 3.

1.1.6 Ecology

1.1.6.1 Diet

As the diet of flatfish species can have an effect on the isotopic composition of species, it is important to note how species' diet differ from each other or how their diet changes throughout their lives to interpret isotopic data. There are three main groups of flatfish species based on diet: crustacean-feeders, fish-feeders, and polychaete/mollusc-feeders (De Groot, 1971). Some families consist mainly of species belonging to one of these groups (Braber & De Groot, 1973). The diet of flatfish also shifts throughout their lives, since they are able to catch larger prey when they grow. The precise diet composition (i.e. relative abundances of prey species), might depend on the locality of a flatfish, the availability of food, and the competition from other species (Livingston, 1987; Darnaude *et al.*, 2001; Guedes & Araújo, 2008).

Pleuronectes platessa feeds on small meiobenthos and crustaceans when they are in the postlarval stadium, and switches to feeding mainly on polychaete worms as juveniles to mainly large molluscs, crustaceans and echinoids (Braber & De Groot, 1973; Ameczua *et al.*, 2003). The diet of *Platichthys flesus* consists of crustaceans, molluscs, polychaetes and fish (De Groot, 1971). *Limanda limanda* also feeds on polychaetes, crustaceans and molluscs, and also on bryozoa, echinoids, sponges, fish and fish eggs. There is a shift in the preferred species throughout the life of *L. limanda* towards a wider diversity of crustaceans (Braber & De Groot, 1973). They do not feed on hard shells of molluscs, but rather seem to eat only the soft siphon of bivalves (Braber & De Groot, 1973). *Microstomus kitt* feeds on polychaetes, crustaceans, molluscs, fish and coelenterata (De Groot, 1971). *Glyptocephalus cynoglossus* feeds on hermit crabs, echinoids, molluscs, polychaetes, and fish (De Groot, 1971; Ameczua *et al.*, 2003; Yazdani, 2009). *Hippoglossus hippoglossus* feeds on fish and crustaceans (De Groot, 1971). *Hippoglossoides platessoides* feeds on crustaceans, echinoids, molluscs and polychaetes (De Groot, 1971).

Scophthalmus maximus and *S. rhombus* feed mainly on fish, such as *Ammodytes* sp., *Clupea* sp., *Gobius* sp., and Gadidae, and also on crustaceans, molluscs and polychaetes. Juvenile *S. maximus* additionally feeds on small crustaceans like shrimps (De Groot, 1971; Braber & De Groot, 1973). *Lepidorhombus whiffiagonis* and *L. boscii* feed on fish, molluscs and crustaceans, such as shrimps (De Groot, 1971; Teixeira *et al.*, 2010). *Zeugopterus norvegicus* feeds on molluscs and crustaceans (De Groot, 1971).
Solea solea feeds mainly on polychaetes throughout its life (Braber & De Groot, 1973), but is found to also eat a large quantity of bivalves and amphipods in the Mediterranean Sea (Darnaude *et al.*, 2001) and also echinoids, crustaceans, and molluscs (De Groot, 1971). *Pegusa lascaris* also feeds mainly on polychaetes and crustacea (Teixeira *et al.*, 2009).
Buglossiudium luteum has a broad spectrum of prey species, feeding mainly on polychaetes, bivalves, gastropods, copepods, and amphipods (Darnaude *et al.*, 2001). The diet of *Microchirus variegatus* consists of hermit crabs, echinoids and fish (Ameczua *et al.*, 2003).
Arnoglossus laterna has a diet that consists mainly of bivalves, amphipods, polychaetes, shrimp-like crustaceans, hermit crabs, and some fish (De Groot, 1971; Darnaude *et al.*, 2001). The diet of *Citharus linguatula* consists of crustacea, molluscs and fish (Bayhan *et al.*, 2009; Carpentieri *et al.*, 2010).

Visual feeders take either swimming food (e.g. *S. maximus, S. rhombus, L. whiffiagonis, Arnoglossus* sp*., H. hippoglossus,* and *Psettodes* sp.) or bottom-living food (e.g., *P. platessa, P. flesus, M. kitt, L. limanda,* and *G. cynoglossus*) (Yazdani, 2009). The first group generally has symmetrical jaws, whereas the latter group has small and asymmetrical jaws (Yazdani, 2009). The eyes are usually more protruding from the head in visual feeders compared to non-visual feeders. Soleidae (*S. solea, B. luteum, M. variegatus*) capture food during the night and only feed on bottom-dwelling invertebrates, relying on their sense of smell to detect prey (De Groot, 1971; Yazdani, 2009). They have highly asymmetrical jaws and the left and right sides can move independently so the blind side can be used for feeding while the eyed side is mainly used for respiration (Yazdani, 2009). Flatfish can either actively move and catch the prey, by a fast attack or a slow stalking movement, or they can wait in ambush till prey passes by. Different behaviours can be observed in one species. Flatfish from the genus *Asterorhombus* from the Indo-West Pacific, lure their prey with a small fleshy protrusion from the first dorsal fin ray that resembles a small fish or invertebrate (Amaoka *et al.*, 1994).

1.1.6.2 Reproduction

The spawning season for flatfish varies per species and per location. *Pleuronectes platessa* has a spawning season from November till May with peak spawn in January and *Solea solea* spawns during late winter- early spring (Metcalfe *et al.*, 2006; Vinagre *et al.*, 2008). During this season, they can migrate to specific spawning sites, which could therefore have an impact when and where certain species are available for fisheries (Wimpenny, 1953, cited by Metcalfe *et al.*, 2006). Their eggs are only a few millimeters in size and can be either pelagic or demersal. The majority of species in the northeast Atlantic spawn pelagic eggs (Gibson *et al.*, 2015). Larger females produce more eggs. The eggs take about a few days to a few weeks to hatch, depending on the species, egg size and water temperature (Russell, 1976, cited by Pauly & Pullin, 1988; Fox *et al.*, 2003). The eggs or larvae can be transported to inshore waters or estuarine nurseries, where the larvae continue to grow (e.g., Jager, 1999; Ramos *et al.*, 2010; Primos *et al.*, 2013), which could leave an isotopic signal of coastal or estuarine environments.

Larvae of flatfish are symmetrical, resembling other teleosts more than their adult conspecifics. At one point during their development, they start to grow asymmetrical and changes in their physiology occur. One eye moves to the other side. Also part of the vestibular system, the hindbrain, pigment cells and even otoliths become asymmetrical in structure, positions, and/or weight (Seikai & Matsumoto, 1994; Helling *et al.*, 2005).

It is during this orbital migration that flatfish commence their benthic lifestyle and further changes in their body, such as in the digestive tract and muscle growth occur (Tanaka *et al.*, 1996; Yamashita *et al.*, 2001). Depending on the species and population, it usually takes a few years for the juvenile fish to mature and start reproducing themselves (Pitt, 1964, cited by Roff, 1982; De Veen, 1976, cited by Roff, 1982; Roff, 1982; Deniel, 1990). Some species, such as *S. maximus* and *S. solea*, can live up to at least 25 years, whereas of others, like *A. laterna* and *L. limanda*, no specimen of over 7 years old was reported along the French coast by one study (Deniel, 1990). The record holding flatfish in terms of age, besides size and depth occurrence, are *Hippoglossus* species that can reach ages of over 50 years old (Munk, 2001; Armsworthy & Campana, 2010). Flatfish species also differ largely in their maximum sizes, ranging between a few centimeters to a few meters (*Aseraggodes andersoni* of 23.5 mm SL[1] vs. *H. hippoglossus* of 4 m) (Robins & Ray, 1986, cited by Froese & Pauly, 2022; Randal *et al.*, 2013). Most species reach a size around 25 cm and only a few species grow larger than 80 cm. Of those larger flatfish, the North Sea is well represented with some 10 species being able to reach sizes over 50 cm TL[2]; i.e. the commercial species.

1.1.6.3 Locomotion

Flatfish move around on the bottom of the seafloor by undulating their anal and dorsal fins. They can also contract their lateral muscles and move the caudal fin to swim around. They usually swim horizontally, but some species are known to swim in a vertical position and even swim straight up to the surface (pers. obs. of *Solea senegalensis* in captivity; *Reinhardtius hippoglossoides* by De Groot, 1970; *Paralichthys dentatus* by Stickney *et al.*, 1973). Flatfish are often depicted lying completely flat on the bottom, but they can lift their head, supported by the pectoral fin on the blind side (Gibson *et al.*, 2015).

Flatfish can bury themselves by shaking their body and head to cover themselves with sandy sediment (Gibson *et al.*, 2015). They do this to avoid detection by predators and prey. Additionally, their eyed side is usually coloured to match the surrounding sediment as camouflage. Changing colour is a trait found in only a handful of taxa, such as chameleons, cephalopods, and several fish groups, including Pleuronectiformes. By changing their colouration in a matter of minutes or days, they can blend in with the sediment and become difficult to see (Sumner, 1911; Kelman *et al.*, 2006).

1.1.6.4 Hybrids

There have been some reports of hybrid flatfish with parents of two different species and genera in the wild (Schultz & Smith, 1936; Garett, 2005) and produced for aquaculture (Riley & Thacker, 1969; Purdom & Lincoln, 1974; Liewes, 1984). Usually the hybrids show

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[1] SL is the standard length of a fish, measured from the tip of the premaxilla or upper lip to the last vertebra on the caudal peduncle.

[2] TL is the total length of a fish, measured from the tip of the premaxilla or upper lip to most posterior tip of the caudal fin.

characteristics coming from one of the two parent species or an intermediate state, as can also be seen in their osteology (Schultz & Smith, 1936). Also species found in the North Sea are known to hybridise in captive situations, e.g., *P. flesus*, *P. platessa*, *L. limanda*, *H. hippoglossus* and *M. kitt* can breed with each other (Riley & Thacker, 1969; Purdom & Lincoln, 1974; Liewes, 1984) as well as *S. maximus* with *S. rhombus* (Liewes, 1984), which must be kept in mind when dealing with morphological and molecular identification methods, especially modern reference material acquired commercially.

1.1.6.5 Conservation

Currently, only 319 out of over 800 species of Pleuronectiformes are assessed by the IUCN, of which 83 are data deficient and 229 of least concern. Seven species are categorised as threatened. The only endangered flatfish currently known is the Atlantic Halibut (*H. hippoglossus*), which is an economically important species in Europe (Sobel, 1996). Many of the modern stocks of flatfish have been overexploited for some time (Rice & Cooper, 2003). No precise information concerning the viability of European stocks or the size of populations are available, indicating the lack of knowledge necessary for conservation of flatfish diversity and sustainability of fisheries. It is estimated that *P. platessa* and *S. solea* are currently being harvested sustainably (FAO, 2011).

1.2 Geographical situation

Part of the Atlantic Ocean, the North Sea (figure 1.3) is a shelf sea located for the most part on the European continental shelf. It has a surface area of around 575 000 km^2. Most of its border is shaped by several countries. Mainland Europe lies to the east with France, Belgium, the Netherlands, the Frisian Islands, Germany and Denmark. Norway lies in the north and the United Kingdom, with England and Scotland, in the west. It is also connected to other marine regions. The Strait of Dover is the boundary between the North Sea and the English Channel. This south border runs between 51°N, 1°55’E (Walde Lighthouse, France) and 51°10’N, 1°23’E (Dover Patrol Memorial at Leathercoat point). Skagerrak Strait and Kattegat Bay connect the North Sea to the Baltic Sea in the northeastern part of the basin. The east border between the North Sea and Skagerrak goes from 57°07’N, 8°36’E (Hanstholm) to 58°N, 7°E (the Naze near Lindesnes). Since the 18th century there has also been a connection between the North Sea and the Baltic Sea through the Eider Canal, which was later replaced by the Kiel Canal. The north of the North Sea is, apart from the presence of archipelagos Orkney Islands and Shetland Islands that form the boundary between the Atlantic Ocean and the North Sea, openly connected to the Norwegian Sea. The north border of the North Sea lies at 61°N between the Shetlands and Norway. The precise coordinates of the North Sea are defined by the International Hydrographic Organization (1953).

Figure 1.3. Map of the North Sea. The southern North Sea is highlighted in red. (retrieved from https://nl.m.wikipedia.org/wiki/Bestand:North_Sea_map-en.png.

The seabed of the North Sea is mainly sandy, with some areas being rather muddy. There is a huge variation in coastlines: cliffs (Dover, parts of Scotland), deep fjords (Norway), pebble or sand beaches (Scotland, Belgium), estuaries, and mud flats with barrier islands (Wadden Islands). The coasts in the north bear the scars made by glaciers during the ice ages, while the coasts in the south consist of glacial deposits. The North Sea is usually rather shallow with an average depth of around 90m, but can reach depths of over 700m at the trench near Norway. A large shallow area between the UK and Denmark/Germany called Dogger Bank is only about 15-30m deep. Warm and salty water from the Atlantic Ocean through the English Channel mixes with the colder water from Skagerrak and the North Atlantic as well as lots of freshwater input from large rivers such as Thames, Scheldt, Meuse, Rhine, Elbe. Being on the shallow continental shelf, the North Sea area was not covered by water during the ice ages of the Pleistocene. Water was trapped in ice during the ice ages and isostatic movements by the land resulted in the sea level being much lower than it is today (Streif, 1990). This area of land that is now covered by the North Sea is called the Doggerland. After the last ice age some 10 000 years ago during the Holocene, the sea level began to rise again, flooding the Doggerland. The highest area of this land, the Doggerbank, was flooded around 5000 BCE, after being an island for some 1000 years. The flooding of this area cut off England from the mainland and resulted in the North Sea as known today (Streif, 1990; Ward *et al.*, 2006). The coastlines of the North Sea have changed considerably during the last 2000 years due to erosion, sedimentation, sea level rise, and human interference (e.g., Denys & Baeteman, 1995; Flemming, 2002; Behre, 2007).

Temperature of the water in the North Sea ranges from 2-8°C in January to 12-18°C in July, with the south being usually slightly warmer than the north (Becker & Pauly, 1996).

During the Medieval period, ca. 800-1300 CE there was a warmer period in the northern hemisphere than before, referred to as the Medieval Warm Period, while the colder period from 1300-1900 CE was called the Little Ice Age (Mann *et al.*, 1999; Mann *et al.*, 2009; Ljungqvist *et al.*, 2012). Sea water temperatures have been estimated as ~1.5-2°C higher in comparison to former and subsequent periods during the Medieval Warm Period, similar to modern day temperature increases (Keignwin, 1996; Cronin *et al.*, 2003; Cronin *et al.*, 2010; Ljungqvist *et al.*, 2012).

The North Sea has an average salinity of around 3.5% percent (Becker & Pauly, 1996), which can be influenced regionally and seasonally by temperature and riverine influx close to the shore (Hoppema, 1990; Agurto Muñoz, 2007).

Stable isotope composition (also see section 1.4.4) can be very varied across the North Sea due to the interplay of many environmental and biological factors. The temperature at both the surface and the bottom of the North Sea influences $^{13}C/^{12}C$ and $^{15}N/^{14}N$ variation (MacKenzie *et al.*, 2014; St John Glew *et al.*, 2018). Using data from modern day jellyfish, it was found that areas in the south of the North Sea are more enriched in ^{13}C than the central and northern open (deeper) sea part between Scotland and Norway. ^{15}N is more enriched on the east and south coasts than in the northwestern area (MacKenzie *et al.*, 2014; St John Glew *et al.*, 2018). The ratio of sulfur ($^{32}S/^{34}S$) is slightly higher in the north of the North Sea than in the south and around the coastal areas due to river influx (St John Glew *et al.*, 2018).

Seasonality can also affect the isotope composition in the ecosystem in the North Sea caused by physiological changes as well as environmental shifts, such as river run-off, throughout the year (Kürten *et al.*, 2013). Kürten *et al.* (2013) showed that different zooplankton species react differently to seasonal changes and geographical variation in their $\delta^{13}C$ and $\delta^{15}N$. Zooplankton seems more enriched in ^{15}N during autumn and winter, and less enriched during spring and summer. For carbon isotopes, the seasonal, geographical and species variation is more complex (Kürten *et al.*, 2013). For example, in Oyster Grounds organisms become less depleted in ^{13}C during spring, but are more depleted in North Dogger, which lies more to the north (Kürten *et al.*, 2013). Similar patterns were found in the German Bight (Agurto Muñoz, 2007). It can be expected that when there is more river run-off, $\delta^{13}C$ and $\delta^{34}S$ can be slightly lower in localised areas.

The difference in $\delta^{15}N$ values between the southern and northern part of the North Sea is related to the depth of those areas. Resuspension of enriched nitrate sources from rivers occurs in the shallow southern part, while the deeper northern part is more stratified and receives relatively less ^{15}N via the northern Atlantic, which combined with a difference in phytoplankton community, results in a different availability of ^{15}N between these two main areas in the North Sea (MacKenzie *et al.*, 2014; Ford *et al.*, 2016).

In general, there also seems to be a correlation between the salinity of water and $\delta^{13}C$ values: the higher the salinity, the less depleted in ^{13}C, as was noted in the estuary of the Great Ouse, UK (Fichez *et al.*, 1993). The closer to the coast, the less depleted in ^{13}C the organic fraction dissolved in water becomes, which could be caused by a difference in vegetation in these areas and changes in the water admixture. During summer and autumn, the difference between $\delta^{13}C$ values between riverine and estuarine areas seem to become less clear, due to changes in turbidity of the river (Fichez *et al.*, 1993).

$\delta^{15}N$ values in the sediment in the North Sea are thought to have increased since the Medieval period due to increased terrestrial run-off as a result of the intensification of agriculture and other anthropological activities (Serna *et al.*, 2010; Serna *et al.*, 2014). Higher $\delta^{15}N$ values occur closer to river mouths than in the open area of the North Sea (Serna *et al.*, 2014). A similar pattern in $\delta^{15}N$ values is found in medieval archaeological cod (*Gadus morhua*) samples from the Medieval and early Post-Medieval period from the North Sea as in modern day jellyfish (Barrett *et al.*, 2011; MacKenzie *et al.*, 2014).

Medieval and early Post-Medieval $\delta^{13}C$ seems to be more depleted than modern day values as measured from sediment cores at the coast of Germany due to eutrophication (Serna *et al.*, 2014), which is opposite of what could be expected by the Suess effect, in which a depletion of modern samples is expected (Keeling, 1979).

1.3 Flatfish and archaeology of fish

Flatfish bones are regularly found in archaeological excavation sites all over the world, from the west-coast of the U.S.A (e.g., Rick *et al.*, 2001; Byram, 2002; Gobalet *et al.*, 2004; Minor *et al.*, 2012), Alaska (Partlow, 2015), Australia (Colley & Jones, 1987), Polynesia (Kirch & Dye, 1979), and Europe (e.g., Makowiecki, 2007; Nicholson *et al.*, 2018; Ritchie *et al.*, 2018; and see below).

One of the oldest records of human consumption of flatfish from archaeological sites in Europe dates from the Magdalenian period (around 17 000 to 12 000 years ago) and Epipaleolithic periods in Spain (Adán *et al.*, 2009; Turrero *et al.*, 2014; Roselló-Izquierdo et al., 2016). Humans have also been using flatfish as inspiration for art and objects since the Magdalenian period, as some drawings and bony objects resembling them have been found in Spain (Altxerri and La Pileta) and France (Mas-d'Azil, Marsoulas, Lespugue les Boeufs), possibly representing species such as flounder, halibut and sole (Citerne & Chanet, 2005; Casasola, 2008), which indicates the early connection people had with flatfish (figure 1.4).

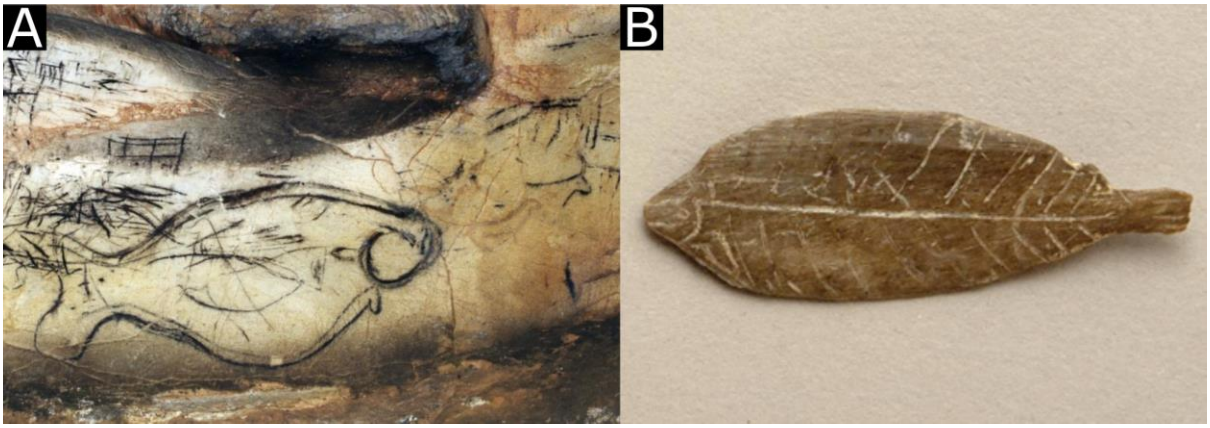

Figure 1.4. Prehistoric art inspired by flatfish. A. cave painting from Le Pileta in Spain; B. bony object from Lespugue les Boeufs in France. (retrieved from https://www.malaga.es/fr/turismo/naturaleza/lis_cd-1691/cueva-de-la-pileta and https://www.hominides.com/html/dossiers/peche-prehistoire-paleolithique.php).

This section will provide an overview of current knowledge originating from archaeological records of changes of fisheries throughout time, focusing mainly on Roman, Medieval, and Post-Medieval periods in different areas around the southern North Sea, namely England, northern France, Belgium, and the Netherlands, as these are the time periods (table 1.3) and geographical areas this study focuses on.

Table 1.3. Table explaining the names of the prehistoric and historical periods with corresponding years in CE per geographical region, comparing continental western Europe and England.

Continental western Europe		**England**	
Dates	**Period**	**Dates**	**Period**
9000 - 5000 BCE	Mesolithic	8000 - 4000 BCE	Mesolithic
5000 - 2000 BCE	Neolithic	4000 - 2200 BCE	Neolithic
2000 - 800 BCE	Bronze Age	2200 - 750 BCE	Bronze Age
800 BCE - 0	Iron Age	750 BCE - 43 CE	Iron Age
0 - 450 CE	Roman	43 - 410 CE	Roman
450 - 750 CE	Merovingian / Early Medieval	410 - 1066 CE	Anglo-Saxon / Early Medieval
750 - 950 CE	Carolingian / Early Medieval		
950 - 1200 CE	High Medieval	1066 - 1154 CE	Norman / High Medieval
1200 - ±1500 CE	Late Medieval	1154 - 1485 CE	Plantagenet / Late Medieval
±1500 - 1789 CE	New period	1485 - 1714 CE	Early Modern / Postmedieval
1789 - 1945 CE	Newest period	1714 - 1901 CE	Modern / Postmedieval
1945 CE - now	Modern	1901 CE - now	Historic / -

1.3.1 Prehistory

The coastal areas of the early Holocene (10 000 BCE - 0) of mainland Europe are difficult to study due to being submerged by the North Sea or poor preservation of material. Areas that are currently close to the coast often used to be further inland. Analysis of fish remains has also been complicated by the lack of sieving of many sites dating from the Mesolithic to the Iron Age (e.g., IJzereef *et al.*, 1992). Osteological and isotopic evidence shows that fish was being consumed locally in western Europe from the Mesolithic period till the Iron Age, although very little evidence for fish exploitation exists for the Iron Age for England and Belgium. It is unsure whether this is due the lack of retrieved fish remains caused by taphonomy or a lack of sediment sieving from this period or if fish simply was not a large part of the diet, for which there are many different explanations suggested in previous research (e.g., Milner *et al.*, 2004; Richards & Schulting, 2006; Dobney & Ervynck, 2007; Rainsford & Roberts 2013).

Fish remains dating from before the Roman Age are scarce in Belgium. No marine products have been found in Belgium. Only freshwater fish bones have been recovered, which would indicate local freshwater consumption of fish. This is confirmed by dietary isotopic analysis of human bones during the Mesolithic and early and middle Neolithic (Bocherens *et al.*, 2007). During the late Neolithic period, however, the contribution of freshwater fish to the diet seems to have decreased (Bocherens *et al.*, 2007).

A Mesolithic site in the Netherlands near Amsterdam, Almere-Hout Zwaanpad, provided many fish bones from mostly freshwater species, as well as eels, some flounder and a single mullet, indicating local freshwater exploitation as both flounder and mullet could have been found that far inland (Niekus *et al.*, 2012). A nearby Mesolithic site also shows the presence of Pleuronectidae, and more specifically, flounder (Hogestijn & Peeters, 2001). The Iron Age coastal settlements in the Netherlands show that people consumed marine fish and other marine animals. These were probably caught by simple catch methods on or close to the coast itself (Dobney & Ervynck, 2007; Van Neer & Ervynck, 2007; Van Neer *et al.*, 2013). During the Bronze and Iron Age in the western Netherlands, fish remains from mostly sturgeon, and some pike, cod and cyprinid have been found in several settlements (e.g., Vlaardingen, Voorne-Putten, Leiden, Heemskerk, and Weesp), which again indicates local capture of fish (IJzereef *et al.*, 1992; Çakirlar *et al.,* 2019).

Isotopic evidence shows that freshwater fish contributed to people's diet in northern France during the Mesolithic period (Drucker *et al.*, 2018). Remains of a fish trap were also discovered from this period (Drucker *et al.*, 2018). In some inland Neolithic sites in northern France, remains of cyprinids and some eel and pike have been found, indicating directed and seasonal local freshwater exploitation, as evidenced by size and otolith growth ring analysis (Clavel & Arbogast, 2005). Also during the Iron Age in Northern France, fish are thought to have been exploited locally, meaning coastal and marine species at coastal sites and freshwater species inland (Oueslati, 2019).

On the other side of the North Sea in England, marine fish was generally more consumed by mesolithic people, but this consumption potentially halted during the Neolithic (Dobney & Ervynck, 2007; Van Neer & Ervynck, 2007).

1.3.2 Roman

During the Roman period, people around the North Sea ate more fish compared to the previous periods. Local fish exploitation was still the norm in this period. Marine fish was consumed in areas close to the coast, while in inland areas people mostly relied on local freshwater species such as pike, cyprinids and perch, as evidenced by the fish remains

(Locker, 2007; W. Wouters pers. comm.). Fish sauce, either made from more southern marine species or the local North Sea species, was brought inland for consumption, as well as marine bivalves. Occasionally, fresh fish from the coast could be brought inland via the Roman road system.

In Belgium Mediterranean species, such as *Scomber japonicus*, were recovered from sites from the Roman period and were most likely transported from the south and the Mediterranean Sea as salsamenta (salted fish) (Van Neer *et al.*, 2010). Sites close to the coast (the coastal sites themselves have been flooded since), occasionally contain some remains of typical North Sea marine species, but they provide no evidence of consistent marine fish exploitation or of transport of fish inland throughout the Roman period in Belgium, except for a few sites, which are relatively close to the coastal area (Van Neer & Ervynck, 2007; Van Neer & Ervynck, 2016). For example, one site in Oudenburg, east of modern-day Oostende, contains many flatfish, sharks and rays, and some freshwater species (Van Neer & Ervynck, 2007; Van Neer & Ervynck, 2016; Ervynck *et al.*, 2017). One single pleuronectid vertebra from either *P. platessa* or *P. flesus* was found in Nevele, close to Gent, and is presumed to originate from the coastal area and not from a nearby river due to its size (Ervynck *et al.*, 1997). A huge amount of solely *P. platessa* was found at the site at Libershies, near Charleroi (Van Neer *et al.*, 2009). Remains from fish sauce found in more inland Roman deposits from the second century CE or later in Tienen, Tongeren, Braives, and Arlon in Belgium also contain some flatfish such as plaice, Scophthalmidae, sole as well as other coastal species that were captured in the North Sea or in estuaries and rivers, indicating people were making local variants of fish sauce (Van Neer *et al.*, 2005; Van Neer *et al.*, 2010). In Tongeren possible remnants of a fish sauce using local freshwater species were also uncovered from the 1st or 2nd century CE (Van Neer *et al.*, 2010). These finds all indicate that there were some transports to inland Belgium of marine fish and their products from the North Sea area during the Roman period. Bivalves, on the other hand, were clearly caught and traded to inland Belgium, presumably for consumption (Van Neer & Ervynck, 2007; Van Neer & Ervynck, 2016).

In the coastal area of the Netherlands marine fish exploitation continued to be frequent during the Roman period (Lotze, 2007; Van Neer & Ervynck, 2007; Van Neer & Ervynck, 2016). Several fish traps dating back to the Roman period have been found all over the Netherlands, which are thought to have been used to catch cyprinids, salmonids, clupeids, pike, and many others (Dütting & van Rijn, 2017). Remains of both marine and freshwater species have been found in inland sites, such as Dorestad, which indicates that also in the Netherlands import of marine fish was happening to inland areas (Brinkhuizen, 1979; 1989).

A similar situation as in Belgium and the Netherlands occurs during the Roman period in France (Oueslati, 2019). Marine species become slightly more abundant inland and are found besides local freshwater species. Mediterranean species have also been recovered from northern French sites. Bivalves seem to have been of particular importance for trade inland (Oueslati, 2019 and references therein).

In England marine or coastal species were imported to more inland sites, e.g. York, and other larger settlements, while many settlements still also relied on local freshwater fish (Locker, 2007). In the North there is a huge number of salmonids and eels, with smaller amounts of flatfish, cyprinids, perch, herring, and pike (Locker, 2007). In the Midlands and especially in the South of England, eels are often recovered in sites. Flatfish, mainly plaice and flounder, are also frequent finds at Roman sites in southern England, especially Roman London (Locker, 2007), although a few bones of turbot, lemon sole, dab, and halibut have also been found (Locker, 2007). Similar to the Belgian sites, fish could be processed and be part of the diet in the form of domestically produced fish sauce, salsamenta, and related products as found in London, Dorchester, and York (Van Neer *et al.*, 2005; Locker, 2007; Van Neer *et al.*, 2010; Reynolds, 2015). Evidence of fish ponds, in which fresh or saltwater species could be kept, were also uncovered in Southern England (Zeepvat, 1988, cited by Locker, 2007).

1.3.3 Early Medieval

Fish consumption gains more importance throughout the Early Medieval period, with an increase of marine fish species being brought inland and consumed throughout this period, while local freshwater fish also remain an important part of the diet. Throughout this period, there is also an increase of zooarchaeological evidence of fish processing, which would mean that there were dedicated economic activities to trade fish from the coastal areas to the growing (proto-)urban settlements.

Trade routes across the North Sea were gradually being re-established throughout this period, with Viking Age Scandinavians expanding the network from mainland Europe, Britain, and Scandinavia to Greenland and the Middle East (Hoffman, 2005).

During the Early Medieval period, people from Scandinavia migrated to other areas across Europe for unknown and probably multiple reasons, and even reached North America (McGhee, 1984). During the 9th and 10th centuries, their culture also reached England and parts of France, Belgium and the Netherlands, where they might have influenced the local cultures (e.g., Verhulst, 1989; Tys & Wouters, 2016). Scandinavians had a much larger tradition of eating marine fish and their influence on the cultures in England and western Europe, might thus have increased the demand for fish in general and probably mostly marine fish (Barrett *et al.*, 1999; Barrett *et al.*, 2001).

In the Early Medieval period few sites with fish remains were uncovered in Belgium and those mainly contain some flatfish, eels (*Anguilla anguilla*), cyprinids, pike, stickleback, some herring and a few other freshwater species (Van Neer & Ervynck, 2007). Based on the fish remains, it seems that Flemish fishers exploited the coastal waters during the second half of the first millennium, and went to open sea around 1000 CE, where they focused on flatfish, gadids (mostly *Merlangius merlangus* and some *Melanogrammus aeglefinus*), and later herring (Van Neer & Ervynck, 2007; Van Neer & Ervynck, 2016). It is hypothesised based on historical records that fish sauce was still being produced during this period (Van Neer & Ervynck, 2007).

In the Netherlands, local marine fish consumption became more regular in this period compared with the Roman period (Lotze, 2007). Oegstgeest, a close-coastal site near Leiden, contains mostly freshwater and marine living species that could have been caught in local freshwater and estuarine/coastal environments (Kerklaan, 2021). Especially Pleuronectidae are abundant in this site, with remains identified to plaice, flounder and dab (Kerklaan, 2021). Also in other early-medieval Dutch settlements fish consumption mostly reflects local catches, but occasionally imported fish is found in settlements along rivers or in large trade hubs, such as Dorestad (Çakirlar et al., 2019 and references therein).

In France, the coastal site Saint-George-sur-l’Aa has a wide variety of fish taxa between the late 9th century and the early 10th century, including remains from pleuronectid flatfish, herring, sticklebacks, eels, thornback rays, with haddock and cod dominating. Of the latter two species, mainly cleithra and head elements were found, indicating that these fish were processed for consumption elsewhere (Oueslati, 2019). A nearby site Barreau Saint-George-Desserte ferroviaire in northern France dates from the late 10th till the beginning of the 11th century and comprises mainly flatfish and some gadid remains (Oueslati, 2019). There is a high abundance of pleuronectid flatfish, with similar numbers of identified flounder and plaice, but most bones have remained unidentified. These fish were probably caught during the winter period. The presence of potential stomach contents from these molluscivorous species and the skeletal element distribution would indicate that these small sized flatfish were brought fresh to the site and consumed locally (Oueslati, 2019).

In England, fish remains are not uncovered from all Early Anglo-Saxon sites, but when they are, a wide variety of species is present (Reynolds, 2015). Most species found in Anglo-Saxon archaeological remains were freshwater and migratory species, such as eels and salmonids, although an increasing amount of herring is also seen through the period (Barrett *et al.*, 2004a,b). Fish weirs, traps, hook, gorges and line, weights, and nets, sometimes using boats, were a common way to catch fish in rivers and shores (Serjeantson & Woolgar, 2006; Reynolds, 2015; Galloway, 2017). Pleuronectidae, such as plaice/flounder, halibut, and also Gadidae are rather rare and are either found at coastal sites, sites close to coasts, or in inland sites connected to the coast by a large river (Reynolds, 2015).

In Mid Anglo-Saxon sites, which were bigger settlements and proto-cities compared with older sites, fish appears to be a bit more frequent, although there could be methodological and taphonomical explanations for this (Reynolds, 2015). Generally, a wider variety of marine species are found, mostly at coastal sites. Some coastal Mid Anglo-Saxon sites, such as Flixborough and Fishtoft, contained lots of marine fish bones, including many plaice/flounder (Reynolds, 2015). Inland sites where marine fish are found are associated with more elite occupations (Reynolds, 2015). Eel remains the dominant species throughout England in this period. Flounder and/or plaice are found in sites in York, Southampton, London, and other southern sites. Other marine species such as clupeids are also common (Reynolds, 2015).

In the Late Anglo-Saxon period, a greater number of fishes have been recovered, including from non-coastal sites (Reynolds, 2015). Herring is found even in rural areas and cod and other gadids also become more abundant, although often found only in urban sites (Reynolds, 2015). Specialised fishing sites start to emerge along the coasts, such as those in Sandwich and Old Winchelsea, as historical texts seem to indicate (Reynolds, 2015). Monasteries consumed a lot of fish and even had fish ponds to keep or even breed fish as their monastic dietary rules imposed the regular consumption of fish (Reynolds, 2015).

While in the areas around the southern North Sea people gradually increased their marine fish consumption during the Early Medieval period, in northern Europe (i.e. Scotland and Scandinavia) and in the Baltic region there was already a focus on gadids and herring, which were also traded inland (Barrett *et al.*, 2004a,b). On the Orkney Islands marine fish became an important part of the diet during the Viking age starting in the 9th century (Barrett & Richards, 2004).

1.3.4 High Medieval

It is during the High Medieval period on the continent and during the end of the Early Medieval period in England that the marine fish event horizon occurs around the North Sea, in which there is a clear shift from mainly freshwater species to marine species that are consumed at sites. This can be attributed to a number of different possible factors (Barrett *et al.*, 2004a; Van Neer & Ervynck, 2016), including the increasing European human population, growing urbanisation, the increasing impact of Christianity with changes in diet requirements, warmer climate, Scandinavian diaspora, the collapse and regulation of freshwater fish stocks, as well as the ready availability of marine fish that were cheap, abundant, and easy to process to retain a longer shelf life (Barrett *et al.*, 2004a; Barrett *et al.*, 2011; Van Neer & Ervynck, 2016). The shift towards more marine species can be more visible in inland sites than in coastal settlements, where people were already consuming more marine species compared to those inland. The evidence for production sites in coastal areas increases after the marine fish event horizon, where fish is processed to be transported inland (Van Neer & Ervynck, 2016).

Even though the Christian Benedictine reform across Europe is thought to be one of the causations of the Fish Event Horizon, it is unsure if everyone around the North Sea was bound to the same rules concerning their diets (Van Dam, 2008). Fish was, and sometimes still is, eaten as a replacement for meat, especially during days of Lent and other days that required abstention. If one follows the rules of Lent and abstains from meat twice a week and on holy days, a Christian diet consists for one third of the year out of fish, eggs, dairy, etc. instead of meat (Van Dam, 2008). In England, any product of a land animal had to be avoided in some cases during lent, including eggs and cheese, while fish and even marine mammals could still be eaten (Harvey, 1995). Documents from the Late Medieval and Post-Medieval periods show that different regions and different groups of people were bound to different rules. For example, besides Lent, people around Liege in Late and Post-Medieval Belgium didn’t eat meat on Fridays and Saturdays, and some documents from the Netherlands and England show that Wednesday was also sometimes a day where meat was replaced by fish or eggs there (Woolgar, 2006; Van Dam, 2008). Monasteries were probably stricter with their diet, whereas the common, rural living people were perhaps less occupied with the specific dietary rules. Coastal sites would be expected to eat more fish than inland sites, however, their coastal position would also make it easier for other meat-replacing products such as dairy and eggs to be available, if these were allowed to be eaten (Dyer, 2006; Van Dam, 2008). Nonetheless, generally these religious dietary requirements would have meant that there was an increase of demand for fish during this period.

A decline of freshwater stocks is also attributed as one of the causes of the marine fish event horizon. This could have been triggered by overfishing, damming, or pollution, which forced people to look for other, marine, sources of fish (Hoffman, 1996). At the same time, these stocks were also increasingly regulated: large fish, such as salmon, could be fished only under regal fishing rights in Namur, Belgium for example (Van Dam, 2008). It is unclear whether the regulations were installed after people noticed the stocks were declining or if there were other reasons. Salmon, eel, and pike were still available throughout the Medieval period since they are found in archaeological sites and historical documents show they were given as gifts or consumed by the wealthier people, albeit their reduced sizes might indicate that the stocks were not healthy (Van Dam, 2008; Van Neer *et al.*, 2009; Harland *et al.*, 2016). According to Van Dam (2008), it was the size of species such as salmon, pike, and even cod, that made them highly valuable and more reserved for the wealthy, when served as a whole fish (also see Maccarinelli, 2021). The imported carp, *C. carpio*, which did not occur in western Europe in a large scale before the Late Medieval period (13th century BE and NL; 14th/15th century in

England), was not readily available yet as a replacement for freshwater fish around the marine fish event horizon (Brinkhuizen, 1979; Database Oceans Past Northern Seas Synthesis).

During the High Middle Ages, European populations increased from 35 to 80-100 million (Russell, 1972). Larger villages were established and natural areas were cleared for more intense farming. Some villages grew into towns with individual governing systems. Following more efficient farming and trade practices, cities offered more employment opportunities, leading to increased populations and further urban development. The increased availability of marine fish in European markets might have led to better-fed populations, which in turn could have led to further population growth.

Cities such as Antwerp, Bruges, Amsterdam, Lyon, and London, became prominent trading hubs. The rise of the Hanseatic League - an influential trade confederation active during the High and Late Medieval period in the North Sea and Baltic Area - united many towns and merchant guilds under new regulations of trade products and routes (Hoffman, 2005; Nedkvitne, 2013).

In the areas around the southern North Sea, an increase of remains from Gadidae and Clupeidae show that species such as cod, haddock, whiting and herring became much more important for the diet during this period. Remains from freshwater taxa such as perch, cyprinids, pike and migratory species such as eels, show that local consumption was still happening as well (Van Neer & Ervynck, 1996; Van Neer & Ervynk, 2007; Barrett *et al.*, 2011).

In Belgium it is noted that haddock (*M. aeglefinus*) has a higher abundance than cod during this period (Van Neer & Ervynck, 2016). Flatfish are dominant mostly during the 10th century and are replaced by Clupeidae and later Gadidae but continue to be an important part of people’s diet in Belgium (Van Neer & Ervynk, 2007; Barrett *et al.*, 2011).

Sites with available fish bone data in the northern Netherlands dating from this period are characterised by a clear absence or very low frequency of freshwater and anadromous species, while marine species like Gadidae and flatfish are abundant (Brinkhuizen, 1979). Historical reports state that freshwater fisheries, for example sturgeon, were still active and of economic interest (Brinkhuizen, 1979). Some sites from the southern part of the Netherlands are characterised by having a mixture of cyprinids, eels, pike, perch, some salmonids, some clupeids, and some gadids. Flatfish are present in only one large site in Vlaardingen (Database Oceans Past Northern Seas Synthesis). It is also during this period that the earliest carp is found in Dutch archaeological sites (Brinkhuizen, 1979; Database Oceans Past Northern Seas Synthesis).

Cod and herring also start to constitute the majority of fish remains in England, even in inland sites, with slight differences in timing and relative abundance between different regions (Barrett *et al.*, 2004b and references therein; Orton *et al.*, 2014). At this point, cod are thought to be mostly caught locally around England in the southern North Sea and brought as a whole to inland sites such as London, with only a small number imported from northern waters of the North Sea, as evidenced by isotope analysis (Barrett *et al.*, 2011; Orton *et al.*, 2014). The freshwater species such as pike, eel and carps are still present, but play a relatively less important role (Orton *et al.*, 2017). Flatfish is present in York, but similar to before and after the High Medieval period, it is only found in low abundances relative to the other species (Harland *et al.*, 2016).

1.3.5 Late Medieval

The Late Medieval period is characterised by the dominance of marine species such as cod and herring, while freshwater species became less important for consumption. Some sites with specific occupancy, such as monasteries or elite households, seem to rely more on freshwater species than households in cities or rural areas. As evidenced by zooarchaeology, isotopes and historical documents, fisheries ventured more out into the sea to capture marine fish to process or sell as whole fish.

Explorations to the East and to America in the Late Medieval period, resulted in new trade networks and the arrival of new products and technology to Western Europe.

Flemish fishers ventured into English and Scottish waters to fish, areas referred to as *Noordover* or *Noordland*, as well as Denmark, northern Netherlands and Doggerbank, presumably to focus more on herring after the 15th century due to a rise in demand from the growing cities (Ervynck *et al.*, 2004; Van Neer & Ervynck, 2007). In Belgian sites, the shift to larger and more fish, including more northern species such as turbot and halibut could indicate a shift to more northern fishing grounds or trade with Scandinavian fishers. The increase in herring exploitation is linked to the shift in technologies, where people started using gill and floating nets instead of trawl nets and seines (Ervynck *et al.*, 2004; Van Neer & Ervynck, 2007). The exploitation of herring was also made easier for Flemish fishers when they were allowed to start gibbing or gutting these fish at the start of the 15th century as well, which allows for better preservation. This made it easier to transport herring from the northern fishing grounds back to Belgium (Ervynck *et al.*, 2004; Van Neer & Ervynck, 2007). Marine fish were caught and brought to Belgian cities near the estuaries of, for example, the Scheldt, from which they were further traded inland (Ervynck *et al.*, 2004).

The following examples show that inland sites and sites with specific occupancy might deviate from the general trends seen elsewhere in the region or the whole North Sea area.

A single event deposit in a pit next to old houses in Raversijde/Walraversijde at the Belgian coast dating from the 15th century consists presumably of mainly *Pleuronectes platessa* of similar sizes between 30-40 cm TL (Van Neer & Pieters, 1997). A notable feature of this peculiar find is the skeletal element distribution, in which cranial elements are overrepresented compared to vertebrae, which would indicate a processing site. This hypothesis is reinforced by the presence of cut marks on cleithra, os anale, precaudal vertebrae, and distal caudal and ultimate vertebrae, and the remnants of bivalve shells found in the pit are thought to be stomach contents from the plaice, which is molluscivorous, meaning the fish were brought whole to the site (Van Neer & Pieters, 1997). Matching growth curves of the plaice from Raversijde using otoliths and vertebrae growth rings with modern material, showed that these fish might be caught in the southern area of the North Sea during spring (Van Neer *et al.*, 1999).

Throughout the Medieval period freshwater fisheries were still active and continued even in the Post-Medieval period. Some areas, e.g., Namur, Belgium, were strictly governed by the elite classes and rules were put in place to prevent overfishing, such as minimum size restrictions, banning fishing in certain periods or seasons, allocated fishing spots etc. Freshwater fish could be sold for a high price (Lentacker *et al.*, 1997). They remained an important and sometimes main source of piscine food in cities and areas far from the sea even in the Late Medieval and Post-Medieval periods (Lentacker *et al.*, 1997; Pigière *et al.*, 2002). Given the large distance from the sea to cities such as Namur, which is well documented and studied zooarchaeologically, imported marine fish was often processed, although wealthy people could also buy fresh, unprocessed fish that had been on the road for a few days. Salted herring was the main food item for the non-elites in Namur during the Late Medieval period. Starting in the 15th century, dried cod was also imported to Namur. A high number of pleuronectid flatfish have been found in Namur in the Late Medieval period and after the Medieval period (Lentacker *et al.*, 1997; Pigière *et al.*, 2002). Marine species were not as popular in remote cities like Namur and only a limited variety reached these places (Lentacker *et al.*, 1997; Pigière *et al.*, 2002).

During the Late Medieval period, the abbey of Ename continued to rely heavily on fish as part of the diet of monks (Van Neer & Ervynck, 1996). Freshwater species made up most of their diet, with the newly available carp and possibly other cyprinids forming the lion’s share of the fish remains. Eels (*Anguilla anguilla*) continued to be an important part of the diet in the abbey of Ename until the end of the Late Medieval period. At the end of the Late Medieval period, a few remains of three anadromous species were also found in the kitchen floor of the abbey: *Acipenser sturio*, *Coregonus* sp., and *Salmo* sp. A large number of marine species were also among the remains found in the kitchen floor, although surprisingly less abundant than the freshwater species. Most of these were probably processed and did not arrive as fresh fish to the abbey. The largest group was herring, followed by Gadidae, flatfish (mainly Pleuronectidae, as well as some *Solea solea* and *Scophthalmus* sp.), and some *Raja clavata*. In the remains found in the abbey, there seems to be no decrease in freshwater fish consumption (without domesticated carp) and only a slight increase in marine fish consumed during the entire Medieval period (Van Neer & Ervynck, 1996).

There is much less information available about fisheries in the Netherlands during this period due to a lack of synthesis publications and fewer articles getting published in journals. In the Netherlands it seems that Gadidae, herring, and flatfish are also the most important species targeted in this period, while freshwater species are still abundant in some sites (Brinkhuizen, 1979; Prummel & Heinrich, 2005; Çakirlar et al., 2019; Database Oceans Past Northern Seas Synthesis).

Cod and herring remain the dominant species in England during the Late Medieval Period. Some Late Medieval sites in England, however, seem to have been specialised sites, where mostly specific species, such as eels, have been uncovered (Barrett *et al.*, 2004a). During the 13th century, cod abundance increased even more in London with more vertebrae and fewer cranial elements, which is thought to represent a switch to processed and imported cod from more northern waters, such as the Arctic, north-east Atlantic and the Baltic region (Barrett *et al.*, 2011; Orton *et al.*, 2014). A slight drop in frequency during the 14th century is thought to be caused by reduced imports (Orton *et al.*, 2014). Little is known about flatfish from excavation reports. As found in historical reports, fresh plaice was brought inland to London from coastal areas, while flounder was caught in the Thames (Galloway, 2017). Freshwater fish, especially those from ponds and larger ones, became a food item associated with elite households and religious establishments and were sold for high prices (Maccarinelli, 2021).

1.3.6 Post-Medieval

Marine fish continue to be the dominant group of fish consumed in most areas and sites. Their importance increased even more after the discovery of new and rich fishing grounds in western parts of the Atlantic Ocean. This allowed the cod trade to boom in Europe during the 16th century CE and impacted the fishing industry as a whole. This increase of marine fisheries

has been called the fishing revolution (Holm *et al.*, 2019). Other fish such as herring remained important as well. Some sites, such as monasteries, still also relied on freshwater species (Ervynck & Van Neer, 1992; Van Neer & Ervynck, 1996).
Flemish fishers probably were fishing more locally in the North Sea during the 15th and 16th centuries due to wars and the economical growth and dominance of the Netherlands and England at this time (Ervynck *et al.*, 2004).

Although cod was more expensive than haddock at this time (Van Neer & Ervynck, 1996), it became the dominant gadid in Flanders from this period on (Van Neer & Ervynck, 2016). In the kitchen area of the abbey in Ename along the Scheldt River in Flanders at least four different flatfish species have been found, dating from 1450-1550: plaice, flounder, turbot and a *Solea* sp., which is thought to be a more expensive fish (Ervynck & Van Neer, 1992). In this site, the relative abundance of *Solea* sp. compared with the other identified species (total 93) is striking, 18% (out of 176 total flatfish bones).

Thanks to one preserved historical document written by Coenen (1577), called *Visboeck* (fish book), there is a lot of information on flatfish fisheries from the 16th century in Belgium and the Netherlands. During the 16th century flatfish could be found close to the coast and in estuaries in the North Sea from February till June (plaice) and June till November (sole). Fishermen would go out to farther waters to catch cod during the winter months. Flounder was captured in rivers and estuaries, such as the Scheldt and Meuse, and was fished by amongst others fishermen from more inland parts of these rivers (Coenen, 1577; Van Dam, 2008). During the 16th century, the main targeted flatfish species were plaice, flounder (in estuaries and rivers), and sole, whereas the other species were found as bycatch of other fisheries (Coenen, 1577; Bennema & Rijnsdorp, 2015). Flatfish were caught using weirs, drag nets, pinks or small boats, with which coastal waters of 3-4m deep could be searched for flatfish. Trawl nets could be used near the shore, whereas hook and line were easier to use further offshore. Sole could be caught using nets. Plaice was often sold dried to places far inland, whereas flounder, halibut and turbot, but also dab and sole were mainly sold as fresh fish to larger cities close to the sea or easy to reach by rivers for the wealthier people (Coenen, 1577; Van Neer & Ervynck, 2007; Bennema & Rijnsdorp, 2015). There was a huge trade market for flatfish, with Dutch fishermen selling fresh flatfish, especially ‘plaice’, to rich people in Antwerp and Brussels and dried flatfish to Germany in Cologne, Mainz and Strasbourg (Coenen, 1577; Bennema & Rijnsdorp, 2015). In inland Denmark (monasteries), Belgium (Tongeren, Brussels, Mechelen, Ename), France, and England (York, London) there are also indications of imported flatfish during the Medieval and Post-Medieval periods (Enghoff, 2000; Clavel, 2001). Fresh plaice and flounder were available for the less wealthy people as well (Coenen, 1577; Bennema & Rijnsdorp, 2015).

Age and size reconstructions of plaice found in Belgian and French sites showed a trend of flatfish becoming smaller and younger through the 12th to 17th century, which could be an effect of intense fisheries (Clavel, 2001; Van Neer *et al.*, 2002). Their ages and sizes indicate that they are probably caught in the southern part of the North Sea, and not in the northern regions, where even today plaice are larger and older than the post-medieval plaice recovered from the southern North Sea, even though market strategies must be kept in mind when dealing with ages and sizes of fish (Van Neer *et al.*, 2002).

In Britain, marine fish, especially cod, was imported to e.g., London from even further regions such as Newfoundland from the 15th century on, as evidenced by isotope and genetic data (Barrett *et al.*, 2011; Orton *et al.*, 2014; Hutchinson *et al.*, 2015). There is no information if flatfish were also caught in places other than the North Sea and imported to south England.

1.3.7 Modern

With the invention of trawlers powered by steam and fossil fuels, the exploitation of flatfish became even more intensive during the last few centuries. Up until the wide-scale introduction of steam powered and fuel powered engines in fisheries, people were often fishing for specific species during delineated seasons. Flatfish are exploited continuously, whenever the cod fishing season is over or when the Gadidae stocks are depleted, such as during the 1980s (Redant, 1997; Lescrauwaet *et al.*, 2010).

In modern-day Europe, flatfish fisheries in the North Sea continue to be of commercial interest. During the last decade, flatfish (mainly plaice and sole) constitute more than half of the total weight of all landed fish (around 60% out of 16 million tons) in Belgium annually and provide more than half of the total value of fisheries (71% out of € 600 000) (Statbel, 2020; 2021). Most flatfish are caught in the shallow areas of the North Sea, except for *H. hippoglossus* which is caught in the deeper water along Norway. *Lepidorhombus whiffiagonis* and *H. platessoides* are also caught in the northern part of the North Sea, whereas the *S. solea* is fished in the south. The main targeted species are *P. platessa*, *H. hippoglossus* and *S. solea*. The less common species such as *G. cynoglossus* and *L. whiffiagonis* are often caught as bycatch (Gibson *et al.*, 2015). In modern times, flatfish are readily available for human consumption and many species such as plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), lemon sole (*Microstomus kitt*), dab (*Limanda limanda*), halibut (*Hippoglossus hippoglossus*), turbot (*Scophthalmus maximus*), brill (*Scophthalmus rhombus*) and common sole (*Solea solea*) can be found in most fish shops.

Other regions in the world also have large flatfish fisheries that originated during the 19th century, exploiting mainly the locally occurring species (Gibson *et al.*, 2015). Some species, *Solea senegalensis, Limanda aspera, Hippoglossus stenolepis,* and *Reinhardtius hippoglossoides*, are imported to Europe nowadays (Viswijzer, 2020).

1.3.8 Summary

Fish and flatfish have been consumed for millenia in Europe. During prehistory, marine fish were initially only consumed near coasts and settlements close to estuaries and rivers, while freshwater fish were consumed where available (Van Neer & Ervynck, 2007). Starting in the Roman period, there is evidence for transport of fresh and processed fish to other regions. Mediterranean species were imported to western Europe and coastal and marine species started to get transported to inland settlements (Brinkhuizen, 1979; Locker, 2007; Lotze, 2007; Van Neer & Ervynck, 2007; Van Neer *et al.*, 2010; Van Neer & Ervynck, 2016; Oueslati, 2019). This trend continued in the Early Medieval period with more and more marine species being recovered from inland sites, although in England there might have been a post-Roman decline at first (Barrett *et al.*, 2004a; Lotze, 2007; Van Neer & Ervynck, 2007; Reynolds, 2015; Oueslati, 2019). At the start of the High Medieval period the amount of Gadidae and herring began to dominate fish assemblages from sites, both coastal and inland. Although some sites have specific uses or occupancy, most sites show that marine species were the most consumed group, while freshwater species became less abundant (Brinkhuizen, 1979; Van Neer & Ervynck, 1996; Barrett *et al.*, 2004a,b; Van Neer & Ervynk, 2007; Barrett *et al.*, 2011; Orton *et al.*, 2014; Harland *et al.*, 2016; Van Neer & Ervynck, 2016). Marine fish was also being caught from regions beyond the local coasts, and there is evidence for international trade from this period, although local fisheries along the coast remained active as well (Barrett *et al.*, 2011; Orton *et al.*, 2014; Galloway, 2017). In the Late and Post-Medieval periods, marine fish remained an important economic and dietary resource around the North Sea (Van Neer & Ervynck, 2007; Barrett *et al.*, 2011; Orton *et al.*, 2014).

It has been argued that there were differences between the eastern and western shores of the North Sea in how quickly the shift to marine species occurred. Van Neer and Ervynck (2016) and Barrett *et al.* (2004a) argue that the marine fish event horizon is clearly delineated in time in England, while this process was more gradual and the transition occurred over a wider time span, starting before the High Medieval period and lasting longer, on the continental side of the North Sea. Although this holds true looking at Gadidae, especially cod, when looking in general at marine species, both sides of the sea seem to have undergone a rather gradual transition starting well before the High Medieval period (see Barrett, 2016).

It seems that pleuronectid flatfish were targeted more than Soleidae and Scophthalmidae throughout the Medieval and following periods (Ervynck & Van Neer, 1992). 'Sole' and 'turbot' were regarded as more expensive or exclusive fish than Pleuronectidae, which might explain why sole seemingly appears more frequently in monastic sites (Ervynck & Van Neer, 1992; Van Neer & Ervynck, 1996; Nicholson, 2015). These values might have shifted since, and flatfish nowadays commonly have similar prices per kilogram, although turbot, brill and sole can sometimes still be more expensive than the Pleuronectid species, excluding halibut (pers. obs.).

Further and more detailed research, however, is needed in order to better understand the flatfish fisheries through time in the North Sea area, which is where this study comes in.

1.4 Review of methodologies

1.4.1 Comparative osteology

Comparative osteology is the study of variation in bone morphologies between different taxa or populations of vertebrates. By analysing ratios of bone dimensions (quantitative) and the absence or presence and shape of structures on and within the bone (qualitative) differences and similarities between groups can be described. This can be used to identify taxa based on remains or to analyse phylogenetic relationships between taxa. This method is often used in taxonomy, palaeontology and archaeology and has been in use for a long time (e.g., Cuvier, 1826; Traquair, 1870; Earle, 1893). It is still commonly used and today can be accompanied by molecular techniques and new technologies, such as X-rays and CT-scans (e.g., Prötzel *et al.*, 2018; Campbell *et al.*, 2019; Zhang *et al.*, 2019).

Comparative osteology can be conducted qualitatively and quantitatively. Qualitative characters can be described, categorised, and illustrated after careful and thorough observations. Due to the nature of qualitative characters, they can be prone to some observation bias, and thus need to be well described in uniform ways, following overview publications, such as Lepiksaar (1994) for fish bones. Quantitative measurements of bones, such as osteometrics or morphometrics, are a more precise method in which specific points along bones are used to measure lengths, surface areas, angles and ratios that can then be compared between groups. These points need to be carefully selected and described to make the comparison between taxa and by different researchers possible. An example of such quantitative methods is Morales and Rosenlund (1979). One specific osteometric method is geometric morphometrics, which will be discussed in the following section. Quantitative morphometrics has also been performed on fish vertebrae (e.g., Huber *et al.*, 2011; Lambrides & Weisler, 2015). It can also be used to estimate the size of an animal based on a single or few measurements of bones, which is more precise than only using visual comparisons to a reference collection (figure 1.5) (e.g., Thieren & Van Neer, 2014; 2016; Jelu *et al.*, 2021) (also see section 1.4.5).

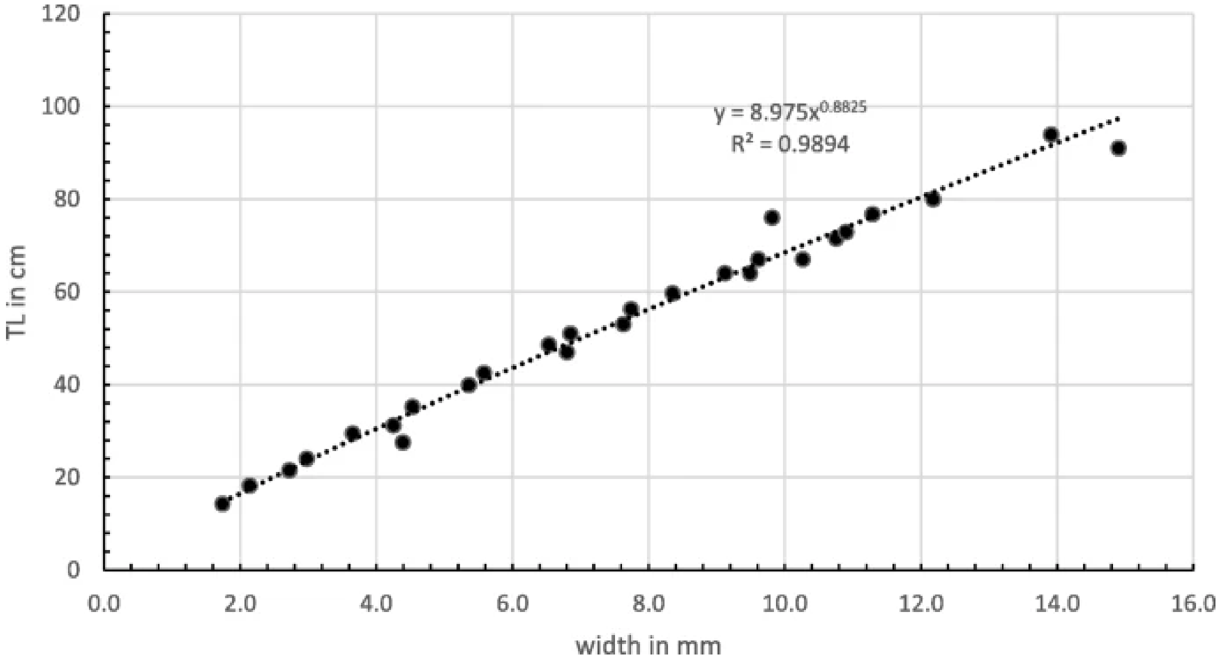

Figure 1.5. The regression model plot from Jelu *et al.* (2021: fig. 5), showing that the width of a vertebra of *Esox lucius* can be used to calculate the total length of the fish.

Descriptive comparative osteology has been conducted for all major vertebrate groups and has proven useful for archaeological studies of faunal assemblages, often accompanied by a reference collection for verification. Several comparative studies on fish bones have been published in the recent years, that can be used to identify disarticulated remains: e.g., Takahashi (2003) on African cichlids, Wouters *et al.* (2007) on European flatfish, Voskoboinikova *et al.* (2010) on eelpouts, Keivany (2014) on high taxon comparisons, Dierickx *et al.* (2017) on tilapia, and Jawad *et al.* (2017) on blennies. This technique is, however, limited sometimes by the absence of diagnostic features between species, which, even when present, can in some cases also be difficult to interpret without a reference collection.

1.4.2 Geometric morphometrics

Geometric morphometrics (GMM) is a landmark-based morphometrics approach to analyse and compare the shape and form of objects. These can be the shape of whole organisms, skulls, single bones, etc., and GMM can be used for example to identify different groups, describe species, relate shape to function, or analyse growth (Bookstein, 1991; Zelditch *et al.*, 2012). Landmarks are coordinates in a Cartesian system that can be either 2D or 3D depending on the object and research question and are defined as specific recognisable morphological structures on an object (Bookstein, 1991; Zelditch *et al.*, 2012). When comparing different taxa, landmarks should be homologous (Zelditch *et al.*, 2012). All landmarks from an object form a landmark configuration, which consists of a list of two (or three in case of 3D analysis) coordinates for all landmarks. There are three different kinds of landmarks (figure 1.6). Type 1 landmarks are defined by a specific anatomical structure with a fixed position in all dimensions, such as a base of a processus of a bone or joining suture lines. Type 2 landmarks have a less fixed position, such as tips of teeth since the length can vary due to wear and age. The third type of landmarks are not defined in one of their dimensions, and are defined by their position to other landmarks. Semilandmarks, or sliding landmarks, are used to define the edge or contour of structures and are not true landmarks. Usually multiple points are placed that follow the intended outline (Bookstein, 1991; Zelditch *et al.*, 2012; Gunz & Mitteroecker, 2013). Once landmarks are obtained from objects their relative position can be used to analyse and compare shapes and forms. However, the landmark configurations need to be corrected for differences in position, rotation and size, since these can influence the analysis. A new set of coordinates, called the shape variables, is obtained after a general procrustes analysis that can then be analysed using a principal components analysis (PCA) (Bookstein, 1991; Zelditch *et al.*, 2012).

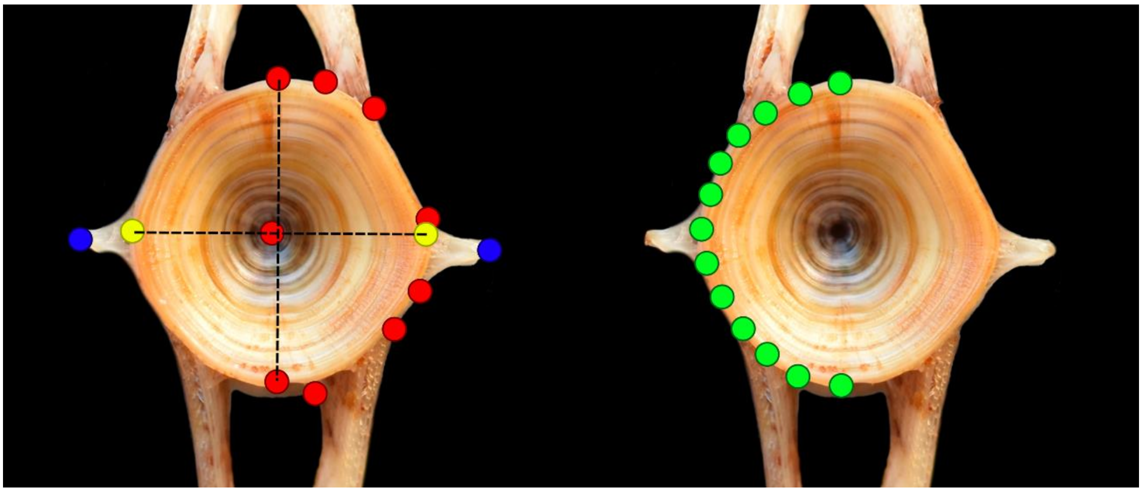

Figure 1.6. Different landmarks types on a fish vertebra. Red: Type 1; Blue: Type 2; Yellow: Type 3; Green: Semilandmarks.

Geometric morphometrics has been applied on flatfish using radiographs of complete specimens (Black, 2014). Some studies applied GMM on scutes, scales, and otoliths of other fish groups, indicating the possibility to use these elements for species identifications (e.g., Ponton, 2006; Ibañez *et al.*, 2007; Thieren & Van Neer, 2016). No study of flatfish vertebrae using geometric morphometric has been performed so far, and the number of studies applying this technique on vertebrae of other fish taxa is also limited. Using only 3-7 landmarks and sliding semilandmarks, modern and archaeological vertebrae from salmonids can be identified to species relatively easily (Guillaud *et al.*, 2016). GMM can also be applied to identify the habitat of archaeological fish remains by comparing the vertebra shape as Indo-Pacific fish inhabiting pelagic or reef habitats differ in the shape of the anterior and posterior sides of their precaudal and caudal vertebrae (Samper Carro *et al.*, 2018). A key thing to note with GMM is that landmarks need to be placed with great care and consistently and not all diagnostic features of a bone are suitable to place landmarks on.

1.4.3 Zooarchaeology by Mass Spectrometry (ZooMS)

Since archaeological remains are often fragmented or the bones are not diagnostic, it can be difficult to identify animal remains to species level. Molecular techniques can be used besides traditional morphological identifications to increase the identification success. DNA analysis is one option, but this can be relatively expensive to do for a large assemblage and is time consuming. Furthermore, DNA can be heavily degraded or easily contaminated due to taphonomy, excavation or lab analysis. Therefore, another molecule was suggested just over a decade ago: collagen, the main bone protein that commonly survives in the burial environment (Collins *et al.*, 2009; Buckley *et al.*, 2009; Collins *et al.*, 2010). The same molecule is also used to analyse stable isotopes (see later) and to radiocarbon date samples.

Collagen is the building block of various types of tissues of the vertebrate body, such as bones, tendons, muscles, skin, organs, cartilage, scales etc. In this work, only the most abundant collagen found in bones (collagen type 1) will be discussed. Collagen is a protein found in the extracellular matrix around bone cells and makes up around 90% of the organic matter. It is produced by osteoblasts as collagen fibrils that form polymers or fibers on which calcium phosphate is deposited to make mineralized bone. A collagen protein consists of three collagen polypeptide α-chains and is about 300 nm long (figure 1.7). Each peptide is a chain of amino acids with one third being glycine (Gly) and with proline (Pro) as another abundant amino acid. Usually they are arranged as Gly-Pro-X or Gly-X-Pro, with X being any other amino acid, usually hydroxyproline, a post-translational change of proline using hydroxyl groups and vitamin C. Together the peptides or chains form a fibrous triple helix, called an α-helix, with hydrogen bonds that are stabilised by hydroxyproline. Lysine can also be changed post-translationally to add glucose or galactose, which help with forming the triple helix structure. The precise amino acid composition determines the ultimate structure and function of collagen, resulting in different types of collagen. The incorporation of collagen within the bone minerals improves the stability of collagen through time (e.g., Collins *et al.*, 2002; Fratzl, 2008; Shoulders & Raines, 2009; Szpak, 2011). In Osteichthyes, the three α-chains differ from each other in their amino acid sequence, since all three are coded by different genes (*COL1A1, COL1A2, COL1A3*). This composition has been observed in several orders of Teleostei, such as Anguilliformes, Salmoniformes, Pleuronectiformes, Gadiformes, and even in Acipenseriformes (Kimura, 1992). In mammals, however, there are only two different genes coding for collagen chains, resulting in a helix that is made from two α1-chains and one α2-chain. This makes fish collagen more diverse and more prone to show diagnostic markers between taxa (Korzow Richter *et al.*, 2011).

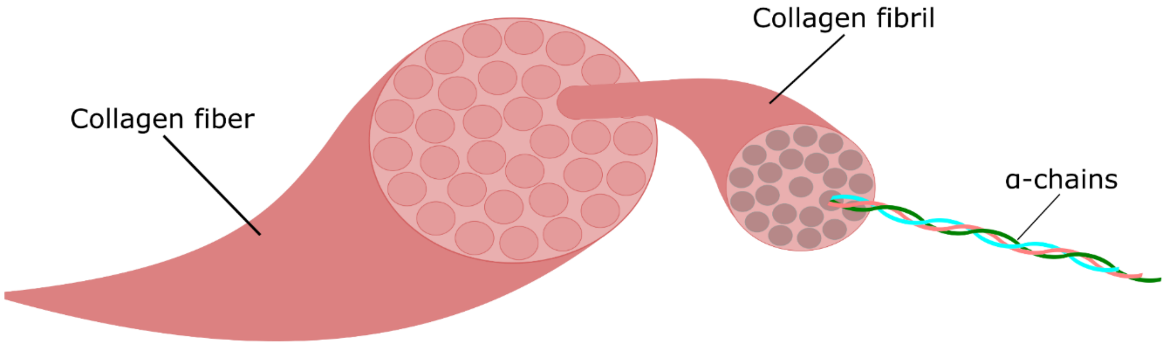

Figure 1.7. Schematic illustration of collagen.

Since the sequences of collagen differ between taxa, they can be used in a similar way as DNA is used to identify species by fingerprinting archaeological remains. Only a few milligrams of archaeological bone is needed for this analysis, which is possible as collagen is abundant in bone tissue and less prone to contamination than DNA, since it is incorporated in the bone matrix. As mentioned before, it is also more robust, preserving longer than DNA in the bone, because of its chemical structure as well as the integration of apatite minerals between the helices (Buckley *et al.*, 2009; Collins *et al.*, 2010). Another advantage over DNA is that all species are analysed in the same way using ZooMS, whereas species specific primers are sometimes needed for DNA. The taxon does not need to be known before the analysis of collagen, but it might be needed for DNA analyses (Korzow Richter *et al.*, 2020).

Different methods have been used over the years to extract collagen from bone for peptide mass fingerprinting. Three protocols have been compared and reviewed recently by Naihui *et al.* (2021): (1) demineralisation of the bone and analysis of insoluble collagen (see chapter 5); (2) demineralisation of the bone and analysis of soluble collagen; and (3) non-destructive analysis of soluble collagen. Demineralisation of a small piece of bone, between 10 and 30 mg, occurs with acid, most often hydrochloric acid (HCl). For the first protocol, once the calcium of the bone is dissolved by the acid, the acid can be removed. To increase and neutralise the pH of the remaining bone, it is rinsed with an ammonium bicarbonate buffer (Ambic) and later gelatinised in a heating block. The enzyme trypsin is added to cut the collagen into strands of peptides at specific sites of the protein with a lysine or arginine amino acid. These peptides differ between taxa because they have been altered during evolution. After stopping the digestion by trypsin, the peptides are purified using C18 ZipTips with buffer solutions. The second protocol uses the acid supernatant obtained during the demineralisation process and filters it to obtain the soluble collagen from the bone, which can then be rinsed, digested and purified in a similar manner as the first protocol. The third protocol does not require demineralisation of the bone, and is thus less/not destructive. The bone sample is placed into an 50mM Ammonium bicarbonate buffer (Ambic) with pH8.0 for a few days, without demineralising it first. The soluble collagen present in the supernatant can then be digested with trypsin and purified using C18 Ziptips. The bone itself can be dried out slowly and stored safely (Nahui *et al.*, 2021). Comparing performance of these three protocols showed that all are good and provide clear spectra allowing identifications. For well preserved samples, the non-destructive Ambic protocol might even be favoured, given time and costs, while the acid insoluble method performs better for poorly preserved bones (Nahui *et al.*, 2021). It is possible to try to extract collagen first using the non-destructive Ambic protocol, and later, if this has failed, to extract the same bone using a destructive demineralisation protocol. This allows for less intrusive analyses of valuable and unique archaeological material (Nahui *et al.*, 2021). Other non-destructive techniques have been used to extract collagen by using erasers to electrically extract collagen (Fiddyment *et al.*, 2015) or by sampling from the plastic bag the bone was stored in (McGrath *et al.*, 2019), which shows that even less invasive methods are possible.

After extraction collagen peptides can be spotted on a plate for MALDI-TOF (matrix-assisted laser desorption/ionisation - time of flight) mass spectrometry analysis. By exciting the crystalised peptides using a laser, these are desorbed from the matrix and become ionised. They are then accelerated in an electric field and hit a detection plate (figure 1.8). By calculating their time of flight through the mass spectrometer, the masses of each peptide can be obtained and plotted in a graph to show the mass spectra of each sample. These mass peaks or m/z markers can be compared to each other and diagnostic peaks are used to identify taxa (e.g., Brown *et al.*, 2021a).

In order to better define these diagnostic markers, it is important to verify if the peptides found in the spectra are indeed collagen and to see if species differ in their amino acid sequences, which then definitely shows that the mass peaks are differentiated. This can be accomplished by running the collagen extracts through a liquid chromatography tandem mass spectrometry system (LC-MS/MS). In this case, the peptides in the samples are excited and run through an electric field twice, which results in first a separation of the peptides based on mass per charge, similar to MALDI-TOF, and later in a separation of the amino acid weights per peptides, from which the amino-acid sequence of the peptides can be deduced (Harvey *et al.* 2018). The resulting peptide sequences can be compared to related species' sequences to verify which peptides are from collagen. Using alignments to publicly available collagen sequences of related taxa, the original collagen sequence of the samples can be reconstructed, which allows to verify the position of each peptide useful for identification, that can then be given a name following its position, as proposed by Brown *et al.* (2021a).

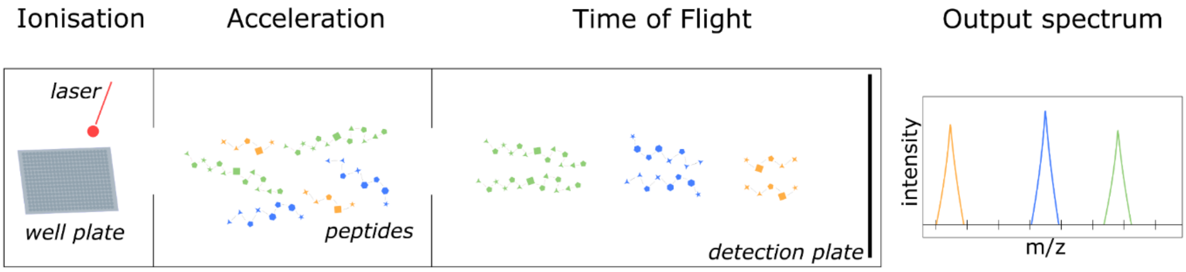

Figure 1.8. MALDI-TOF mass spectrometry set-up and methodology.

Important for identification by ZooMS is access to a good reference library. Modern samples of known identification need to be analysed first to see for which peptide markers taxa differ. With these diagnostic masses, archaeological samples can then be analysed. Previous studies have shown that ZooMS and morphological identifications are complementary and combining both can result in an increased number of identified samples, especially since ZooMS can identify worked and heavily fragmented bones (Buckley *et al.*, 2014; Welker *et al.*, 2015; Brandt *et al.*, 2018; Harvey *et al.*, 2018). Some species can be difficult to identify based on bones, but ZooMS can provide an alternative identification method, which can resolve some in-depth questions concerning animal use such as distinguishing between sheep and goat bones (e.g. Buckley *et al.*, 2010; Pilaar Birch *et al.*, 2019). Although ZooMS can help to improve the identification success of an assemblage, this technique is limited by the collagen amino acid sequence and whether or not taxa differ in the mass of the detectable collagen peptides.

Pitfalls of ZooMS include mainly the absence of diagnostic m/z markers between species or the absence or poor preservation of collagen in archaeological samples, resulting in poor spectra quality, which makes identification difficult to impossible. Even though collagen is viewed as a well-preserved molecule compared to DNA, it can still degrade or be damaged over time due to microbial attack, loss of stability due to loss of apatite mineral in the bone, and chemical deterioration of collagen, and it occurs faster when temperatures are higher (Nielsen-Marsh *et al.*, 2007; Smith *et al.*, 2007). Archaeological bones could have been treated by humans in the past by boiling or cooking them. Some simple results of testing these treatments on bones show that cooking and short boiling does not have an effect on the marker patterns, whereas treating bones with enzyme-containing cleaning products or long boiling makes the bones unuseable for ZooMS (Korzow Richter *et al.*, 2011). Boiling, however, can make the bone more prone to degradation afterwards (Roberts *et al.*, 2002). Taphonomic processes can also decrease the quality of collagen, depending on burial duration, temperature, deviation from neutral pH, hydrology and microbial activity (Collins *et al.*, 2002). If the bone minerals are degrading because of microbial or chemical processes, then collagen is more exposed, resulting in poorer preservation (Collins *et al.*, 2002; Pestle & Colvard, 2012). Bacterial enzymes that break down collagen can more easily degrade fish bones since collagen is less densely packed compared with mammal collagen (Szpak, 2011). Even when collagen is badly preserved, the amino acid sequence appears to remain unaltered (Pestle & Colvard, 2012).

ZooMS has mainly been used to identify bones, teeth, skin, and antlers of a wide variety of taxa (e.g., Buckley *et al.*, 2009; Buckley *et al.*, 2010; van der Sluis *et al.*, 2014; Charlton *et al.*, 2016; Buckley *et al.*, 2017; Brandt *et al.*, 2018; Buckley *et al.*, 2018; Desmon *et al.*, 2018; Hofman *et al.*, 2018; Amsgaard Ebsen *et al.*, 2019; Harvey *et al.*, 2019; Brandt & Mannering, 2021; Culley *et al.*, 2021; Marković *et al.*, 2021; Peters *et al.*, 2021), but also eggshells (e.g., Stewart *et al.*, 2013; Presslee *et al.*, 2017; Demarchi *et al.*, 2020) and to identify human remains (e.g., Brown *et al.*, 2016; McGrath *et al.*, 2019; Brown *et al.*, 2021b). The oldest bones analysed using ZooMS so far are at least 3.4 million years old (Rybczynski *et al.*, 2013).

There is a growing number of publications applying ZooMS on fish remains. The first article proposing and testing ZooMS for archaeological fish bones was that of Collins *et al.* (2009), which showed that European cyprinids can be distinguished using this method. Differences in collagen sequences of some distantly related orders of fish are shortly described in Buckley *et al.* (2018). The first large study that used fish collagen fingerprints to identify fish remains is Korzow Richter *et al.* (2011). Eight European species were included as modern reference material. These were compared with archaeological remains from Great Yarmouth, UK, and using discriminant analysis grouped according to species. The success rate of ZooMS can be much higher than morphological identification (Korzow Richter *et al.*, 2011). This study also showed that the absence of a species in the reference material together with small sample sizes can result in a different identification at order level, when using discriminant analysis (Korzow Richter *et al.*, 2011). Another large study on fish collagen fingerprinting in an archaeological context is Harvey *et al.* (2018). They analysed and published the collagen spectra of 34 different species found in the Baltic Sea, including five flatfish species: *L. limanda, P. flesus, P. platessa, S. rhombus* and *S. maximus* (Harvey *et al.*, 2018). One species specific marker capable of distinguishing the species of the genus *Scophthalmus* was found and described (Harvey *et al.*, 2018). These m/z markers results were applied to analyse 114 archaeological remains from the Baltic area, showing that ZooMS and morphological identifications differ in only 6 cases and in 32 cases ZooMS was able to refine the identification to a lower taxonomic level. ZooMS was not possible for 29 bones (Harvey *et al.*, 2018). The latest publications describing markers for Xiphiidae, Scombridae and Salmonidae, show the increasing quality of this technique to identify archaeological fish remains to genus and even species level (Rick *et al.*, 2019; Korzow Richter *et al.*, 2020; Buckley *et al.*, 2021). A recent study proposed to use collagen amino acid sequences of Actinopterygii for phylogenetic analysis in cases where DNA approaches might not be possible (Harvey *et al.*, 2021). Building on Harvey *et al.* (2018), Buckley *et al.* (2022) provided ZooMS data (mass spectra and mass peaks) on many more species from European waters and applied their results on an archaeological assemblage (n=77) of a shipwreck found in Newport, UK, dating to the 15th century. Their results confirm that ZooMS can be used to identify species, but the study lacked a clear comparison between osteological identification and ZooMS. Additional markers for *P. flesus*, *P. platessa*, *S. rhombus*, *S. maximus* and new markers for *H. hippoglossus, L. limanda, M. kitt, L. whiffiagonis* and *S. solea* were described by Buckley *et al.* (2022).

1.4.4 Stable isotope analysis

Isotopes are atoms of the same chemical element with different numbers of neutrons which results in them having differing masses. There are two categories of isotopes: stable and radioactive. The latter type undergoes radioactive decay by which it loses particles. This happens at a certain rate, often written as the half-life of a radioactive isotope, i.e. the time it takes for half of the original amount to decay. This is used for chronometry such as ^{14}C dating. Stable isotopes on the other hand, are not observed to undergo radioactive decay.

Stable isotopes of the same chemical element have similar characteristics, since the electron and proton compositions are the same. Due to the mass difference, isotopes have a slight difference in reaction speed (kinetic isotope effect) or transport processes. This causes isotopes of the same element to move through ecosystems or tissues differently, resulting in fractionation (Topalov *et al.*, 2012).

There are many elements with sometimes multiple stable isotopes. Most commonly analysed and studied in this work and more widely in archaeology are the stable isotopes of carbon (^{12}C and ^{13}C), nitrogen (^{14}N and ^{15}N) and sulfur (^{32}S and ^{34}S).

The stable isotope value of a sample is calculated with the following formula: $\delta(‰) = R_{sample}/R_{standard} - 1$; with R the ratio of the stable isotopes, e.g., $^{13}C/^{12}C$, within a sample. The standards are internationally agreed upon definitions. For $^{13}C/^{12}C$ this is Vienna Pee Dee belemnite (Fry, 2006; Topalov *et al.*, 2012; see table 1.4-5). The standard for $^{15}N/^{14}N$ is the atmospheric value (Fry, 2006; Guiry *et al.*, 2020; see table 1.4-5). For $^{34}S/^{32}S$ the Vienna-Canyon Diablo used (Fry, 2006; see table 1.4-5). A positive value means the sample is enriched in the high mass isotope compared to the standard, a negative value means depleted compared with the standard (Topalov *et al.*, 2012).

Table 1.4. Relative natural abundances of different isotopes (Fry, 2006).

Element	Low Mass	Low Mass abundance	High Mass	High Mass abundance
Carbon	^{12}C	98.89	^{13}C	1.11
Nitrogen	^{14}N	99.64	^{15}N	0.36
Sulfur	^{32}S	95.02	^{34}S	4.21

Table 1.5. Isotope standards composition (Fry, 2006).

Standard	Ratio	Value of ratio	%Heavy isotope	%Light isotope
PeeDee Belemnite (PDB)	$^{13}C/^{12}C$	0.011180	1.1056	98.8944
Air (AIR)	$^{15}N/^{14}N$	0.0036765	0.36630	99.63370
Vienna-Canyon Diablo	$^{34}S/^{32}S$	0.0441626	4.19719	95.03957

Plants tend to form the base of the food chain as primary producers as they store carbon from the atmosphere. ^{13}C is less favoured than ^{12}C during photosynthesis, which results in a depleted carbon composition in primary producers (O'Leary, 1988). Terrestrial plants can use carbon from the atmosphere for photosynthesis, while marine photosynthesizing organisms, such as cyanobacteria, algae and marine plants, use the dissolved CO_2 in ocean water as a carbon source, which is enriched in ^{13}C compared with the atmosphere's CO_2. Therefore, in terrestrial ecosystems plants usually have a $\delta^{13}C$ of -28‰, while marine phytoplankton have a $\delta^{13}C$ of -19‰ to -24‰ (Fry, 2006). In terrestrial systems, the difference between C4 or C3 plants, which use different pathways during photosynthesis, result in different isotopic ratios, with organisms using the C4 pathway being less depleted in ^{13}C (O'Leary, 1988). Freshwater systems can either rely on carbon input produced by terrestrial plants or by aquatic primary producers, such as bacteria and algae. The latter can use carbon dissolved from the atmosphere, but also from the rock bedding and detritus (Fry, 2006). Therefore, freshwater systems depend more on the local environment and can show a range of $\delta^{13}C$ values (Fry, 2006). As primary producers in an ecosystem provide the carbon for the whole food chain, the differences between $\delta^{13}C$ values can also be found higher up the food chain. With each trophic level increase, $\delta^{13}C$ increases by 1‰ (Topalov *et al.*, 2012).

Nitrogen is mostly present in the atmospheric air as N_2. It can be taken up by organisms through direct fixation, ammonium or nitrate in the soil water, or from nitrogen in the soil. The ratio of ^{15}N increases with each trophic level by 2-6‰ as ^{14}N is lost faster than ^{15}N (Topalov *et al.*, 2012).

Sulfur has four different stable isotopes: ^{32}S, ^{33}S, ^{34}S, and ^{36}S. Further, only the relation between ^{32}S and ^{34}S will be discussed. Sulfur in ecosystems comes from the atmosphere, and weathering of minerals, rocks and evaporites. Microbes and plants capture sulfur into the amino acids cystein and methionine by chemical reactions of naturally occurring sulfur-containing molecules such as hydrogen sulfide, sulfate, sulfur dioxide, and carbonyl sulfide, which fractionates the isotopes (Johnston, 2011). With each trophic level, $\delta^{34}S$ can change from -1‰ to +2‰ (Mekhtiveya *et al.*, 1976, cited by Privat *et al.*, 2007). Ocean water has a relatively stable ratio of sulfur isotopes of around +17 to +21‰ (Rees *et al.*, 1978), while terrestrial systems can show a much larger variation depending on the bedrock, minerals, sediments, etc. in a local area (Privat *et al.*, 2007; Nehlich, 2015). Plants can thus show a variable ratio as well, depending where they grow, but it is usually about 1.5‰ lower than the sulfate found in the surrounding area (Trust & Fry, 1992). Inland their ratio is usually between -7‰ to +8‰, while plants close to oceanic water can have a slightly higher ratio (Chukhrov *et* *al.*, 1980; Privat *et al.*, 2007). This variation between the primary producers depending on their closeness to seawater and the small change in isotope ratio between trophic levels allows marine and terrestrial systems to be differentiated by $\delta^{34}S$ (Leach *et al.*, 2003). Freshwater plants and organisms, however, can show a much wider range of $\delta^{34}S$ between -22‰ and +22‰ due to the local environment and bedrock, which could complicate the distinction between freshwater and marine dietary sources (Privat *et al.*, 2007). Because of the potential local variation of sulfur isotope ratios, isoscapes are necessary to make conclusions about the origin of organisms using $\delta^{34}S$ (Nehlich, 2015).

Several environmental factors can influence local isotope values. Compared with marine systems, the isotope value is much more related to the freshwater river system itself and can differ between different basins due to the differences between the surrounding terrestrial systems and the hydrology (Fry *et al.*, 2002; Kennedy *et al.*, 2005; Finlay & Kendall, 2007; Ciancio *et al.*, 2008; Guiry, 2019). Also other environmental factors can influence stable isotope signatures in both freshwater and marine environments. Climatic change, seasonality, ecological succession, and human impacts on nature can influence factors such as temperature, pH, salinity, precipitation, etc., that as a result will affect the isotopic availability and fractionations in organisms, especially in primary producers (Resco *et al.*, 2011; Guiry, 2019). The combination of abiotic and biotic factors will determine the availability of ^{13}C, ^{15}N, and ^{34}S for organisms (Bauer *et al.*, 2000; Laiolo *et al.*, 2015). A change in the environment or the introduction/extirpation of organisms will therefore result in a change in the isotope composition of organisms (Vander Zanden *et al.*, 1999; Barnum *et al.*, 2013; Rogosch & Olden, 2020). It is therefore important to try to select reference species from the same locality and time period when analysing stable isotopes of an organism (Guiry, 2019).
The temperature from both the surface and the bottom of the North Sea influences ^{15}N and ^{13}C variation, as was modelled using data from modern day jellyfish (*Cyanea capillata*) (St John Glew *et al.*, 2018). Areas in the south are more enriched in ^{13}C than the central and northern open (deeper) sea part between Scotland and Norway. Nitrogen is less depleted on the east and south coasts than in the northwestern part. Although this might be caused partly by the influx of modern-day agriculture around the southern part of the sea, a similar pattern is found in medieval archaeological fish samples (Barrett *et al.*, 2011; MacKenzie *et al.*, 2014; St John Glew *et al.*, 2018). Since modern and medieval samples show the same pattern, it can be assumed that there hasn’t been much change due to anthropogenic effects since the Medieval period (MacKenzie *et al.*, 2014). The difference in $\delta^{15}N$ between the southern and northern part of the North Sea is related to the depth of those areas. Resuspension of enriched nitrate sources from rivers is easier in the shallow southern part, while the deeper northern part is more stratified and receives isotopically depleted nitrogen from the northern Atlantic, which combined with a difference in phytoplankton community results in a different availability of ^{15}N between these two main areas in the North Sea (MacKenzie *et al.*, 2014; Ford *et al.*, 2016). Seasonality can also affect the isotope composition in the ecosystem in the North Sea caused by physiological changes as well as environmental shifts, such as river run-off, throughout the year (Kürten *et al.*, 2013). A seasonal study of flatfish in a French estuary showed slight variations between seasons, dependent on the species of flatfish and the location in the estuary (Bouaziz *et al.*, 2021). Seasonality was also observed in a wide range of fish taxa from the English Channel on carbon, nitrogen and sulfur isotope composition, as well as a correlation between the isotope values and the weight of the fish (Cobain *et al.*, 2022).

The variation in sulfur isotope ratios across the North Sea is related to influx of freshwater, which is higher in the southern part of the North Sea. Therefore, there is a small gradient from south to north of increasing $\delta^{34}S$ from 20‰ to 22‰ and slightly depleted values at coastal areas (St John Glew *et al.*, 2018).

Isotope studies on animal remains usually use the organic component, or collagen, present in bones (see above). To extract collagen from bones, acid can be used to demineralise the mineral component and to gelatinise collagen. This is not always successful and depends on the preservation of collagen in the bone. Once extracted, collagen can be analysed using a mass spectrometer for which it is first burned to make the components gaseous (CO_2, N_2, and SO_2). The spectrometer separates the isotopes of the elements by mass and can provide the relative ratio of each isotope. Analysis can be in bulk, analysing a tissue, or compound specific, in which a specific molecule such as an amino acid is analysed.

In fish, bone (bioapatite $Ca_{10}(PO_4)_3(OH)_2$ and collagen) grows continuously throughout their lifetime (Witten & Huysseune, 2009). Collagen constitutes around 20% of the weight of a bone (Guiry *et al.*, 2016b). For growth, bone is first formed as woven bone and later remodelled into lamellar bone by which bone can be resorbed (Witten & Huysseune, 2009). Bone can also be repaired after fractures or can be changed to accommodate mechanical stresses. In fish, it is also used for mineral homeostasis (Witten & Huysseune, 2009; Shahar & Dean, 2013; Atkins *et al.*, 2014).

Different tissues of organisms show different isotopic signatures due to fractionation differences and a difference in turnover rate (Jardine *et al.*, 2005; Heady & Moore, 2012; Xia *et al.*, 2013; Busst & Britton, 2017). Bone collagen is regarded as one of the slowest tissues to change isotope composition, and therefore provides a more general long-term average of an animal's life (Philips & Eldridge, 2006; Hobson, 2019). The turnover rate of collagen in fish is unclear, and might differ immensely between species and fish of different ages (Tzadik *et al.*, 2017). Basal teleosts with cellular bone seem to undergo much remodelling, while derived teleosts, Percimorphs such as flatfish, have acellular bone and undergo less remodelling (Witten & Huysseune, 2009; Shahar & Dean, 2013; Atkins *et al.*, 2014).

As mentioned in the section on ZooMS above, bone collagen can be affected by taphonomic processes resulting in contamination or alteration and it can degrade over time (see above). In order to verify if values obtained from analysing archaeological bones have not been impacted by taphonomy and diagenesis, some quality control criteria have been developed (DeNiro, 1985; Ambrose, 1990; Hoke *et al.*, 2018; Guiry & Szpak, 2020; Guiry & Szpak, 2021). For modern fish, the C:N ratio has to be between 3.00 and 3.30, while archaeological samples can have a wider range (2.9-3.6) (DeNiro, 1985; Ambrose, 1990; Hoke *et al.*, 2018; Guiry & Szpak, 2020), although a stricter range for coldwater fish between 3.2 and 3.4 is advised (Guiry & Szpak, 2021). The C:S ratio should be 175±50 and the N:S 60±20 for fish (Nehlich & Richards, 2009). The weight percentage can also be used to assess the quality. For carbon, the weight percentage should be at least 13% in archaeological collagen samples, for nitrogen at least 4%, and 0.4-0.8% for sulfur (DeNiro, 1985; Ambrose, 1990; Nehlich & Richards, 2009; Guiry & Szpak, 2020; Guiry & Szpak, 2021). Also, the yield, i.e. the weight of extracted collagen by the weight of the original bone sample, can indicate whether a sample has been preserved well, or if it endured lots of degradation (Ambrose, 1990; Guiry & Szpak, 2020). Certain taphonomic processes can result in the presence of humic acids, which can impact stable isotope values. These can be removed by treating archaeological bones with NaOH prior to gelatinisation (Lowry *et al.*, 1941). In previous studies it has been reported that an NaOH wash does not impact the stable isotope values of archaeological samples, only the collagen yield (Kennedy, 1988; Katzenberg, 1989; Liden, 1995; Ambrose, 1990; Guiry & Szpak, 2020). Collagen extractions can in some cases be difficult due to the composition of collagen in certain species as in the case of *G. morhua* (Harvey *et al.*, 2021). Fish having fatty tissues and bones may also be prone to more difficult collagen extraction and value interpretation (Guiry *et al.* 2016). The presence of lipids in bones could also impact stable isotope values, since lipids are less enriched in ^{13}C than collagen (Katzenberg, 2008). Therefore, lipids have been extracted from archaeological remains in some studies (cf. Kates, 1986; Liden *et al.*, 1995). It is, however, not well known whether the lipid extraction procedure in itself alters the stable isotope values of the collagen samples. One study reported that lipid extraction should not have a significant effect on the values if the collagen yield of the extraction is sufficient (Tsutaya *et al.*, 2018). In order to avoid interpretations based on values obtained from untreated bones, which might have been affected by the presence of lipids, samples that show a clear correlation between C:N and δ^{13}C can be discarded (Hyland *et al.*, 2021).

Carbon, nitrogen, and sulfur stable isotope analysis is mainly used to study the diet of animals, and especially humans in past environments or societies, as well as their health (Hobson & Clark, 1992; Katzenberg, 2008). A variety of research questions can be answered using stable isotope analysis. Following are some examples of research questions that can be studied, with a few specifically on fish:

- <u>C3 vs C4 plants</u>: photosynthesizing plants can follow two systems, C3 or C4 photosynthesis, which have a different fractionation for ^{13}C. Analysing ^{13}C of animals and humans can uncover which plants they have been eating throughout their life (e.g., van der Merwe, 1982).
- <u>Marine vs terrestrial diets</u>: analysing human remains for ^{13}C, ^{15}N, and ^{34}S can uncover the diet and differentiate between food items of terrestrial, freshwater and marine origin, due to the producers in those habitats following different pathways for their ^{13}C (C3 vs. C4), having different trophic level composition, or a different δ^{34}S due to the local environment (e.g., Leach *et al.*, 2003; Privat *et al.*, 2007; Nehlich *et al.*, 2010; Müldner & Richards, 2007; Sayle *et al.*, 2013). One study analysing human remains from York dating from the Roman till Post-Medieval period found a gradual change in the isotope compositions indicating a shift in diet through time. It is thought that this is caused by the growing importance of off-shore marine fish starting in the Medieval period (e.g., Müldner & Richards, 2007), which corresponds to the growing amount of marine fish remains from later periods (Barret *et al.*, 2004; Harland *et al.*, 2016).
- <u>Trophic level diet / weaning age</u>: nitrogen stable isotope ratio is a proxy for the trophic level of an organism and analysing it can give more insight into the diet (e.g., Hedges & Reynard, 2007). In a similar way, weaning of mammals can also be analysed by ^{15}N ratios throughout infancy (e.g., Schurr, 1998; Reynard & Tuross, 2015). In fish the potential trophic level of an individual is determined by its size. As fish generally become more predatory of other fish as they get larger, their bodies are enriched in ^{15}N compared with smaller conspecifics (Jennings *et al.*, 2008; Miszaniec *et al.*, 2021). ^{34}S can also be used to estimate the weaning age of mammals (Nehlich *et al.*, 2011).
- <u>Diet composition:</u> analysis of animal, plant and human remains from a site combined can give a better understanding of the general and detailed diet composition of humans or specific animals using ^{13}C, ^{15}N and ^{34}S (e.g., Richards *et al.*, 2001; Leach *et al.*,

2003; Müldner & Richards, 2005; Privat *et al.*, 2007; Tykot *et al.*, 2009; Nehlich *et al.*, 2010; Nehlich *et al.*, 2011; Fernandes *et al.*, 2014). Dietary composition studies using $\delta^{34}S$ can also be used as a proxy for mobility and migration of humans and animals (e.g., Vika, 2009).

- Marine vs freshwater fish: carbon, nitrogen and in some cases sulfur have been used to differentiate between fish species or populations living in marine, estuarine and freshwater environments (e.g., Fry, 2002; Fry & Chumchal, 2011; Fuller *et al.*, 2012; Nehlich *et al.*, 2013; Drucker *et al.*, 2016; Robson *et al.*, 2016). Also fish species and ecotypes can be distinguished in archaeological material using this approach (Guiry *et al.*, 2016a; Guiry *et al.*, 2020). The ratio of nitrogen can be higher in marine environments than in terrestrial and freshwater environments, due to having more trophic levels. ^{34}S analysis can be used to even distinguish between estuarine and marine habitats of fish, with coastal fish showing higher $\delta^{13}C$ and $\delta^{34}S$ compared with estuarine fish from the same species (Leakey *et al.*, 2008). Sulfur isotopes of cod bones have been used to uncover the provenance of traded cod (Nehlich *et al.*, 2013; Kyselý *et al*., 2022).
- Provenancing: Using $\delta^{15}N$ the geographical origin of fish can be determined as different regions seems to show a different average value, e.g., Baltic versus North Sea (Barrett *et al.*, 2011; Robson *et al.*, 2016) and Mediterranean and Atlantic (Llorente-Rodríguez *et al.*, 2022).
- Chronological stable isotope analysis of organisms is possible by using continuously or intermittently growing tissues. In fish this is possible with otoliths (e.g., Weidman & Millner, 2000), spines (e.g., Acosta-Pachón *et al.*, 2015), and vertebrae (e.g., Matsubayashi *et al.*, 2017) due to the incremental bone formation of those elements. These studies can uncover behaviour (e.g., migration) and shifts in ecology (e.g., short term environmental impacts).

Many studies have analysed fish isotopes from western and northern Europe (see table 1.6), either as part of a human dietary study or to specifically analyse and compare fish from an area. The number of dedicated European fish isotopes studies is increasing (e.g., Barrett *et al.*, 2008, 2011; Fuller *et al.*, 2012; Hutchinson *et al.*, 2015; Haberle *et al.*, 2016; Robson *et al.*, 2016; Ervynck *et al.*, 2018; Olafsdottir *et al.*, 2021). Most work so far has focused on Gadidae, specifically *G. morhua*, to uncover trade across Europe (e.g., Barrett *et al.*, 2008, 2011; Orton *et al.*, 2011; Nehlich *et al.*, 2013; Hutchinson *et al.*, 2015; Olafsdottir *et al.*, 2021). Only a handful of isotope studies have included flatfish (table 1.6 and figure 1.9). Of these, Fuller *et al.* (2012, Belgium), Robson *et al.* (2016, Baltic Sea), and Ervynck *et al.* (2018, Belgium) tried to uncover the catch environment of these fish. Two flatfish samples are thought to have been estuarine catches from the Baltic Sea in Denmark (Robson *et al.*, 2016). All samples from Mesolithic/Neolithic Denmark have remarkably lower $\delta^{15}N$ values and higher $\delta^{13}C$ than the samples from Roman/Medieval/Postmedieval Germany, Belgium and the UK from the North Sea. It is possible that this is caused by the presence of seagrass in the Baltic Sea, which is enriched in $\delta^{13}C$ (Röhr *et al.*, 2016; Guiry *et al.*, 2021).

Pleuronectes platessa, H. hippoglossus and about half of *P. flesus* from Belgium, Germany and the UK seem to have been captured from marine environments, whereas the other half of *P. flesus*, especially the smaller ones, seem to have been captured from a freshwater environment (Müldner & Richards, 2005; Fischer *et al.*, 2007; Müldner & Richards, 2007; Antanaitis-Jacobs *et al.*, 2009; Fuller *et al.*, 2012; Göhring *et al.*, 2016; Dahliwal *et al.*, 2019; Ervynck *et al.*, 2018). The small freshwater *P. flesus* are more enriched in ^{15}N than the larger

P. flesus and *P. platessa*, which is probably due to the change in diet throughout its life from crustaceans to molluscs and feeding more on other fish species than *P. platessa* (Fuller *et al.*, 2012; Ervynck *et al.*, 2018). No isotope data is available on non-Pleuronectid flatfish species.

In order to have a better understanding of the relative stable isotope ratios between different environments, the analysis of other species with a stricter habitat (i.e. non-migratory marine or freshwater), can be used to compare the species in question to (Fuller *et al.*, 2012; Robson *et al.*, 2016). For the North Sea area, *Gadus morhua* is a common species from a typical marine habitat. For freshwater habitats, species such as *Esox lucius* and Cyprinidae should be good candidates, since these are non-migratory and therefore should show a clear freshwater signature (or estuarine in the case for some populations).

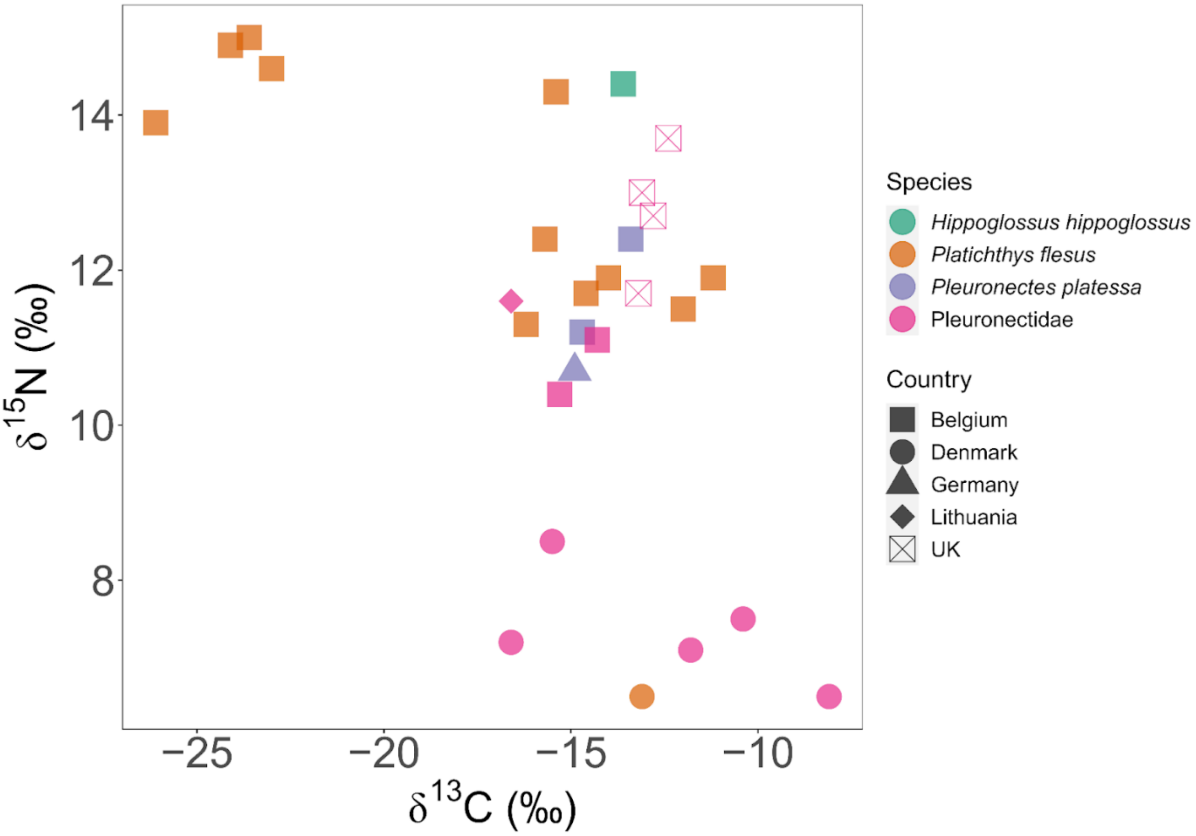

Figure 1.9. Plot of δ^{15}N against δ^{13}C of published isotope data on Pleuronectidae species from different countries and periods (for details and references see table 1.6). Green: *H. hippoglossus*; Red: *P. flesus;* Purple: *P. platessa*; Pink: unknown Pleuronectidae; Circle: Belgium; Triangle: Denmark; Square: Germany; Diamond: Lithuania; Crossed square: UK.

Table 1.6. Overview of published isotope values of flatfish from various studied areas and periods in Europe (Müldner & Richards, 2005; Fischer, 2007; Müldner & Richards, 2007; Antanaitis-Jacobs *et al.*, 2009; Fuller *et al.*, 2012; Göhring *et al.*, 2016; Robson *et al.*, 2016; Ervynck *et al.*, 2018; Dahliwal *et al.*, 2019).

Taxon	**Locality**	**Period**	**Size est. (cm)**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**C:N**	**%C**	**%N**	**Reference**
Platichthys flesus	Nivågård DK	mesolithic		-13.1	6.5	3.3	40.3	14.4	Fischer *et al.* (2007)
Pleuronectidae	Šventoji 4 LT	Early Subboreal (5000-4000)		-16.6	11.6	3.3			Antanaitis-Jacobs *et al.* (2009)
Pleuronectidae	Asnæs Havnemark DK	ca. 4300-4100 cal. B.C.		-15.5	8.5		27.4		Robson *et al.* (2016)
Pleuronectidae	Dragsholm DK	ca. 5000-3500 cal. B.C.		-11.8	7.1				Robson *et al.* (2016)
Pleuronectidae	Dragsholm DK	ca. 5000-3500 cal. B.C.		-16.6	7.2				Robson *et al.* (2016)
Pleuronectidae	Nederst DK	ca. 5400-3950 cal. B.C.		-8.1	6.5		44.3		Robson *et al.* (2016)
Pleuronectidae	Nederst DK	ca. 5400-3950 cal. B.C.		-10.4	7.5		42.3		Robson *et al.* (2016)
Pleuronectidae	Tournai BE	3rd-4th	30-40	-14.3	11.1	3.2			Fuller *et al.* (2012)
Pleuronectidae	Ghent BE	10th-12th	ca. 40	-15.3	10.4	3.3			Fuller *et al.* (2012)
Pleuronectes platessa	Schleswig DE	1070–1350		-14.9	10.7				Göhring *et al.* (2016)
Pleuronectidae	Beverley UK	14-15th		-13.2	11.7	3.3	5.4		Müldner & Richards (2005)
Pleuronectidae	Beverley UK	14-15th		-12.4	13.7	3.2	6.1		Müldner & Richards (2005)
Pleuronectes platessa	Raversijde BE	15th	ca. 40	-13.4	12.4	3.1			Fuller *et al.* (2012)
Pleuronectidae	York UK	Late Medieval		-13.1	13	3.2	44	15.7	Müldner & Richards (2007)
Platichthys flesus	Dendermonde BE	16th	10-20	-26.1	13.9	3.3	40.7	14.5	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	10-20	-24.1	14.9	3.2	37.6	13.7	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	20-30	-15.7	12.4	3.3	39.2	14	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	20-30	-23.6	15	3.3	27.1	9.5	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	20-30	-23	14.6	3.2	42.8	15.6	Ervynck *et al.* (2018)
(Platichthys flesus	Dendermonde BE	16th	30-40	-23.9	13.9	4.2	20.2	5.7	Ervynck *et al.* (2018))
Platichthys flesus	Dendermonde BE	16th	30-40	-14.6	11.7	3.4	39.4	13.6	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-16.2	11.3	3.4	39.5	13.7	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-11.2	11.9	3.2	35.5	13	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-12	11.5	3.2	48.8	18	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-14	11.9	3.1	40.4	15	Ervynck *et al.* (2018)
Pleuronectidae	Chichester UK	medieval/postmedieval		-12.8	12.7				Dahliwal *et al.* (2019)

Table 1.6 continued

Taxon	**Locality**	**Period**	**Size est. (cm)**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C:N**	**%C**	**%N**	**Reference**
Pleuronectes platessa	Antwerpen BE	17th	ca. 30	-14.7	11.2	3.3			Fuller *et al.* (2012)
Platichthys flesus	Antwerpen BE	17th	25-30	-15.4	14.3	3.4			Fuller *et al.* (2012)
Hippoglossus hippoglossus	Antwerpen BE	17th	80-90	-13.6	14.4	3.4			Fuller *et al.* (2012)

1.4.5 Size reconstruction on bones

Archaeological bones can provide information about the size of a fish. There are multiple techniques possible: visual comparison with known reference samples, geometric morphometric calculations, and regression analysis. To do regression analysis, bones can be measured following standardised methods, such as the one described in Morales and Roselund (1978) for many different bones and Lambrides and Weisler (2015) for vertebrae.

The reconstruction of fish sizes using regression analysis of measurements allows for more in-depth analysis as well as providing a more standardized approach, which makes it possible to more confidently compare sites analysed by different people.

Fish grow throughout all their lives, with slower or faster growth depending on season, food availability, stress, etc. Their size can in some way be used as a proxy for age, however corrections should be made when dealing with very large fish, since the growth rate slows down when the fish gets older (e.g., Choat *et al.* 2006). Growth rates can differ between populations (Hewett & Kraft, 1993).

Size of fish is important when it comes to analysing archaeological fish exploitation and commercialisation of fish. In general, large fish can be more easily captured and are more favoured on the markets. Some researchers have used the size of fish to infer social status of households (e.g., Kirch & Jones O'Day, 2003; Maccarinelli, 2021). Sudden changes in sizes of fish through time in an area can be linked to economic, social, or ecological factors. For example, decrease of cod bones in Quoygrew during the Medieval period was observed which was linked to a shift in the economic organisation of fisheries (Harland & Barrett, 2012). Also, for several other fish species in Medieval England the local economy might have played a role in the distribution of certain sized fish (Maccarinelli, 2021). Due to overexploitation, which causes bigger fish to be removed from a population and thus leaving only smaller fish, the average size of the fish population becomes smaller. If overexploitation continues for a long time or if there are environmental stresses which impedes growth, there might be evolutionary selection for fish to remain small and/or have slower growth rates (e.g., Bianchi *et al.*, 2000; Schilberschneider *et al.*, 2012). It is therefore important for interpretations to differentiate between small and young fish in a normal population and small and old fish from an overexploited or stressed population. This can be done by analysing the growth rings of otoliths and vertebrae, which correspond to the number of growth seasons the fish has experienced, which in most cases is similar to how many years the fish has lived (e.g., Van Neer *et al.*, 2002; Ólafsdóttir *et al.*, 2014). In some cases, it is also possible to infer the catch season and place based on size of fish in an assemblage, like Tilapia in Northern Africa (Van Neer & Lesur, 2004).

One study analysing flatfish remains from Raversijde calculated sizes, ages and growth rates of plaice using vertebrae and otoliths to infer catch locality and season (Van Neer *et al.*, 1999).

Chapter 2. Archaeological assemblages

This chapter will discuss the thirteen archaeological assemblages analysed during this research project by firstly giving an overview of the sites and what has been discovered by previous studies and later by comparing the zooarchaeology of the sites after recording the bones.

2.1 Overview of the archaeological sites

All sites analysed in this study (figures 2.1 and 2.2) have previously been studied and excavation reports are available for all of the sites. The sites were selected based on their location (i.e., southern North Sea area), dating of the features (between 600 and 1600 CE), reported amount of Pleuronectiformes bones (minimum ca. 10 per family per dated phase), and accessibility to the material during the project. These sites themselves therefore do not represent the whole southern North Sea area.

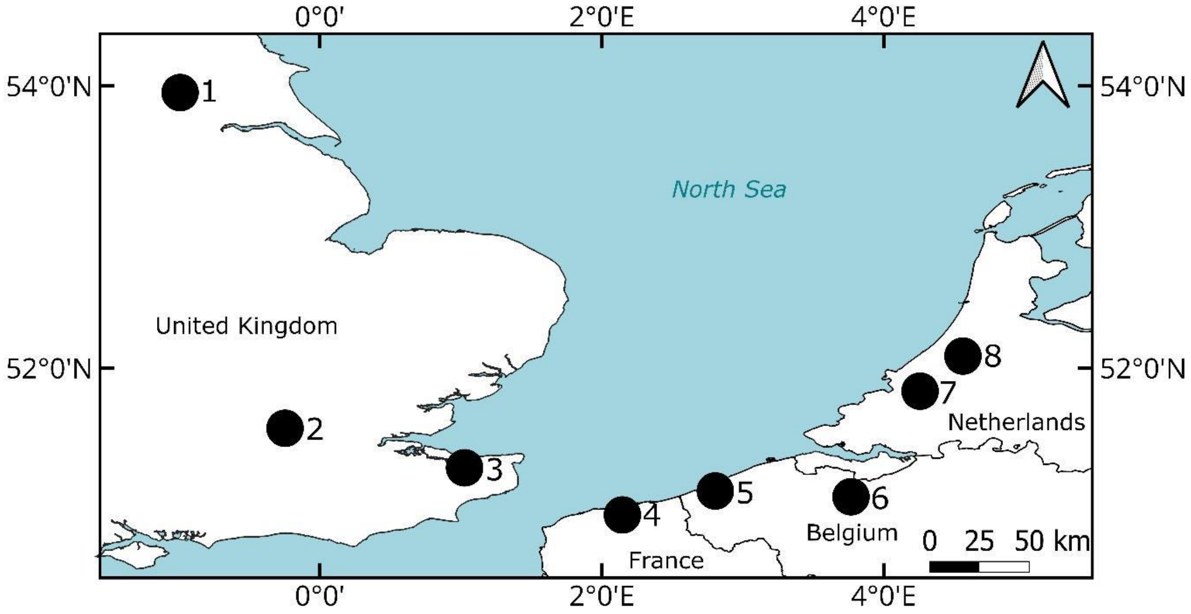

Figure 2.1. Map of the southern North Sea basin with the 13 archaeological sites in 8 locations. 1. York with *16-22 Coppergate* and *Blue Bridge Lane*; 2. London with *CAO96*, *GSJ06*, *SGA89*, and *SOT89*; 3. Canterbury with *Tradescent Lane*; 4. Saint-George-sur-l'Aa with *Barreau Saint-George-Desserte ferroviaire*; 5. Koksijde with *Hof ter Hille*; 6. Gent with *Zwarte Laag*; 7. Vlaardingen with *Gat in de Markt*; 8. Leiderdorp with *Kastanjelaan* and *Plantage*.

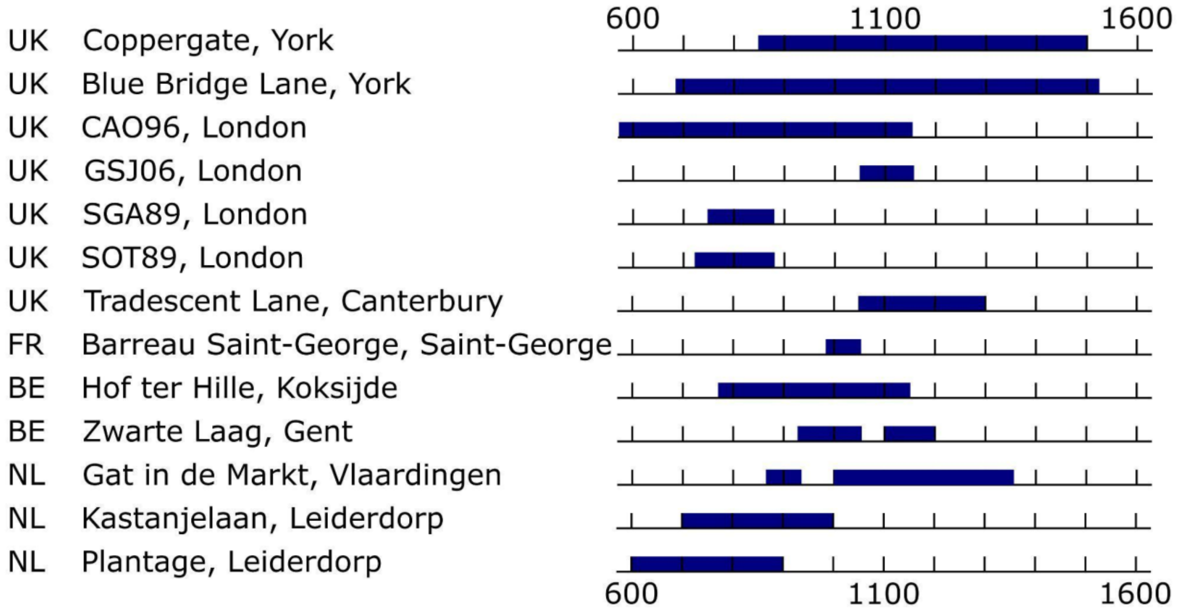

Figure 2.2. Chronological overview of the sites.

2.1.1 York

Remains of human activity in this city have been uncovered dating back to the Neolithic and Bronze Age. York became an important settlement during the Roman period between the 1st and 4th centuries CE. Near the York minster area, there was a Roman military fortress, built as part of the Roman military occupation of northern England in the later 1st century. On the south bank of the Ouse there was a civilian town (colonia), while elsewhere in the city an economy for military purposes existed. After the Roman period, York became inhabited by Angles and Saxons subsequently. During the 9th century, Vikings raided and conquered York. York grew large during the Viking Age and it became an important trading hub. During the 10th and 11th centuries, English and Norman rulers took over York. During the Medieval period, York remained an important trading hub and political center.

2.1.1.1 16-22 Coppergate

16-22 Coppergate (from now on “Coppergate”) is located in the city center of York, northern England, UK (53°57'27.4"N, 1°04'51.5"W). The site is located between the rivers Ouse and Foss which connect via the Humber into the North Sea. It was excavated extensively during the 1970s (1976-1981) after the discovery of finds from the Viking Age by the York Archaeological Trust (O’Connor, 1989; Bond & O’Connor, 1999; York Archaeological Trust, 2021).

In total an area of ca. 1000 m² was excavated on the site going 9 m deep. The material is exceptionally well preserved due to the peaty and moist condition of the soil between the two rivers. More than five tons of animal bone was recovered, as well as building remnants, timbers, pottery, and many other interesting objects, which all provided a unique insight into the lives of people, especially during the Viking Age (ca. 800 - 1050 CE) (O’Connor, 1989; Bond & O’Connor, 1999; York Archaeological Trust, 2021).

On the Coppergate site signs of occupation as well as remains from a cemetery dating from the Roman period were uncovered. After the Roman period, the first centuries show very little signs of occupation. After the Vikings took over the area, the site became inhabited once more by Anglo-Scandinavians following the 9th century CE. Remnants of buildings indicate the change through time and how this occupation was organised. After ca. 935 CE four aligned buildings were present, which had backyards with many pits filled with domestic rubbish. In the following period, after ca. 975 CE, other buildings had replaced the older ones, but their set-up was very similar. One part of the site shows signs of a longer occupancy than the other parts. The people who occupied these buildings are thought to have included craftsmen. These buildings became abandoned at some point in time without more info on it. During the 11th and 12th centuries, most of the site became buried under 2 m of soil. The medieval deposits, comprising some 3 m of soil, came mostly from the part of the site at the side of the River Foss. The Coppergate site had a steep slope in the middle during medieval times, making parts of the site less interesting to build on, except for the part facing Coppergate Street. Starting from the 13th century, the site became more inhabited and constructed again. Towards the end of the Medieval period, more stone constructions appeared (O’Connor, 1989; Bond & O’Connor, 1999; York Archaeological Trust, 2021).

During the Anglo-Scandinavian period, mostly eels and herring were exploited, besides pike, Cyprinidae and Salmonidae. There is a decline in Salmonidae and Cyprinidae between Phases 3, 4, and 5A (mid-late 800s - ca. 955/956), and Phases 5B and 5Cr (ca. 955/956 - mid-later 1000s), while the amount of cod and other Gadidae increase, which could indicate a more marine oriented exploitation. Most typical marine species are lacking during the Anglo-Scandinavian period, while herring are very abundant. Given the species’ behaviour of moving inshore during summer months, it is possible that these herring were caught in estuaries, the Humber, and possibly other rivers nearby and that these herring would indicate freshwater exploitation. Flatfish, mostly Pleuronectidae, have been recovered from this site. Only some bones were identified as plaice, flounder, halibut and turbot (Harland *et al.*, 2016).

2.1.1.2 Blue Bridge Lane

Blue Bridge Lane site is situated at Blue Bridge Lane south of the walled city center of York located at the east bank of the Ouse River at its confluence with the river Foss (53°57'5.6"N, 1°4'34.5"W). The site was excavated in 2000-2002 by the York Archaeological Trust (Spall & Toop, 2005).

The Fishergate area has been inhabited since the late Roman period in York. Remains from the Anglo-Scandinavian period show that the Fishergate area was a densely populated part. It might have served as a trade hub since the Anglo-Saxon period, as several objects from southern England and the continent were found. The settlement south of the walled city seems to have become less important during the Viking Age in York. During the Medieval period the area south of the walls was still inhabited and probably was a suburb with local parishes. Crafts seem to have been an active industry during the Viking and Medieval period (Spall & Toop, 2005). In the Late Medieval and Post-Medieval periods, a cemetery was in use on this site (Spall & Toop, 2005).

The fish remains from this site have been sieved with 2- and 4-mm fractions. Preservation of the bones is good (Harland *et al.*, 2016). A clear switch from freshwater species to estuarine or marine species is seen during the 10-11th centuries (Harland *et al.*, 2016), with herring being the most dominant species. During the Medieval period, herring continued to be the most abundant taxon (Keaveney, 2005; Harland *et al.*, 2016). From the 10th century onwards Gadidae became increasingly more important throughout the Medieval period, with first cod and later haddock (Harland *et al.*, 2016). Freshwater and migratory species were relatively more common before the 10th century (Harland *et al.*, 2016). Flatfish were also recovered from Blue Bridge Lane, especially from the late 7th to mid-9th centuries and late-12th to mid-14th centuries. Several plaice and a single flounder have been identified (Harland *et al.*, 2016). It is thought that herring were mostly local captures instead of imports (Keaveney, 2005; Harland *et al.*, 2016). Based on stable isotope analysis, it seems that some late-medieval cod were imported from northern areas (Barrett *et al.*, 2011; Harland *et al.*, 2016).

2.1.2 London

London is situated in the southeast of England and is built around the Thames, which connects the city to the southern part of the North Sea as well as deeper inland to the west.

London has been inhabited since the Roman period, when it was called Londinium, during which it also served as a military settlement, civilian town and administrative capital. The city was situated north of the Thames between the modern Tower of London and the Blackfriars. A port for seafaring ships was also present in the city at this time.

Following the end of Roman rule in Britain, Londinium was abandoned. West of Londinium, there was an Anglo-Saxon settlement called Lundenwic in the Aldwych area. This urban settlement also had a port for ships and it is thought that trade with the continent was happening at this time (e.g., Loveluck & Tys, 2006). During the Late-Saxon period, the area of Londinium, i.e. the old walled city, started to be inhabited again as London grew larger during the following periods. London became the capital of England during the Late Medieval period.

Previous studies on fish assemblages in London have shown that the marine fish event horizon happened in the city during the second half of the 11th century with people relying more on Gadidae and herring afterwards, although the transition might have occurred earlier (Barrett *et al.*, 2004a; Orton et al., 2017). By the 11th and 12th centuries, cod might have been imported in small numbers from northern areas and after the 13-14th centuries, the majority of cod was probably being imported from areas outside the southern North Sea (Barrett *et al.*, 2011; Orton *et al.*, 2014). Fish, including flatfish such as “flounder”, were captured in the Thames near or in the city of London, and potentially many other species of flatfish observed there during the past few centuries, such as plaice, dab, sole and brill (Galloway, 2021).

2.1.2.1 CAO96

CAO96 or Gateway House is situated in London at 25 Cannon Street (51°30'47.0"N, 0°05'44.6"W) a few hundred metres north of the Thames. This site was excavated in 1996 by MoLAS (Bowsher, 1996; Bowsher, 1998; Elsden, 1999).

Excavated parts of this site contained Roman remains from the 1st and 2nd centuries, medieval remains from the 11th and 12th centuries, and post-medieval remains from the 17th and 18th century, including flatfish. The Roman settlement is thought to be a residential area. One of the structures dating to the Medieval period is the St John Evangelist church, while other remains were mostly pits, wells, and cesspits (Bowsher, 1996; Bowsher, 1998; Elsden, 1999).

Fish remains found on the site were mostly Gadidae (hand-collected and sieved), Pleuronectidae (hand-collected and sieved), *Anguilla anguilla* (eel) (sieved), Cyprinidae (sieved), *Raja* sp. (ray) (sieved), *Clupea harengus* (herring) (sieved), although many fish remains were unidentified. During the Roman period consumption of marine species is already apparent, with several cod bones found from this period besides some Pleuronectidae, a few *Anguilla anguilla* and *Clupea harengus*, and a single cyprinid bone. During the Medieval period, the amount of fish increased. Gadidae, mostly cod, are the most abundant group. Pleuronectidae are also represented by some finds. Some Cyprinidae, *A. anguilla*, and several marine species, such as *Scomber scombrus* (mackerel) and *C. harengus*, have also been found from the Medieval period (Elsden, 1999; MOLA database).

2.1.2.2 GSJ06

GSJ06 is located at 54-66 Gresham street, London (51°30'48.0"N, 0°05'47.8"W) a few hundred metres north of the Thames. The site was excavated in 2006 by MoLAS (Pennington & Wroe-Brown, 2008).

Excavations from this site included Roman and medieval remains, including flatfish. This area of London used to have many tributaries of the Thames that ran across the area. During the Roman period, the site was firstly used as a quarry and later several buildings were constructed. At the end of the Roman period, the site became abandoned. Several Saxon pits and some remains from constructions were found. In the southern part of the site, medieval pits and constructions were recovered. Several cuts and pits from Post-Medieval periods were also uncovered (Pennington & Wroe-Brown, 2008).

The site was well-sampled for environmental analysis and hand-sieved, which recovered around 4000 animal bones. During the Medieval period, the diversity of fish increased. Gadidae are the most abundant. *Anguilla anguilla*, *C. harengus* and Pleuronectidae are also quite common, as well as *Osmerus eperlanus* (European smelt). Other species recovered from this site include *Raja* sp., *Scomber scombrus*, Triglidae, Salmonidae, and Cyprinidae. Only one *Acipenser* sp. (sturgeon) was also found (Pennington & Wroe-Brown, 2008; MOLA database).

2.1.2.4 SGA89

2-26 Shorts Gardens and 19-41 Earlham Street (SGA89) is located in the little area enclosed by Shorts Gardens, Earlham Street and Neal Street in London (51°30'50.3"N, 0°07'35.5"W). During the Early Medieval or Saxon period, the site was located at the north-western border of Lundenwic, west of the Thames (Cowie *et al.*, 2012). The site was excavated in 1989 by DGLA (Cowie *et al.*, 2012).

The site seems to have been an industrial area with evidence of hearths and industrial buildings, but also a domestic house (Cowie *et al.*, 2012). A Middle Saxon eel/fish trap has been recovered. Several alluvium deposits would indicate some inundations and floods have occurred on the site throughout the Saxon period (Cowie *et al.*, 2012).

Lundenwic excavations showed that Anguillidae, Clupeidae, Cyprinidae and Pleuronectidae were the most abundant groups of fish in the Saxon settlement. In the later period there seems to have been a slight decrease in the number of Cyprinidae and a slight increase in the number of Gadidae (Cowie *et al.*, 2012).

2.1.2.3 SOT89

26-27 Southampton Street (SOT89) is located on the western bank of the Thames (51°30'40.2"N, 0°07'21.5"W). It was located in the central part of the Saxon settlement of Lundenwic, which is now Covent Garden. The site was excavated in 1989 by DGLA (Cowie *et al.*, 2012).

The site has several short periods of Mid and Late Saxon occupation with several pits, dumps and building features (Cowie *et al.*, 2012).

Lundenwic excavations showed that Anguillidae, Clupeidae, Cyprinidae and Pleuronectidae were the most abundant groups of fish in the Saxon settlement. In the later period there seems to have been a slight decrease in the number of Cyprinidae and a slight increase in the number of Gadidae (Cowie *et al.*, 2012).

2.1.3 Tradescent Lane, Canterbury

Canterbury is a city in the southeast of the United Kingdom (51°16'44.3"N, 1°05'18.1"E), located about 15-20 km inland from the southernmost part of the North Sea. It is connected to the sea by the River Stour. The site was excavated in 2014 by the Canterbury Archaeological Trust.

Tradescent Lane is part of the Scheduled Monument of St Augustine's Abbey, a former abbey founded at the end of the 7th century. Canterbury has been occupied since before the Iron Age and the city was expanded by the Romans. After the Romans left, the city decayed, until Anglo-Saxons started to occupy the center again. During the Medieval period, Canterbury became an important location for the Church, with a large abbey and later many pilgrims visiting the city. Being close to the English Channel and having city walls originally constructed by the Romans, Canterbury was of military importance. During the Early and High Medieval periods, the city was invaded by Vikings and taken over by William the Conqueror, and later the French Prince Louis (English Heritage, 2021).

During the excavation two trenches were dug, with most fish remains coming from the first trench. Most remains were uncovered by sieving, and a few by handpicking. The material from Tradescent Lane dates from the mid-11th century till the end of the 13th century and is divided into three phases, with the middle phase (3) being the richest in fish bones and best preserved. The fish bones come from features related to the abbey complex. It is thought that, since there are small vertebrae and scales recovered from phase 3, that these bones were kitchen waste where fresh fish was prepared. A number of *Acipenser sturio* (European sea sturgeon) scute fragments has been found, which could indicate a high-status occupation – not uncommon for abbeys. The freshwater species are rather infrequent and small in size, with only a handful of Cyprinidae and Salmoniformes recovered. Eel is more frequent, but could also have been captured in estuarine and marine environments. The marine species are much more diverse and numerous. Most of these species can however be captured close to shore or near estuaries as well. A large number of *Raja clavata* (thornback ray) denticles have been found. Gadidae are also present in this assemblage, although not as abundant as in other contemporary sites. It is assumed that the monastery, due to its status/wealth and easy access to the fishing ports at the coastline, preferred fresh fish, rather than the traded and dried Gadidae (Nicholson, 2015).

2.1.4 Barreau Saint-George-Desserte ferroviaire, Saint-George-sur-L'Aa

The city of Saint-George sur-L'Aa is situated in the north of France in Nord Pas de Calais region, slightly northeast of Calais and southwest of Dunkirk. The town is located close to the coastline in the southernmost part of the North Sea and is connected to the sea by the river Aa. The site was excavated in 2007-2008 (Herbin & Oueslati, 2016; Oueslati, 2019).

In Roman times, the current coastal area in northern France was flooded. After the 7th century, the North Sea retreated and settlements were built on the drier areas of this polder. During medieval times, this region was part of the Flemish region.

The excavation of "Barreau Saint-George-Desserte ferroviaire" (50°58'27.8"N, 2°10'7.6"E) (Eng.: Well of Saint-George at the train tracks), from now on Barreau Saint-George, uncovered unique building structures (Herbin & Oueslati, 2016; Oueslati, 2019). The buildings on poles were occupied between the end of the 10th century till the beginning of the 11th century. Mollusc remains on the site indicate local coastal consumption of marine and estuarine fauna. Both hand picking and sieving (mesh sizes of 4, 2 and 0.5 mm) were used to obtain the 901 fish remains from the site in at least 6 pits. Most of the fish material comes from two pits, 215 (20L sieved, 749 bones) and 47 (16.5L sieved, 125 bones). The fish material was identified to only 3 different families: 847 Pleuronectidae (35 *P. platessa*, 56 *P. flesus,* and 756 unidentified), 1 Soleidea (*S. solea*), and 53 Gadidae (28 *G. morhua*, 2 *M. merlangus,* and 23 unidentified). The high abundance of coastal flatfish is remarkable. The analysis of the growth rings of flatfish vertebrae indicates that they were caught in winter months (Oueslati, 2019). They were mostly small and medium sized fish, smaller compared to other sites in the area. The site was probably a consumer site, since the vertebrae and cleithra of flatfish are overrepresented compared to the cranial elements and burn marks were found on the bones. Molluscs that could be gut content from flatfish could indicate that the gut was only removed from the fish on site, which means the fish was probably brought in fresh. Gadidae on the other hand were mostly large fish of 1 meter or larger and mostly consisted of remains after processing, with an overrepresentation of cranial bones. Pit 215 might have been a dump for waste and human faeces, since bone deformities related to passing through the gut have been found. No cod bones were found in pit 215 (Herbin & Oueslati, 2016; Oueslati, 2019). There were also some cetaceans remains in this site, that had been used as tools (Herbin & Oueslati, 2016; Oueslati, 2019). Other faunal remains on the site consisted of a lot of cows, some pigs (including a needle made from a fibula), some caprines, some horses, cats, as well as geese and ducks (Herbin & Oueslati, 2016).

2.1.5 Hof ter Hille, Koksijde

Koksijde is a city on the Belgian coastline close to the river Yser. The archaeological site "Hof ter Hille" (51°6' 38.6"N, 2°41'39.6"E) (Eng.: Court on the hill) was extensively studied and excavated between 2008 and 2012 on the golf terrains of Koksijde Golf ter Hille by Monument

Vandekerckhove nv (Lehouck *et al.*, 2014). The terrain was first geophysically analysed, which uncovered structures in the ground that could then purposely be excavated, as well as a system of creeks that gradually got buried during the Roman and High Medieval period. The area probably wasn't occupied until the High Medieval period (5-6th century) due to high water levels and tidal influences, and it is estimated that occupation was not possible until at least the 7th century. The first signs of occupation on the site date from the 10-11th century. The structures recovered from this period are thought to have been farm houses owned by wealthy farmers. Typical for these kinds of structures in Flanders from that time is the central rectangular wooden house with smaller buildings close by, as well as the presence of water wells on the sites. Each property was surrounded by ditches and creeks. During the 11th century, the design of the buildings changed and the occupation became more economically oriented, with a clear separation between occupation and agriculture with a surrounding moat. The different phases of occupation are dated using pottery and the find of a coin (Lehouck *et al.*, 2014). Later analysis using ^{14}C-dating of wood confirmed these initial datings (Van der Meer *et al.*, 2018). The occupation of this site lasted until the end of the 12th century or early 13th century. One reason for the end of the occupation might be the competition of larger farms nearby. Starting in the 14th century, this site, thereafter called "Hof ter Pikegny" became a monastic grange of the Ten Duinen Abbey, which was located a few kilometres to the west. The Ten Duinen Abbey had been part of the Cistercian Order since the 12th century (Lehouck *et al.*, 2014).

The faunal material of two of the four zones excavated has been fully analysed. These two zones, 1 and 2, appear to have been inhabited between the 10th and 12th century (875-1150 CE). The habitation period during the High Medieval period can be divided into two phases defined by the structure of the buildings. The first phase has two large buildings surrounded by a ditch, while the second phase both structures have their own ditch. It is thought that these buildings were inhabited by rich and/or elite households (Lehouck *et al.*, 2014; Van der Meer *et al.*, 2018). Ovicaprids are the most common domestic animal uncovered from the site, which is to be expected given the high salinity content of the surrounding area and the economic importance of wool during this period in Flanders. Remains of cattle, horses, pigs, dogs, cetaceans and many species of bird were also excavated (Van der Meer *et al.*, 2018).

The fish remains from this site indicate a primarily marine or estuarine fish exploitation (Van der Meer *et al.*, 2018). Most species recovered are marine species. Some sharks and ray remains have been found. Only a few Cyprinidae and pike bones were found, but it is known that these groups can also tolerate rather brackish environments. Given the distance to the coast and the mouth of the Yser of the site, this can be expected, although import from freshwater areas cannot be excluded. Further, remains of eels, Clupeidae, Gadidae, Triglidae, large Moronidae, Carangidae, Mugilidae, Scombridae, and flatfish have been identified from the site. It is remarkable that Gadidae only constitute 5% of all remains and they appear to have been brought to the site as whole fish based on the element representation. Flatfish are the most abundant group of fish recovered from the site. Pleuronectidae constitute 78% of all identifiable fish remains. Only one *L. limanda* has been reported. Of the other identified remains of flatfish it seems that 90% are *P. platessa* and 10% *P. flesus*. Most flatfish were between 20 and 40 cm SL large, with *P. platessa* being a bit larger on average than *P. flesus*. Smaller flatfish from 10-30 cm SL seems to have been processed more than the larger flatfish (>30 cm SL), which is indicated by the underrepresentation of cranial bones. Larger flatfish are more difficult to process and dry, and were probably brought to the site as whole and perhaps fresh fish, whereas the smaller flatfish were processed and dried elsewhere before coming to the site. This might also explain why there seems to be an overrepresentation of *P. platessa* at first: the actual number of *P. flesus* might be higher but they are more difficult to identify using only vertebrae. Few remains of *Scophthalmus* sp. and *S. solea* have been recovered. Based on the skeletal representation of flatfish and eels, it seems that most of the remains of the site are table or kitchen refuse. Based on the sizes of the fish (absence of juveniles typically found in estuarine and brackish waters; small Gadidae) and the fish species, it is assumed that most fish were captured along the coast of the southern North Sea (Van der Meer *et al.*, 2018).

A pit excavated on the same site dating from the 14th century shows a clearly different fish species spectrum, where Gadidae and *Clupea harengus* become the most abundant and more frequent than flatfish, and Cyprinidae are slightly more frequent (Van der Meer *et al.*, 2018).

2.1.6 Zwarte Laag, Gent

Gent is a city in Belgium in the north western part of the country situated at the confluence of the Leie and Scheldt rivers, the latter by which it is connected to the North Sea.

Settlements in Gent date back to the Iron Age and Stone Age. There are also remains dating to the Roman period found. During the High Medieval period, multiple settlements started to grow and fuse together. Two abbeys, St-Bavo and St-Pieter, formed the center of Gent at the time. During the 9th century, the city was pillaged and briefly inhabited by Vikings twice. Afterwards, another center with a harbour formed at the location of the site. A moat surrounded this new center, and due to population increase and urbanisation, the center expanded westward. The excavated site was originally outside the moat (Ervynck *et al.*, 1999; Deforce, 2017). As part of the political center of the County of Flanders, Gent was one of first larger cities in Europe and grew immensely during the same time as the site material was deposited. During the 13th century there might have been 50-60 000 people living in Gent (Caenegem & Geens, 1989; Verhulst, 1999). The city had a lot of wool production during the High Medieval period and was largely autonomous (e.g., Hutton, 2018).

Throughout history, the influence from the sea and the course of the Scheldt changed. The Scheldt is a river with headwaters in Northern France that courses through the western part in Belgium from south to north and mouths into the North Sea at Antwerp in modern days. The upper part of the river down till Gent is called Upper-Scheldt. The “Zeeschelde”, the part between Gent and Antwerp, and the “Westerschelde”, the lowest part between Antwerp and the North Sea, form the estuarine part of the Scheldt that undergoes tidal fluctuations. During prehistoric and Roman times, the Scheldt had a more northerly mouth than it has today around the Goeree-Overflakkee island. During the High Medieval period, the main mouth of the Scheldt was the “Oosterschelde”, while at the end of the High Medieval period, an additional mouth at the “Westerschelde” was formed. This part only became the dominant mouth of the river after the 12th century. During the Early Medieval and High Medieval period Gent was also connected by a small river directly north to the Honte, the old name for the Westerschelde before it became the dominant mouth of the Scheldt, which allowed small boats to sail (e.g., Kiden & Verbruggen, 2001).

With the Scheldt being estuarine from its mouth up to Gent, the species found there today consist of a mix of estuarine and freshwater species. *Platichthys flesus* is even nowadays regularly found in the Zeeschelde (Waarnemingen.be).

The site Zwarte Laag (51°03'13"N, 3°43'28"E) (Eng.: Black Layer) has been excavated in 1996 at the Emile Braun plein in the historic city center of Gent at the location of the old, and no longer present, Korte Ridderstraat (Ervynck *et al.*, 1999). The site material was deposited as refuse in a street and is well-layered that allowed precise dating with 11 small and overlapping intervals dating from the mid-10th century till the end of the 12th century. Only one short period is absent in the layers (1050 - 1100), which might be caused by a cleaning event of the street (Ervynck pers. comm.).

Preliminary analysis on the material from this site showed that flatfish and herring are the dominant fish species at the beginning of the Medieval period, while Gadidae gradually increased in abundance throughout the Medieval period. Herring remained the most abundant species. A slight decline of freshwater species is noted throughout the Medieval period. At the beginning of the High Medieval period within Gadidae mainly *Merlangius merlangus* was consumed and later *Melanogrammus aeglefinus*. *Gadus morhua* didn't become the dominant species until the Post-Medieval period (Ervynck *et al.*, 2004).

Several studies have analysed fish remains from this site as well as from sites in nearby cities along the Scheldt. Fuller *et al.* (2012) analysed several taxa from this site. A Pleuronectid from about 40 cm SL had isotopes values of -15.3‰ δ^{13}C and 10.4‰ δ^{15}N with 3.3 C:N, which is a marine signal consistent with two samples from usually marine species from the same site and study: *Melanogrammus aeglefinus* of around 60cm SL with -14‰ δ^{13}C, 14.5‰ δ^{15}N, and 3.3 C:N, and *Clupea harengus* of around 20-25cm SL with -15.2‰ δ^{13}C, 10.6‰ δ^{15}N, and 3.7 C:N. An adult *Acipenser* sp. had values of -14.5‰ δ^{13}C, 13.1‰ δ^{15}N, and 3.3 C:N (Fuller *et al.*, 2012). Barrett *et al.* (2011) analysed two *G. morhua* bones with -13.5 and -11.7‰ δ^{13}C and 15.4 and 17.5‰ δ^{15}N, with C:N 3.3. An analysis of *P. flesus* from the Scheldt excavated in Dendermonde found that smaller flounder (10-20cm SL) have a more freshwater signal with δ^{13}C ranging between -26.1‰ to -24.1‰, while larger flounder (30-40cm SL) are less depleted in ^{13}C (-11.2 to -16.2‰). The small flounder are more enriched in ^{15}N (13.9-14.9‰) than the larger flounder (11.3-11.8‰), which is probably due to the change in diet throughout its life from crustaceans to molluscs (Ervynck *et al.*, 2018).

2.1.7 Gat in de Markt, Vlaardingen

Vlaardingen is a city in the Netherlands, just west of Rotterdam, connected to the North Sea by the rivers De Lek and Meuse. The oldest occupation in this city dates back to the Iron Age and continues to the Roman period. Based on pollen data, it seems there were no people inhabiting the region and that the landscape returned to a natural state (bog/peat-like) during the Early Medieval period. From the 8th century onward, people returned to this area. Based on some historical references, the "Noormannen" (Norsemen) settled down here first. The city expanded during the Medieval period and became one of the prominent cities in the Westfrisian county. Vlaardingen was home to elite households. During the 11th century, the castle of the town was expanded and fortified and multiple invasions of the castle indicate that this period was tumultuous. The city was hit by floods regularly and dikes were built and expanded in the High Medieval period, although these would break once in a while (Van Loon & de Ridder, 2006).

The site “Gat in de Markt” (Eng.: Hole in the town square) was excavated south of the main church (51°54'27.01”N, 4°20'32.81”E) in 2002 by VLAK (Vlaardings Archeologisch Kantoor) prior to new constructions. The material is mostly hand collected and some soil samples were sieved. Three pits were made to excavate the site (Buitenhuis *et al.*, 2006).

At this site used to be an old dike to hold back the waters of the Meuse, as well as a terp during the Medieval period. 45 skeletons, both children and adults, were uncovered, which were buried in a graveyard next to the main church. The people seem to have been generally healthy, although many show signs of injury (although it is unsure if these were the cause of death) (Groen & de Ridder, 2007).

About half of the fish remains were hand collected and the rest came from sieved material. Period 5 (High Medieval and Post-Medieval) contains the most fish remains. Most of the remains come from marine species. There is no indication of fish having been processed prior to arriving at the site. Little to no signs of cooking and burning were found, and only a few remains show cut marks. Gadidae and some of the flatfish are large specimens that were probably caught using lines, while fishing with nets seems to have been less common, as is seen by the low frequency of smaller species such as herring (although sieving was done extensively) (Buitenhuis *et al.*, 2006).

2.1.8 Leiderdorp

Leiderdorp is a town east of Leiden in the Netherlands. It lies at the Old Rhine river, which was the main waterway of the Rhine river during the High Medieval period. Via the Rhine, there was an easy route to the North Sea to the west and deeper inland to the east.

There are indications of humans living in the area since prehistory. The earliest settlement in Leiderdorp, Munnikkenpolder, dates from the Iron Age. Roman settlements from the 1st till 3rd century CE were uncovered nearby, since the Rhine was the northern border of the Roman empire. Also objects from local people dating from the Roman period were found. The high water table made habitation in Leiderdorp difficult throughout the Roman period and the first part of the Medieval period, but clear signs of habitation, such as excavated dikes, buildings and many objects, are found from the 6th century and later. The area probably consisted of a system of creeks, which had tidal influences (Houken, 2014; Dijkstra *et al.*, 2016). During the High Medieval period the town consisted of three main districts, called Leithons. Due to the expansions of Leiden, Leiderdorp gradually became smaller throughout the Late Medieval period. Due to marine river deposits from inundations during the Medieval period, stone baking could become an interesting economic activity in the area (Dijkstra *et al.*, 2016).

Two sites from this city have been included, Kastanjelaan and Plantage, that are situated about 500 m from each other and were located at the same trench river.

2.1.8.1 Plantage

The archaeological site Plantage in Leiderdorp was excavated in 2013 and is situated at Leithonpark (52°09'09.8"N, 4°31'46.3"E) (Dijkstra *et al.*, 2016).

The only Roman age object from this site is a water well from the 2-3rd century (Dijkstra *et al.*, 2016).

During the Medieval period a settlement was situated next to a small part of the sheeted trench river. Throughout the High Medieval period, the trench rivers often changed course and they were largely sheeted. Several structures indicating different kinds of constructions, such as houses, sheds, ovens and wells, were found. An incredible number of well-preserved objects were recovered dating from between the 7th till 9th century from wood, stone, ceramics, metal, rope, glass, leather, bone, and antler. In terms of mammal bones on this site, remains from mostly cattle and some sheep, pigs, horses, dogs, and whales were found. Botanical remains indicate that the people used a variety of crops. Textile production was an important activity. The people from this town seem to have traded with southern and northern areas for grain, ceramics, etc. (Takken *et al.*, 2008; Dijkstra *et al.*, 2016). The site was abandoned after 840 CE for a few centuries, which was probably caused by the combination of floods, Viking invasion and reduced economical activities (Takken *et al.*, 2008; Dijkstra *et al.*, 2016).

Remains of fishing gear, including nets, spears, and traps, were found on the site, as well as over 2000 fish bones from at least 19 different species. One kind of trap was designed for eels. A previous study on flatfish from this site has used size estimations to distinguish between locally captured *P. flesus* and marine caught *P. platessa*. Small Pleuronectidae up to 35 cm were identified as freshwater *P. flesus*, Pleuronectidae larger than 56 cm as marine *P. platessa*, and Pleuronectidae between the two sizes as marine *P. flesus* or *P. platessa*. Together with Cyprinidae and Percidae, Pleuronectidae are the most common group of fish recovered from this site, each with around 400-500 specimens. Only a handful of Pleuronectidae were identified to species, and both freshwater and marine *P. flesus* and marine *P. platessa* were represented (although it has to be verified whether the methodology used resulted in correct identifications). A variety of other species, including catfish, stingray, and Salmonidae, were found as well. Remarkable is the limited amount of Gadidae (only larger ones were found), Anguillidae and Clupeidae from this site. Local freshwater species and migrating groups of fish seem to have been the most targeted taxa in this site, whereas the few marine specimens must have come from the coastal area down the Rhine. A slight trend through time is noticeable, in which during the later period there is an increase of species such as pike and perch and a decrease of Cyprinidae. Fish bones with signs of digestion and burning and with cut and chop marks were also noticed (Beerenhout, 2016).

Comparisons of this site with other sites in the area from the same period, show that multiple sites along the Rhine River and surrounding areas were mostly consuming local freshwater species, except for the coastal sites, and the further away from the coast, the fewer flatfish remains were found. In Dorestad, which lies deep inland and was a large and important trading hub between the Dutch coastline and Germany along the Rhine, many Clupeidae remains were uncovered, which could have been brought there as preserved herring, while Gadidae seem to have been rare during the High Medieval period (Beerenhout, 2016).

2.1.8.2 Kastanjelaan

The archaeological site Kastanjelaan in Leiderdorp was excavated in 2011 and is situated at Kastanjelaan (52°09'03.5"N, 4°31'32.3"E) (Houken, 2014).

Medieval constructions seem to have used Roman debris, originating from nearby castellums that were abandoned. The precise occupation type and use of the site is unclear due to disturbance of later exploitation of the soil. The site consists of a trench with sheeting remains at the Old Rhine. It is thought that this place was used to moor boats in the Old Rhine, which was located south of this site. This part of Leiderdorp is thought to have been inhabited since around 745 CE, based on dating of wooden poles used for sheeting the banks of the river. The small number of mammal remains indicate a small community without much trade that only kept animals for its own use (Houken, 2014).

Nearly 2000 fish remains were found in this site from contexts dated to the 8-10th centuries. Most fish remains come from one context, nr. 148. The most abundant taxa were *Anguilla anguilla* and Cyprinidae, while Percidae and Pleuronectidae form a smaller part of the assemblage. There are only a few Gadidae and Clupeidae found at this site. The absence of the latter cannot be explained by the excavation method used, since sieving was applied on the contexts analysed for fish remains. Within Pleuronectidae there is no data on the species representation. This species assemblage indicates that people fished rather locally mostly on freshwater taxa and possibly small flatfish. Vertebrae seem to be overrepresented compared with cranial elements across the assemblage, which might indicate that fish were being processed elsewhere in the settlement before being brought for consumption to Kastanjelaan. It is also possible that some of the larger marine taxa were brought in as dried fish from the coastal regions, such as the bigger Gadidae and Pleuronectidae; the former potentially being traded from Scandinavia. Objects related to fishing, such as spears, net weights and possible remains from traps, were also uncovered at the site (Kerklaan, 2014; Beerenhout, 2016).

2.2 Zooarchaeological analysis of the assemblages

2.2.1 Methodology of zooarchaeological analysis

All selected archaeological sites were re-analysed and each available fish bone recorded by the author. This was done firstly to have a more detailed overview of the availability of all flatfish remains (i.e., Pleuronectidae, Scophthalmidae, and Soleidae) and other relevant taxa in each site for further sampling (see chapters 4, 5, and 6) and secondly to consistently record the fish assemblage, as different reports have different methodologies and for some of the selected sites no original data files were available. The recording was performed for the author's own purposes, rather than providing an in-depth systematic comparative analysis of the sites. As not all fish bones were recorded due to time constraints, the proportion (i.e. relative frequency) of flatfish in a site is only calculated by comparing the numbers of identified flatfish to the numbers of identified freshwater taxa such as Esocidae and Cyprinidae, marine taxa such as Gadidae and Clupeidae, and the catadromous Anguillidae. Although other families are present in the assemblages too, their numbers are relatively low and their presence is not consistent across all sites, making it difficult to compare regions. These selected taxa were analysed to family and, if possible, species by using modern reference collections where available, housed in University of York, Royal Belgian Institute of Natural Sciences, or Museum of London Archaeology, or by using osteological guides (e.g., Lepiksaar, 1994; Watt *et al.,* 1997; Wouters *et al.,* 2007). For every fish bone from the 13 assemblages, the following characteristics were recorded:

- Site (name, year of excavation, geographical coordinates);
- Context/pit (phase, dating, depth);
- Collecting method and sieving mesh size if known (although no in-depth analysis (e.g., Barrett *et al.,* 1999) was performed, the differences in sieving and collection method was used to make interpretations on taxa, element and size distributions in the discussion);
- Taxon: every level possible with notes of diagnostic criteria (for flatfish to family level, as the species identification of flatfish will be discussed in more detail in chapters 3-5);
- Skeletal element: which bone, left or right, and which fragment, based on zonation system used by Harland and Barrett (2003);
- Size of the bone (maximum length);
- Measurements following Morales and Rosenlund (1979);
- Pathologies, cut marks, and other types of surface modifications (e.g., Butler & Schroeder, 1998; Çakırlar *et al.,* 2014; Guillaud *et al.,* 2017; Harland & Van Neer, 2018);
- Colour using the Munsell colour charts to detect differences in preservation and burial environment.

Size estimations were done by comparing the archaeological bone to the equivalent element in modern reference specimens of known sizes. As precise estimations are difficult to get using this method, a size estimation class (in cm SL) was noted for each specimen (mostly for flatfish), as precise as possible. This was usually in bins of 10 cm, and preferably from multiples of 10. Occasionally other size classes, e.g., 15-25 cm SL, or larger classes, e.g., 20-40 cm SL were used if it was difficult to determine the size class. Size classes are further analysed and compared only for flatfish to see if there are any differences in preferred/available sizes between sites or if there was a change in size of the fish through time, which could reflect either economic preferences or ecological effects. Regression analyses for flatfish (e.g., Brinkhuizen, 1989) were not applied as these do not exist for all skeletal remains of flatfish, which would have limited the samples available for size comparisons, and are not always species-specific, which can over- or underestimate the sizes.

To compare the element representation of flatfish bones across sites and periods, all elements are grouped into categories depending on potential processing of fish. Traditionally, two main groups exist: the cranial group, containing the neurocranium, jaw apparatus, suspensorium, hyoid arch, and opercular series, and the postcranial group, containing mostly the vertebra. However, a common way of fish processing is by chopping the head off from the body, which usually occurs behind the cranium and cleithrum. The precise chopping area could however depend on the butcher’s experience and processing style for example. This could result in the precise chop happening at slightly different places and across different elements. Therefore, a third category is created that included the most common bones that contain chop marks or lie in the same line of common chop marks, called “border”: atlas, basioccipital, cleithrum, posttemporal, supracleithrum and coracoid. For this analysis, the postcranial includes all the vertebrae, as well as the basipterygium and os anale, which are characteristic for flatfish and often recovered. The cranial category includes all the head bones such as those from the jaw apparatus, neurocranium, suspensorium, hyoid arches, and opercular series.

To compare sites more easily, all phases from each site were recategorised to the larger periods (table 2.1). The number of identified specimens (NISP) was used to quantitatively compare regions and time periods for the relative abundance of flatfish, relative flatfish element representation, and relative size distribution. Data was collected in Microsoft Office Excel 16.0. Analysis of data was done using R (R Core Team (2022), version 4.1.1 (2021-08-10) -- "Kick Things") and plots were made using ggplot() (ggplot2 package; Wickham, 2016).

Table 2.1. Overview of the time periods used.

Period	Abbreviation	Start (CE)	End (CE)
Roman period	R	0	500
Early Medieval 1	EM1	600	900
Early Medieval 2	EM2	850	1050
Early/High Medieval	E/HM	875	1150
High Medieval	HM	1000	1300
High/Late Medieval	H/LM	1025	1500
Late Medieval	LM	1200	1600
Post-Medieval	PM	1550	1800

Some remarks regarding the methodology have to be made prior to discussing the results. Due to time constraints, only some sites were analysed in full with certainty: Zwarte Laag, Gat in de Markt, Kastanjelaan, Plantage, Barreau Saint-George, and Tradescent Lane. Coppergate was analysed completely as well, except at least one box with animal bones which was not available (but more than 20 others were, so this loss of data should be minimal). Some bags with Clupeidae material might have not been available when analysing the Blue Bridge Lane data, which will impact the species representation for this site. This is suspected as the reported amount of Clupeidae in the Early Medieval period by Harland *et al.* (2016) is much higher than what was found during this study. Hof ter Hille had to be analysed very quickly due to time constraints, resulting in a recording bias of only flatfish and some taxa that might have been useful for isotope analysis. This will result in an overabundance of Pleuronectidae and other flatfish taxa in the analysis. All London sites (CAO, GSJ, SGA, SOT) were all rather small and therefore any bone sample will have a large effect on the proportional data. Proportions calculated for these sites should therefore be interpreted cautiously. Furthermore, these four sites were also analysed rather quickly with the idea of getting subsamples for further analysis and it is unsure if all material was available for study.

Roman and Post-Medieval periods will not be included to make interpretations as these were not consistently analysed when available.

Taphonomic processes can impact the preservation of bones, and thus influence the results of zooarchaeological analyses. Fish are a very diverse group with many different species from different sizes, ecology, and even with slightly different bone characteristics. Some species have robust bones, e.g., bony plates from sturgeons and the dentary of pike, while others have fragile and thin bones, such as most opercular bones and clupeid cranial bones. These differences can cause differential preservation of certain species or skeletal elements due to physical, biological or chemical processes (Struever, 1968; Von Endt & Ortner, 1984; Shaffer & Sanchez, 1994; Stahl, 1996; Smith *et al.,* 2007). The size of the bones also has an effect as small bones can be more easily translocated than larger ones. Larger bones might be easier to break, but they are still more likely to be recovered and recognized than smaller ones that have been broken. Furthermore, the recovery of smaller bones and fragments is more difficult than that of larger bones, as sieving methods are generally needed to make sure they are not overlooked (Struever, 1968; Shaffer & Sanchez, 1994; Stahl, 1996). As this has not always been done consistently and in the same manner in all archaeological excavations, comparing sites with different excavation methods can cause large misinterpretations. Also, smaller bones are in general less well described in osteological studies (see chapters 1 and 3), creating a bias towards reporting only the bigger and more known bones, species or skeletal elements, as researchers are less able to identify the smaller bones or certain skeletal elements (e.g., fin rays, orbital bones). These notes have to be kept in mind when analysing and comparing data from zooarchaeological assemblages.

2.2.2 Results of zooarchaeological analysis

Detailed tables of the results of the zooarchaeological recording of the assemblages can be found in tables A1-A5 in appendix part A.

Slight differences between sites were noticed for the colouration of the bones, reflecting the burial environment. In several sites some fish bones showed colouration which could be linked to exposure to heat and some were (partially) burned, but these were a minority.

2.2.2.1 Species representation

Figure 2.3 visualises the proportion of each of these selected families per site. Details can be found in table A1 in the appendix. Flatfish constitute a huge part of the assemblage in Barreau Saint-George, northern France (95.77%), while only a minor part in Blue Bridge Lane, northern England (<10%), which has a large focus on Clupeidae. The Early Medieval sites of Leiderdorp (i.e. Kastanjelaan and Plantage in the Netherlands) have a relatively large focus on Cyprinidae and Kastanjelaan also has a large proportion of Anguillidae. Gadidae seem to be only dominant in High and Late Medieval CAO, London. The high abundance of Pleuronectidae in Hof ter Hille, coastal Belgium, is an artefact of the methodology, as described above.

Figure 2.4 provides a chronological overview of all the sites analysed; for details per site see Table A1 in the appendix. In Coppergate (York) and CAO (London) Pleuronectidae became more abundant compared to the other families in the Late Medieval period compared with the earlier periods (see table A1). Also in Vlaardingen (Gat in de Markt, NL) there is a slight increase of Pleuronectidae during the Late Medieval period. Esocidae seem to have only been of some importance in both York sites during the Early and High Medieval periods. CAO, GSJ, Coppergate and Vlaardingen already have a high proportion of Gadidae during the High Medieval periods, but these sites do not show an increase in the Late Medieval period. In fact, there seems to be a slight decrease in most of these sites for Gadidae. The apparent switch from Pleuronectidae to Clupeidae seen in Blue Bridge Lane is an artefact from the methodology as not all material was available for study.

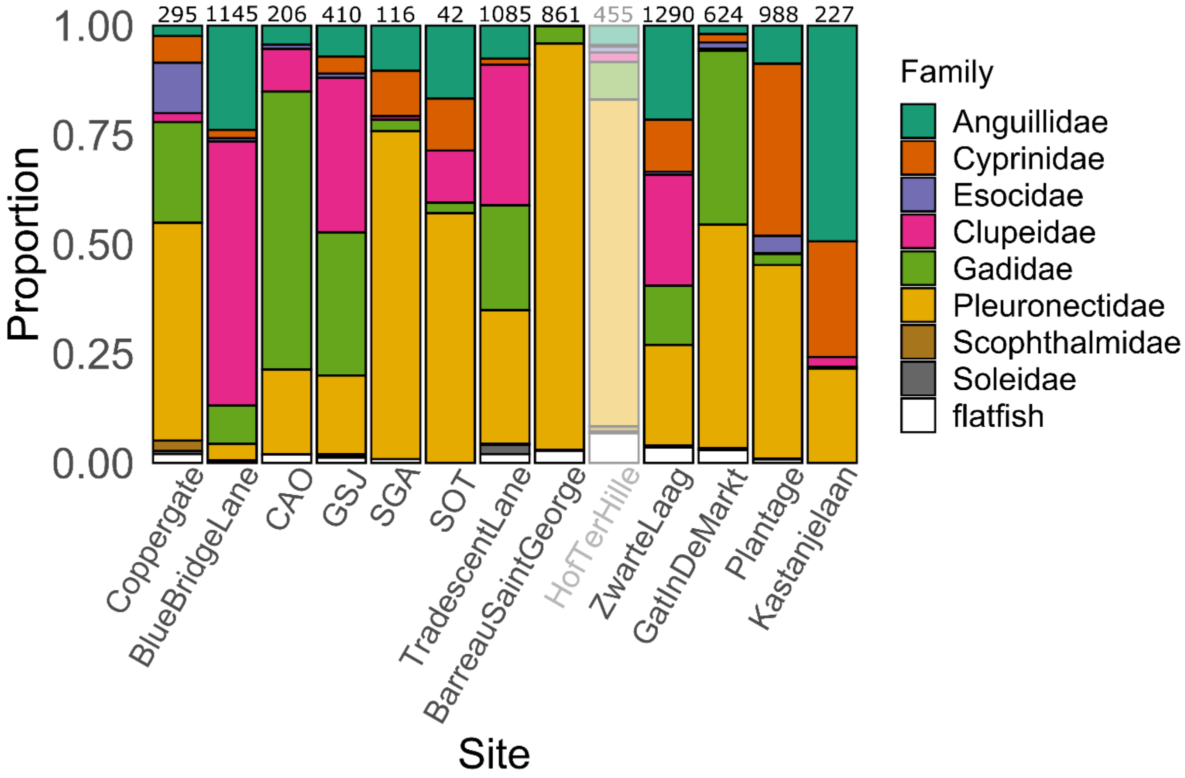

Figure 2.3. Proportion of flatfish NISP per family level compared with certain taxonomic groups per site. The total NISP per site is noted above each bar. Hof ter Hille is greyed out due to methodological issues explained above.

Due to limitations of identifying flatfish remains to species, the relative species proportions of flatfish are not further discussed. A more focused analysis will be done in chapter 5 using collagen peptide mass fingerprinting. So far, a low diversity of flatfish has been encountered in the assemblages based on osteological identifications. Most of these identifications occur with cranial bones or cleithra as these show more diagnostic features compared with vertebrae.

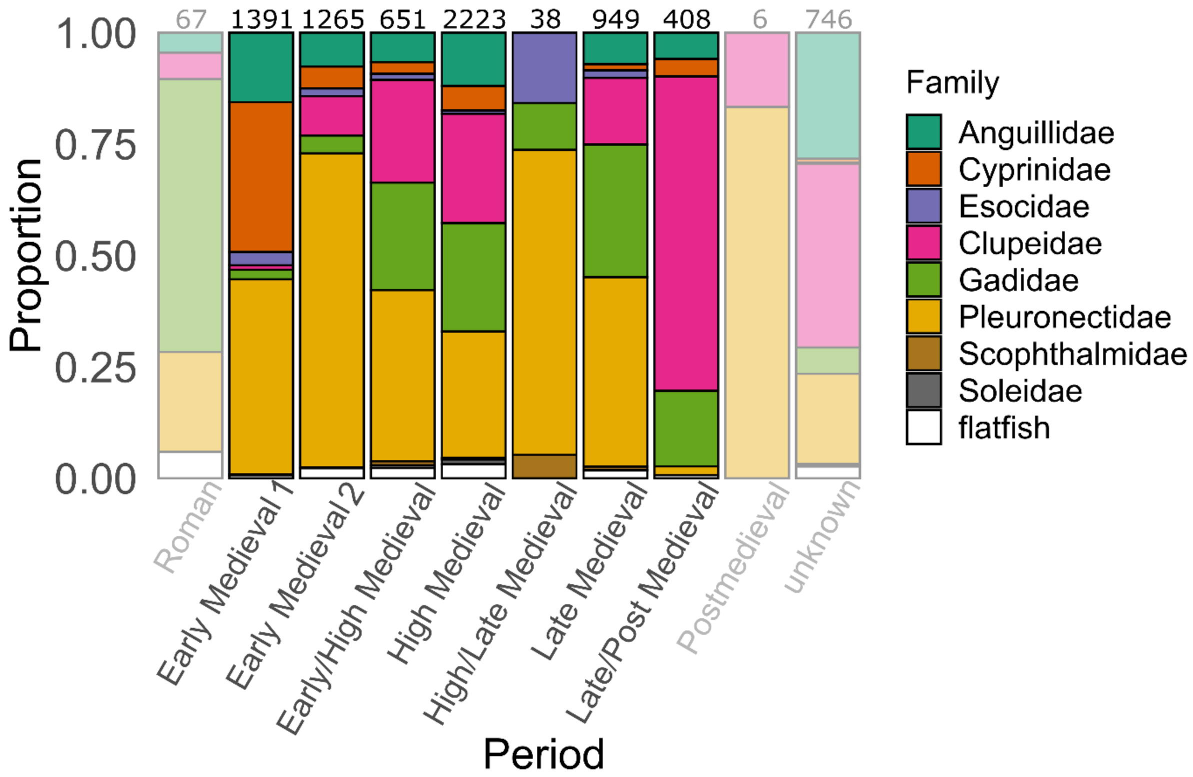

Figure 2.4. Proportion of flatfish NISP per family level compared with certain taxonomic groups per period. The total NISP per period is noted above each bar. Roman, Post-Medieval, and unknown periods are greyed out due to methodological issues explained above.

2.2.2.2 Element representation

The element distribution differs slightly per site (figure 2.5), with the coastal sites (figure 2.7) having relatively slightly fewer postcranial bones compared to the inland sites (figure 2.7). Especially in the four London sites, the high abundance of the postcranial bones is noticeable. Throughout the Medieval period there is a very slight trend visible across all sites showing a slight relative decrease in the postcranial bones and a relative increase of the cranial bones (figure 2.6), which only shows in the inland sites (2.7). Due to methodological concerns stated earlier, no statistical tests were performed to test for differences between sites and periods. As the sites were excavated differently, such as using different sieving methods, a bias towards bigger bones might be present in some sites, which would favour the generally larger postcranial elements. Due to the lack of sieving information on the three London sites excavated in the 1980-90s, it is thought that the overabundance of postcranial bones could reflect a methodological artefact, instead of a reflection of human behaviour during the Medieval period. However, as the total number of flatfish bones in these sites were small, this might just as well be an artefact of the small sample size. CAO has a relatively high proportion of cranial bones compared to the other sites from the same city. Also see tables A2, A4 and A5 in the appendix.

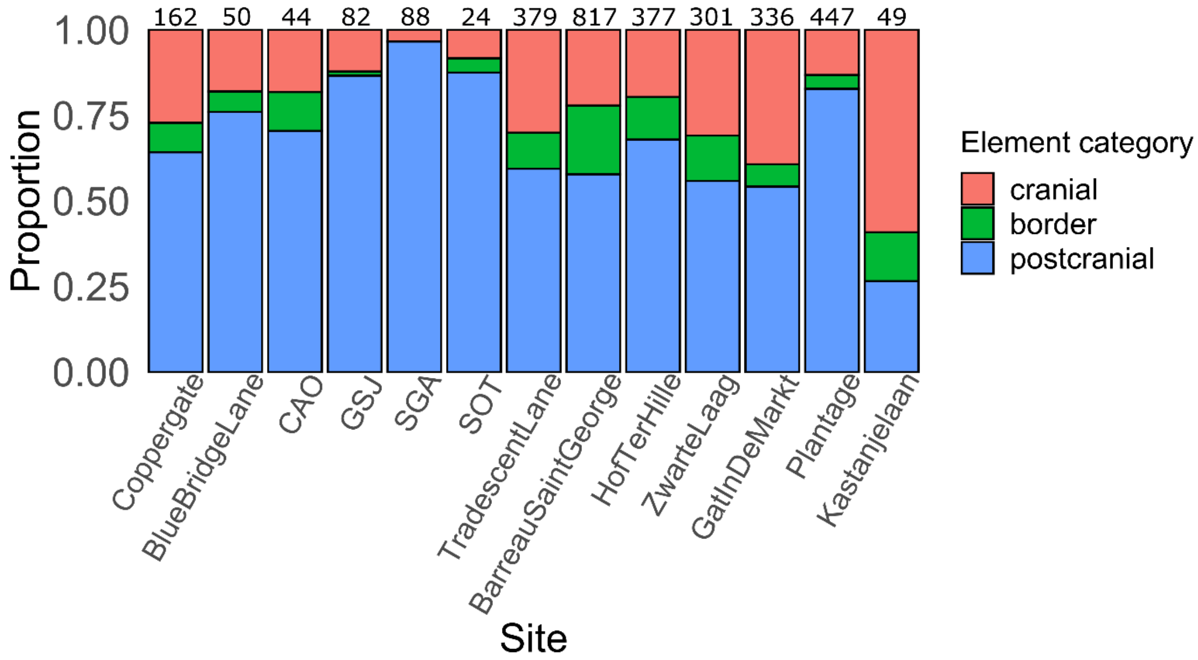

Figure 2.5. Proportional element representation of flatfish bones per element category across the sites. The total NISP per site is noted above each bar.

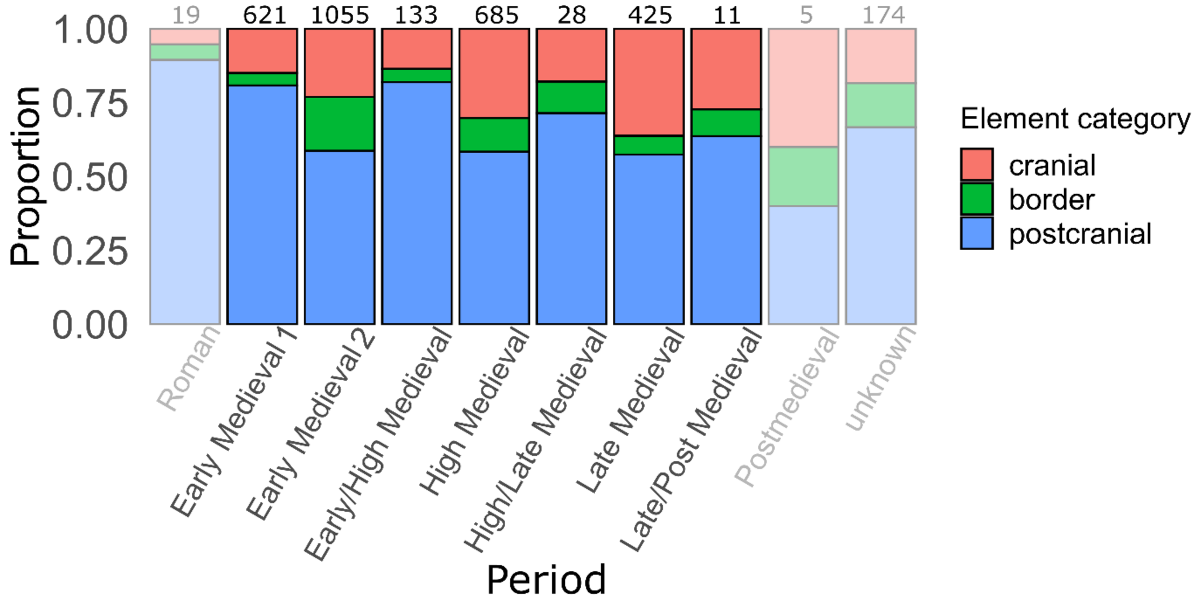

Figure 2.6. Proportional element representation of flatfish bones per element category across the periods. The total NISP per period is noted above each bar.

In Hof Ter Hille we see a slight increase in postcranial elements during the High Medieval period compared to the Early Medieval period, which is also the moment when the site slightly changes in occupation type.

Gat in de Markt has a slightly higher proportion of cranial bones throughout the Medieval period, even compared with the other coastal sites, which could mean that this coastal site was a processing site intended for export of fish meat. However, only 1 flatfish bone from this site showed cut marks.

Kastanjelaan has a remarkable overrepresentation of cranial bones, which might indicate some form of processing of the fish in this location after which the meaty part of the fish was transported elsewhere while the cranial bones remained on site as waste. Fish head was also regarded as a delicacy in some cases. In the site Plantage, within the same city as Kastanjelaan, we see, however, a slight overrepresentation of the postcranial bones, which could indicate that this is one of the places where the meaty parts of the fish were transported to.

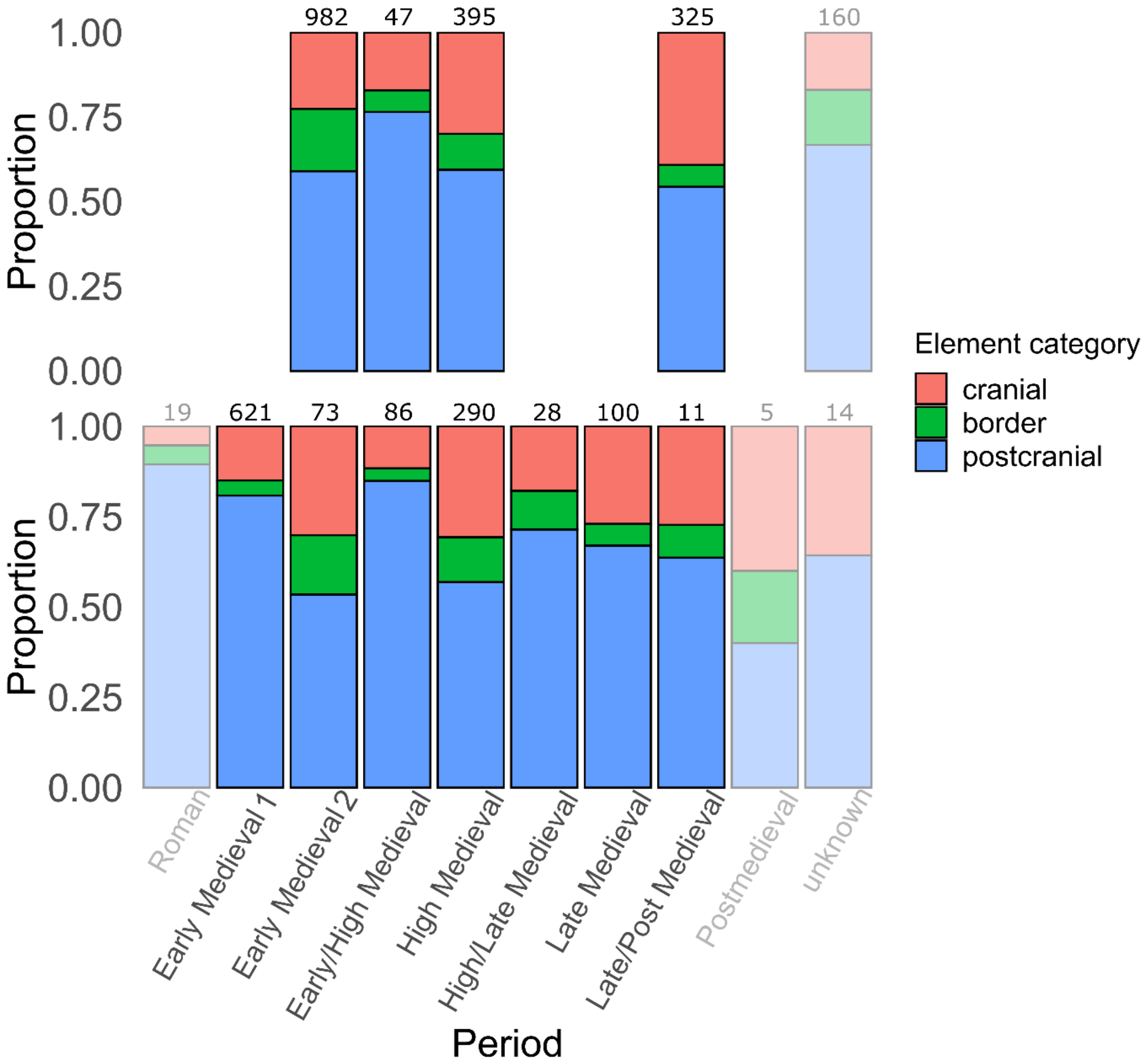

Figure 2.7. Proportional element distribution per grouping of element per time period for the coastal site in Canterbury, Saint-George, Koksijde, and Vlaardingen (above) and the inland sites in York, London, Gent, and Leiderdorp (below). The total NISP per period is noted above each bar.

2.2.2.3 Size distribution

SGA and SOT sites have a high proportion of unknown size class, as these two sites were analysed without having a reference collection at hand for comparisons. In all sites most size classes are represented (figure 2.8). Barreau Saint-George is characterised by having a dominance of very small flatfish (less than 20 cm SL). The largest size class is slightly more abundant in Zwarte Laag and Coppergate than in the other sites, while no large flatfish were recovered from CAO, GSJ, and Kastanjelaan. In the case of both these London sites, there could be some larger flatfish bones that were unavailable for study as these might have been stored in boxes with larger, hand collected, fish material which were not sorted out from the large mammal bones and therefore due to time constraints not studied. Kastanjelaan also has a specific species and element distribution, which could indicate that this was a production site of local, and therefore small, flatfish.

When looking at the size classes per period (figure 2.9), there seems to be a slight decrease in abundance of the smaller classes (5-20 and 20-30 cm SL) and a slight increase in abundance of the larger classes (30-40 and 40-60 cm SL) throughout the Medieval period. In all sites there seems to be a slight increase in abundance of larger flatfish in later periods (especially High and Late Medieval) compared with earlier periods (especially Early Medieval). There seems to be a dominance of large flatfish in Gat in de Markt in the Early Medieval 2 and High Medieval periods, but it has to be noted that there are only a handful of flatfish bones from those periods (n=3 and n=11). Also see tables A3, A4, and A5 in the appendix.

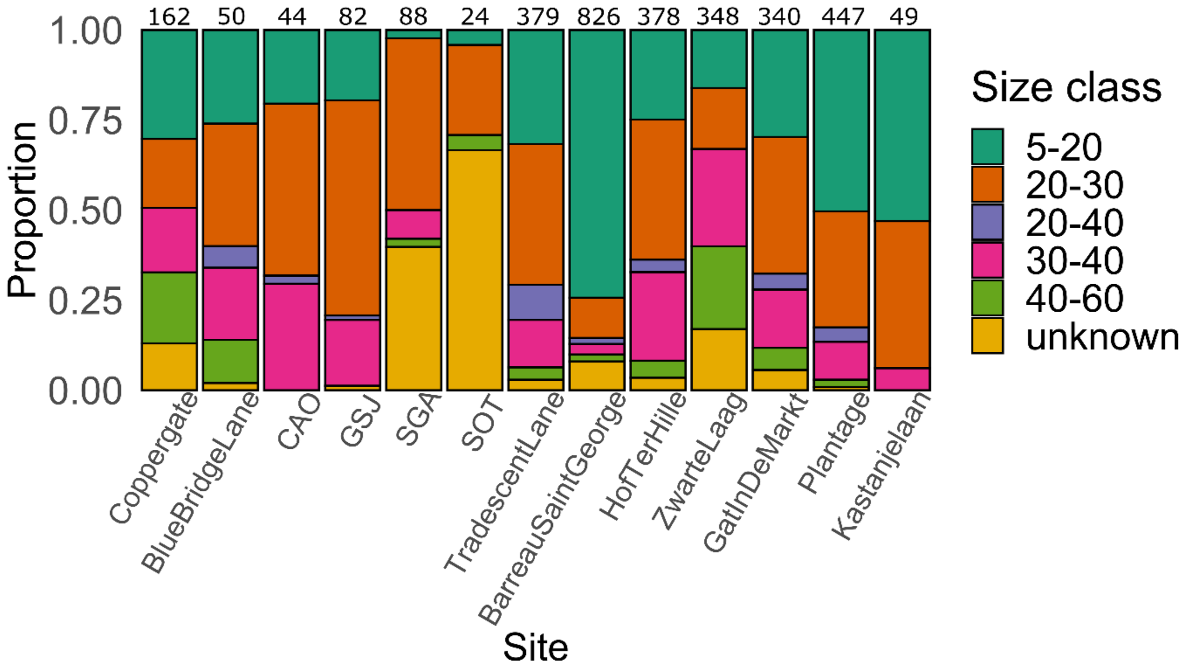

Figure 2.8. Size classes of flatfish per site. The total NISP per site is noted above each bar.

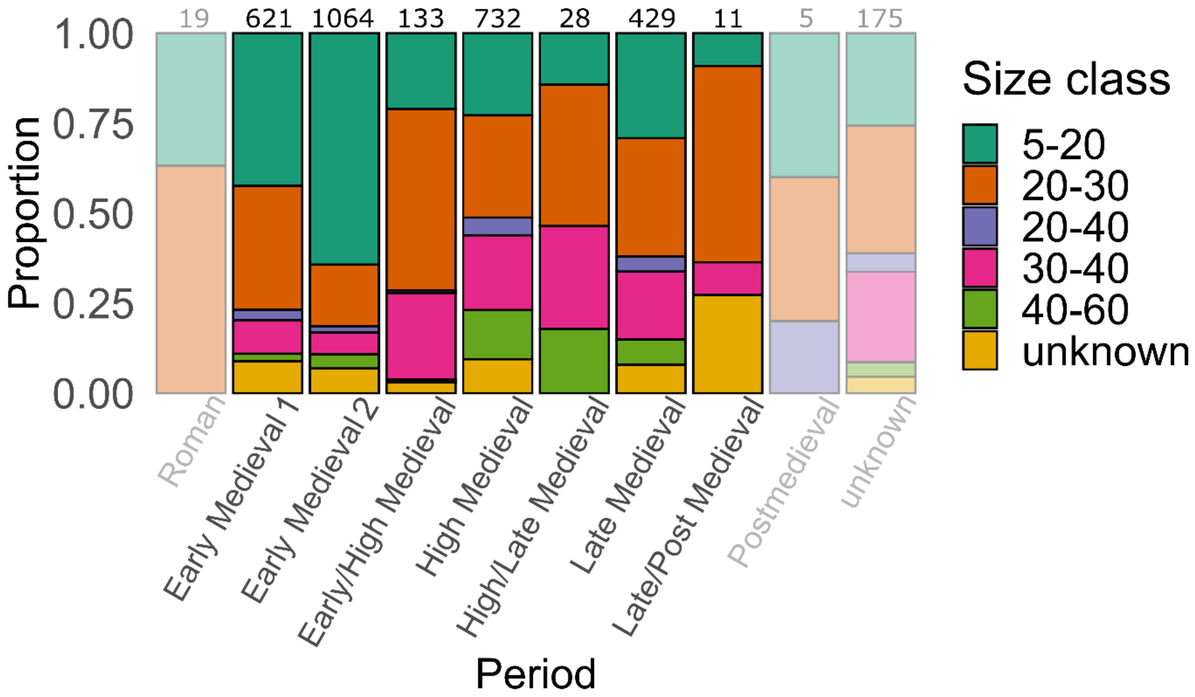

Figure 2.9. Size classes of flatfish per period. The total NISP per period is noted above each bar.

As Van der Meer *et al.* (2018) noticed a slight difference in element distribution between size classes in Hof ter Hille, a similar comparison is performed to test whether there has been some preference of processing certain sized flatfish over other across sites and periods. There seems to be no clear trend with certain sized flatfish being more or less processed compared to the other size classes across sites or periods. In Hof ter Hille, Zwarte Laag, Tradescent Lane, Barreau Saint-George, and Gat in de Markt seem to show a slight overabundance of cranial bones for the larger size classes and a slight overabundance of postcranial bones for the smaller size classes. In the London sites there seems to be a preference for smaller sized fish to be processed, i.e. having an overrepresentation of postcranial bones, but as mentioned before, there are some methodological concerns regarding these sites.

2.2.3 Discussion

As only certain fish families were considered here for methodological reasons, this also avoids certain taphonomical issues when comparing different taxa. For example, Salmonidae have not been included in this analysis, as the preservation of their bones is subject to debate, as their bones might be more prone to chemical dissolution during burial compared with bones from other taxa (Orton, pers. comm.). On the other hand, eels have many vertebrae, which can skew interpretations of abundance and their relative importance can be overestimated. Clupeidae have small bones, which are less easy to uncover and study and therefore might be overlooked more easily. Their abundance might have been underestimated in this analysis. Further, potential issues with taphonomy and recovery could also impact these results. The sites in London, for example, might not have been sieved as in detail as some of the other sites, creating a skew in the taxon and element distributions.

In the three sites that have both Early Medieval and Late Medieval sites (CAO96, Coppergate, Gat in de markt; Blue Bridge Lane not counted here) there seems to be a slight increase in the abundance of Pleuronectidae and a preference of larger flatfish in Coppergate in the later period, which coincides with the hypothesis that people would rely more on marine species, such as adult plaice, than on local freshwater/estuarine sources, which might also include small flounder.

Skeletal element distribution shows that the postcranial bones seem more abundant in the Early Medieval period in the inland sites than during the High and Late Medieval periods. This would suggest that there is a decrease of processed fish, although the taphonomic effect of the London sites should not be ignored here, as this might skew the element distribution for the Early Medieval period towards more postcranial bones, and therefore perhaps processed fish.

We see no difference in element representation between the coastal and inland sites in the Late Medieval period, which would indicate that flatfish were brought to all sites as whole fish. This matches some historical reports by Coenen in the *Visboeck* (Coenen, 1577; Bennema & Rijnsdorp, 2015) where it is said that in Holland people would buy and eat whole fresh plaice and flounder, whereas the processed (i.e. salted and/or dried) was transported to inland Germany (e.g., Cologne, Juliche, Kleve), which is much further away from the coastal areas than the inland sites included in this study and therefore required processing of fish to arrive in time before spoiling.

The increase of average fish size throughout the Medieval period could indicate that people shifted from local (riverine, estuarine, near-coastal) exploitation to marine exploitation as the larger adult flatfish can usually be found in open marine environments while smaller juveniles are mostly found in coastal areas and estuaries.

Coppergate has a high abundance of Pleuronectidae throughout all periods, with a slight decrease due to a shift to Gadidae during the High Medieval period which corresponds to the marine fish event horizon. There is also a high amount of pike in Coppergate, which is not noticed in any of the other sites. These could have been exploited in the local environment. There seems to be only a slight overrepresentation of postcranial bones of flatfish in both Coppergate and Blue Bridge Lane, which would indicate some level of processing of flatfish, but it is likely that most fish were brought to the site as whole fish. In both York sites there seems to be a slight increase in the general size of flatfish throughout the Medieval period, which would also suggest a more marine oriented exploitation, but this has to be confirmed with stable isotope analysis.

In London there seems to be a clear difference between the sites and/or time periods. The Saxon/Early Medieval sites SOT89 and SGA89 have a dominance of flatfish and a decent amount of freshwater and catadromous taxa, while the High Medieval CAO96 and GSJ06 have a dominance of Gadidae and some Clupeidae, with CAO96 showing an increase of Pleuronectidae again in the High Medieval period, similarly to Coppergate. This matches the trend described for the marine fish event horizon (Barrett *et al.*, 2004a). In all periods except the Post-Medieval, there is an overrepresentation of postcranial bones of flatfish across all four sites, which could indicate some form of processing of flatfish. All flatfish, except those during the High and Late Medieval periods in CAO96, are rather small, which are also more represented by postcranial bones compared with the larger specimens. This would suggest a preference to process the smaller fish, which are expected to be easier to dry than the larger flatfish (Van der Meer *et al.*, 2018), but it could also reflect a methodological artefact.

In Tradescent Lane in Canterbury there is a slight decrease in the proportion of flatfish during the Late Medieval period compared to the High Medieval period, while the amount of Clupeidae and Gadidae increase, but those Late Medieval flatfish are mostly larger sized, indicating that the abbey might have preferred the more marine adult flatfish in this period. This site also shows the highest proportion of Soleidae, which is a group associated with more elite occupation, but is also simply more abundant in the southernmost part of the North Sea. Based on the element representation of flatfish, which is similar to Barreau Saint-George in the Early Medieval period, it is thought that the fish were brought to the site as whole fish, which is possible in Tradescent Lane due to the closeness to the coast in Canterbury. Interestingly, the largest sized fish are mostly represented by cranial bones, which is especially the case for those from the Late Medieval period, although the sample size is only 13.

Although there is only High Medieval material present in Barreau Saint-George, it is clear that this site had a much larger focus on flatfish exploitation compared to the contemporaneous sites. Because of the location of the site and the distribution of the elements, it is thought that flatfish were brought as whole fish to the site. The overabundance of very small flatfish would indicate that exploitation occurred in nearby estuaries.

As the material of Koksijde Hof ter Hille was not properly analysed, it is difficult to make any kind of conclusion about the presence of non-flatfish taxa. Within the site, there is a slight increase of postcranial bones and a clear decrease of cranial bones during the High Medieval period together with a focus of larger sized flatfish. This switch not only matches with the general concept of the marine fish event horizon, it might also be linked to the change in the occupation of the site during the High Medieval period.

Although the dating resolution of Zwarte Laag in Gent is more precise than what is discussed here, it is clear that there is a decrease in the abundance of freshwater fish and a clear increase of marine fish, especially Gadidae and some Pleuronectidae, from the Early Medieval period to the High Medieval period. Within flatfish there is a slight increase in postcranial elements and a decrease in the smallest size class, which would also suggest a more marine oriented fish exploitation with fish being more often processed prior to arriving on the site.

In Vlaardingen, the Gat in de Markt site shows a clear switch from freshwater to marine exploitation during the High Medieval period with a sudden increase in Gadidae and slight increase in Pleuronectidae. Throughout the Medieval period there is also an increase in the proportion of postcranial bones. The Early Medieval period shows a very high abundance of cranial bones, indicating that this might have been a processing site, while a more averaged abundance of cranial and postcranial bones during the High and Late Medieval periods would indicate that people were bringing more whole flatfish to the site at this point. In the Early Medieval period the town was much smaller than in the High and Late Medieval periods. It is possible that people had a more dedicated fish landing and potentially processing site somewhere else in Vlaardingen once the town became more prominent during the High Medieval period.

Both sites in Leiderdorp show a clear difference in fish bones, with Plantage having a higher proportion of Pleuronectidae and postcranial bones and Kastanjelaan more local freshwater Cyprinidae and catadromous Anguillidae and very high proportion of cranial bones of flatfish. In the Plantage site, remains of houses and sheds have been found, while Kastanjelaan is more associated with the riverbanks and only consists of an old trench river. All this might suggest that both sites had specific uses, with Plantage being more of a consumer site, whereas Kastanje might have been the landing site where fish were processed.

2.2.4 Conclusion

In conclusion, it seems that there are small trends throughout the Medieval period that could be linked to an increase of marine fish consumption due to the shift in abundance of marine fish taxa and the increasing amount of larger flatfish. Some sites diverge from the general trends, which is most likely due to specific occupation types (e.g., Tradescent Lane being a monastic site, Kastanjelaan being a processing site). Precise exploitation shifts of freshwater to marine environments should still be confirmed by applying molecular methods such as stable isotope analysis (see chapter 6). Checking the species shifts within flatfish is limited due to the lack of diagnostic features on some bones (chapter 3), but with ZooMS this can be analysed using a subset of samples for each site (chapter 5). When comparing the results of ZooMS and osteology, however, it seems that the osteological identifications are still very prone to misinterpretations. Therefore, it was decided not to focus too much on the species identifications of these sites using osteology, and only discuss results in the context of family-level identifications.

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Chapter 3. Comparative osteology study of North Sea flatfishes

Authors: Katrien Dierickx, Wim Wouters

This is a paper that will be submitted soon. Katrien Dierickx selected the reference specimens, completed the analysis and drafted the paper. It has received input from Wim Wouters (Royal Belgian Institute of Natural Sciences), who trained Katrien Dierickx in fish bone analysis, provided access to museum specimens and helped assessing the diagnostic features of the skeletal elements.

The figures showing the morphological features for each element and species have sometimes photos or sketches instead of drawings. These photos and sketches are placeholders that will be replaced with final drawings for the publication. For the thesis, the photos will remain as placeholders as there was not enough time before submission to finish these drawings.

Abstract

The identification of flatfish remains in archaeozoological studies has often been limited to higher taxonomic levels or species groups. Bones from disarticulated skeletons of eleven main commercial species of flatfish present in the North Sea were compared to define diagnostic criteria allowing species identification. Out of the thirty-four studied skeletal elements often recovered in archaeological assemblages, ten proved to be very reliable for species identification and often allowed the distinction between right-eyed and left-eyed flounder. Fourteen elements were found to be less consistent to differentiate species. The other ten elements did not possess clear diagnostic features to distinguish the different taxa. The diagnostic details of each element are summarised and illustrated, leading to a clear identification guide for this particular group of fishes. More precise species identifications can provide more insight in the zoogeographical distribution of flatfish and will be useful in reconstructing the transition from inshore fisheries to deep water fishing.

Key words: Pleuronectiformes; Scophthalmidae; Pleuronectidae; Soleidae; comparative osteology

3.1 Introduction

Flatfishes were and are an important group of fish used as staple food and they had a great economic trade value through history, which is reflected by their common occurrence in archaeological sites (e.g., Barrett *et al.*, 2004a; Ervynck *et al.*, 2004; Harland *et al.,* 2016; Oueslati *et al.*, 2019) and historical records (e.g., Coenen, 1577).

Despite their common occurrence, early reports from archaeological studies on North Sea material stated that fish bones of flatfish were difficult to identify to species (e.g., Lepiksaar & Heinrich, 1977, Heinrich, 1987). Many skeletal elements remained unidentified or were at best only identified to order, family or species complex level. Typically, only 1 to 15% of flatfish bones are identified to species level, while the majority of remains are classified as the species complex plaice/flounder/dab (*Pleuronectes platessa*, *Platichthys flesus*, *Limanda limanda*) or summarised as Pleuronectidae (e.g., Ervynck & Van Neer, 1992; Enghoff, 1999; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019). Several zooarchaeological reports did identify some flatfish remains, but did not provide any description of their morphology (e.g., Lepiksaar & Heinrich, 1977; Enghoff, 1986; Heinrich, 1987; Brinkhuizen, 1989; Enghoff, 1989; Clavel, 1997). Within the Scophthalmidae also, bones were mostly assigned to family level or genus level (e.g., Nicholson, 2009; Harland *et al.*, 2016). The identification of flatfish vertebrae is even more difficult than that of cranial bones (e.g. Clavel, 1997). Bad preservation of archaeological flatfish bones, such as broken or fragmented elements, can only partially explain this problem.

Comparative osteology of flatfish species or elements has been rather sporadic and hardly well substantiated. Otoliths of flatfish and other North Sea species were described by Härkönen (1986). Roselló (1986) described the dentary and articular of six species. Dermal denticles were used in some archaeological studies to identify *P. flesus* and *S. maximus* (Enghoff, 1986, 1999). The pteroticum and sphenoticum of *P. flesus* can easily be distinguished from other flatfish, especially *P. platessa* and *L. limanda*, by a nodose-serrated margin (Enghoff, 1989). Lepiksaar (1994) illustrated elements from the axial skeleton and two os anale bones from flatfish without further comments. Watt *et al.* (1997) provided details to distinguish the premaxillae and vertebrae for 13 species of flatfish from the North Sea. A breakthrough was reached on the initiative of Luc Muylaert which resulted in the publication of Wouters *et al.* (2007). Here, 38 skeletal elements from three species, i.e., *Pleuronectes platessa*, *Platichthys flesus* (right- and left-eyed), and *Limanda limanda* were systematically studied. This study proved that species identification was successful for a number of elements, but not always for all the species. It further emphasised the need for a good reference collection which remains essential to improve the identification rate. Pure anatomical descriptions about flatfishes in general and specifically focussed on certain species are available (e.g., Gregory, 1933; Hubbs, 1945; Futch *et al.*, 1972; Cooper & Chapleau, 1998; Hoshino, 2001; Chanet, 2003; Díaz de Asterloa, 2005; Yazdani, 2009; Voronina, 2010; Märss *et al.*, 2017. Although these studies are intended for anatomical purposes, useful information and description needed for comparative osteology is often lacking.

At least 18 species of flatfish, or Pleuronectiformes, have been reported from the North Sea area in modern times (table 3.1). They belong to 4 families: Bothidae, Scophthalmidae, Pleuronectidae and Soleidae (Nielsen, 1986; Heessen *et al.*, 2015). Occasional reports also mention the presence of Cynoglossidae and Citharidae and other Soleidae and Scophthalmidae (Nijssen, 1966; Nijssen & De Groot, 1974; Nielsen, 1986; Heessen *et al.,* 2015; Froese & Pauly, 2021).

Table 3.1. All flatfish species commonly found in the North Sea and their maximum recorded total length (Heessen *et al.*, 2015).

Family	**Species**	**Author**	**Common name**	**Size$_{max}$**
Scophthalmidae	*Lepidorhombus whiffiagonis*	(Walbaum 1792)	megrim	61 cm
Scophthalmidae	*Scophthalmus maximus*	(Linnaeus 1758)	turbot	100 cm
Scophthalmidae	*Scophthalmus rhombus*	(Linnaeus 1758)	brill	61 cm
Scophthalmidae	*Zeugopterus norvegicus*	(Günther 1862)	Norwegian topknot	12 cm
Scophthalmidae	*Zeugopterus punctatus*	(Bloch 1787)	common topknot	25 cm
Scophthalmidae	*Zeugopterus regius*	(Bonnaterre 1788)	Ekström's topknot	20 cm
Bothidae	*Arnoglossus laterna*	(Walbaum 1792)	scaldfish	19 cm
Pleuronectidae	*Glyptocephalus cynoglossus*	(Linnaeus 1758)	witch	60 cm
Pleuronectidae	*Hippoglossoides platessoides*	(Fabricius 1780)	long-rough dab	48 cm
Pleuronectidae	*Hippoglossus hippoglossus*	(Linnaeus 1758)	halibut	254 cm
Pleuronectidae	*Limanda limanda*	(Linnaeus 1758)	dab	42 cm
Pleuronectidae	*Microstomus kitt*	(Walbaum 1792)	lemon sole	66 cm
Pleuronectidae	*Platichthys flesus*	(Linnaeus 1758)	flounder	51 cm
Pleuronectidae	*Pleuronectes platessa*	Linnaeus 1758	plaice	91 cm
Soleidae	*Buglossidium luteum*	(Risso 1810)	solenette	15 cm
Soleidae	*Microchirus variegatus*	(Donovan 1808)	thickback sole	33 cm
Soleidae	*Pegusa lascaris*	(Risso 1810)	sand sole	40 cm
Soleidae	*Solea solea*	(Linnaeus 1758)	sole	70 cm

Pleuronectiformes species are usually left- or right-eyed, but occasionally an individual can show the opposite sidedness. *Platichthys flesus* is especially known to have a variable proportion of left- versus right-eyed fishes. Distinguishing between these two forms could reveal more about the populations and ecology of exploited *P. flesus*, as the abundance of left-eyed *P. flesus* is geographically dependent and could impact the ecology of the individual fish (Fornbacke *et al.,* 2002; Russo *et al.,* 2012). Only several left-eyed *P. flesus* have been recorded from the archaeological record so far (e.g., Enghoff, 1994; Fornbacke *et al.*, 2002) Other flatfish species are less prone to this feature. Cunningham (1907) described a whole small reversed specimen of *S. maximus*. Gudger (1935) listed all reversed specimens described in older literature. His list included one Scophthalmidae (*S. maximus*), four Pleuronectidae (*P. platessa, L. limanda, P. flesus, H. hippoglossus)*, and one Soleidae (*S. solea*). Bruno and Fraser (1988) mentioned a very rare reversed *L. limanda*. Macdonald (2013) mentioned the single find of a reversed *L. whiffiagonis*. Recently, a reversed specimen of brill (*Scophthalmus rhombus*) and three reversed *Solea solea* were found by a fishmonger in Leuven, Belgium (Wim Wouters, unpublished data). Archaeological traces of reversed species other than *P. flesus*, however, are unknown so far. Remains of a reversed left-eyed *P. flesus* were identified for the first time by Enghoff (1984).

The aim of this study is to provide additional osteological diagnostic criteria for species and skeletal elements that were not previously described, which can improve the identification rate of genera and species of flatfishes found in the North Sea. This will allow more in-depth analysis of the flatfish bones found in archaeological contexts in this region which may lead to new insights about the abundance of these fishes through time. Improved identification rates may illustrate the historical development of fishing techniques as some species are known to live in estuaries and rivers, while others prefer the sea (Froese & Pauly, 2021). Another, often neglected, aspect is the side-effect that more material for other kinds of analytical research like isotope studies becomes available with better osteological identification. Such techniques can further provide insight into the historical exploitation of flatfish.

3.2 Material and methods

Dry, disarticulated specimens of flatfish housed at the University of York (YZL) and the Royal Belgian Institute of Natural Sciences (RBINS) were used for this study. All specimens originate from European waters and represent the main commercial and frequently occurring species currently found in the North Sea: *Pleuronectes platessa*, *Limanda limanda*, *Platichthys flesus* (normal right-eyed and reversed left-eyed), *Glyptocephalus cynoglossus*, *Hippoglossus hippoglossus*, *Hippoglossoides platessoides*, *Microstomus kitt*, *Scophthalmus maximus*, *Scophthalmus rhombus*), *Lepidorhombus whiffiagonis*, and *Solea solea*. Because several common names exist in English for some species and to avoid confusion for the reader, we will always refer to each species using only the scientific name. Table 3.2 provides an overview of the specimens used in this study; details can be found in table B1 in the appendix.

Table 3.2. Overview of the specimens used in this study. Details can be found in table B1 in the appendix.

Species	**Number of specimens**	**Min-max SL (cm)**	**Remarks**
Pleuronectidae			
Glyptocephalus cynoglossus	7	25-41	
Hippoglossoides platessoides	15	10-32	
Hippoglossus hippoglossus	14	35-240	
Limanda limanda	13	11-31.5	
Microstomus kitt	15	15-36.55	
Platichthys flesus	8	16-35.5	left-eyed
Platichthys flesus	6	20.6-32.9	right-eyed
Pleuronectes platessa	17	15-56	
Scophthalmidae			
Lepidorhombus whiffiagonis	8	25-35	
Scophthalmus maximus	15	18.2-48.5	
Scophthalmus rhombus	14	14.5-54.5	
Soleidae			
Solea solea	18	9.5-56	

Zeugopterus regius is only an occasional guest in the North Sea. Its main habitat is found in the English Channel. *Zeugopterus punctatus* is also rare for the southern North Sea. For this reason, they were not retained in this study. Other species reaching smaller maximum sizes than 20 cm TL were also excluded from this research. Fishes rarely grow to the potential full length and the bone remains of these species are too small for normal recovery. Moreover, these species were considered as fishes of low economic importance. The remains of scaldfish (*Arnoglossus laterna*), Norwegian topknot (*Zeugopterus norvegicus*) and solenette (*Buglossidium luteum*) are so far absent in archaeological material. The sand sole (*Pegusa lascaris*) was not retained either because it is a fish which prefers the English Channel. Nielsen (1986) doesn't mention its presence in the North Sea, while Heessen *et al.* (2015) shows how this species is moving up into the North Sea nowadays. The last species which is not studied here is the thickback sole (*Microchirus variegatus*). This is also a smaller sized fish, up to 20 cm SL according to Nielsen (1986). This species is absent from the east side of the North Sea and lives only in western waters. It is considered of minor economic importance and specimens larger than 17 cm SL are not present in the reference material in York or Brussels. It is clear that our specimen table doesn't cover the complete species spectrum present in the North Sea. However, we may state that in the case of *P. lascaris*, *B. luteum, M. variegatus,* and *A. laterna*, the elements have the typical shape on family level but are still very distinctive from the species studied here. In case elements differ strongly from the species described here, it is wise to check these other species too.

The osteology of *P. platessa*, *P. flesus* and *L. limanda* is already extensively described in Wouters *et al.* (2007). These are retained here and compared with the other species for consistency in the descriptions of the characteristics. Both right-eyed and left-eyed *Platichthys flesus* are analysed and compared (Table 3.2).

The final selection of elements was based on the proportion of all elements which reached the highest abundance over several sites in Flanders. These elements often collectively constitute 1 to 10% of all flatfish bones found in sites: premaxilla, maxilla, dentary, articular, metapterygium, ectopterygoid, palatine, quadrate, hyomandibula, operculum, preoperculum, interoperculum, posttemporal, cleithrum, supracleithrum, urohyal, vomer, parasphenoid, basioccipital, os anale, coracoid, basipterygium, basihyal, ceratohyal, epihyal, upper and lower hypohyal, pharyngeals II, III, IV, and V, first vertebra, first caudal vertebra and ultimate vertebra. Although vertebrae, fin rays and most of the branchial elements are more commonly found, their morphology does not allow adequate species identification, so they were not retained. Several head elements, used to distinguish *P. platessa*, *P. flesus* and *L. limanda* in Wouters *et al.* (2007) were not studied here: nasal, alisphenoid, praefrontal, frontal, pteroticum, sphenoticum, and supraoccipital. In the archaeological material of the other species treated here, these bones are rarely found. Only in the case of *S. solea* are they often abundant, but fortunately they are very characteristic and unique in shape (see Futch *et al.*, 1972).

Diagnostic characteristics are based on the presence/absence of certain morphologies as well as proportions and differences in overall shape. When describing the observed differences, the terminology of Lepiksaar (1994), complemented by Wouters *et al.* (2007), was used as much as possible. Illustrations are provided that show the observed differences. For paired elements, it is always the left bone that is illustrated, unless there are clear morphological differences between the left and right sides; then a drawing of the right bone is also included.

3.3 Results

The differentiation of all skeletal elements are summarised for each species, based on the comparison of complete bones. Only the most essential diagnostic criteria are mentioned in the text and main figures (3.1-35). When identifying fragmented bones, the additional tables (B1-45) and figures (B1-18) provide details about diagnostic criteria for specific characteristics of each bone part. Good diagnostic bone parts are indicated in bold in the tables in the appendix which allows the user to quickly find other criteria to check the identification. Some criteria are so diagnostic that such extra check is not necessary but for most of the bones, a combination of criteria is recommended. Elements are arranged according to their diagnostic ability with first the elements that allow clear and easy differentiation of all genera or species (more than half of species is easily identified), secondly elements that allow clear differentiation between families and some species (species can be identified but less straightforward), and thirdly the elements without diagnostic differences.

An overview of the identifiable elements is provided in table 3.3. Elements with clear diagnostic features and thus admitting fast and precise identification are indicated with E (easy). Elements without such straightforward criteria and thus showing minor diagnostic differences or differences that are difficult to interpret between a few species are indicated with D (difficult) for those species. Also elements that can only be identified after very careful comparison with an extensive reference collection are marked with a D (difficult). Elements that cannot be used to identify a species are indicated with a N (not possible).

3.3.1 Elements that allow easy differentiation of all genera

3.3.1.1 Premaxilla

The premaxilla is the only tooth-carrying part of the upper jaw. The teeth are implanted on the ventral side. Anteriorly on the corpus is the processus anterior with right behind it the processus articularis. In general, the premaxilla has an L-shape, although proportions vary between Pleuronectiformes species. The corpus is often curved ventrally and medially. The left and right premaxilla meet at the symphysis. When viewed laterally, the processus anterior is on the left side in the left premaxilla, and on the right side in the right premaxilla.

The lateral view of the left premaxilla is given in figure 3.1. Additionally, the medial and ventral view can be found in the appendix together with the detailed analysis for each species (table B2; figure B1). This bone allows easy identification to all the genera. *Solea solea* differs from all other species by having a strongly curved corpus (1) and a very broad and parabola shaped tooth area (2). *Microstomus kitt* has a very high and short corpus, that is as long as the processus anterior (3), and no indent between both processus. In the other Pleuronectidae and Scophthalmidae, the corpus is (slightly) longer than the processus anterior and a clear indent (4) between both processus is present. In Scophthalmidae there are 3 or more tooth rows (2) on the anterior part of the corpus, while in Pleuronectidae there are only 1 or 2 tooth rows. *Hippoglossus hippoglossus* differs from all other Pleuronectidae by having large teeth that are placed irregularly, and by having a large and broad symphysis (5). The corpus is very long, the teeth somewhat irregularly implanted, and the medial top of the processus anterior protrudes anteriorly in *H. platessoides*, while the corpus is not as long, the teeth implanted regularly, and the medial tip does not protrude anteriorly in *P. flesus*, *P. platessa*, *L. limanda*, and *G. cynoglossus*. Left-eyed *P. flesus* can easily be distinguished from other Pleuronectidae by not having a protruding symphysis and teeth on the posterior part of the corpus. *Limanda limanda* has a broader tip of the processus anterior and a posteriorly protruding angulus of the processus articularis (6), which is not the case in right-eyed *P. flesus*, *P. platessa*, and *G. cynoglossus*. The indent (4) between the processus anterior and the processus articularis is usually deep in right-eyed *P. flesus* and shallow in *P. platessa* and *G. cynoglossus*. The latter two species can be distinguished by the relative corpus length (short in *P. platessa*, long in *G. cynoglossus*) and the absence (*G. cynoglossus*) or presence (*P. platessa*) of the medial processus (7) at the base of the processus anterior. *Lepidorhombus whiffiagonis* can be identified from the *Scophthalmus* sp. by the bulb (8) of the processus articularis, which is higher than or the same height as the crista (9) in *L. whiffiagonis* and (barely) lower than the crista in *Scophthalmus* species. No criteria were found that allow distinction of both *Scophthalmus* species.

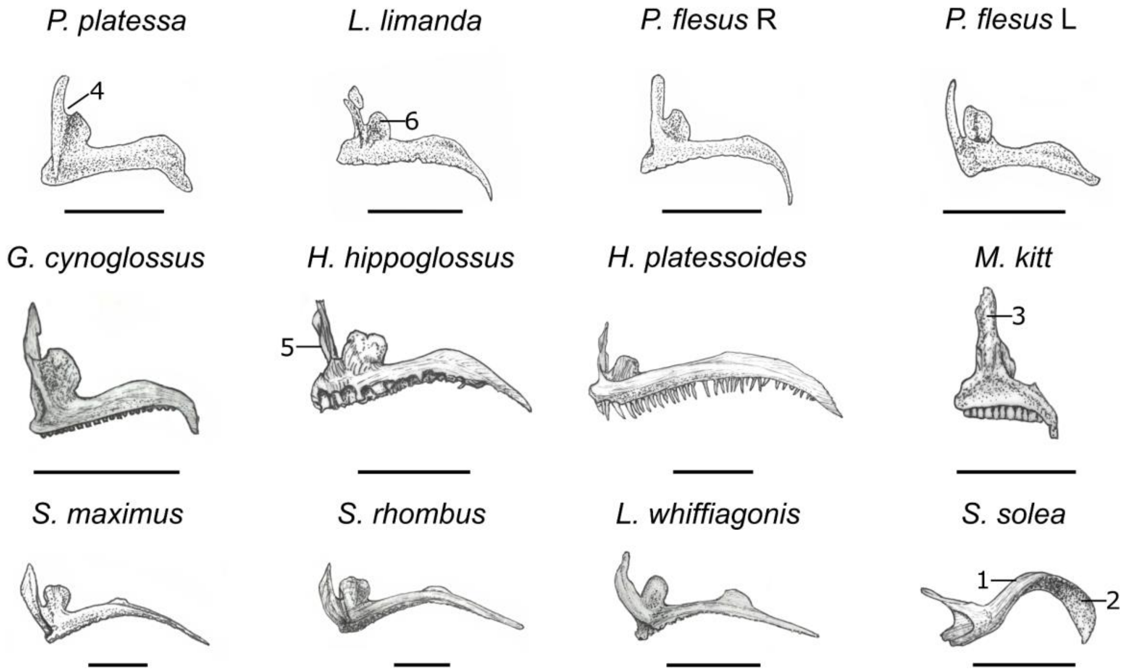


Figure 3.1. Lateral view of the left premaxilla of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the right premaxilla is given in figure 3.2. Additionally, the medial and ventral view can be found in the appendix together with the detailed analysis for every species (table B3; figure B2). This bone allows easy identification to all the genera. *Microstomus kitt* and *Solea solea* have characteristic shape and no teeth that differs strongly from the other taxa. Scophthalmidae differ from Pleuronectidae by having 3 or more tooth rows (2) on the anterior part of the corpus, while the Pleuronectidae have (0)1-2(3) tooth rows. *Hippoglossus hippoglossus* has very large alveoli placed irregularly with large gaps in between and broad processus anterior (3). *Pleuronectes platessa* has only 3-6 teeth till halfway the corpus, while in *G. cynoglossus, H. platessoides, L. limanda* and *P. flesus* there are more than 6 teeth that reach further than halfway the corpus (1). *Hippoglossoides platessoides* has a very long corpus compared with other Pleuronectidae. Left-eyed *P. flesus* is easily distinguishable by its protruding symphysis (5). The corpus is about as long as the processus anterior in *G. cynoglossus*, while it is longer than the processus in right-eyed *P. flesus* and *L. limanda*. *Limanda limanda* is characterised by having a thin and slenderer corpus with small tooth alveoli, while right-eyed *P. flesus* has a thick and longer corpus with large alveoli. *Lepidorhombus whiffiagonis* can be identified from the *Scophthalmus* sp. by the bulb (8) of the processus articularis, which is higher than or the same height as the crista (9) in *L. whiffiagonis* and (barely) lower than the crista in *Scophthalmus* species. No criteria were found that allow distinction of both *Scophthalmus* species.

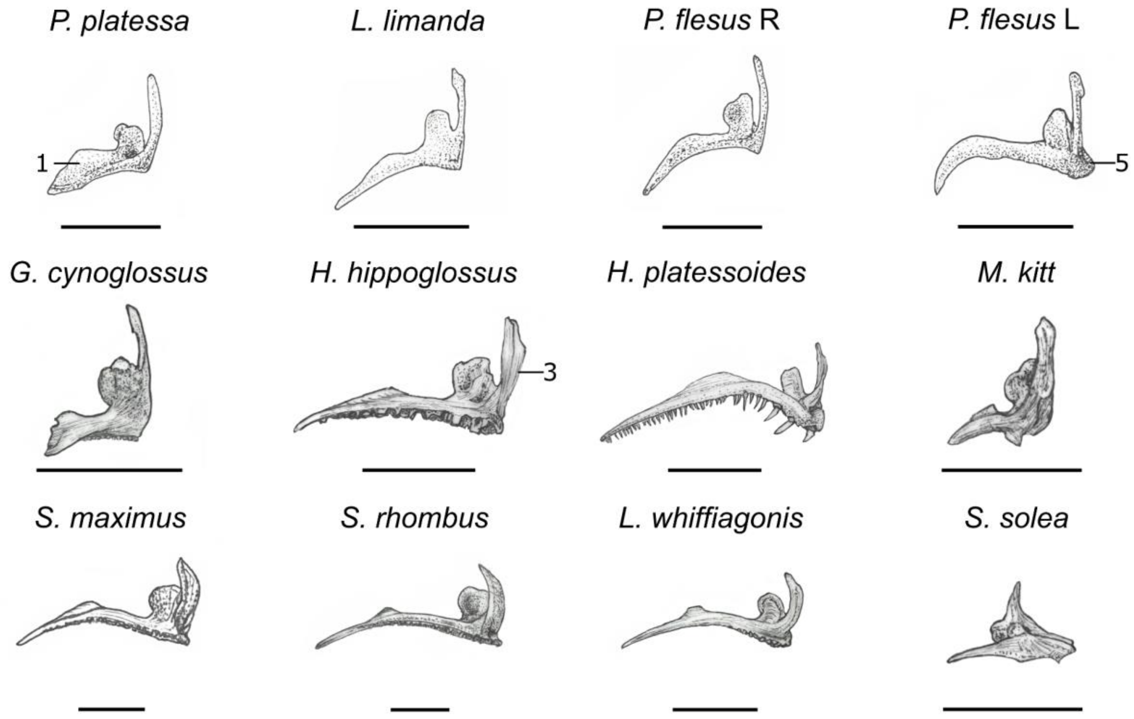


Figure 3.2. Lateral view of the right premaxilla of all twelve species. The black bar under each species represents 1 cm.

3.3.1.2 Maxilla

The maxilla lies posteriorly of the premaxilla and is also part of the upper jaw. There are no teeth on this bone in Pleuronectiformes. The corpus of the maxilla is usually long and slender, with often a crista maxillaris. A collum maxillare connects the crista maxillaris to the caput maxillare, which is the anterior part of the maxilla and consists of a dorsal bulb and two anterior/ventral processus: processus internus medially and processus externus laterally. Sometimes there is a tuberositas processus externus posterior of the processus externus on the lateral side. Often there is a foramen inside the caput, which is also visible from the posterior or lateral side. The caudal part of the maxilla is the pars caudalis, which is often broader than the corpus. Viewed dorsally, the left maxilla caput is curved to the right, and the right maxilla caput to the left.

The lateral and medial view of the left maxilla is given in figure 3.3. Additional descriptions can be found in the appendix (table B4). This bone allows easy identification to all the species. *Solea solea* is the only species in which the processus externus (1) is barely visible and *M. kitt* has a very stocky shape, making these species very distinct. The pars caudalis (2) doesn’t broaden in *L. whiffiagonis*, and broadens in the other Scophthalmidae and Pleuronectidae. In *Scophthalmus* sp. there is a gradual broadening of the pars caudalis and the spina on the processus internus (3) is oriented laterally, while in Pleuronectidae the broadening of the pars caudalis is clear and abrupt and the spina is oriented anteriorly. *Scophthalmus rhombus* differs from *S. maximus* by having a posterior spina, which looks like it overhangs posteriorly, on the caput (4) and a short spina on the processus internus, while *S. maximus* does not have an overhanging caput and has a long spina on the processus internus. *Hippoglossus hippoglossus* differs from the other Pleuronectidae by having a hollow medial side of the pars caudalis and a large foramen (5) on the processus internus sometimes, both structures that are absent in the other species. The caput is at its broadest in the middle in *G. cynoglossus*, while in the lower half in other Pleuronectidae. *Hippoglossoides platessoides* has an upward oriented spina on the processus internus, while the other Pleuronectidae have an anteriorly oriented spina. Left-eyed *P. flesus* has a forward bend caput, while right-eyed Pleuronectidae has a non-bend caput. In *P. platessa* the spina barely reaches more anterior than the ventral tip of the processus internus (6) and the pars caudalis is strongly broadened, while in right-eyed *P. flesus* and *L. limanda* the spina often reaches (a bit) further than the ventral tip of the processus internus and the pars caudalis broadening is less clear. *Limanda limanda* has a slenderer corpus (7) compared with right-eyed *P. flesus* and a caput that has no posterior spina. Right-eyed *P. flesus* sometimes has a slightly overhanging caput.

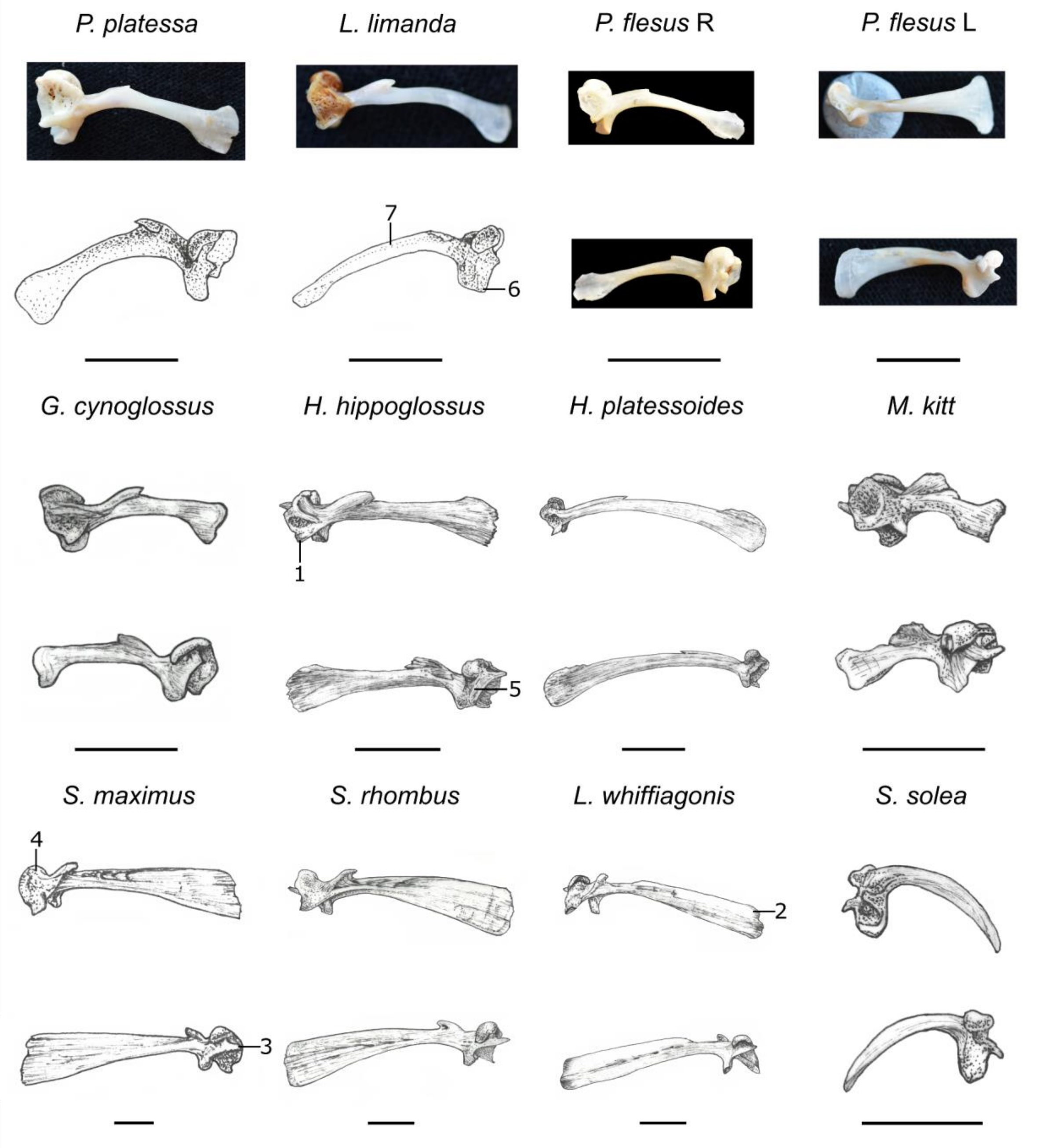


Figure 3.3. Lateral (top) and medial (bottom) view of the left maxilla of all twelve species. The black bar under each species represents 1 cm.

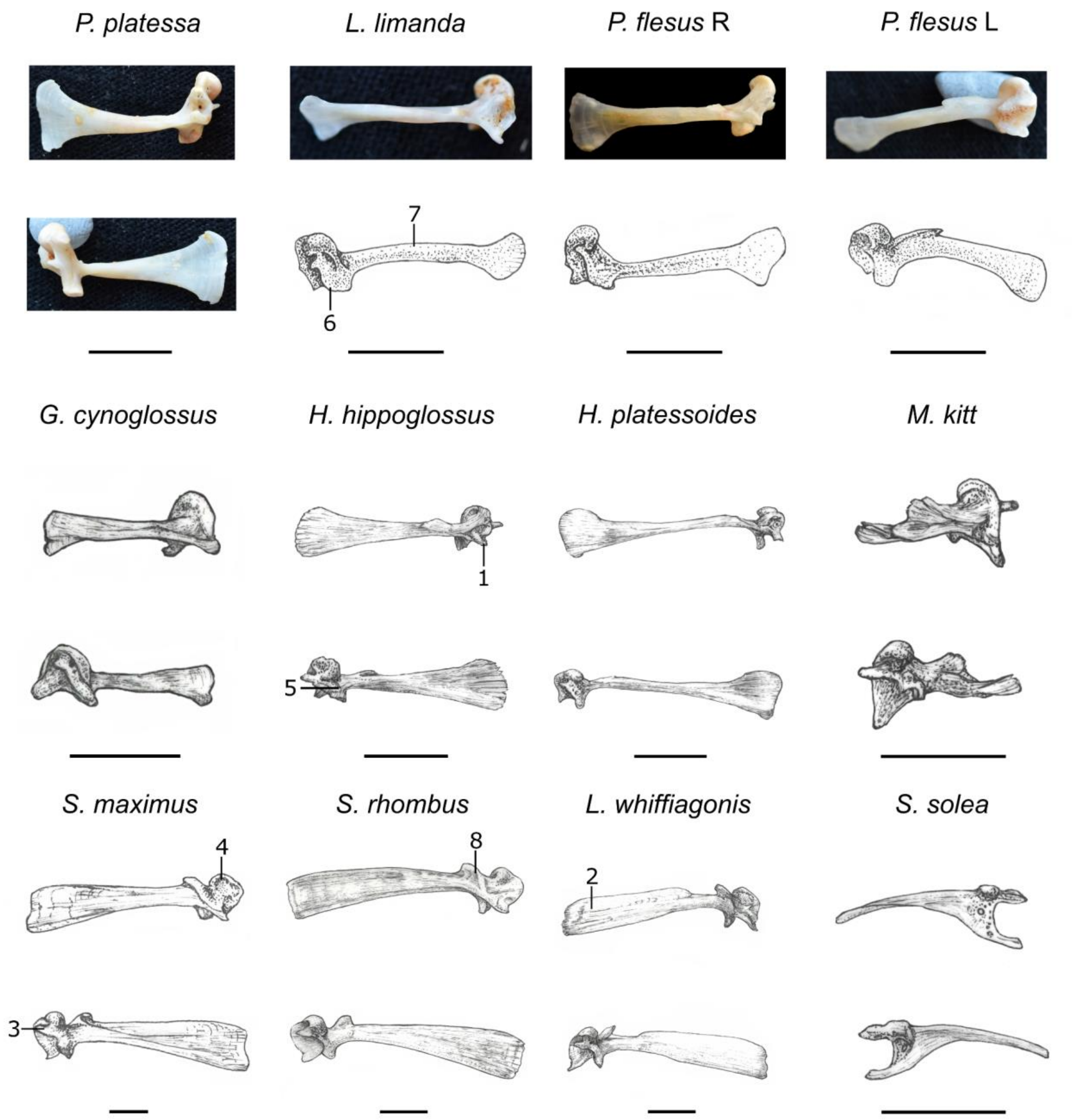


Figure 3.4. Lateral (top) and medial (bottom) view of the right maxilla of all twelve species. The black bar under each species represents 1 cm.

The lateral and medial view of the right maxilla is given in figure 3.4. Additional descriptions can be found in the appendix (table B5). This bone allows easy identification to all the species. S*olea solea* is the only species in which the processus externus (1) is barely visible and *M. kitt* has a very stocky shape, making these species very distinct. The pars caudalis (2) doesn’t broaden in *L. whiffiagonis*, and broadens in the other Scophthalmidae and Pleuronectidae. In *Scophthalmus* sp. there is a gradual broadening of the pars caudalis, while in Pleuronectidae the broadening of the pars caudalis is clear and abrupt. *Lepidorhombus whiffiagonis* can be distinguished from *Scophthalmus* sp. on the relatively smaller lateral ridge on the crista articularis (8) and the relatively longer processus internus (6). *Scophthalmus rhombus* differs from *S. maximus* by having a spina on the posterior side of the caput (4) and a relatively shorter spina on the processus internus (3). *Hippoglossus hippoglossus* differs from the other Pleuronectidae by having a large foramen (5) on the processus internus, which is absent in the other species. The processus externus in *G. cynoglossus* is longer than the processus internus and the notch is weakly delineated. The corpus (7) is very long and slender and the caput high and slender in *H. platessoides.* Left-eyed *P. flesus* does not have a laterally protruding ventral part of the processus externus, while that is present in the other Pleuronectidae. The corpus is thin and slender and the pars caudalis slightly curved around its axis in *L. limanda*, while in right-eyed *P. flesus* and *P. platessa* the corpus is thick and the pars is strongly curved around its axis. Right-eyed *P. flesus* has a slenderer appearance and a relatively longer corpus for maxilla with the same caput width compared with *P. platessa*.

3.3.1.3 Dentary

The dentary is the only tooth-carrying part of the lower jaw. The teeth are implanted on the dorsal side. Posteriorly there are two processus, the superior and inferior, that are implanted on the corpus. There is often a slight medial curve of the processus superior. The left and right dentary meet at the symphysis. On the lateral side are often some foramina from the lateral line system on the corpus and processus inferior. Other foramina are possible too. When viewed laterally, the symphysis is on the left side in the left dentary and on the right side in the right dentary.

The lateral view of the left dentary is given in figure 3.5. Additionally, the medial and ventral view can be found in the appendix together with the detailed analysis for every species (table B6; figure B3). This bone allows easy identification to all the genera. *Solea solea* and *M. kitt* are easily distinguished from all other flatfish species by their unique and short shape. The large size of the lateral foramen (1) on the processus inferior (2) distinguishes *G. cynoglossus* very easily from the other species. Scophthalmidae differ from Pleuronectidae by having 3 or more tooth rows (3) at the anterior part, while Pleuronectidae only have 1 or 2 rows. *Hippoglossus hippoglossus* differs from all other Pleuronectidae by having large teeth that are placed irregularly. Left-eyed *P. flesus* can easily be distinguished from the other Pleuronectidae by having teeth only till the split of the processus (4) and a high symphysis (5). *Hippoglossoides platessoides* is characterised by having a very long, much longer than high, dentary with at least 30 teeth. In *Pleuronectes platessa* the teeth are very tidely implanted, while rather tidy or slightly chaotically implanted in right-eyed *P. flesus* and *L. limanda*. The former species also has a straight symphysis and a strongly laterally curved processus superior (6), while the latter two species have an inclined symphysis and only a slightly laterally curved processus superior. The processus inferior is as long as the processus superior in *L. limanda*, while longer than the processus superior in right-eyed *P. flesus*. The ventral indent (7) is long in *L. limanda*, and short in right-eyed *P. flesus*. The dorsal border of *L. whiffiagonis* is curved while the elements of both *Scophthalmus* have a straight board. Moreover, the depression halfway the element (8) is very large and always open in *L. whiffiagonis*. When this depression is open, it is most likely *S. rhombus*. When this depression is closed, it is most likely *S. maximus*. If these last criteria are less clearly visible, it is advised to restrict identification to *Scophthalmus* sp.

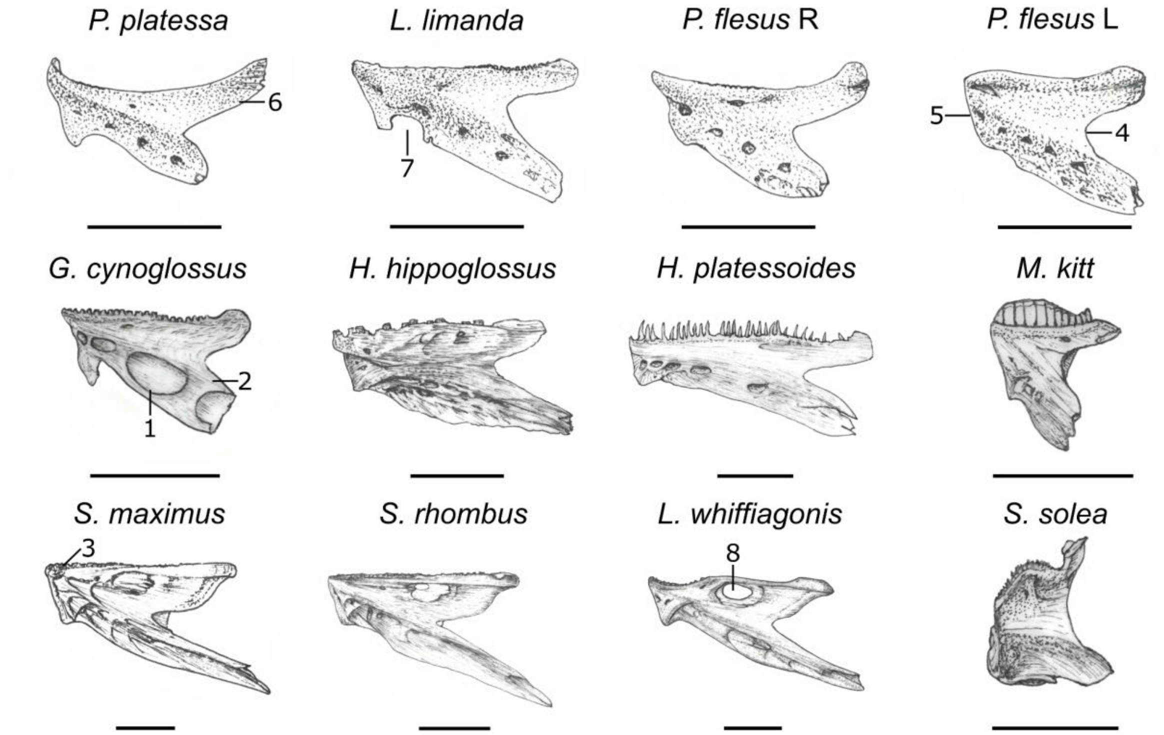


Figure 3.5. Lateral view of the left dentary of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the left dentary is given in figure 3.6. Additionally, the medial and ventral view can be found in the appendix together with the detailed analysis for every species (table B7; figure B4). This bone allows easy identification to all the genera. The shape is characteristic for *M. kitt*. The dorsal edge and shape of the right dentary of *S. solea* is also very characteristic. The large size of the lateral foramen (1) on the processus inferior (2) distinguishes *G. cynoglossus* very easily from the other species. In Scophthalmidae, the processus inferior is much longer than the processus superior (6) and the processus superior has no upward pointed posterior tip. In Pleuronectidae, the processus superior has a clearly upward pointed tip. Left-eyed *P. flesus* can easily be distinguished from the other Pleuronectidae by having a processus superior that is much longer than the processus inferior and has a strong lateral curve. *Hippoglossus hippoglossus* differs from all other Pleuronectidae by having large teeth (3) that are placed irregularly. *Hippoglossoides platessoides* is characterised by having a convex dorsal margin of the processus superior and irregularly implanted teeth. *Pleuronectes platessa* has only 4-8 teeth at the most anterior part of the dentary, while in *L. limanda* and right-eyed *P. flesus* there are more than 10 teeth that reach till the split of the corpus (4). *Limanda limanda* differs from right-eyed *P. flesus* by having a deep ventral indentation (7) usually and a long ventral protrusion of the symphysis (5), while right-eyed *P. flesus* has a shallow ventral indentation and a short ventral protrusion of the symphysis. The dorsal border of *L. whiffiagonis* is curved while the elements of both *Scophthalmus* have a straight board. Moreover, the depression halfway the element (8) is very large and always open in *L. whiffiagonis*. When this depression is open, it is most likely *S. rhombus*. When this depression is closed, it is most likely *S. maximus*. If these last criteria are less clearly visible, it is advised to restrict identification to *Scophthalmus* sp. Usually the crista at the split of the processus (9) is not visible laterally in *S. rhombus*, while it is visible usually in *S. maximus.*

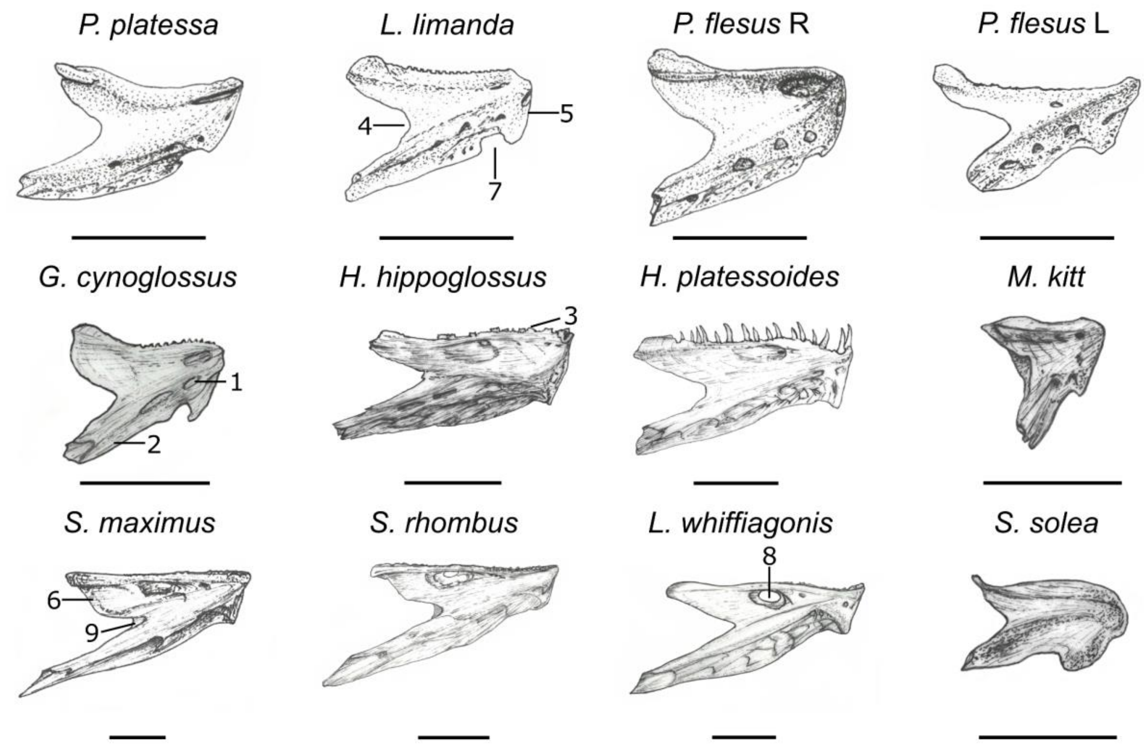
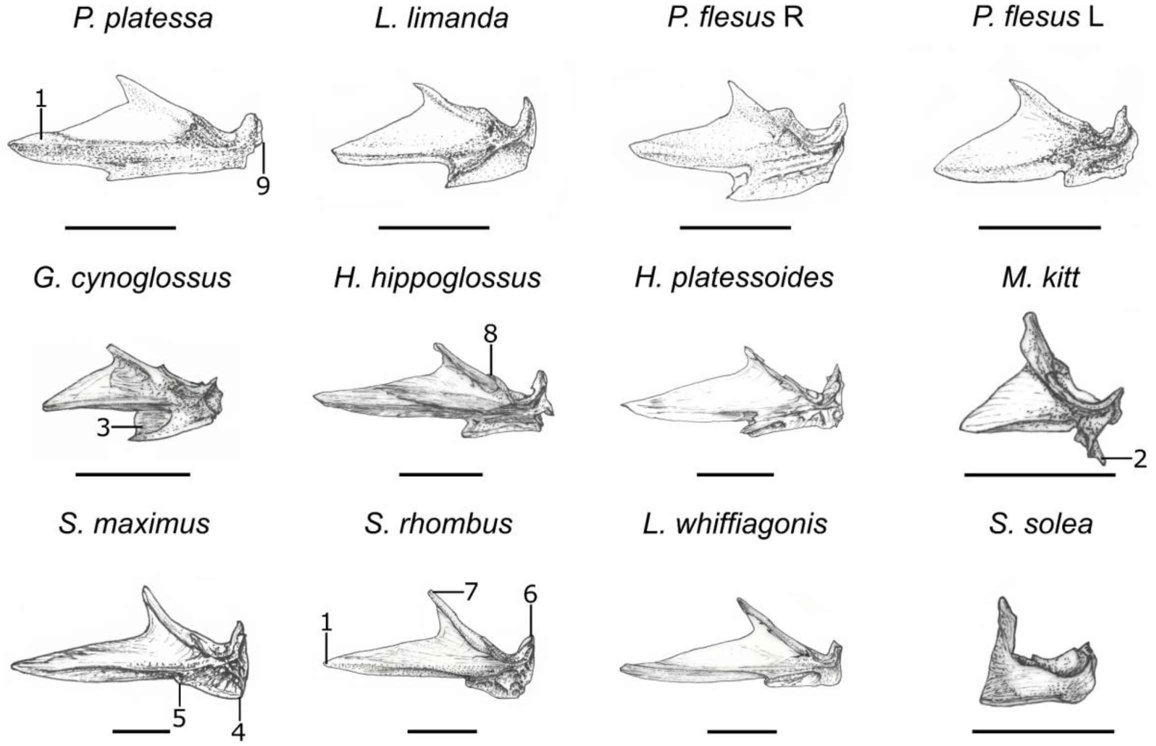


Figure 3.6. Lateral view of the right dentary of all twelve species. The black bar under each species represents 1 cm.

3.3.1.4 Articular

The articular lies posteriorly of the dentary. The processus coronoides is the dorsally oriented processus from the corpus, the processus anterior the anteriorly oriented, and the processus ventralis the ventral oriented processus. The processus ventralis often shows the anterior tube of a lateral line channel. The posterior tube of this channel can be seen on the posterior side. At the posterior base of the processus coronoides lies the facies articularis quadrati, of which the posterior edge can look like a spina. When viewed laterally, the processus anterior is pointed left in the left articular, and right in the right articular.

The lateral view of the left articular is given in figure 3.7. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B8; figure B5). This bone allows easy identification to all the species. *Solea solea* is characterised by having no clear processus anterior (1). *Microstomus kitt* has a ventrally oriented processus ventralis (2). Enlarged tubes of the channel (3) are typical for *G. cynoglossus.* Scophthalmidae can be distinguished by having a posterior edge (4) of the processus ventralis that is higher than the anterior tip (5), while it is lower in the Pleuronectidae. *Lepidorhombus whiffiagonis* has a long and thin bone compared with *Scophthalmus* sp., and a slight concave ventral margin of the processus ventralis, while it is slightly convex in *Scophthalmus* sp. In *S. maximus* the spina (6) is much higher than in *S. rhombus*. Both *Scophthalmus* sp. also differ in the angle of the processus coronoides (7) with the processus anterior (1), with *S. maximus* having a larger angle than *S. rhombus*. In *H. hippoglossus* and *H. platessoides* the spina is higher than the anterior edge of the facies (8), while it is lower or similar in height in *L. limanda*, *P. platessa*, and *P. flesus*. In *H. hippoglossus*, the tip of the processus coronoideus lies in front of the angulus ventralis while in *H. platessoides* these two are at the same level. *Pleuronectes platessa* has a low posterior margin (9) and slightly protruding processus ventralis, while *L. limanda* and *P. flesus* have a high posterior margin and strongly protruding processus ventralis. In *L. limanda* often and left-eyed *P. flesus*, the tip of the processus coronoideus lies in front of the angulus ventralis, while in right-eyed *P. flesus* these two are at the same level. *L. limanda* never has a second spina on the posterior edge and a more angular lower posterior corner (4), while there are often two spina and a more irregular or rounded lower posterior corner in right-eyed *P. flesus*.


P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure 3.7. Lateral view of the left articular of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the right articular is given in figure 3.8. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B9; figure B6). This bone allows easy identification to all the species. *Solea solea* has a processus coronoides (7) that is oriented posteriorly, which is characteristic for this species. *Microstomus kitt* has a ventrally oriented processus ventralis (2). Scophthalmidae can be distinguished by having a posterior edge (4) of the processus ventralis that is higher than the anterior tip (5), while it is lower in the Pleuronectidae. *Lepidorhombus whiffiagonis* has a long and thin bone compared with *Scophthalmus* sp., and a slight concave ventral margin of the processus ventralis, while it is slightly convex in *Scophthalmus* sp. In *S. maximus* the spina (6) is much higher than in *S. rhombus*. Both *Scophthalmus* sp. also differ in the angle of the processus coronoides (7) with the processus anterior (1), with *S. maximus* having a larger angle than *S. rhombus*. In *H. hippoglossus* and *H. platessoides* the spina is higher than the anterior edge of the facies (8), while it is lower or similar in height in *G. cynoglossus, L. limanda*, *P. platessa*, and *P. flesus*. In *H. hippoglossus*, the tip of the processus coronoideus lies in front of the angulus ventralis while in *H. platessoides* these two are at the same level. *Pleuronectes platessa* has a low posterior margin (9) and slightly protruding processus ventralis, while *G. cynoglossus, L. limanda* and *P. flesus* have a high posterior margin and strongly protruding processus ventralis. In left-eyed *P. flesus,* the tip of the processus coronoideus at the same level as the angulus ventralis, while in front in *P. platessa, L. limanda, G. cynoglossus* and right-eyed *P. flesus*. *Pleuronectes platessa* has a low posterior margin and slightly protruding processus ventralis, while the other Pleuronectidae have a high posterior margin and strongly protruding processus ventralis. *Glyptocephalus cynoglossus* has a relatively shorter right articular compared with *L. limanda* and right-eyed *P. flesus*, with a much shorter processus anterior. *Limanda limanda* never has a second spina on the posterior edge and a more angular lower posterior corner, while there are often two spina and a more irregular or rounded lower posterior corner in right-eyed *P. flesus*.

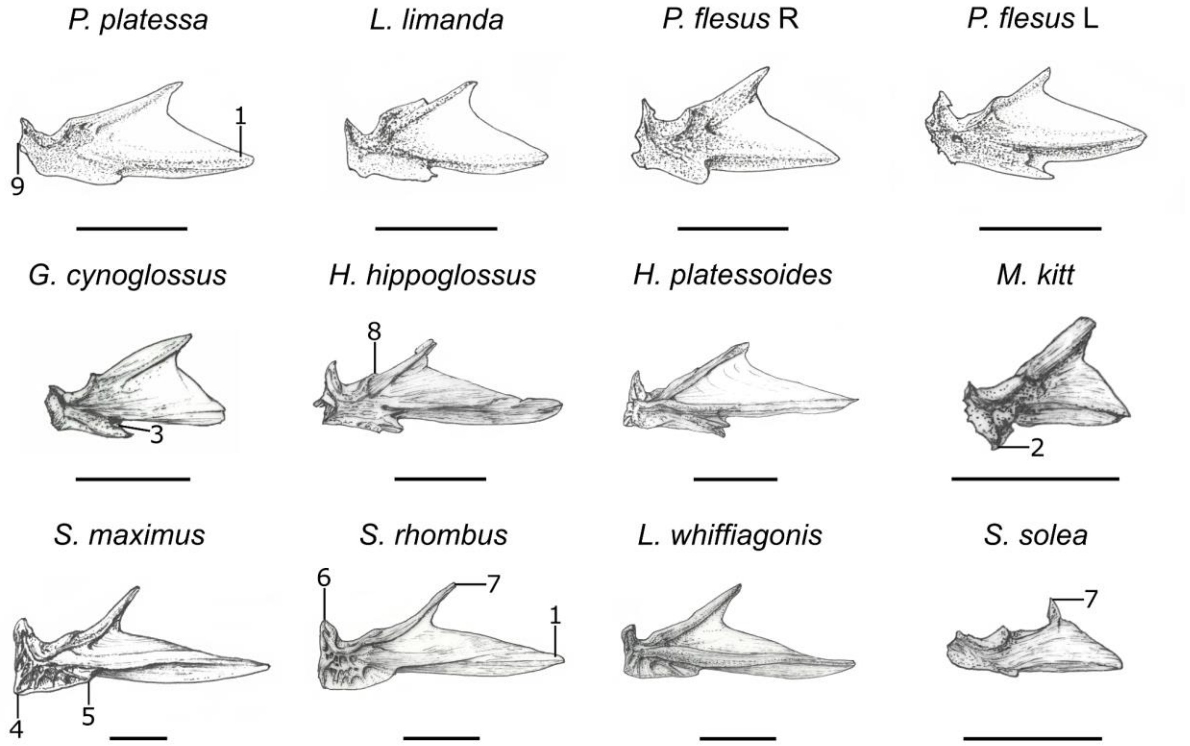


Figure 3.8. Lateral view of the right articular of all twelve species. The black bar under each species represents 1 cm.

3.3.1.5 Hyomandibula

The hyomandibula is situated behind the eye at the neurocranium and supports the jaw system as well as the articulation of the operculum. The hyomandibula has a caput dorsally with three processus: pr. articularis sphenoticus anteriorly, pr. articularis pteroticus dorsally, and pr. articularis opercularis posteriorly. On the ventral side there is a long processus inferior. Laterally along the length of the hyomandibula there is a crista preopercularis. On the anterior side, the crista anterior is implanted below the pr. a. sphenoticus. Foramen are possible on the hyomandibula on the posterior and medial sides, as part of the canalis hyomandibularis. When viewed laterally, the crista anterior is on the left side in the left hyomandibula and on the right side in the right hyomandibula.

The lateral view of the left hyomandibula is given in figure 3.9. The right hyomandibula (figure 3.10) shows similar criteria to distinguish species as the left, although relative proportions differ. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species for the left hyomandibula (table B10; figure B7) and the right hyomandibula (table B11; figure B8). This bone allows easy identification to all genera. *Microstomus kitt* differs from all other species by having a concave processus articularis (pr. a.) pteroticum (1) and a very short and wide processus articularis opercularum (2). The processus articularis sphenoticum (3) is as wide as the tip of the processus inferior and the small crista anterior (4) attaches about halfway the processus inferior (5) in *S. solea*. In *Scophthalmus* sp., *H. platessoides*, and *H. hippoglossus* the posterior tip of pr. a. pteroticum is lower than or of similar height as the posterior tip of pr. a. sphenoticum, while in *L. whiffiagonis*, *G. cynoglossus*, *L. limanda*, *P. platessa*, and *P. flesus* the anterior tip of the pr. a. pteroticum is higher than the posterior tip of the pr. a. sphenoticum. *Hippoglossus hippoglossus* has a very long posterior part of the caput (6) and a very slender crista anterior that doesn't reach further than the pr. a. sphenoticum or only slightly. The crista anterior reaches clearly further than the pr. a. sphenoticum in *H. platessoides* and *Scophthalmus* sp. *Hippoglossoides platessoides* differs from *Scophthalmus* sp. by having a long pr. a. opercularis. The anterior tip of the pr. a. pteroticum is higher than the posterior tip in *H. platessoides* and of the same height in *Scophthalmus* sp. *Scophthalmus rhombus* and *S. maximus* differ slightly but show a lot of overlap, making identification of these species difficult. *Lepidorhombus whiffiagonis* has a characteristically slender hyomandibula, with a crista anterior that barely reaches further than the level of the pr. a. sphenoticum. *Glyptocephalus cynoglossus* is characterised by having a large foramen (7) posterior of the crista preopercularis (8) below the caput. The crista (9) between pr. a. pteroticum and pr. a. opercularum is slenderer than pr. a. pteroticum in *L. limanda*, while as wide as pr. a. pteroticum in *P. platessa* and *P. flesus*. The former species also has a slenderer appearance compared with the two latter species. *Pleuronectes platessa* is difficult to distinguish from *P. flesus*, although the transition (10) between pr. a. opercularum and pr. inferior is somewhat deeper (in the left) or narrower (right) in *P. platessa* than in *P. flesus* and *P. flesus* can show a dorsal constriction in the middle of the pr. a. pteroticum. Right-eyed and left-eyed *P. flesus* can not confidently be distinguished, although subtle differences might be present.

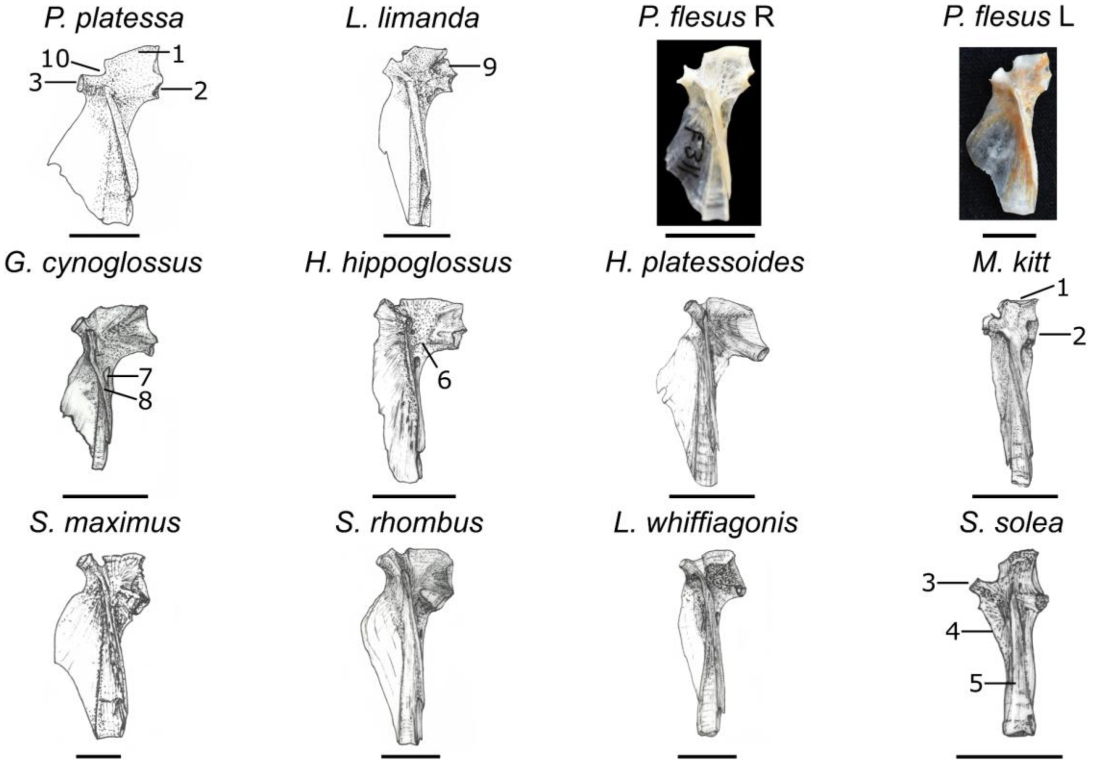


Figure 3.9. Lateral view of the left hyomandibula of all twelve species. The black bar under each species represents 1 cm.

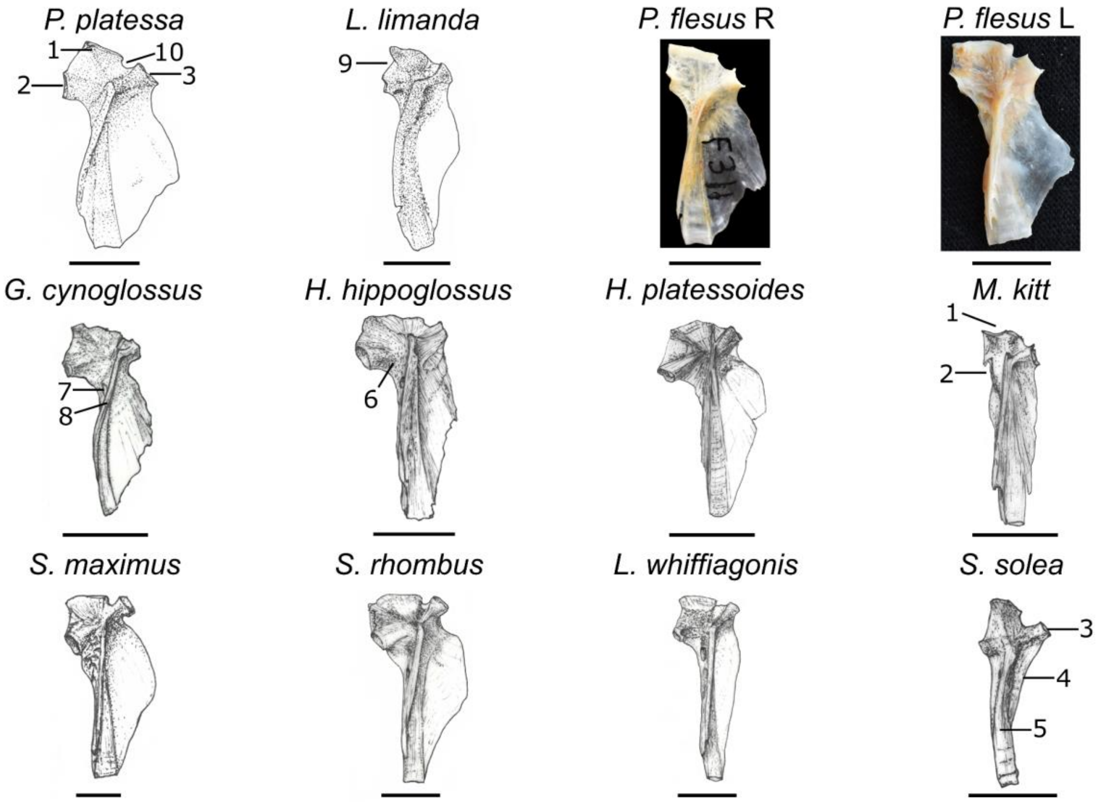


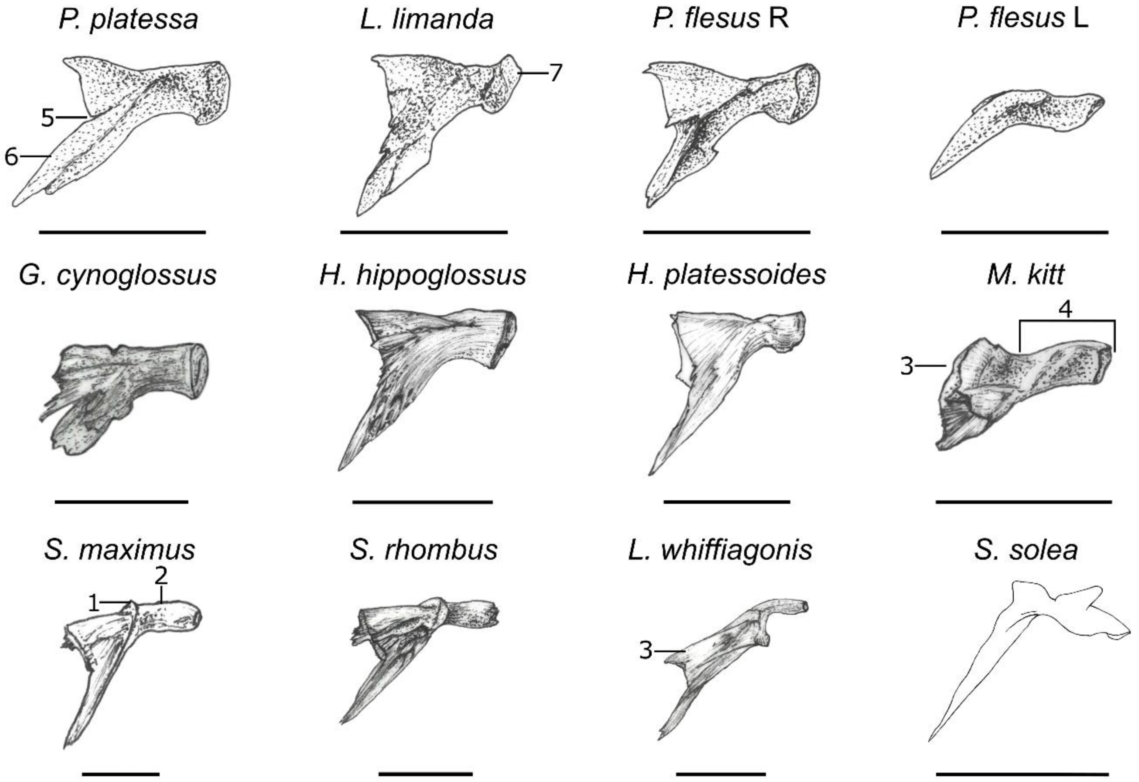
Figure 3.10. Lateral view of the right hyomandibula of all twelve species. The black bar under each species represents 1 cm.

3.3.1.6 Palatine

The palatine lies at the anterior part of the neurocranium above the upper jaw. It has no teeth in Pleuronectiformes. It has a caput and collum anteriorly, that can show processus and tubercles and make up the processus maxilaris. The elongated ventral part of the palatine is the processus inferior, which is connected to the ectopterygoid. The broad thin crista at the posterior side is the pars hypopterygoidea. The left and right palatine differ strongly in shape. When viewed dorsally the caput is curved to the right in the left palatine and to the left in the right palatine.

The lateral view of the left palatine is given in figure 3.11. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species for the left palatine (table B12; figure B9). This bone allows easy identification to all the species. The left palatine of *S. solea* is very distinct and easily recognizable. Left-eyed *P. flesus* also has a distinct left palatine, which resembles the right palatine of the right-eyed *P. flesus*, but in mirror-image. Scophthalmidae have a dorsal transverse ridge (1) on the collum (2), which is absent in Pleuronectidae. The pars hypopterygoidea (3) is longer and slenderer in *L. whiffiagonis* compared to *Scophthalmus* sp. The dorsal transverse ridge is stronger in medial view in *S. maximus* than in *S. rhombus*. The pars hypopterygoidea is very short and the processus maxillaris (4) is relatively long and curved in *M. kitt.* The pars hypopterygoidae is very broad and short in *G. cynoglossus*. There is a slight indent (5) between the pars hypopterygoidea and the processus inferior (6) in *P. platessa* and *H. platessoides*, which is not the case in the other Pleuronectidae. The left palatine is broader in *P. platessa* than in *H. platessoides*. Right-eyed *P. flesus* has a long collum compared with *L. limanda* and *H. hippoglossus*. The caput

(7) of the processus maxillaris is clearly broader than the collum in *L. limanda*, while barely and more gradually broader in *H. hippoglossus*.



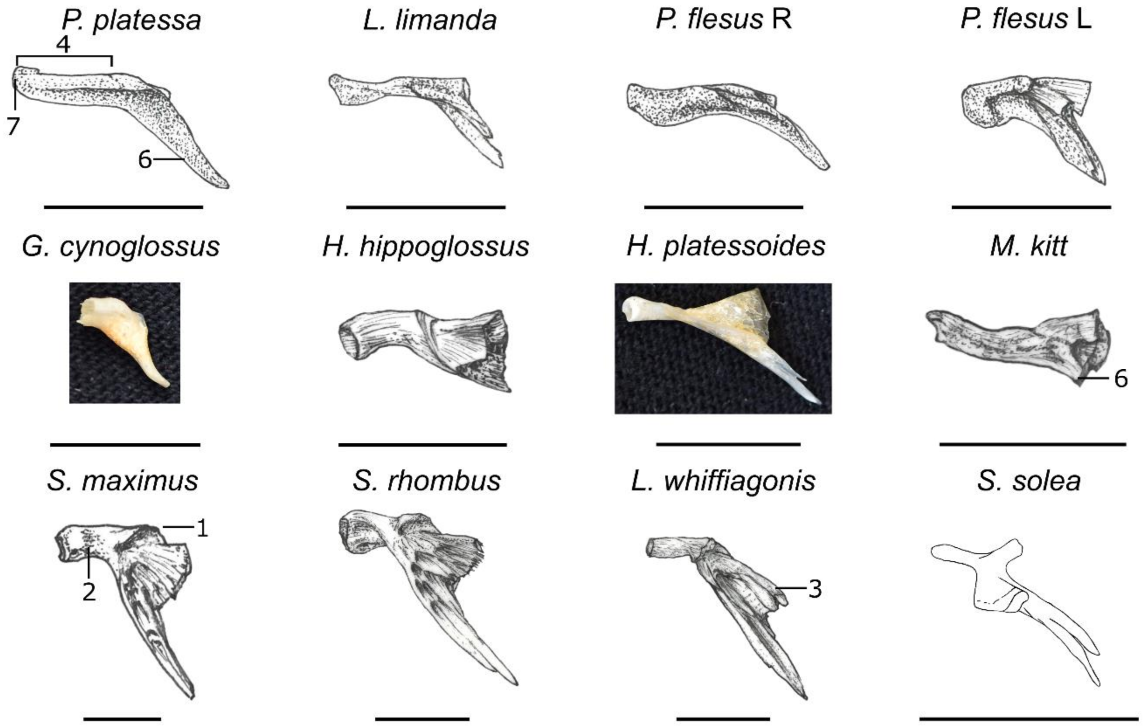
P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure 3.11. Lateral view of the left palatine of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the right palatine is given in figure 3.12. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species for the right palatine (table B13; figure B10). This bone allows easy identification to all the genera. The right palatine of *S. solea* and left-eyed *P. flesus* are unique in shape and cannot be confused with the other flatfish. Left-eyed *P. flesus* has a distinct right palatine, which resembles the left palatine of the right-eyed *P. flesus*, but in mirror-image. Scophthalmidae are characterised by having a clear dorsal transverse ridge (1) on the collum (2). The pars hypopterygoidea (3) is very long and slender in *L. whiffiagonis,* while shorter and broader in *Scophthalmus* sp. *Scophthalmus* sp. can barely be distinguished from each other. The right palatine of *M. kitt* has a very long collum and short processus inferior (6) and pars hypopterygoidea. *Glyptocephalus cynoglossus* has a thin palatine with a large foramen in the processus inferior. *Hippoglossus hippoglossus* differs from *H. platessoides, P. platessa, L. limanda* and right-eyed *P. flesus* by having a shorter and broader right palatine. *Hippoglossoides platessoides* differs from the latter three by the larger and higher pars hypopterygoidea, while this structure is low and not protruding much in the latter three species. The processus maxillaris (4) is rather straight and the tip (7) is rather broad in *P. platessa*, while it is more curved and the tip is slenderer in *L. limanda* and right-eyed *P. flesus*. The collum is broader in right-eyed *P. flesus* than it is in *L. limanda*.



P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure 3.12. Lateral view of the right palatine of all twelve species. The black bar under each species represents 1 cm.

3.3.1.7 Vomer

The vomer is the most anterior part of the neurocranium. It can have teeth in Pleuronectiformes. The dorsal part consists of two ventral bulbs with lateral/caudal wings or partes ethomoidales and are connected anteriorly. The bulbs usually have clear edges on the lateral and ventral sides. The caudal apophysis posterior connects the vomer to the neurocranium.

The ventral and sinistral lateral view of the vomer is given in figure 3.13. Additionally, the dorsal and dextral lateral view can be found in the appendix together with the detailed analysis for every species (table B14; figure B11. This bone allows easy identification to all the species. *Solea solea* has a characteristically very slender vomer with high ventral bulbs (1) and ventrally oriented partes ethmoidales (2). Scophthalmidae and Pleuronectidae have caudally oriented partes ethmoidales. A few alveoli (3) for teeth, visible in ventral view just under the top of the apical part (4), characterise the Scophthalmidae. *Scophthalmus* sp. have a higher right bulb and stockier apophysis posterior (5), while in *L. whiffiagonis* the bulbs are symmetrical and the apophysis posterior long and thin. Both *Scophthalmus* sp. can be distinguished by the dorsal structure (6) of the apical part in the dorsal view. *Scophthalmus maximus* has a strong ridge which ends in a clearly marked hook while in *S. rhombus* both are less expressive. Left-eyed *P. flesus* differs from all other Pleuronectidae by having the right bulb and pars ethmoidalis as the longest, instead of the left one. *Microstomus kitt* is distinct from the others through the unique shape with small partes ethmoidales (2), which extend in lateral direction, and pars praefrontalis (7). The partes ethmoidales and pars praefrontalis are very large in *H. platessoides* compared to the thin apophysis posterior (5). When looking from the front, *H. hippoglossus* has a wider than high vomer. The right bulb (8) is protruding laterally in *G. cynoglossus*, while in *P. platessa,* right-eyed *P. flesus* and *L. limanda* the bulb only protrudes slightly and more caudally. *Limanda limanda* has a much slenderer apex (4) compared to the width of the partes ethmoidales, than right-eyed *P. flesus* and *P. platessa*. The right bulb is more caudally oriented in right-eyed *P. flesus* than in *P. platessa* in which the left bulb (9) has a more anteriorly positioned frontal surface.

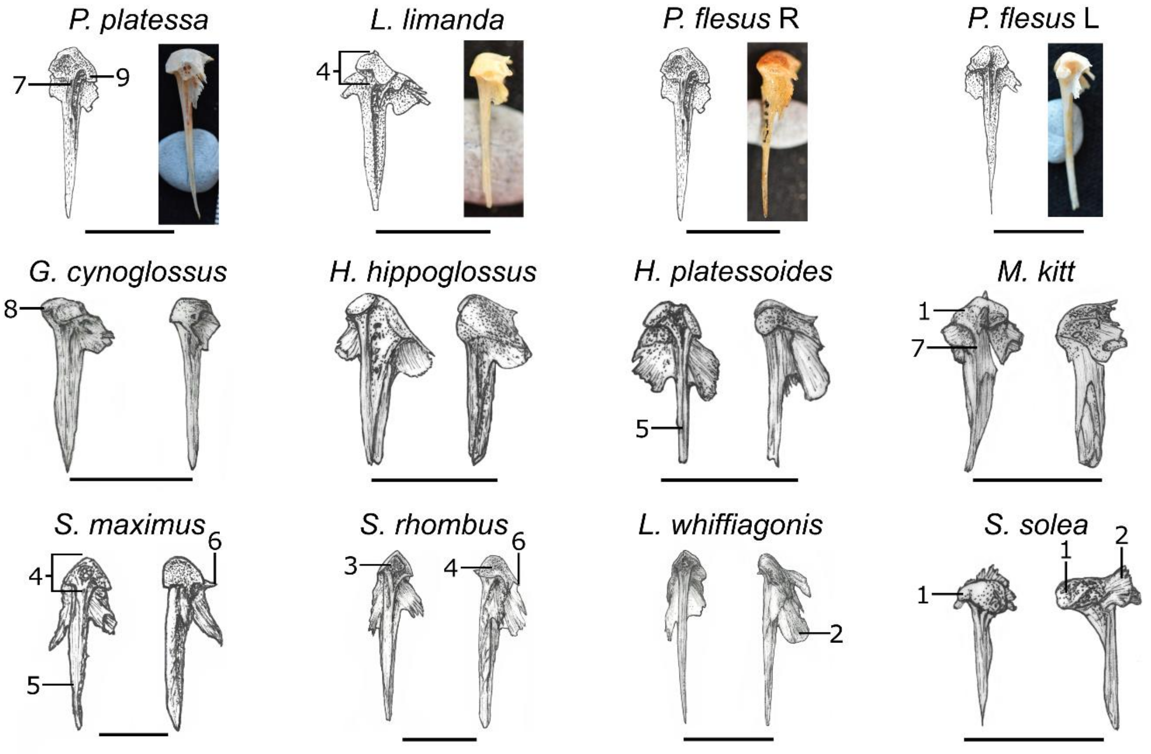
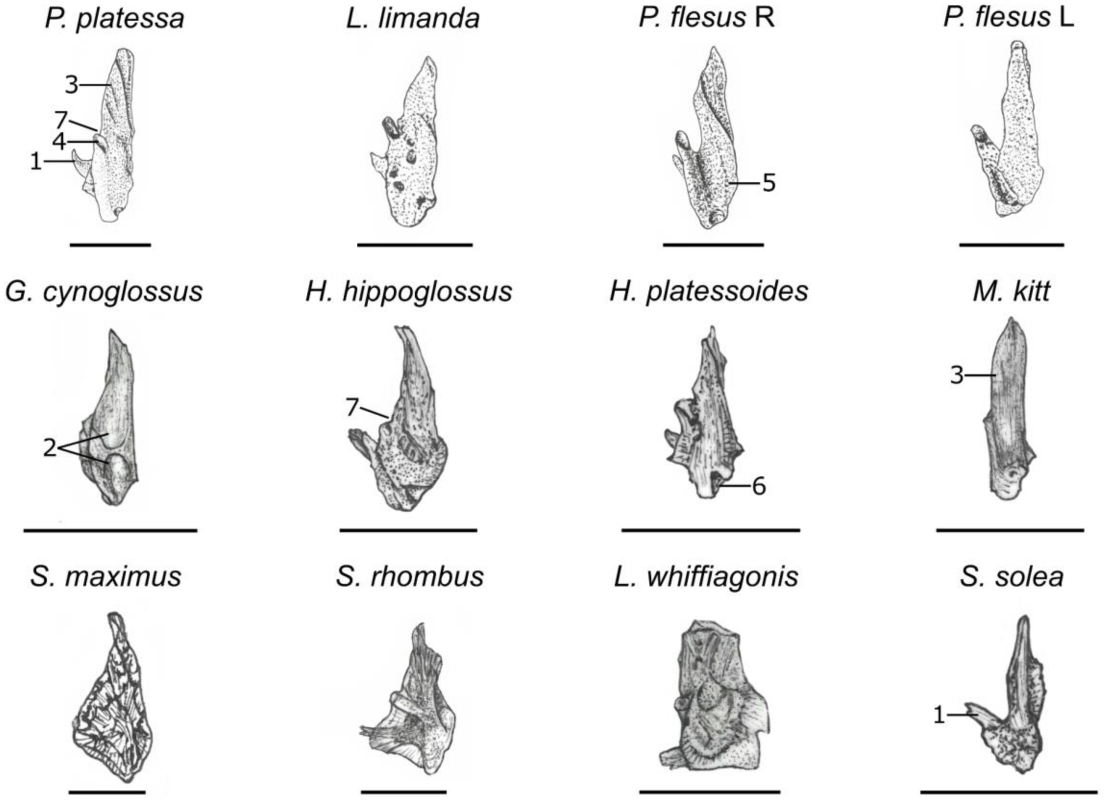


Figure 3.13. Ventral (left) and sinistral lateral (right) view of the vomer of all twelve species. The black bar under each species represents 1 cm.

3.3.1.8 Posttemporal

The posttemporal has three processus. Dorsally the processus superior is often long, rather flattened and sometimes curved. On the medial side in the middle of the corpus there are the processus medialis and processus inferior, which are implanted on the anterior side. On the lateral side, the canalis lineae lateralis is visible as two tubes. The caput is the most ventral part of the corpus. When viewed medially, the processus medialis is oriented right in the left posttemporal, and left in the right posttemporal.

The lateral view of the left posttemporal is given in figure 3.14. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B15; figure B12). This bone allows easy identification to all the species. A long processus medialis (1) is detached from the slender, straight corpus in *Solea solea*. Two large foramina (2) on the lateral side distinguish *Glyptocephalus cynoglossus* from all other species. Since the foramen are only separated by a small ridge, however, the bone might be less identifiable when the ridge is broken off, as could be the case in archaeologically preserved bones. *Microstomus kitt* has a straight posttemporal with a round processus superior (3) and without a processus inferior (4) nor a processus medialis. *Lepidorhombus whiffiagonis* has a characteristically round, broad and barely protruding processus superior. *Scophthalmus* sp. have a very flat and broad posttemporal with a heavily striated lateral side. Both *Scophthalmus* sp. can only be distinguished comparing bones of the same size. The processus medialis is always longer and thinner in *S. rhombus* than in *S. maximus*. Since this difference is difficult to assess and shows some variation, confident identification of these species is rarely possible. *Platichthys flesus* shows tubercles (5) along the lateral surface, which can be unclear in archaeological samples. Similar structures are present on other neurocranial bones in this species, which allows easy species identification (also see Enghoff, 1989). The tube incision (6) of the processus inferior on the lateral side is deep in *H. platessoides* and shallow in *H. hippoglossus, L. limanda* and *P. platessa*. The processus superior is slightly curved anteriorly and the incision (7) between the processus inferior and the corpus is very short in *H. hippoglossus*, while in *P. platessa* and *L. limanda* the processus superior is straight and the incision short and as deep as the processus inferior is long. The posttemporal is much slenderer in *L. limanda* than in *P. platessa* and also the processus superior is broader in *P. platessa* than in *L. limanda*.


P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure 3.14. Lateral view of the left posttemporal of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the right posttemporal is given in figure 3.15. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B16; figure B13). This bone allows easy identification to all the species. The characteristics to identify the species are similar as the ones for the left posttemporal, except for *H. hippoglossus, P. platessa* and *L. limanda*. The right posttemporal of *P. platessa* has a large bump (9) on the lateral side along the channel (8) on the right posttemporal, which is unique to this species; it is not present in the left posttemporal. The posttemporal is much slenderer in *L. limanda* than in *H. hippoglossus* and also the processus superior is broader and the incision between the processus inferior and the corpus shorter *H. hippoglossus* than in *L. limanda*.

Right- and left-eyed *P. flesus* cannot be distinguished, but there are subtle differences that show some overlap: in the left posttemporal the processus superior is slightly curved (the anterior side more medially oriented) in right-eyed *P. flesus* and straight in left-eyed *P. flesus*; in the right posttemporal, the opposite is found.

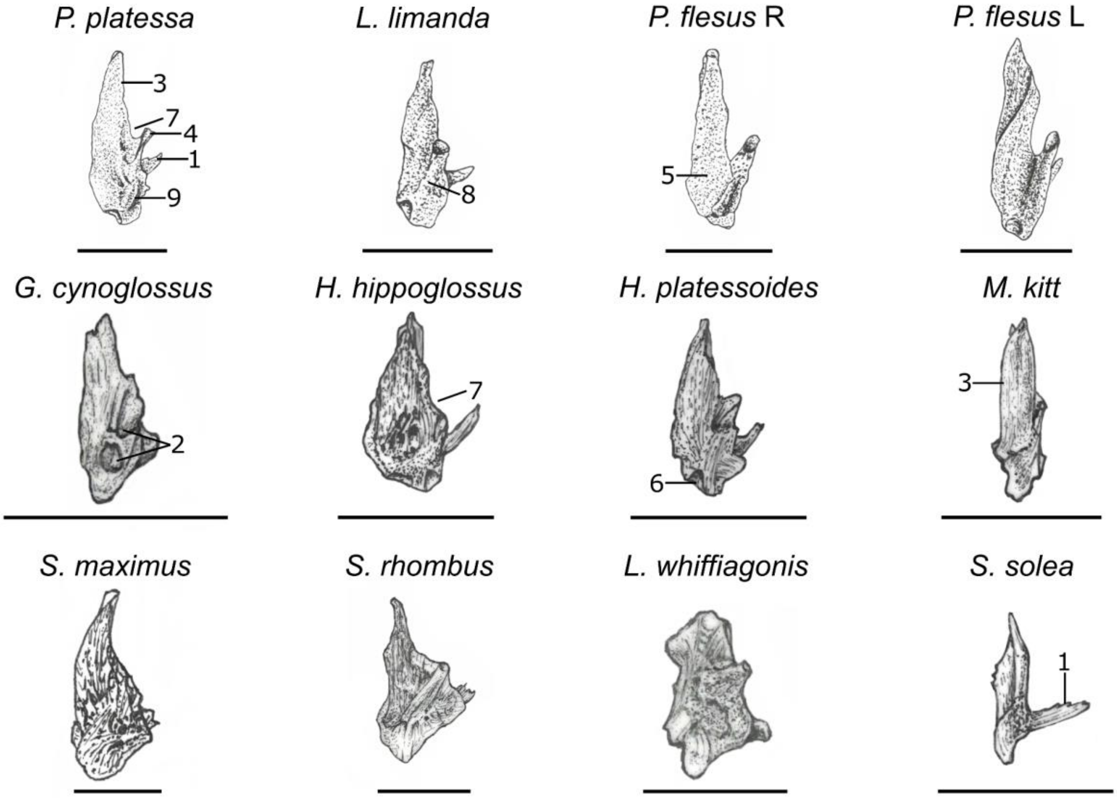

P. platessa · *L. limanda* · *P. flesus* R · *P. flesus* L · *G. cynoglossus* · *H. hippoglossus* · *H. platessoides* · *M. kitt* · *S. maximus* · *S. rhombus* · *L. whiffiagonis* · *S. solea*

Figure 3.15. Lateral view of the right posttemporal of all twelve species. The black bar under each species represents 1 cm.

3.3.1.9 Urohyal

The urohyal is an unpaired bone that can be L- or U- shaped around the incisura collis. The urohyal has two angulus, angulus inferior and processus hypohyalis, that both can have a thicker edge and a crista. The posterior caput is usually flat laterally but can have lateral cristae (crista lateralis).

The lateral view of the urohyal is given in figure 3.16. Additional descriptions can be found in the appendix (table B17). This bone allows easy identification to all the genera although there is no distinction possible between right-eyed and left-eyed *P. flesus*. *Solea solea* has a distinct L-shape with slender angulus inferior (1) while *L. whiffiagonis* is distinct from other flatfish through the lack of a clear and deep incisura collis (2). *Scophthalmus* sp. and *M. kitt* can also easily be differentiated from Pleuronectidae and Soleidae by the parallel position of processus hypohyalis (3) and the angulus inferior (1). In *M. kitt*, the length of the incisura collis (2) is equal to the height of the bone while in both *Scophthalmus* sp. it is very elongated. The distinction between these two species is difficult to make. *Glyptocephalus cynoglossus* can be distinguished from other Pleuronectidae by the long length of the caput (4). *Hippoglossus hippoglossus* and *H. platessoides* have processus hypohyalis (3) that are twice as long as the width of the crista angulus inferior (5), while *P. platessa*, *P. flesus* and *L. limanda* all have a processus hypohyalis that is about as long as or slightly longer than the crista angulus inferior. Compared with *H. hippoglossus*, *H. platessoides* is much thinner, and can have a slightly ventrally curved angulus inferior (1). The angulus inferior and processus hypohyalis are almost parallel in *L. limanda*. The tip of the angulus inferior is curved ventrally in *P. flesus*, while it is straight or slightly posterior in *P. platessa*.

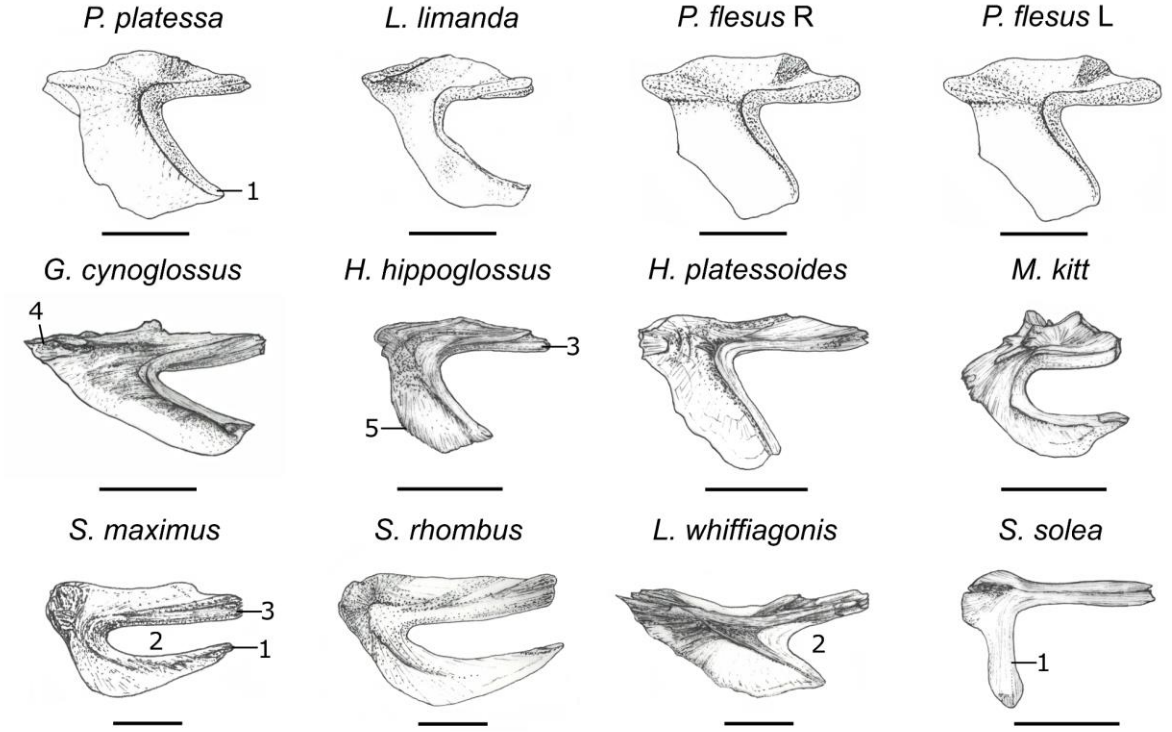


Figure 3.16. Dextral lateral view of the urohyal of all twelve species. The black bar under each species represents 1 cm.

3.3.1.10 First precaudal vertebra

The first vertebra connects the spine to the neurocranium. The center has two anterior condyli on its dorsal side that connect to the basioccipital. There is a neural arch that can have zygapophyses protruding from it.

The anterior and lateral view of the first precaudal vertebra is given in figure 3.17. Additional descriptions of the first precaudal vertebra are summed up in the appendix (table B18). This bone allows easy identification to species but differentiation between right-eyed and left-eyed *P. flesus* is not possible. *Solea solea* is easily distinguished by the lack of a complete neural arch (1), which should not be confused with broken neural arches in other species when dealing with archaeological material, and of pre-(2) and post-(3) zygapophyses on the neural arch. In *Scophthalmus* sp. the condyli (4) protrude dorsally and lie against each other diagonally, while in Pleuronectidae and *L. whiffiagonis* there is usually a clear or a slight distance between the rather horizontally or slightly diagonally condyli. The length of the corpus (5) in lateral view is much larger in *S. rhombus* compared to *S. maximus*. The edge of the condyli protrude dorsally in *H. platessoides*, but not in the other Pleuronectidae. *Microstomus kitt* has a horizontally flat dorsal edge of the center (6), while this is curved in other flatfish. *Hippoglossus hippoglossus* can be distinguished by having condyli that are sometimes shaped like an 8 with the lateral lobes being broader than the medial lobes and a very broad neural arch. *Lepidorhombus whiffiagonis* has an anteriorly curved neural arch. *Glyptocephalus cynoglossus* has laterally strongly protruding condyli. *Pleuronectes platessa*, *L. limanda* and *P. flesus* differ from each other by the implantation of the neural zygapophyses and the shape of the neural arch and condyli as mentioned in Wouters *et al.* (2007).

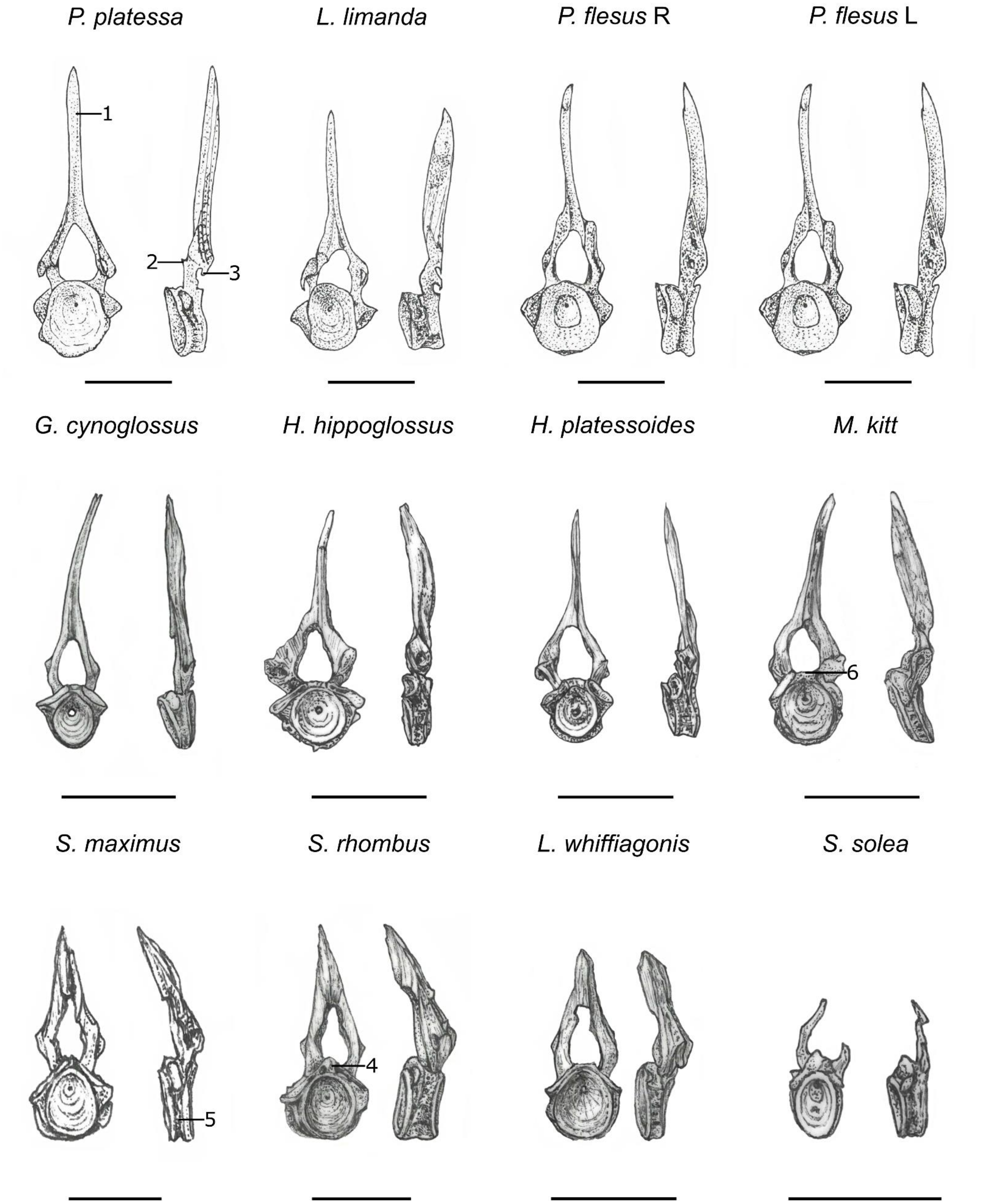


Figure 3.17. Anterior (left) and sinistral lateral (right) view of the first precaudal vertebra of all twelve species. The black bar under each species represents 1 cm.

3.3.2 Elements that allow clear differentiation of families and some species

The following elements can be used to identify families and several species, although some species can not be confidently distinguished from others without using a reference collection or careful consideration of the diagnostic criteria.

3.3.2.1 Metapterygium

The metapterygium is a thin bone situated between the hyomandibula, the quadrate and the eye. It has a rather square or round shape. It has an articulation tube on the anterior side to the quadrate. The posterior side sometimes has a protruding processus ventralis, while on the dorsal side a processus dorsalis can be seen as a broad or slender and pointed protrusion. The corpus sometimes has slightly thicker bone that can have a slight ridge on the lateral side. In lateral view, the articulation is on the left side in the left metapterygium and on the right side in the right metapterygium, although siding can be very difficult due to the subtle or lack of clear differences between the medial and lateral sides. Often the lateral side is slightly more convex and the medial side more concave.

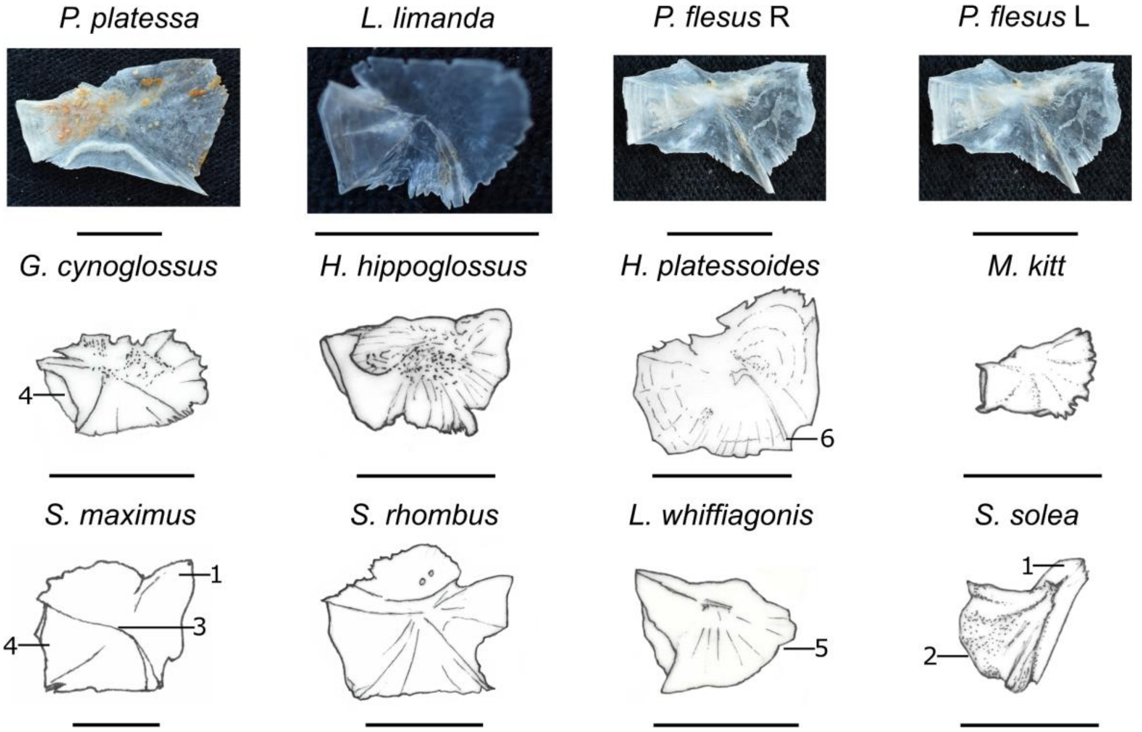


Figure 3.18. Lateral view of the metapterygium of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the left metapterygium is given in figure 3.18. Additional descriptions can be found in the appendix (table B19). This bone allows easy identification to all the species. Left and right metapterygium are similar and show the same diagnostic features, so only the left element is illustrated. Because the metapterygium is very thin and fragile, however, recovering this bone might be problematic. Metapterygia of small fishes cannot be identified to species, because they lack clear details in the bone. The metapterygium from *S. solea* has a triangular shape thanks to the pointed processus dorsalis (1) and the semi-circular margo inferior (2), which articulates with the quadrate. *Microstomus kitt* has a slender margo inferior and a strongly ossified appearance. In *Scophthalmus* species the processus dorsalis protrudes strongly, while it is protruding only slightly or barely in Pleuronectidae and *L. whiffiagonis*. *Scophthalmus* species can be distinguished due to the proportionally more ossified texture of the corpus (3) in *S. maximum* compared to *S. rhombus,* although this characteristic is prone to subjective interpretation. The metapterygium of *Lepidorhombus whiffiagonis* is very transparent and only the dorsal border of the tube (4) is a bit more ossified than the corpus. The posterior margo (5) is semi-circular in shape and lower than the anterior part. The posterior part is usually higher than the anterior part in Pleuronectidae, except in *H.*

hippoglossus and *G. cynoglossus* where both sides are of similar height. The metapterygium of *H. hippoglossus* is squarish in shape and doesn't show much texture. The surface is ossified and striated. *Hippoglossoides platessoides* and *G. cynoglossus* have a very weakly delineated tube. The tube is longer than high in the former species and as long as high in the latter. The anterior tube is longer than high in *P. platessa* and about as high as long in *L. limanda* and *P. flesus*. The processus ventralis (6) is long in *P. flesus* and short in *L. limanda.* Differentiation between right- and left-eyed *P. flesus* seems impossible.

3.3.2.2 Basioccipital

The basioccipital is the posterior ventral bone of the neurocranium and articulates with the first vertebra. Ventrally it has a groove with two ridges, called the facies articularis parasphenoidalis. Laterally it has 2 crista, crista lateralis dextra and c.l. sinistra. Dorsally, there can be a short or long ridge, the articularis dorsalis.

The ventral, lateral and caudal views of the basioccipital are given in figure 3.19. Additional descriptions can be found in the appendix (table B20). This bone allows easy identification to all the genera. *Solea solea* is characterised by having high and round ventral condyli (1). *Hippoglossus hippoglossus* is very recognisable by the very wide and shallow facies articularis parasphenoidalis (2). *Microstomus kitt* is the only species with parallel running borders (3) of the facies articularis parasphenoidalis and a very high basioccipital with dorsally oriented lateral cristae (4). The facies articularis parasphenoidalis is much wider near the facies articularis vertebralis (5) in the Scophthalmidae than in the Pleuronectidae. The anterior prolongation of the facies articularis parasphenoidalis extends much farther than the anterior part of the lateral crista in Scophthalmidae than in Pleuronectidae. Criteria to distinguish *L. whiffiagonis* from both *Scophthalmus* species were not found. Slight differences were noticed, but their diagnostic value is unsure. The lateral cristae of the basioccipital extend slightly broader in *L. whiffiagonis* than in both *Scophthalmus* species. *Scophthalmus* sp. show differences in the shape of the lateral cristae and the shape of the facies articularis vertebralis, but are difficult to distinguish. Two bony ridges (6) close to the facies articularis vertebralis are characteristic for *G. cynoglossus*. The lateral cristae protrude ventrally beyond the corpus of the basioccipital in *H. platessoides* (not clear on illustration). This species is also characterised by a stronger widening of the facies articularis parasphenoidalis anteriorly. The lateral cristae widen strongly anteriorly and the facies articularis parasphenoidalis is broad in *L. limanda*, while the wings barely widen and the facies is rather slender in *P. platessa* and *P. flesus*. The latter two species differ by the relative height and orientation of the lateral cristae, but this characteristic is difficult to assess. There is no difference between right-eyed and left-eyed *P. flesus*.

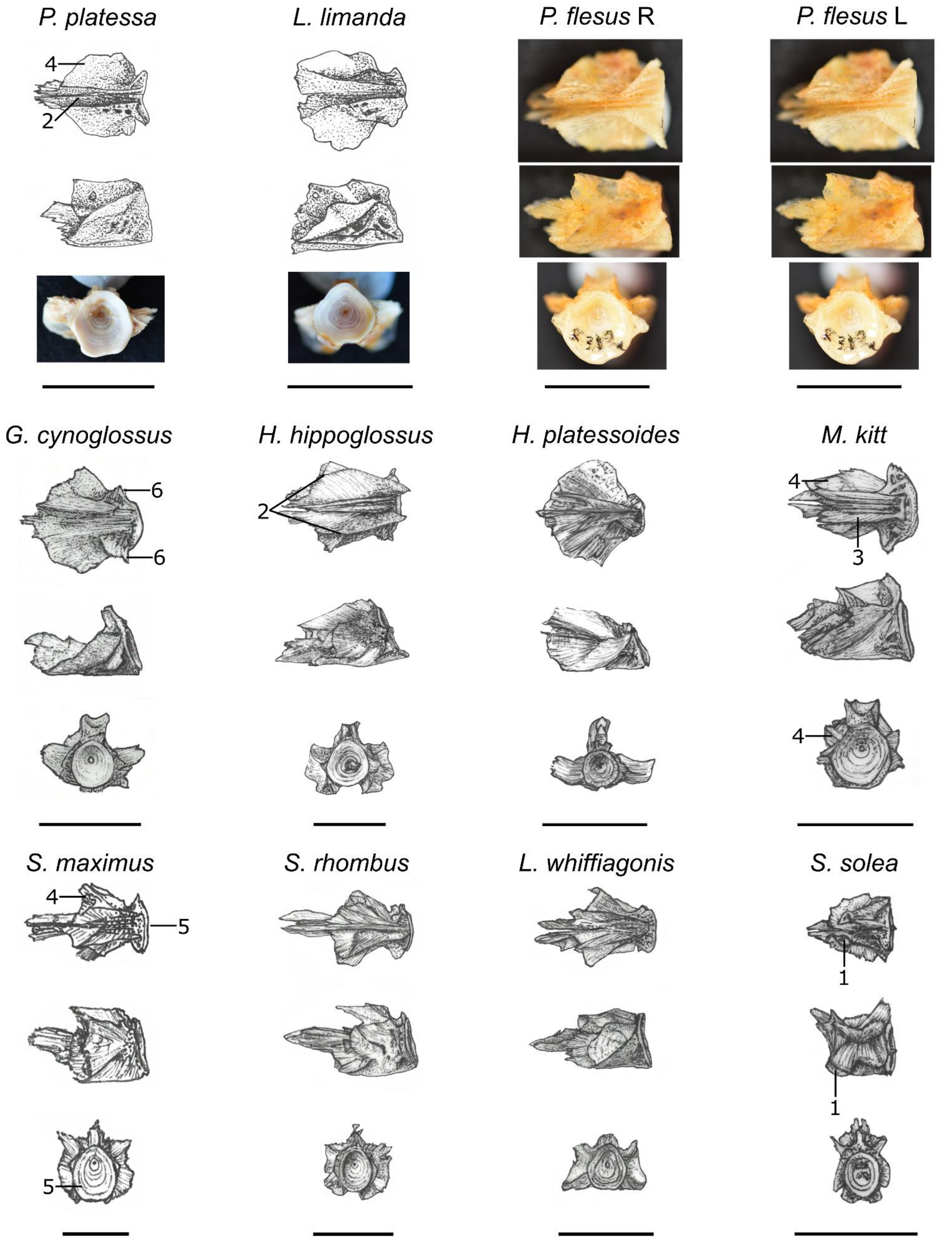


Figure 3.19. Ventral (top), sinistral lateral (middle), and posterior (bottom) view of the basioccipital of all twelve species. The black bar under each species represents 1 cm.

3.3.2.3 Cleithrum

The cleithrum is a large bone that is part of the pectoral girdle. On the dorsal part of the bone is a processus dorsalis implanted on the angulus superior. The anterior part of the cleithrum is the angulus anterior. The dorsal and medial parts of the angulus anterior are, respectively the lamina dorsalis and lamina medialis, that are joined dorsally but have separate margo inferiors. When viewed laterally, the angulus anterior points to the left in the left cleithrum and to the right in the right cleithrum.

The lateral and caudal view of the left cleithrum is given in figure 3.20. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B21; figure B14). This bone is often found in archaeological assemblages and is very useful in distinguishing species. *Pleuronectes platessa* and often left-eyed *P. flesus* and sometimes right-eyed *P. flesus* are easily distinguished from the other species by having a deep and broad indent (1) at the corner (2), which is also very broad. These two species are however difficult to distinguish. The cleithrum of *S. solea* doesn't have a clear crista articularis (3) and its processus dorsalis (4) has two tips. In the Pleuronectidae, the margo anterior (5) is thick while the margo posterior (6) is thin. In the Scophthalmidae, both the margo anterior and posterior are thin, surrounding a thick and broad rib (7) in the corpus. In *L. whiffiagonis* the lamina medialis (8; also see appendix for medial view) is sometimes clearly visible from the lateral side and the anterior crista of the angulus superior very broad. The anterior crista of the angulus superior is rather slender in *Scophthalmus* sp. The depression (9) in the lamina dorsalis (10) is almost invisible or very shallow in *S. rhombus*, while clearly outlined in *S. maximus*. The use of this characteristic needs to be checked on reference bones of the same size. In *M. kitt* the corner is very broad, but has no indent. This species also has a flat angulus anterior (11) tip, a deep medial impressio supracleithralis on larger specimens (12; also see appendix for medial view), a strongly ossified margo anterior of the angulus superior, and a short angulus superior. *Hippoglossus hippoglossus* has a shallow indent at the lamina dorsalis, a very thick medial side of the angulus superior, and a striated texture of the surface. *Hippoglossoides platessoides* and *L. limanda* have a slender corner and a lamina medialis that does not reach the tip of the angulus anterior. The former species has a slightly smaller angle (13) between the anguli and a medially placed ventral groove (14). The latter species has a slightly larger angle between the angulis and a rather centrally place ventral groove. *Platichthys flesus* and *G. cynoglossus* have a lamina medialis that reaches the tip of the angulus anterior and have a broad corner. The former species has a broader lamina dorsalis, a rather low lamina medialis, a rather slender ventral groove, and a rather broad tip on the processus dorsalis. The latter species has a slenderer lamina dorsalis, a high lamina medialis, a broad ventral groove, and a slender tip on the processus dorsalis. Convincing arguments to distinguish between right-eyed and left-eyed *P. flesus* were not found.

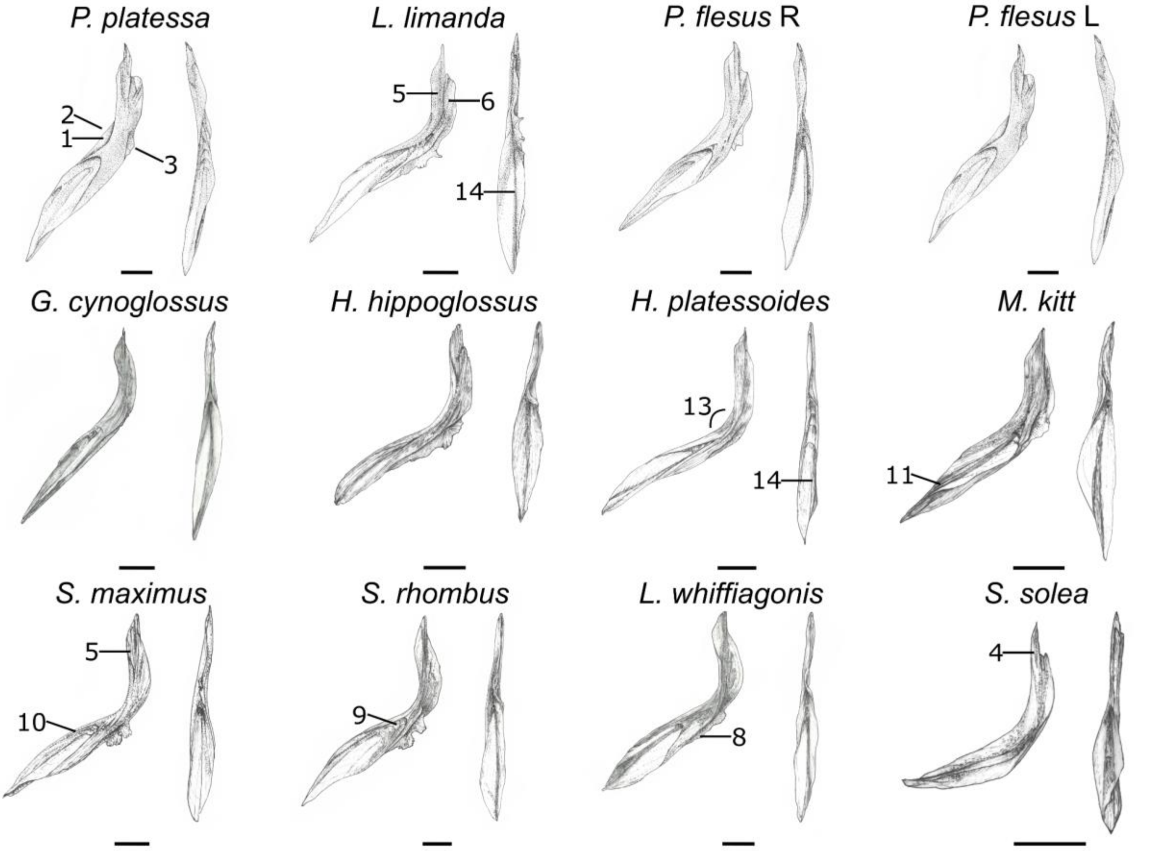


Figure 3.20. Lateral (left) and ventral (right) view of the left cleithrum of all twelve species. The black bar under each species represents 1 cm.

The lateral and caudal view of the right cleithrum is given in figure 3.21. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B22; figure B15). This bone distinguishes most of the species. The criteria described for the left preopercular are similar for the right in the following species: *P. platessa, S. solea, L. whiffiagonis, S. maximus, S. rhombus, M. kitt, H. hippoglossus, H. hippoglossoides,* and *L. limanda*. *Platichthys flesus* differs from the other remaining Pleuronectidae by having a broad bone and often an indent at the corner, while the others have no or only a slight indent and a usually slender corner. Convincing arguments to distinguish between right- and left-eyed *P. flesus* were not found. *Glyptocephalus cynoglossus* can, however, have a rather broad corner and differs from *H. platessoides* and *L. limanda* by having a lamina medialis that reaches the tip of the angulus anterior, while the latter two species have a slender corner and a lamina medialis that does not reach the tip.

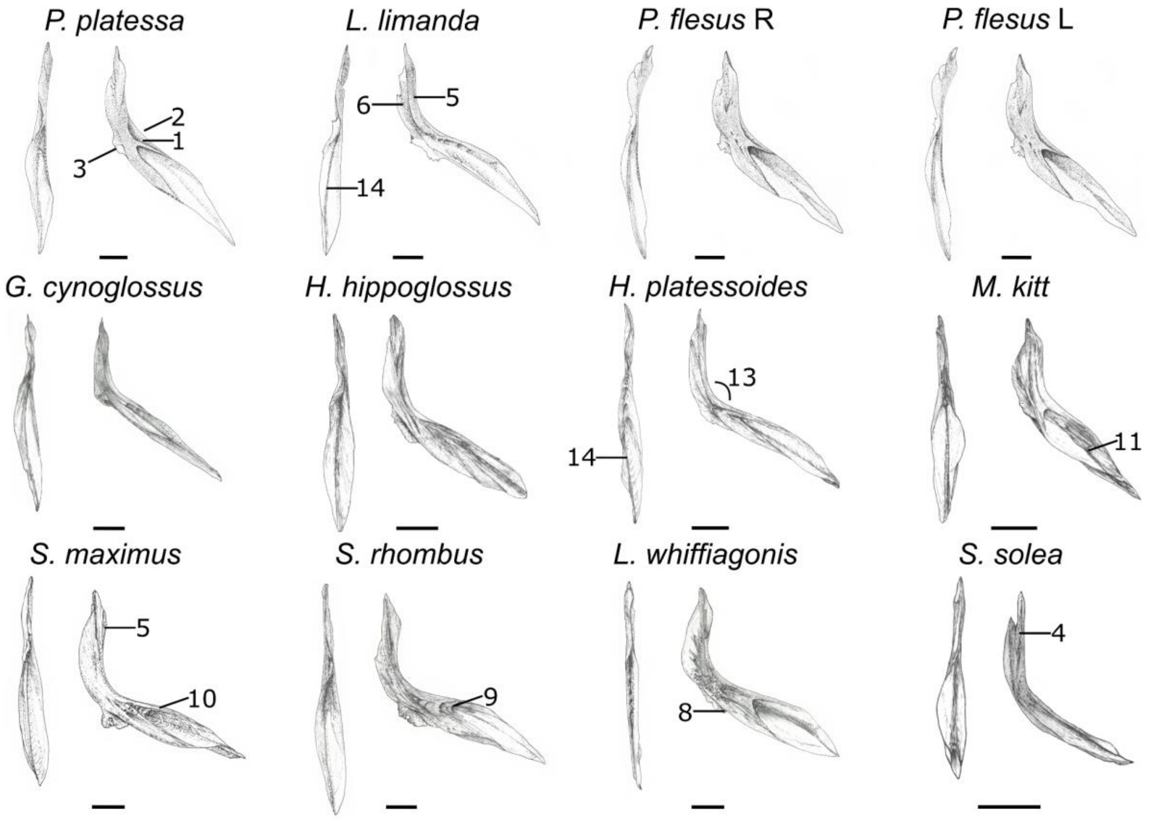


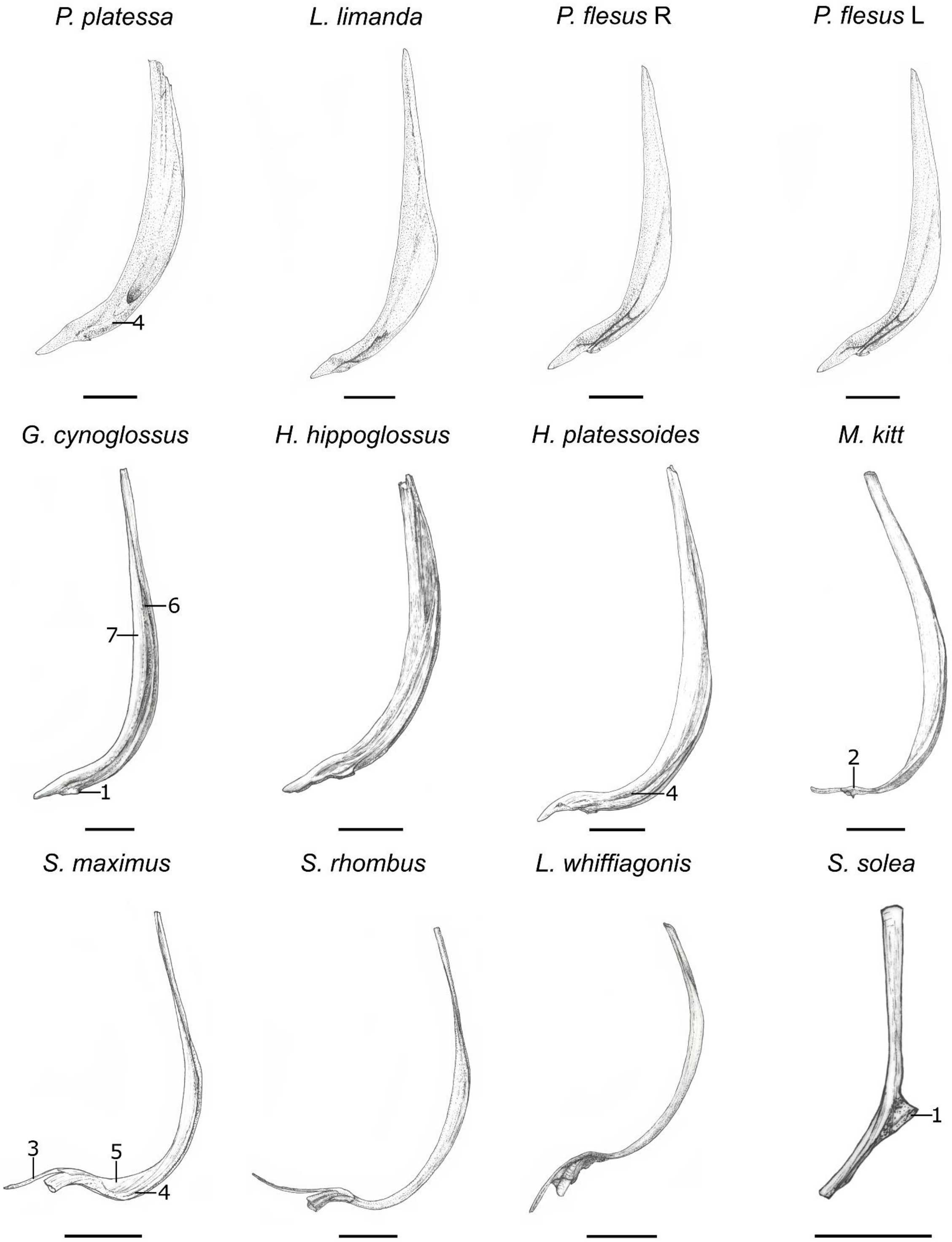
Figure 3.21. Lateral (right) and ventral (left) view of the right cleithrum of all twelve species. The black bar under each species represents 1 cm.

3.3.2.4 Os anale

The os anale is the first, enlarged, pterygiophore of the anal fin. It usually has a L- or J-shape, with the anterior part the angulus anterior and the upper part the angulus superior. The angulus anterior can be enlarged near the corner or neck. Sometimes there are striations on the neck and the rest of the bone. On its ventral side there can be an articulation. In some groups, the angulus anterior has an enlarged processus anteriorly. The posterior side of the os anale has often ridges on both sides. On the lateral side there is sometimes an indent, called the sulcus.

The lateral view of the os anale is given in figure 3.22. Additional descriptions of the os anale are summed up in the appendix (table B23). This bone allows easy identification to species but differentiation between right-eyed and left-eyed *P. flesus* is not possible. The anal bone of *S. solea* is rather straight with just a simple outcrop for the ventral articulation for the first ventral finray (1), looking very similar to its other pterygiophores. *Microstomus kitt* is the only species that has a flattened and wider than high angulus anterior (2), with a tube ending in a horizontal position. The angulus anterior has two bumps dorsally in *L. limanda*. In *L. whiffiagonis* and both *Scophthalmus* species, the articulation with the first finray has the shape of an open tube of which dorsally an anterior processus (3) is implanted. There are no lateral indentations (4) of the angulus anterior in *L. whiffiagonis*, and there are in *Scophthalmus sp*. *Scophthalmus maximus* has a dorsal crista (5) that is higher than the corpus of the angulus anterior, while in *S. rhombus* these structures have the same height. *Hippoglossus hippoglossus* has a ridge along the angulus anterior laterally, but no lateral indent (4), which is present in *P. platessa, P. flesus, G. cynoglossus* and *H. platessoides*. As seen ventrally, the width of the ventral articulation (1) of the angulus anterior is as wide as the corpus in *G.*

cynoglossus and *H. platessoides*, while it is slenderer than the corpus in *P. platessa*, and *P. flesus*. In *G. cynoglossus*, the posterior ridges (6) get broader and diverge slightly, making the posterior edge broader than the anterior edge of the angulus superior (7). In *H. platessoides* the posterior ridges remain slender and parallel, so both edges of the angulus superior have the same width. *Pleuronectes platessa* has long lateral indentations (4) while these are shorter in *P. flesus*.


P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure 3.22. Sinistral lateral view of the os anale of all twelve species. The black bar under each species represents 1 cm.

3.3.2.5 Quadrate

The quadratum is connected to the lower jaw and allows it to move. It is a thin and triangular or square shaped bone. The processus preopercularis is broader than the rest of the bones. At the ventral side of the processus there are two condyli, a lateral and a medial one. The crista has two margins, the anterior (margo ectopterygoidalis) and dorsal margin. Between the dorsal margin and the processus preopercularis there can be an incisura symplecti, which is usually deeper and more defined in the medial side. When viewed medially the processus preopercularis is on the left side in left quadrates and on the right in right quadrates.

The lateral and anterior view of the left quadrate is given in figure 3.23. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B24; figure B16). This bone allows identification to family and some species. The margo ectopterygoidalis (1) and margo posterior (2) have an almost equal length in *S. solea* which gives the bone a high and slender shape. *Microstomus kitt* is characterised by the combination of a short margo dorsalis (3), very large condyli (4) and a very broad margo ectopterygoidalis. In *Scophthalmus* sp. the margo ectopterygoidalis is two thirds the length of the margo posterior and the crista (5) is implanted in the middle of the processus preopercularis (6). There are no clear differences between *S. maximus* and *S. rhombus*, except that *S. maximus* has a proportionally more striated lateral surface of the crista, extending to the margo dorsalis. In *S. rhombus* this striation is only visible in the lower part of the bone. This characteristic is not clear in the quadrate of fishes with an SL of less than 25 – 30 cm SL. *Lepidorhombus whiffiagonis* is easily distinguishable by its slender appearance. In *H. hippoglossus* the transition (7) between the margo dorsalis and the processus preopercularis is smooth, straight and gradual, while deep or with a clear bend in the remaining species. *Hippoglossoides platessoides* is characterised by having a clear v-shaped bend between the condyli, while the other Pleuronectidae have a rounded bend between them. The difference between *G. cynoglossus* and *L. limanda*, *P. flesus* and *P. platessa* is subtle. The lateral condylus (8) is much larger than the medial (9) and more angular in shape in *G. cynoglossus*. In *L. limanda* the implant of the crista, which is also wider in this species, is rather in the middle instead of clearly laterally. Its margo dorsalis also reaches relatively higher on the processus preopercularis than in *P. flesus* and *P. platessa*. Right-eyed *P. flesus* and *P. platessa* have too many overlapping criteria and cannot be distinguished from each other. In right-eyed *P. flesus* and *P. platessa* the medial condyli is implanted a bit more ventrally as seen in the posterior view, while both condyli are implanted at equal level in the left-eyed *P. flesus*.

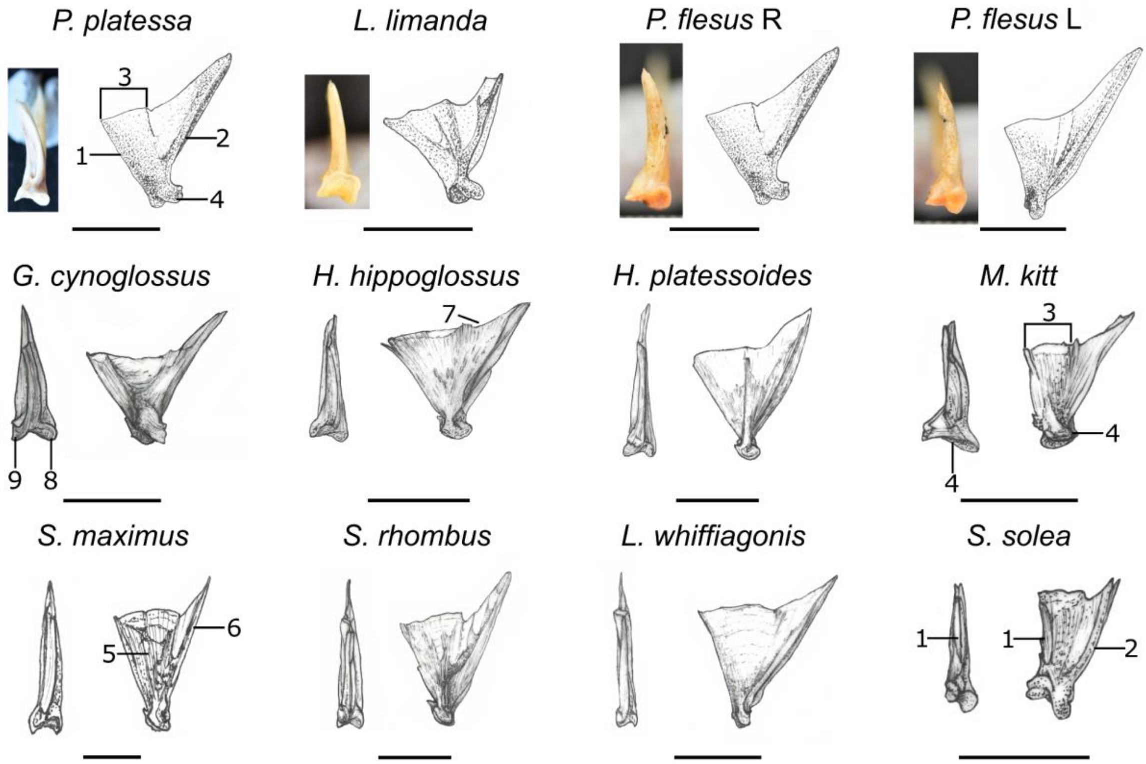


Figure 3.23. Lateral (right) and anterior (left) view of the left quadrate of all twelve species. The black bar under each species represents 1 cm.

The lateral and anterior view of the right quadrate is given in figure 3.24. Additionally, the medial view can be found in the appendix together with the detailed analysis for every species (table B25; figure B17). This bone allows identification to family and some species. The margo ectopterygoidalis (1) and the margo posterior (2) are short in *S. solea*, with proportionally large condyli (4). The diagnostic features are the same as in the left quadrate for the Scophthalmidae, *M. kitt, and H. hippoglossus*. The remaining species can be difficult to distinguish. *Hippoglossoides platessoides* is characterised by having very short condyli with a clear constriction in the middle of both condyli, while *P. flesus*, *G. cynoglossus*, *P. platessa* and *L. limanda* have long condyli with no clear constriction. The margo dorsalis (3) is shorter in length than the margo ectopterygoidalis in right-eyed *P. flesus* and *P. platessa,* longer in *G. cynoglossus* and left-eyed *P. flesus,* and similar in *L. limanda*. The margo posterior can also be more laterally curved around its axis than in the other species. Left-eyed *P. flesus* has a more posteriorly protruding lateral condylus (8) and a less curved margo ectopterygoidalis than *G. cynoglossus*. *Limanda limanda* differs from *P. platessa* and right-eyed *P. flesus* by having a higher margo dorsalis. Right-eyed *P. flesus* and *P. platessa* have too many overlapping criteria and cannot be distinguished from each other. In *P. platessa* the lateral condylus is a bit more posteriorly curved and the anterior edge of the lateral condylus is more defined and sharper compared with right-eyed *P. flesus*.

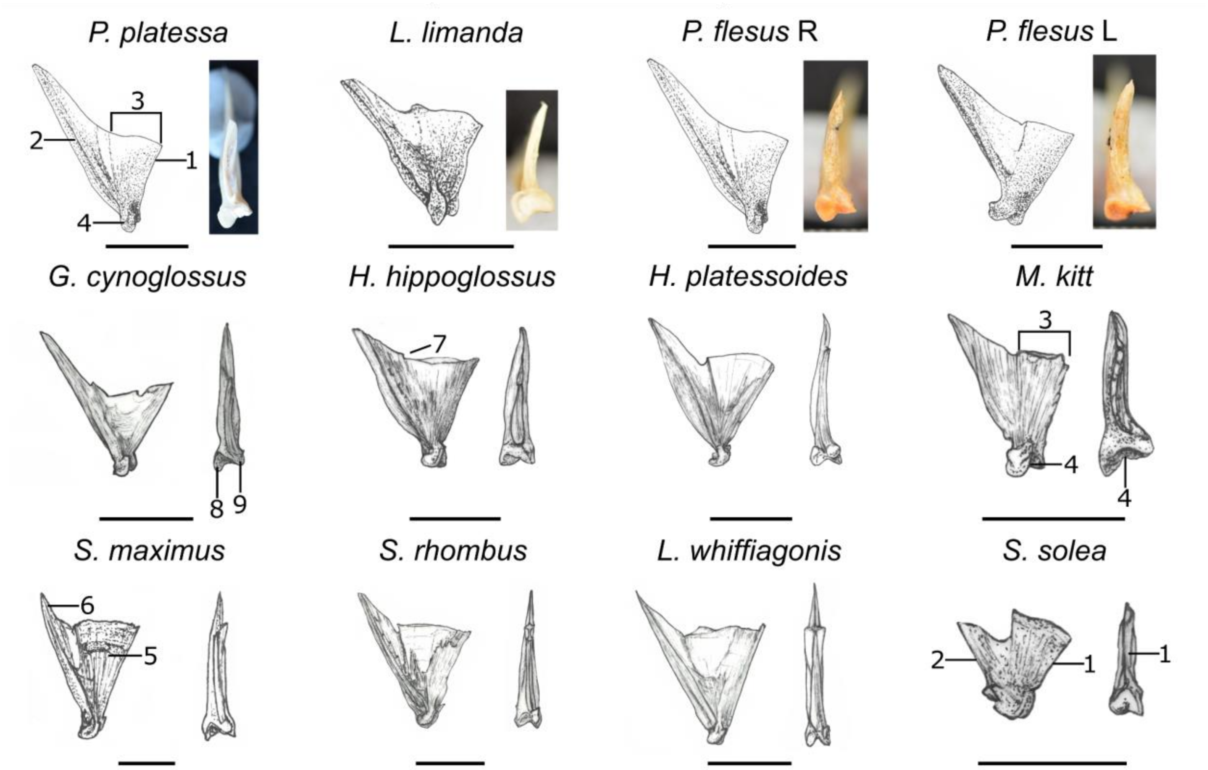


Figure 3.24. Lateral (left) and anterior (right) view of the right quadrate of all twelve species. The black bar under each species represents 1 cm.

3.3.2.6 Ectopterygoid

The ectopterygoid connects the quadrate with the upper jaw. It is L-shaped and consists of two crura, the crus anterius that connects to the palatine, and the crus posterius that connects to the margo anterior of the quadrate. Where the two crus join, there is an angulus dorsalis. When viewed laterally (non-hollow side; medial side visible on crus posterius), the angulus anterius points to the left in the left ectopterygoid and to the right in the right ectopterygoid.

The lateral view of the left ectopterygoid is given in figure 3.25. Additional descriptions of the left ectopterygoid are summed up in the appendix (table B26). This bone allows identification to genus, but identification for smaller bones is not feasible. Even in complete bones of larger fish, characteristics are not always that clear and are better identified at family level. *Solea solea* can easily be distinguished by the robust and thick crus posterius (1) and the clear groove between the medial and dorsal ridge of this crus and dorsal orientation of the angulus dorsalis (2). The crus posterius is short and very thick in *M. kitt* and the crus anterius (3) is also short. The fossa (4), marking the articulation with the palatine, is shallow. *Microstomus kitt* also has a smaller angle (5) between the crura compared to the other species. The crus posterius and the crus anterius are also shorter in *G. cynoglossus*, with the crus anterius shorter than the crus posterius. The fossa is bigger and the angle between the crura smaller in *G. cynoglossus* than in *M. kitt*. The crus posterius is only half the size of the crus anterius in *H. platessoides* while the angulus dorsalis is strongly reduced in this species. The three species of the Scophthalmidae are characterised by the fine and long crura and the deep fossa in the crus anterius. Both crura are thinner in *L. whiffiagonis* compared to an ectopterygoid of both *Scophthalmus* sp. of the same size. Differentiation between these last two species is impossible. The remaining species can be difficult to confidently identify, even when the ectopterygoid is complete, since many characteristics are prone to subjective interpretation. Left-eyed *P. flesus* can be identified from all species by the processus (6) at the base of the crus anterius (not visible on illustration). Right-eyed *P. flesus* has a slightly shorter crus anterius compared to *P. platessa, H. hippoglossus* and *L. limanda*. *Limanda limanda* has a slenderer appearance compared to *P. platessa, H. hippoglossus* and *P. flesus*. The crura are slightly broader and the fossa slightly deeper in *P. platessa* than in *H. hippoglossus*. *Hippoglossus hippoglossus* has a crus anterius that is relatively longer than the crus posterius compared to *P. platessa*.

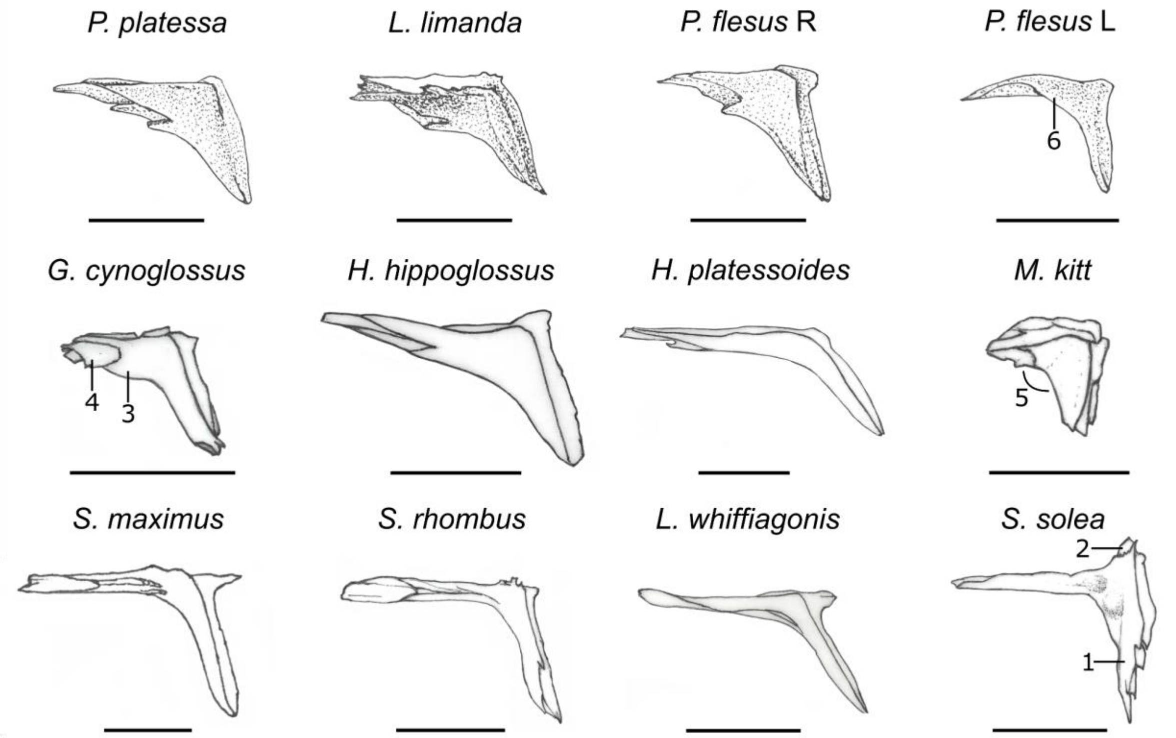


Figure 3.25. Lateral view of the left ectopterygoid of all twelve species. The black bar under each species represents 1 cm.

The lateral view of the right ectopterygoid is given in figure 3.26. Additional descriptions of the left ectopterygoid are summed up in the appendix (table B27). This bone allows identification to genus, but identification for smaller bones is not feasible. Even in complete bones of larger fish, characteristics are not always that clear and are better identified at family level. *Microstomus kitt* differs from all other species by the stocky and thick appearance and the strong reduction of both crura. *Solea solea* can easily be distinguished by the posterior extension (7) in the middle of the crus posterius (1). The blunt crus anterius (3) in *G. cynoglossus* is very short compared to the crus posterius. The long groove for the articulation with the palatinum (4) is typical for the right ectopterygoid in the Scophthalmidae, alongside the large angle (5) between the crura and the slender appearance. The crus anterius is only a bit longer than the crus posterior in *L. whiffiagonis*. These proportions change to far longer in both *Scophthalmus* sp. but both species cannot be distinguished from each other. The remaining species can be difficult to confidently identify, even when the ectopterygoid is complete, since many characteristics are prone to subjective interpretation. *Hippoglossoides platessoides* is characterised by having a long and slender appearance, slight lateral curvatures of the crura, and a reduced angulus dorsalis (2). *Hippoglossus hippoglossus* differs by the lack of a clear fossa and a thick appearance. Left-eyed *P. flesus* has no processus (6) at the base of the crus anterius, which is present in *P. platessa, L. limanda* and right-eyed *P. flesus*. *Limanda limanda* has a rather slender appearance compared to *P. platessa* and *P.*

flesus. *Pleuronectes platessa* has a slightly stockier (shorter and broader) crus posterius than *P. flesus*.

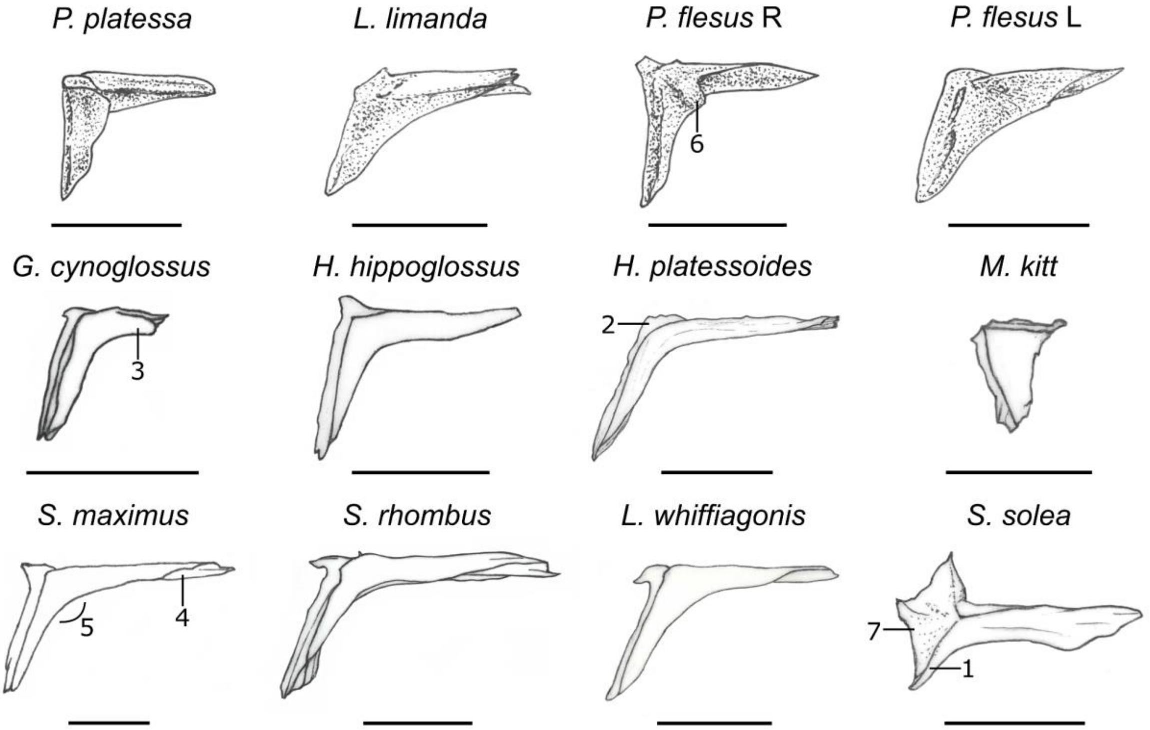


Figure 3.26. Lateral view of the left ectopterygoid of all twelve species. The black bar under each species represents 1 cm.

3.3.2.7 Preoperculum

The preoperculum lies anteriorly of the operculum. It is L-shaped. The upper part is the angulus superior and the anterior part the angulus anterior. On the lateral side and on the tips of both angulus foramen of the lateral line system are present. In the corner between the angulus a small processus s. limbus anterior can sometimes be seen. When viewed laterally, the angulus anterior is on the left side in the left preoperculum and on the right side in the right preoperculum.

The lateral and medial view of the left preoperculum is given in figure 3.27. Additional descriptions of the left preoperculum are summed up in the appendix (table B28). This bone allows easy identification to most species. *Glyptocephalus cynoglossus* differs from all other species by four large foramina (1) in lateral view. These foramina are rather small or absent in the other species. This element is very thick in *S. solea* and *M. kitt* compared to the width of the angulus. In *S. solea* the margo opercularis (2) bends smoothly into the margo interopercularis (3). In *M. kitt*, the transition between the margo opercularis (2) and the margo interopercularis (3) is sharp and makes a 90° turn. In Scophthalmidae the crista hyomandibularis (4) is as wide as the angulus superior (5), while in Pleuronectidae, it is wider. The angle between the angulus anterior (6) and superior exceeds clearly the 90° in *L. whiffiagonis.* This species also has a thinner bone in general than *Scophthalmus* sp. The base of the angulus anterior is always smaller in width in *S. rhombus*. The surface is proportionally always more striated in *S. maximus* than in *S. rhombus*. In *P. flesus* and *P. platessa* the angulus anterior is clearly longer than or of similar length as the angulus superior and clearly shorter in *H. hippoglossus, H. platessoides,* and *L. limanda. Hippoglossus hippoglossus* is characterised by having a wide angulus anterior, a shallow anterior transition (7) between the angulus, a striated surface, and a slightly forward curved angulus superior. *Limanda limanda* has broader crista than *H. platessoides*. No clear differences could be established to distinguish *P. platessa* from *P. flesus* nor between the right- and left-eyed form of the latter.

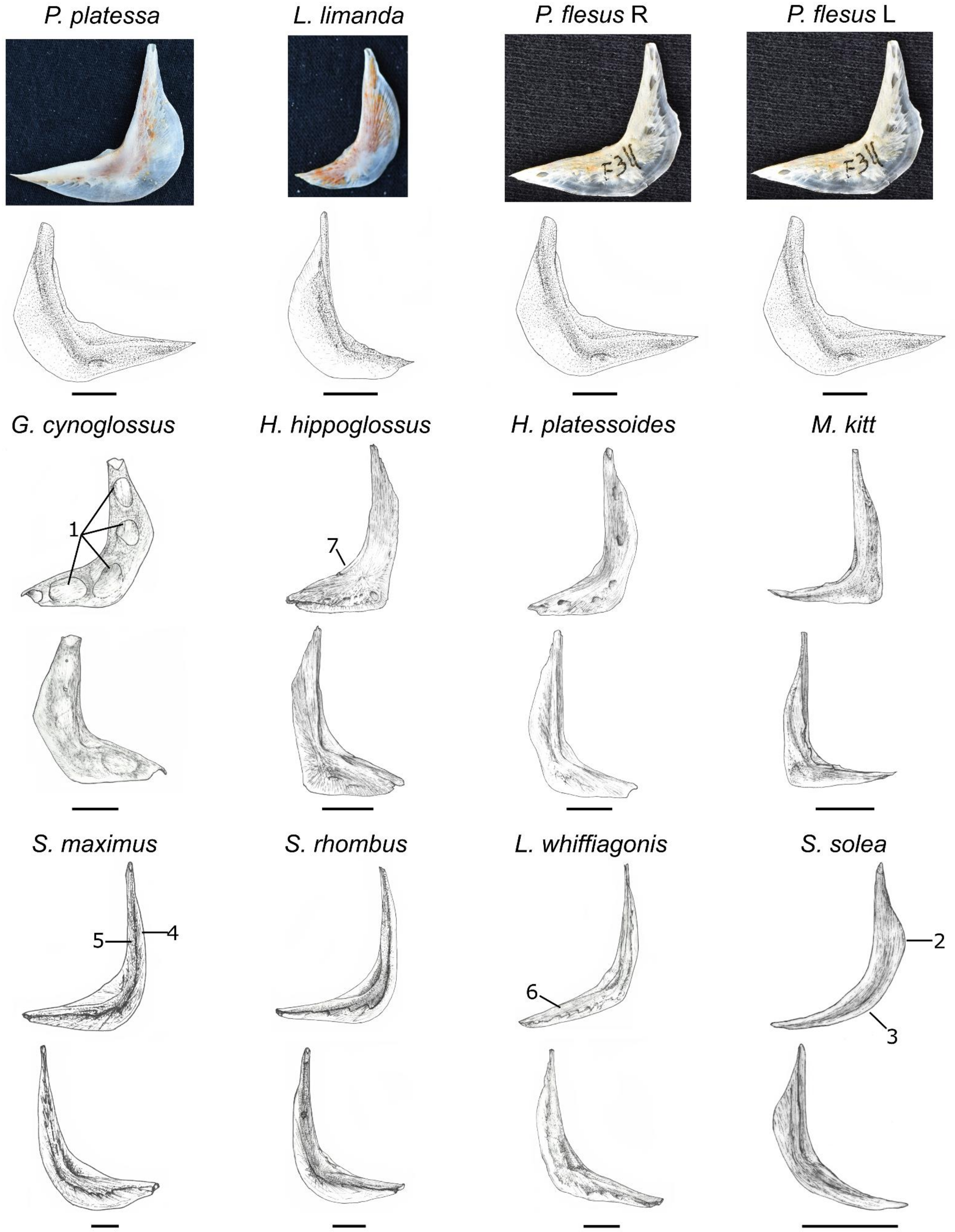


Figure 3.27. Lateral (upper) and medial (bottom) view of the left preoperculum of all twelve species. The black bar under each species represents 1 cm.

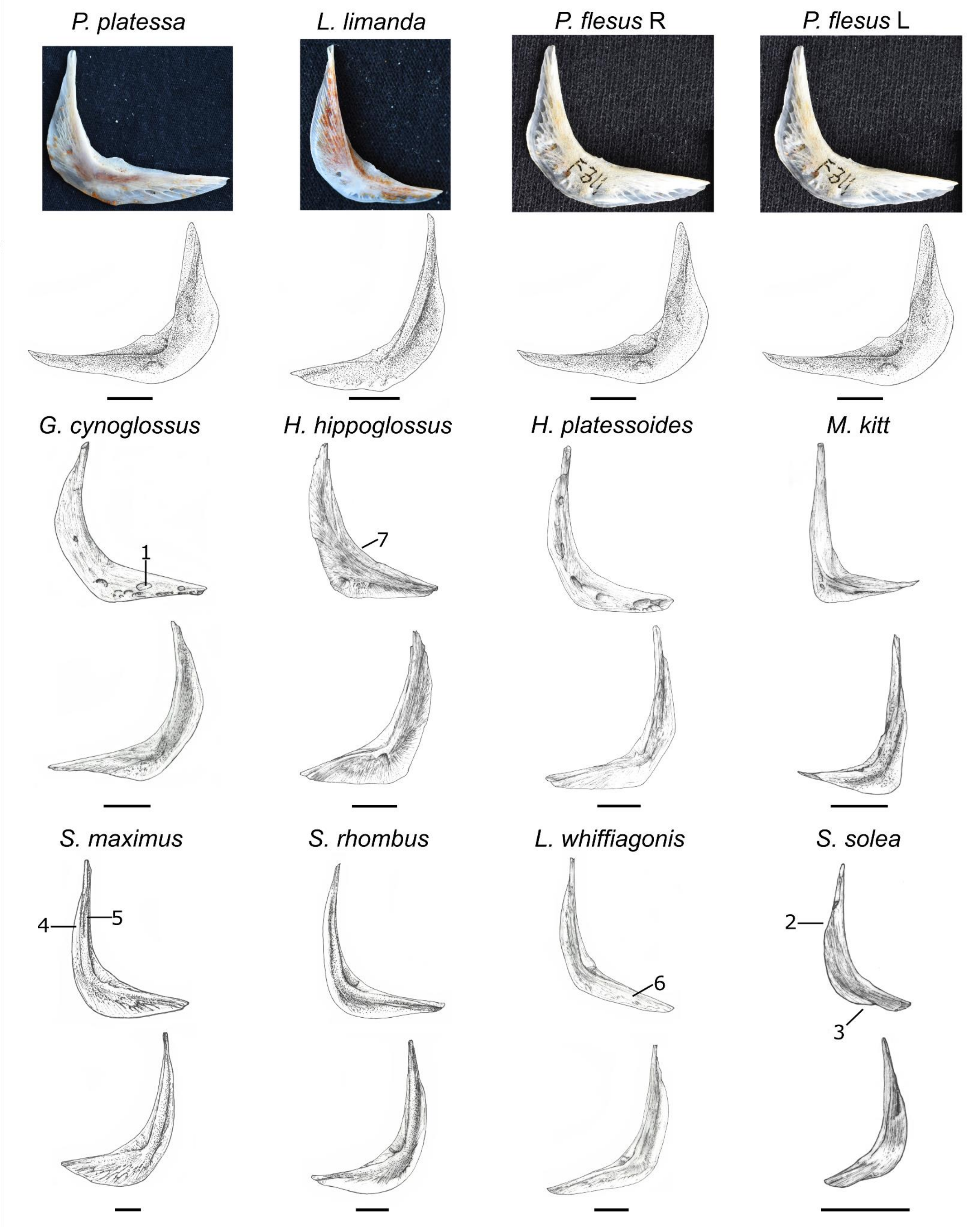


Figure 3.28. Lateral (upper) and medial (bottom) view of the right preoperculum of all twelve species. The black bar under each species represents 1 cm.

The lateral and medial view of the right preoperculum is given in figure 3.28. Additional descriptions of the right preoperculum are summed up in the appendix (table B29). This bone allows easy identification to most species. The criteria, described for the left preopercular are similar for the right in the following species: *S. solea*, *M. kitt*, *S. maximus*, *S. rhombus* and *L. whiffiagonis*. The foramen (1) are larger in *G. cynoglossus* and *H. platessoides* than in the other species. *Glyptocephalus cynoglossus* can be distinguished from *H. platessoides* by having a slightly concave margo ventralis of the angulus anterior (6) and a more angular posterior transition (8) between the angulus and larger curvature in general. The L-shape of the preopercular in *H. hippoglossus* is less outspoken than in the left element, but it is still far different from the other Pleuronectidae. The striated surface is also very typical for this species. The angulus anterior is slightly shorter than the angulus superior (5) in *L. limanda*, while longer in *P. platessa* and *P. flesus*. In *L. limanda* there is also a slight concave indent in the margo ventralis of the angulus anterior, which is not present in *P. flesus* and *P. platessa*. No clear differences could be established to distinguish *P. platessa* from *P. flesus* nor between the right- and left-eyed form of the latter.

3.3.2.8 Interoperculum

The interoperculum is a thin oval shaped bone below the operculum. Anteriorly there is a small spina often on the dorsal side, called the spina anterior. The dorsal margin or margo superior is often a bit thicker. The posterior margin has two angulus, one superior and one inferior. The bone can be thin and fragile, mostly in smaller specimens. The interoperculum on the eyed side of the fish can be more elongated and have slightly different proportions compared with the one on the blind side, but has no different morphological structures. When viewed laterally, the angulus are on the right side in the left interoperculum and on the left side in the right interoperculum.

The medial view of the left interoperculum is given in figure 3.29. Additionally, the medial view of the right interoperculum can be found in the appendix together with the detailed analysis for every species (table B30; figure B18). This bone allows identification of some species. A clear, straight rib marks the margo superior (1) in the three Scophthalmidae species. *Lepidorhombus whiffiagonis* differs from the other species by the squarish, elongated shape with only a very limited amount of dense bone (2) in the centre that is not clearly delineated. Both *Scophthalmus* sp. can be differentiated if bones of the same size are compared. The density of the element is heavier in *S. maximus* and the ventral delineation of dense bone towards the margo inferior (3) is also stronger. These criteria should not be used in bones of fish smaller than 30 cm SL. *Solea solea* is the only species where the margo superior (1) is densely ossified in the anterior part (4). The margo posterior (5) is deeply incised in *G. cynoglossus*. The ventral delineation of dense bone towards the margo inferior (3), reaching more than half of the height distinguishes *H. hippoglossus* from the other species. Next to it, the heavy striated surface is also very diagnostic. The dorsal medial rib is dense and has a slightly protruding edge in *M. kitt*, which is absent in the other species. The remaining Pleuronectidae are difficult to identify, but slightly differ by the transition between both angulus (6) on the margo posterior, the shape of the angulus, the thickness of the margo dorsalis, the size of the spina (7). *Hippoglossoides platessoides* has a barely denser margo dorsalis, while *L. limanda* has a slightly dense margo dorsalis and *P. platessa* and *P. flesus* have a clearly dense margo dorsalis. Right- and left-eyed *P. flesus* might be identified by the relative size and shape of the interoperculum, for which a reference collection is advised.

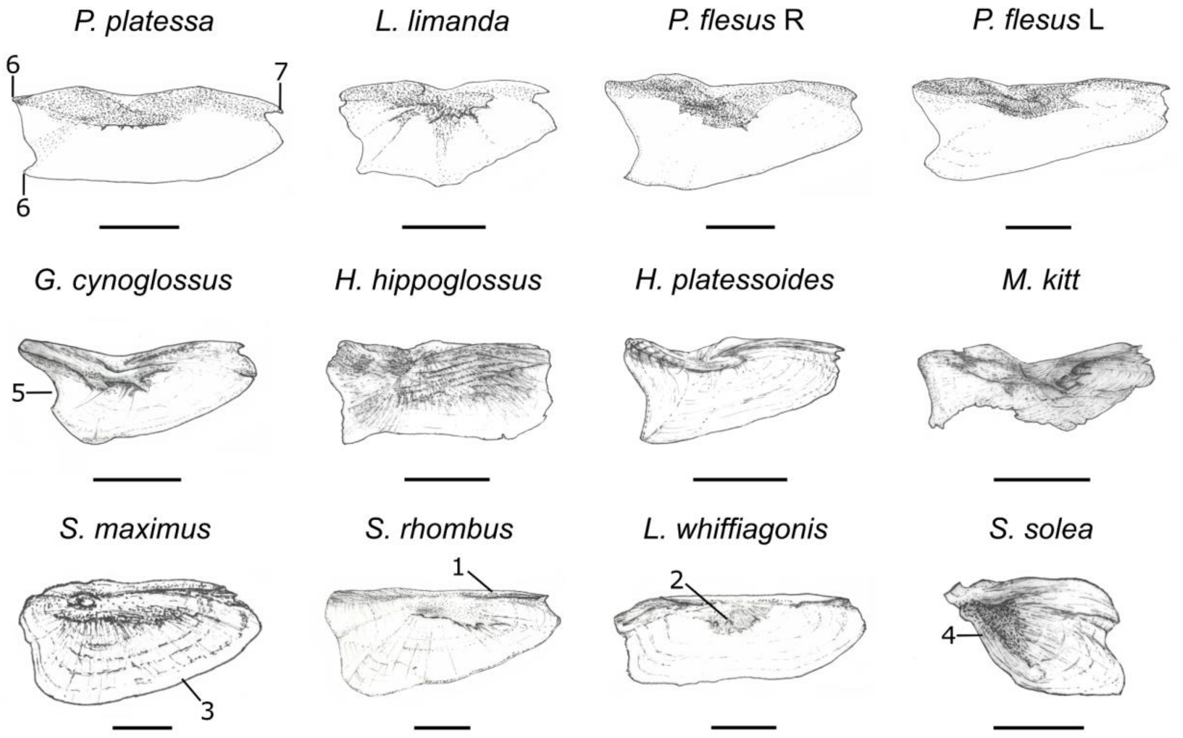


Figure 3.29. Medial view of the left interoperculum of all twelve species. The black bar under each species represents 1 cm.

3.3.2.9 Parasphenoid

The parasphenoid is a long bone on the ventral part of the neurocranium. The posterior side, which articulates with the basioccipital, has a groove in the facies articularis basioccipitalis. In the mid part of the parasphenoid, there are two lateral cristae: crista lateralis sinistra and dextra. Ventrally on the midpart there is a crista ventralis. The angulus anterior is long and often a bit curved.

The ventral and lateral view of the parasphenoid is given in figure 3.30. Additional descriptions of the parasphenoid are summed up in the appendix (table B31). This bone allows easy identification to families and some species. *Solea solea* differs from all other flatfishes by the strong dorsal indentation of the margo ventralis (1) in lateral view. In Scophthalmidae and left-eyed *P. flesus* the angulus anterior (2) of the anterior part is curved to the left, while in the other Pleuronectidae it is curved to the right. The margo ventralis (1) makes a sharp turn to the left in ventral view just before the facies articularis basioccipitalis (3) in *L. whiffiagonis*, while it is only slightly bend in *Scophthalmus* sp. and straight in left-eyed *P. flesus*. *Scophthalmus* sp. can not be distinguished. Within the Pleuronectidae, *M. kitt* is easily distinguished by a ridge (4) between the facies articularis basioccipitalis and the lateral cristae (5) and by the short and deep facies articularis basioccipitalis. The appearance of *H. hippoglossus* is unique due to its broad and flattened appearance distinguishing it from the other Pleuronectidae. *Glyptocephalus cynoglossus* is the only Pleuronectidae that has a clear ventral bend or curvature of the angulus anterior, while the other species have a dorsal curvature or a straight ventral margin. *Hippoglossoides platessoides*, right-eyed *P. flesus*, *L. limanda* and *P. platessa* cannot be identified confidently. The facies basioccipitalis is widest in the middle in *H. platessoides* and *L. limanda*, while it is widest at its base in *P. platessa* and *P. flesus*, but this feature is prone to subjective interpretation. The groove of the facies basioccipitalis is deeper in *H. platessoides* and *P. flesus* than in *P. platessa* and *L. limanda*, but this is again prone to subjective interpretation.

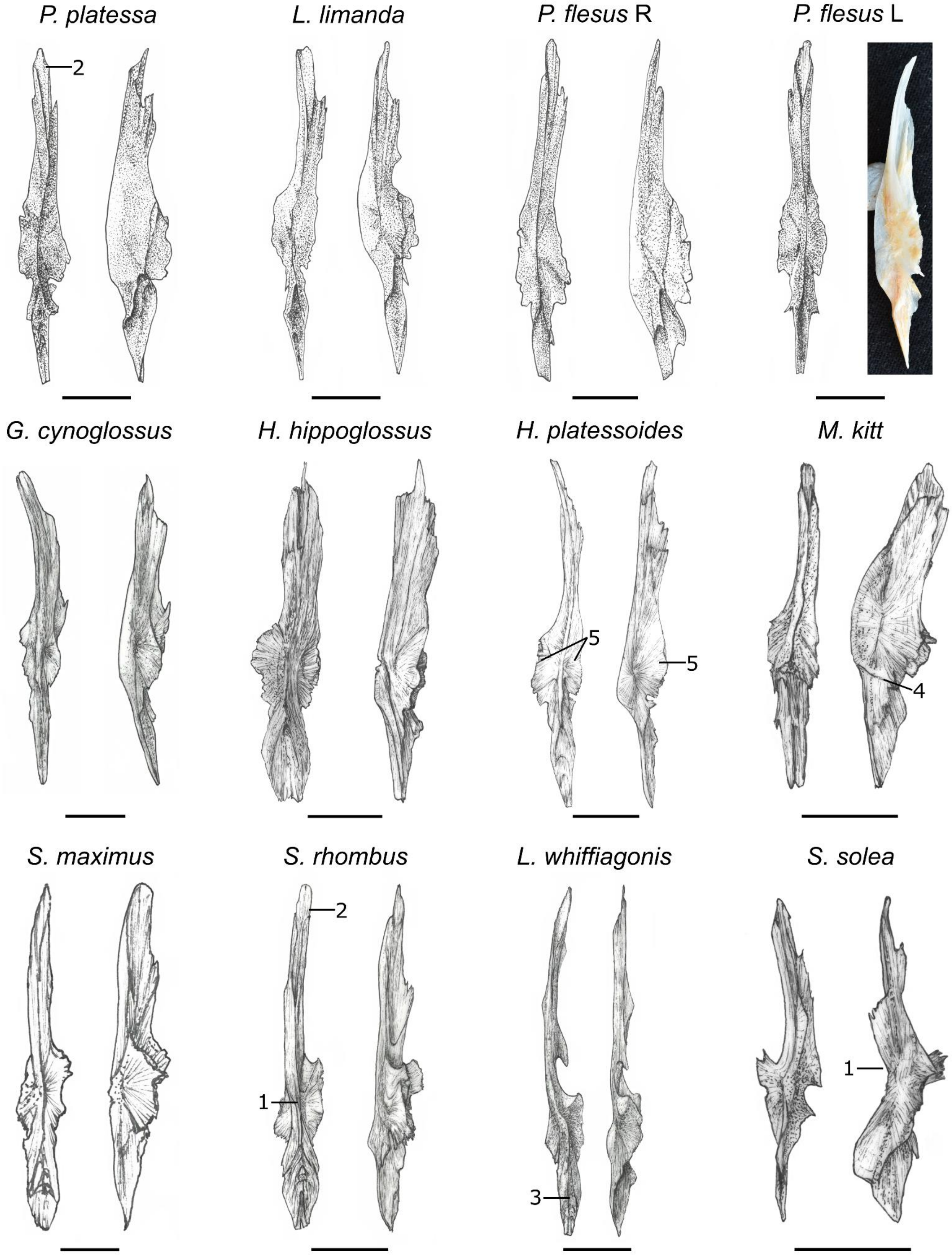


Figure 3.30. Ventral (left) and sinistral lateral view (right) of the parasphenoid of all twelve species. The black bar under each species represents 1 cm.

3.3.2.10 Ceratohyal

The ceratohyal has a long and rather straight margo ventralis. Foramina and small processus might be present along this margo. The ceratohyal articulates with the epihyalis at the margo synchondrosis. Anteriorly, a long and slender processus ceratohyalis is present, that along the posterior and anterior sides can have crista. The dorsal margin of the corpus is often broad and in the middle of the corpus the foramen externum, visible as an elongate horizontal groove or foramen, can sometimes be present. On the anterior side of the corpus, a processus hypohyalis dorsalis is present, that is shorter than the processus ceratohyalis. When viewed medially (hollow side), the processus ceratohyalis is on the left side in the left ceratohyal and on the right side in the right ceratohyal.

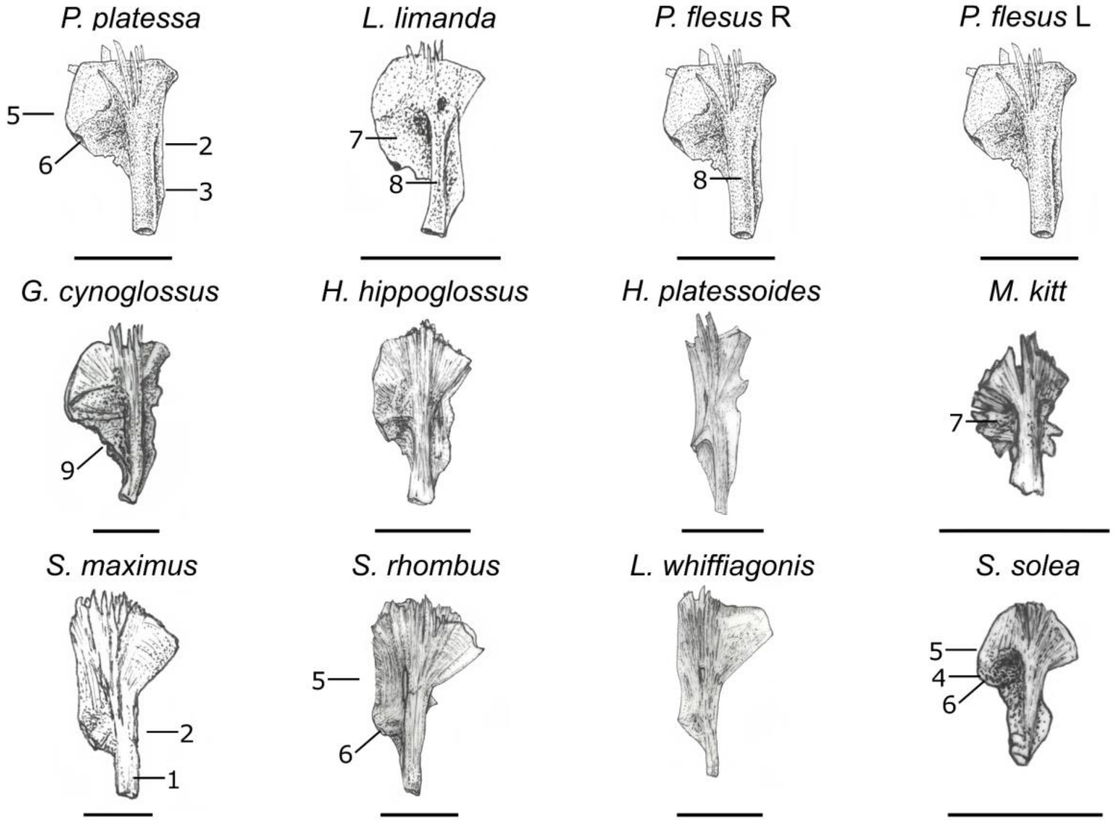


Figure 3.31. Medial view of the left ceratohyal of all twelve species. The black bar under each species represents 1 cm.

The medial view of the left ceratohyal is given in figure 3.31. Additional descriptions of the parasphenoid are summed up in the appendix (table B32). This bone allows easy identification to most species. Left and right ceratohyal are similar and show the same diagnostic features, so only the left element is illustrated. The processus ceratohyalis (1) of the Scophthalmidae forms the ventral board of the element for approximately 2/3 of the bone. In all other species, the margo ventralis (2) is shaped by a ventral crista (3) that originates quickly from the processus ceratohyalis (1). *Lepidorhombus whiffiagonis* is slenderer and thinner compared to both *Scophthalmus* sp. which cannot be distinguished from each other. *Solea solea* is characteristic due to the relatively thick ridge (4) of the margo dorsalis (5) at the basis of the processus hypohyalis (6). *Hippoglossoides platessoides* has a very elongated ceratohyal with a concave margo dorsalis. *Hippoglossus hippoglossus* has a slightly longer margo dorsalis and an irregular shape of the ridge on the margo ventralis. The processus hypohyalis is oriented posteriorly or is absent, and the corpus (7) is small and irregular in *M. kitt.* The base (8) of the processus ceratohyalis is slenderer than the tip in *L. limanda* and *G. cynoglossus*, while it remains broad in *P. platessa* and *P. flesus*. The transition (9) between the margo dorsalis and the processus ceratohyalis is more gradual and longer in *G. cynoglossus* than in

L. limanda. The corpus also is about half or less of the length of the ceratohyal in *G. cynoglossus*, while more than half in *L. limanda*. *Pleuronectes platessa* and *P. flesus* are difficult to distinguish, with *P. flesus* showing a slightly wider corpus, a feature that is almost impossible to use with confidence. There is no difference between the right-eyed and left-eyed *P. flesus.*

3.3.2.11 Epihyal

The epihyal is a rather square or triangular bone that is connected to the ceratohyal by the margo synchondrosis. The posterior part of the bone is the apex epihyalis, which is often a bit curved to the dorsal side. Anterior of the apex epihyalis there is a slight articulation for the interhyal, called the incisura anterior. In Pleuronectiformes the margo ventralis is often short and more inclined vertically. Along the medial side there can be bulbous enlargements anterior of the apex epihyalis and impressios. When viewed laterally (hollow side), the apex epihyalis is on the left side in the left epihyal and on the right in the right epihyal.

The lateral and medial view of the epihyal is given in figure 3.32. Additional descriptions of the epihyal are summed up in the appendix (table B33). This bone can only be used to identify some species of flatfish. Left and right epihyal are similar and show the same diagnostic features, so only the left element is illustrated. The apex epihyalis (1) is not individualised and widens immediately in *Solea solea* and *M. kitt*. The margo synchrondrosus (2) of *S. solea* is wide, while slender in *M. kitt*. In general, the bone is almost squarish in *S. solea* while rounded rectangular in *M. kitt*. The epihyal has a perfect triangular shape in both *Scophthalmus* sp. but no valid criteria exist to distinguish the two species from each other. These two species differ sometimes slightly in the presence of ridges (3) medially below the apex epihyalis. The margo ventralis (4) is long and the margo synchrondrosus reaches till almost halfway the height of the epihyalis in *H. hippoglossus, H. platessoides,* and *L. whiffiagonis*. A thick rib (5) is extending from the apex epihyalis (1) into the corpus in *L. whiffiagonis*. This rib is fine in *H. platessoides* and extends in the margo synchondrosus. The margo synchondrosus (2) of *H. hippoglossus* is very irregular and the general striated appearance is also characteristic. *Pleuronectes platessa*, *Limanda limanda*, *Platichthys flesus*, and *Glyptocephalus cynoglossus* can’t be distinguished from each other.

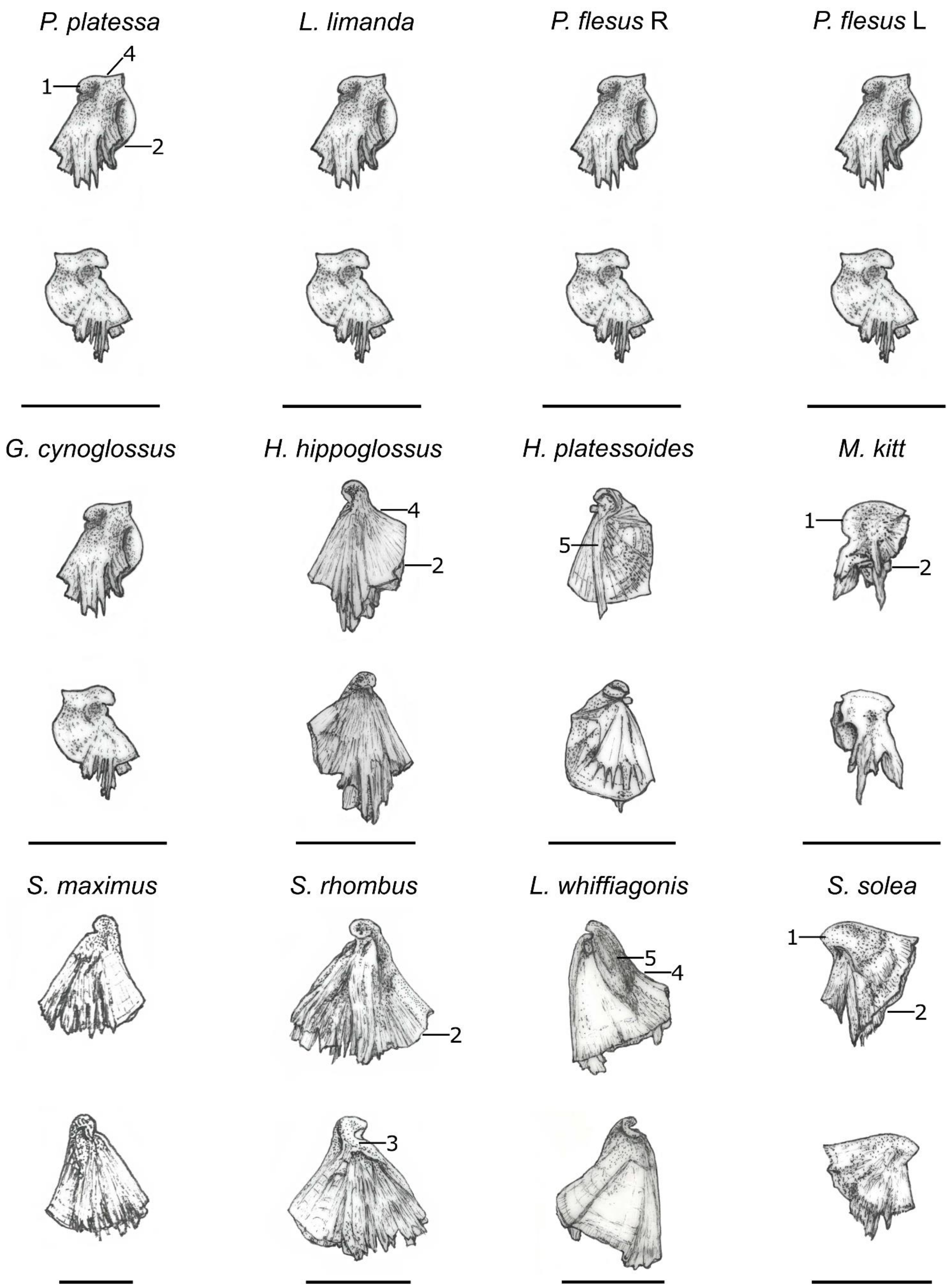


Figure 3.32. Lateral (upper) and medial (bottom) view of the left epihyal of all twelve species. The black bar under each species represents 1 cm.

3.3.2.12 Upper hypohyal

The upper hypohyal is a square or rectangular bone that articulates with the ceratohyal by the articularis ceratohyalis on the margo posterior, and the lower hypohyal with the articularis hypohyalis on the margo hypohyalis inferior. Anteriorly it has an apex hypohyalis. In the middle of the corpus there is usually a foramen. When viewed laterally (ridged side) with the articulation on the bottom, the apex is on the left side in the left upper hypohyal and on the right side in the right upper hypohyal.

The medial view of the left upper hypohyal is given in figure 3.33. Additional descriptions of the upper hypohyal are summed up in the appendix (table B34). Left and right upper hypohyal are similar and show the same diagnostic features, so only the left element is illustrated. The upper hypohyal can be used to distinguish the families and some species. The bones of both *S. solea* and *G. cynoglossus* have a squarish appearance, being about as long as high, although the margo hypohyalis inferior (1) is somewhat rounded. The foramen (2) lies close to the apex hypohyalis (3) and the corpus is hollow in *G. cynoglossus,* while the foramen lies central in *S. solea* and the corpus is completely bony. *Solea solea* can also show a protruding ventral spina at the margo anterior (4), but this is less present in very large specimens. The upper hypohyal of *M. kitt* and *H. platessoides* are much longer than high. The margo hypohyalis inferior in *M. kitt* is hollow in the middle and the foramen is only visible in medial view. It doesn't pierce the bone. The margo posterior (5) is long and forms a fine tube in *H. platessoides* while the foramen is positioned close to the apex hypohyalis. All other species have an upper hypohyal with a rectangular shape. The apex hypohyalis is as thick as the margo hypohyalis inferior in the *Scophthalmidae* while much finer than the margo in the Pleuronectidae (except *H. platessoides* and *G. cynoglossus*). In *Scophthalmus* the articulares connection (6) is filled with bone, while it is hollow or closed in Pleuronectidae and *Lepidorhombus*. *Scophthalmus* rhombus has a slightly more elongated upper hypohyal compared to *S. maximus*. Further differentiation within these two families seems very tempting. Several differences have been found between species, but their use for identification should be done with caution. *Hippoglossus hippoglossus* has a ridge above the foramen on the lateral side, which is not present in *P. platessa, L. limanda, P. flesus,* and *L. whiffiagonis*. In *L. whiffiagonis* the margo dorsalis (7) is straight or convex, while in the other species it is usually concave or rather straight in smaller specimens. *Pleuronectes platessa*, *L. limanda* and *P. flesus* are difficult to distinguish. The former species can subtly differ from the latter two by having a slightly inclined ventral posterior part, which is not inclined in the latter two species. In *L. limanda* the foramen is usually large compared with those in *P. flesus*, and the articularis hypohyalis can be oval and long in *L. limanda*, while usually round in *P. flesus*. There is no difference between the right-eyed and left-eyed *P. flesus*.

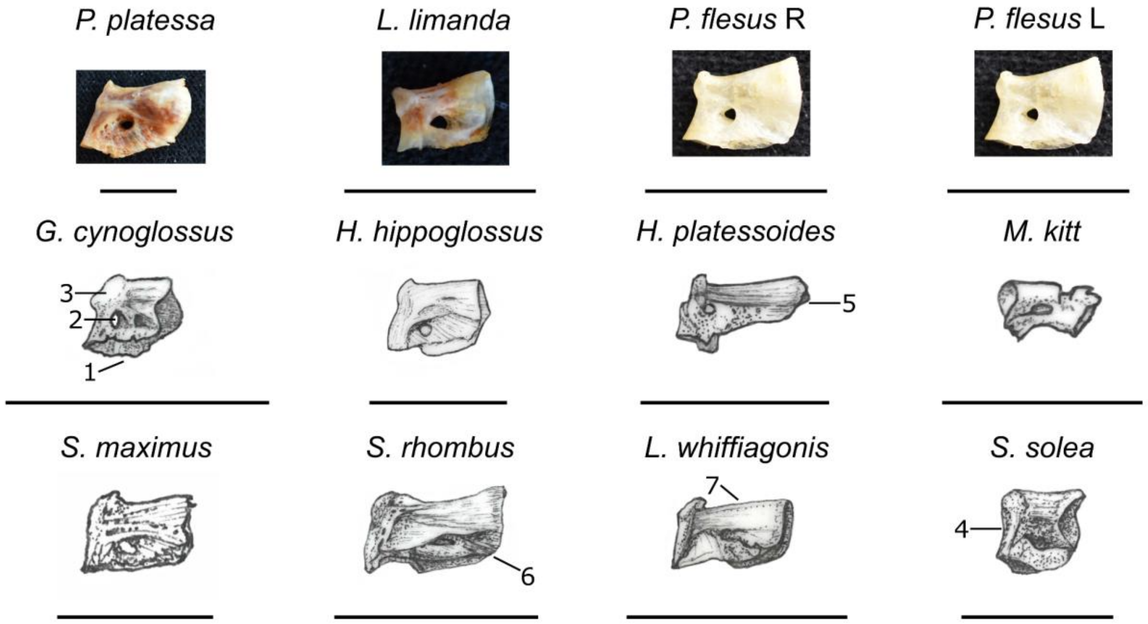


Figure 3.33. Medial view of the left upper hypohyal of all twelve species. The black bar under each species represents 1 cm.

3.3.2.13 Infrapharyngeal V

The infrapharyngeal V is a bone ventrally in the back of the mouth between the cleithra. It is an elongated bone that is often slightly curved. Anteriorly and posteriorly it has tubes, with the anterior ones being slightly larger than the posterior ones. On the ventral side there can be a crista ventralis. The tooth area covers most of the dorsal side of the bone, except for some part of the tubes. In some species the tooth area, and sometimes the corpus as well, is broader than the tubes. When viewed dorsally with the larger tube on the top, the concave side of the tooth area with smaller tooth alveoli is on the left side in the left pharyngeal and on the right side in the right pharyngeal.

The ventral and dorsal view of the left lower pharyngeal V is given in figure 3.34. Additional descriptions of the lower pharyngeal V are summed up in the appendix (table B35). Left and right lower pharyngeal V are similar and show the same diagnostic features, so only the left element is illustrated. Identification of the family level is easy by using the number of teeth and the shape of the bone (see appendix). The lower pharyngeal V of *P. platessa* and *P. flesus* are very broad and triangular in shape and differ in their teeth implantation and tooth shape Wouters *et al.* (2007). All other flatfish have an elongated and slender pharyngeal V. In Scophthalmidae and Soleidae the tooth surface (1) is broader than the corpus (2), while it is slenderer in Pleuronectidae. The bone is straight in *L. whiffiagonis* and both *Scophthalmus* sp. but clearly curved in *S. solea*. *Lepidorhombus* differs from *Scophthalmus* by having an anteriorly positioned and thin ventral crista (3), while *Scophthalmus* sp. have a more posteriorly placed and broad ventral crista. *Scophthalmus* sp. are difficult to distinguish from each other. The other Pleuronectidae are a bit more difficult to distinguish from each other. The bone of *M. kitt* is short and straight and that of *L. limanda* is short and curved. The tooth sockets (4) of the inner and outer row from *H. platessoides* differ clearly in size while this difference is minimal in the other species. The cross section in the middle of the bone is triangular in *G. cynoglossus* while rectangular in *H. hippoglossus*.

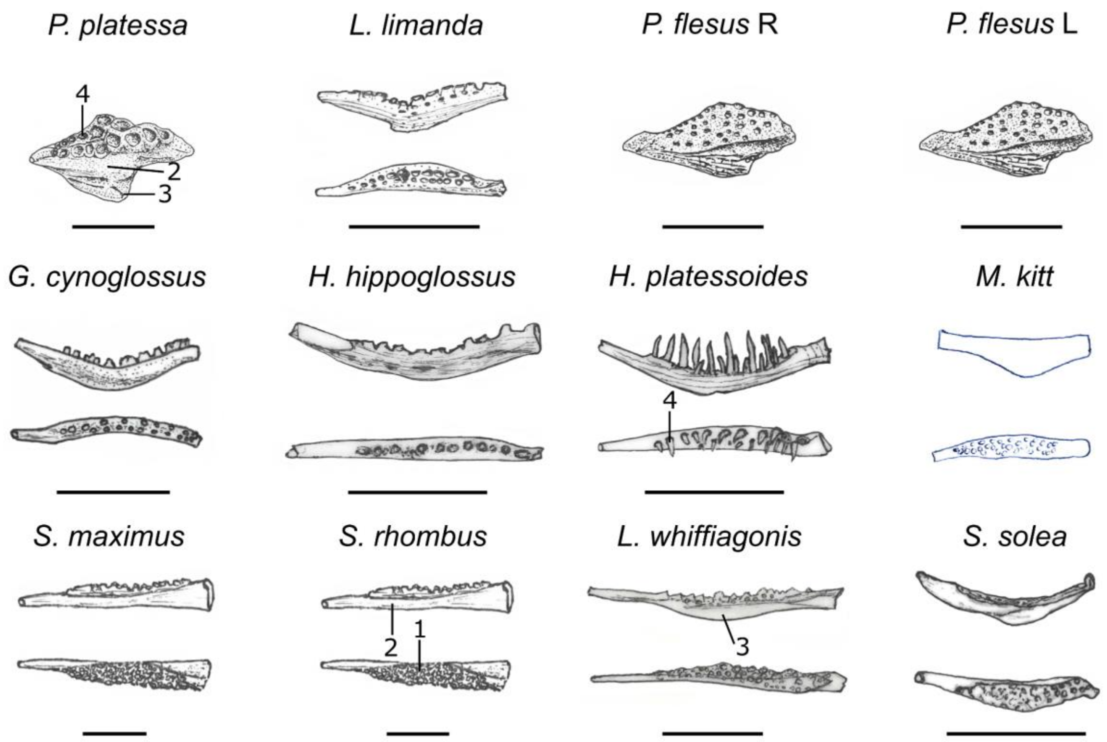


Figure 3.34. Dorsal (upper) and sinistral lateral view (bottom) of the left lower pharyngeal V of all twelve species. The black bar under each species represents 1 cm.

3.3.2.14 First caudal vertebra

The first caudal vertebra is characterised by the large haemal arch on the ventral side with large lateral cristae. This vertebra has both a neural and a haemal arch that can or cannot be connected to the lateral spina anteriorly and posteriorly. At the anterior and posterior bases of both arches there can be small spina present. The lateral side of the center often has ridges and pits. The base of the neural arch often has a foramen laterally.

The anterior and sinistral lateral view of the first caudal vertebra is given in figure 3.35. Additional descriptions of the first caudal vertebra are summed up in the appendix (table B36). This bone allows precise identification for some species if the archaeological bone material is well preserved. This vertebra is easy to distinguish from all other caudal vertebrae thanks to very broad ventral haemapophysis which form the haemal arch (1) in Pleuronectidae and Scophthalmidae. Soleidae are easily distinguished by the short haemal arch (1) and the strongly curved neural arch (2). Relative to size, the corpus (3) is also squarish and the lateral rib thick and clearly aligned (4) in *S. solea*. Both *Scophthalmus* species have a rough and usually irregular lateral surface (5), while Pleuronectidae and *L. whiffiagonis* usually have ridges on the lateral side or a smooth surface. *Scophthalmus* sp. cannot be distinguished. *Hippoglossus hippoglossus* has a rather smooth lateral side without a pit above the lateral side, while in the other Pleuronectidae there are usually ridges and an upper pit (6). A double or triple rib separated by deep pits is characteristic for *L. whiffiagonis* and the anterior spine is absent here. Pleuronectidae have both an anterior (7) and posterior (8) spine. The anterior lateral processus is connected to the crista (9) of the haemal arch in all Pleuronectidae, except in *G. cynoglossus.* The remaining species are difficult to distinguish. *Platichthys flesus* and *P. platessa* cannot be distinguished from each other. Left-eyed *P. flesus* might be distinguished from other Pleuronectidae by the subtle asymmetry of the vertebra.

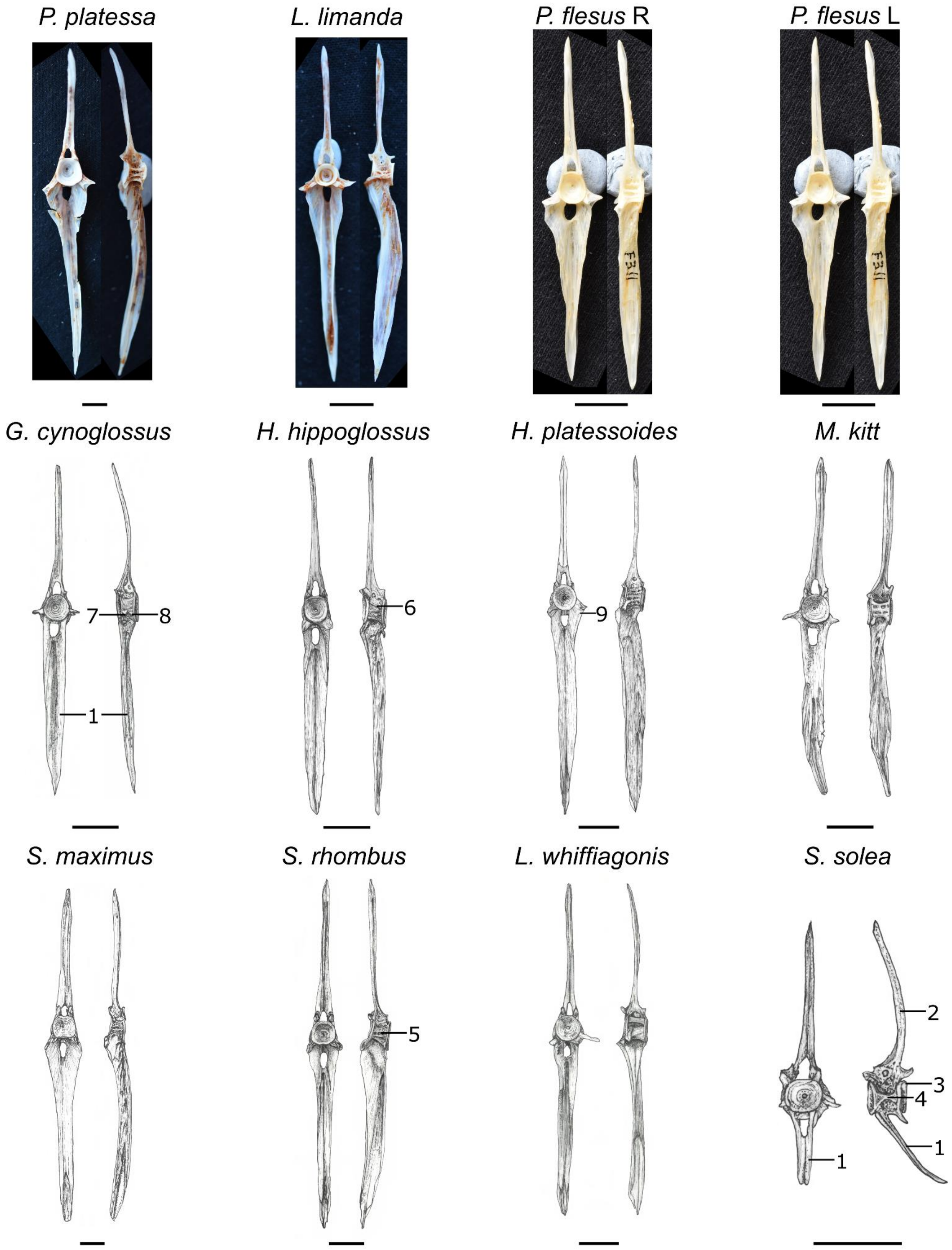


Figure 3.35. Anterior (left) and sinistral lateral view (right) of the first caudal vertebra of all twelve species. The black bar under each species represents 1 cm.

3.3.3 Elements which do not differentiate families or species

Some other elements frequently found in archaeological contexts were also compared but no well-defined distinguishing criteria were found to identify the flatfish species. These elements are: opercular, supracleithrum, basipterygium, lower hypohyal, pharyngeal II, III and IV, coracoid, basihyal, and the ultimate vertebra (see appendix B3; tables B37-46).

3.4 Discussion

It can be said that a distinction of most Pleuronectiformes species from the North Sea is possible using most of the frequently recovered skeletal elements. Out of 34 skeletal elements analysed, ten can be easily used to identify most of the main flatfish species from the North Sea area, considering fragmentation and preservation. Fourteen skeletal elements were found to be quite useful to distinguish between families and most species. The remaining ten elements are considered to be unreliable for species identification, allowing only family level identification and a few species in some cases.

Compared with previous osteological studies, we provided many additional diagnostic criteria and a clear overview containing multiple families and species of flatfish found in the North Sea. Eight skeletal elements from this study had not been analysed in published studies before for these flatfish species: metapterygium, epihyal, upper and lower hypohyal, operculum, basipterygium, coracoid, and basihyal. Of these, the metapterygium can be used to identify most species. Two other elements, epihyal and upper hypohyal, can provide some taxonomic information. For some species, there were many other elements included for the first time as well in an osteological comparative study.

Morphologically, flatfish come in two main groups: left-eyed, such as Scophthalmidae and left-eyed *P. flesus*, and right-eyed, such as most Pleuronectidae and Soleidae. The two groups can easily be distinguished due to the asymmetry present in many bones. This makes family-level identification and distinction of left-eyed *P. flesus* quite straightforward in many bones.

Compared with Wouters *et al.* (2007), some additional diagnostic criteria were found, allowing better distinction between *P. platessa* and right-eyed *P. flesus*. These species differ in the shape of the spina on the processus internus of the left maxilla, the shape of the corpus, and the relative length of the processus of the maxilla. Both species can be identified by the shape of the transitions between the processus and the shape of the processus of the hyomandibula. They can be distinguished using the vomer by the shape of the frontal indent and the presence of ridges and folds on the lateral sides. The basioccipital lateral wing shape is also different between *P. platessa* and *P. flesus*.

In this study, additional criteria were found that allow distinction between right-eyed and left-eyed *P. flesus* in the posttemporal, cleithrum, preoperculum, and the interoperculum, although none of these are easy to use and can show overlapping characteristics, making identification very tentative. Unfortunately, there were no additional criteria found besides those reported by Wouters *et al.* (2007) to improve the identification of *P. platessa* and *P. flesus* using the quadrate, preoperculum, ceratohyal, supracleithrum, the first caudal vertebra, and the ultimate vertebra. These species remain undistinguishable in these elements.

The posterior part of the parasphenoid, which contained the diagnostic features according to Wouters *et al.* (2007), however, was found to be too variable in shape and too prone to subjective interpretation to be used for species identification. Furthermore, the ventral groove of the lateral crista of the cleithrum, as described in Wouters *et al.* (2007) was not found to be clearly visible and distinct between *P. platessa* and *P. flesus* in this study. Due to fragmentation of remains, it is also not often usable in zooarchaeological analyses.

Table 3.3. Overview of the taxa able to be identified per skeletal elements. E: easy; D: difficult, requiring reference collection or prone to subjectivity; N: not possible.

	Pleuronectidae										**Scophthalmidae**					**Soleidae**
Skeletal element	*Family level*	*P. platessa*	*L. limanda*	*P. flesus*	*right-eyed P. flesus*	*left-eyed P. flesus*	*G. cynoglossus*	*H. hippoglossus*	*H. platessoides*	*M. kitt*	*Family level*	*Scophthalmus sp.*	*S. maximus*	*S. rhombus*	*L. whiffiagonis*	*S. solea*
premaxilla	**E**	**E**	**E**		**E**	**E**	**E**	**E**	**E**	**E**	**E**	D	N	N	D	**E**
maxilla	**E**	**E**	**E**		**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**
dentary	**E**	**E**	**E**		**E**	**E**	**E**	**E**	**E**	**E**	**E**	D	D	D	D	**E**
articular	**E**	**E**	**E**		**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**
hyomandibula	**E**	D	**E**	D	N	N	**E**	**E**	**E**	**E**	**E**	**E**	D	D	**E**	**E**
palatine	**E**	**E**	**E**		**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	D	D	**E**	**E**
vomer	**E**	D	D		D	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**	**E**
posttemporal	**E**	D	D	**E**	D	D	**E**	D	**E**	**E**	**E**	**E**	D	D	**E**	**E**
urohyal		**E**	**E**	**E**	N	N	**E**	**E**	**E**	**E**		**E**	D	D	**E**	**E**
first vertebra		D	D	D	N	N	**E**	**E**	**E**	**E**		**E**	D	D	**E**	**E**
metapterygium		D	D	D	N	N	D	**E**	**E**	**E**		**E**	D	D	**E**	**E**
basioccipital	**E**	D	**E**	D	N	N	**E**	**E**	**E**	**E**	**E**	D	D	D	D	**E**
cleithrum	**E**	**E**	D	D	D	D	D	**E**	D	**E**	**E**	**E**	D	D	**E**	**E**
os anale	**E**	D	**E**	D	N	N	D	**E**	D	**E**	**E**	**E**	D	D	**E**	**E**
quadrate	**E**	D	D		D	D	D	**E**	**E**	**E**	**E**	**E**	D	D	**E**	**E**
ectopterygoid		D	D		D	**E**	**E**	D	**E**	**E**	**E**	D	N	N	D	**E**
preoperculum	**E**	N	D		N	N	**E**	D	D	**E**	**E**	**E**	D	D	**E**	**E**
interoperculum	**E**	D	D		D	D	**E**	**E**	D	**E**	**E**	D	D	D	D	**E**
parasphenoid	**E**	N	N		N	**E**	D	**E**	D	**E**	**E**	**E**	N	N	**E**	**E**
ceratohyal	**E**	D/N	**E**	D/N	N	N	**E**	D	**E**	**E**	**E**	D	N	N	D	**E**
epihyal		N	N	N	N	N	N	D	**E**	**E**		**E**	D/N	D/N	**E**	**E**
upper hypohyal		D/N	D/N	D/N	N	N	**E**	D	D	**D**		**E**	D	D	D	**E**
pharyngeal V	**E**	**E**	D/N	**E**	N	N	D/N	D/N	D/N	D/N	**E**	D	D/N	D/N	D	**E**
first caudal vertebra		N	D	D/N	D/N	D/N	D	D	D	D		**E**	N	N	D	**E**

As also noticed by Wouters *et al.* (2007), *P. platessa* and *P. flesus* of less than 20-25 cm SL show less pronounced diagnostic criteria, making it more difficult to identify juvenile fish. This issue seemed to be less relevant for the other species in this study. The remaining Pleuronectidae are generally easily distinguished with most elements. Remarkably, *Microstomus kitt*, which is currently classified as a Pleuronectidae (Fricke *et al.*, 2022), shows many aberrant morphological characteristics and is in some cases more similar to Scophthalmidae. Genetic analysis shows that this species falls within the Pleuronectidae clade (Vinnikov *et al.*, 2018), which would mean that this species has undergone far more morphological adaptations compared with the other species of this family.

Lepidorhombus whiffiagonis can in most cases be easily distinguished from *Scophthalmus* species. *Scophthalmus maximus* and *S. rhombus* are very similar in many elements, which hinders species identification. Only using a handful of elements is it possible to confidently distinguish between these congeners: maxilla, articular, metapterygium, vomer, cleithrum, os anale, first vertebra, and upper hypohyal.

Solea solea is easily recognisable as a separate species from the other included species due to clear morphological changes in its skeletal elements. As there are other Soleidae present in the North Sea, caution is advised and to verify identifications using a reference collection, especially when dealing with bones from very small specimens. Further, it was also noticed that *S. solea* with the same standard length as a Pleuronectidae species has much smaller and thinner bones. This could potentially lead to a survival and recovery bias of archaeological samples, with *S. solea* being less frequently found and reported because of osteological features (e.g., Struever, 1968; Von Endt & Ortner, 1984; Shaffer & Sanchez, 1994; Stahl, 1996; Smith *et al.*, 2007). The vertebrae of *S. solea* further do not share some of the typical characteristics of Pleuronectidae and Scophthalmidae. The center of a *S. solea* vertebra is longer, more constricted in the middle, lacks a clear haemal arch (especially in the first caudal vertebra), and has its spina implanted differently on the arches and center than the other flatfish species. This could result in identification issues, with *S. solea* not being recognised as a Pleuronectiform bone, and therefore remaining unidentified or being erroneously identified as another taxon.

Certain skeletal elements are more fragile and thinner or much smaller than others, making them less likely to be recovered and identified. The metapterygium, for example, is very thin and can easily be broken down by biological and chemical degradation in the soil (Von Endt & Ortner, 1984; Smith *et al.*, 2007). Also, certain structures on other bones, such as cristae and thin processus and angulus, can become too degraded or broken to be used for identification, while they might otherwise be of great use (e.g., preoperculum, interoperculum, quadrate, hyomandibula). *Hippoglossoides platessoides* and *Glyptocephalus cynoglossus* generally have much thinner and more fragile bones than other Pleuronectidae, which might be one of the reasons why these are rarely recovered and reported from archaeological sites. The latter species is also characterised by large foramina in the dentary, preoperculum, and posttemporal, which are only separated by small ridges and are the most diagnostic criteria for this species. These small ridges and very thin bone surrounding the foramina might be simply too delicate to be preserved, and therefore make the species very difficult to recognize in archaeological remains.

For some elements, flatfish species show differences in shape proportions, which are prone to subjective interpretations by the analyst. It is therefore recommended not to rely solely on those morphologies and to use a reference collection to compare bones with, which is an indispensable tool for zooarchaeological analyses anyway, certainly if the researcher is not familiar with such bones. The reference collection should consist of several specimens of small, medium and large size of different species. It is desirable to compare bones of specimens with approximately the same length, certainly in cases when proportions are an important diagnostic feature. Experience with Pleuronectiformes bones is also an added benefit.

There are still many of the smaller elements that are usually not recovered in archaeological sites, and were thus not included here, that lack clear osteological descriptions in the literature. The recovery issue can be solved by consistent sieving and flotation methods during archaeological excavations (e.g., Struever, 1968; Shaffer & Sanchez, 1994; Stahl, 1996). Also, the osteology of the other, smaller and rarer North Sea and other eastern Atlantic species has barely received any attention. It has to be remarked that, although *Limanda limanda*, or dab, is a very common species of the southern part of the North Sea area that can grow up to 45 cm SL, it is only rarely reported from archaeological sites (e.g., Nicholson, 2009). Also, very few finds of other common Pleuronectidae species, such as *Hippoglossus hippoglossus* and *Microstomus kitt*, or of *Scophthalmus rhombus* are reported (e.g., Nicholson, 2009; Cerón-Carrasco, 2013; Harland *et al.*, 2016). These issues should be addressed as well in the future in order to completely understand the presence of Pleuronectiform species in archaeological sites from the North Sea area. Since there are still some species that cannot be distinguished using certain elements or elements that have little to none diagnostic morphologies, other techniques, such as ZooMS (Dierickx *et al.*, 2022) or DNA (e.g., Kijewska et al., 2009; Pappalardo & Ferrito, 2015), might sometimes still be needed to complement visual identifications of flatfish remains.

3.5 Conclusion

Archaeological studies of fish remains from sites around the North Sea are still hindered by the low identification success rate of flatfish bones (see above). With these new diagnostic criteria for bone identification of the majority of commercially interesting species from this area, a better insight in the species composition of archaeological sites should be possible with more consistent identification criteria than were available before. This will improve the general understanding of flatfish consumption through time, how and where they fished, with whom people traded, which species preferences different social statutes had, and so on, using a very accessible method.

Acknowledgements
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Chapter 4. Geometric morphometric analysis of Pleuronectiformes vertebrae: a new tool to identify archaeological fish remains?

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This is a paper that will be submitted soon. Katrien Dierickx is responsible for making the photographs, performing the analysis and interpreting the results, making the figures, and drafting the paper. The paper has received input from Antonio Profico (University of Pisa), who trained Katrien Dierickx in geometric morphometrics and assisted with the coding of the script for the analysis.

Abstract

Flatfish (Pleuronectiformes) vertebrae are difficult to identify to species due to the lack of diagnostic features. This has resulted in a lack of understanding of the species abundances across archaeological sites, hindering interpretations of historical fisheries in the North Sea area. We use a new approach, utilising a combined 2D landmark-based geometric morphometric analysis as an objective and non-destructive method for species identification of flatfish vertebrae from the North Sea area. Modern specimens were used as a reference to describe the morphological variation between taxa using principal component analysis (PCA) and to trial an automated classification using linear discriminant analysis. Although there is limited distinction between taxa using PCAs, the classification shows high accuracies, indicating that flatfish species identifications using geometric morphometrics are possible. Bone samples (n=105) from two archaeological sites in the UK and France were analysed using this approach. The success rate of species identification was usually less than 50%, indicating that this technique has limited applicability due to preservation/fragmentation of archaeological fish bone. Nonetheless, this could prove a valuable tool for modern and non-fragmented samples. Furthermore, the technique applied in this study can be easily adapted to work on other landmark datasets.

Key words: Zooarchaeology; Ichtyoarchaeology; Fish remains; North Sea

4.1 Introduction

Studying flatfish bones from archaeological sites around the North Sea area can help to better understand shifts in the environment, economy, fisheries, and human diet throughout history. There are currently over 20 species of Pleuronectiformes reported from the North Sea (Heessen *et al.*, 2015). Of all flatfish species in the North Sea *Platichthys flesus* (Linnaeus 1758) (flounder) and *Pleuronectes platessa* Linnaeus 1758 (plaice) are very similar in morphology and rarely get confidently identified to species based on a single vertebra from archaeological remains. It is, however, of great interest to correctly identify these two species, since they are the most commonly reported species from archaeological sites around the North Sea and have been of economic importance for this area for centuries (e.g., Locker, 2007; Van Neer & Ervynck, 2007; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019). Differentiating between species that can occur in freshwater environments, such as *P. flesus*, from the marine species could be useful to better understand changes in fisheries through time. Also identifying species that are known from the more northern or southern areas from the North Sea, such as for example *Hippoglossus hippoglossus* (Linnaeus 1758) and *Solea solea* (Linnaeus 1758) respectively, can help to uncover environmental changes in the North Sea as well as potentially expose the trade of fish (Ervynck *et al.*, 2004).

Archaeological studies on disarticulated fish remains from the North Sea in Europe often show that many flatfish (Pleuronectiformes) bones can be difficult to identify at the species level, although they are very commonly recovered from these sites. This difficulty resulted in many skeletal elements remaining unidentified or only being identified to a higher taxonomic level (e.g., Ervynck & Van Neer, 1992; Enghoff, 1999; Wouters *et al.*, 2007; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019). This issue is especially true for vertebrae of flatfish. Vertebrae are difficult to use to identify species due to the lack of clear diagnostic criteria between species (e.g., Clavel, 1997; Wouters *et al.*, 2007). To date, there has been no in-depth study of flatfish vertebrae shape and how it can be used to identify species. Only a few publications provide descriptions of vertebra morphology of some flatfish species found in the North Sea (e.g., Watt *et al.*, 1997; Wouters *et al.*, 2007).

Geometric morphometrics (GMM) is a landmark-based morphometrics approach to analyse and compare the shape and form of objects by comparing the relative position of landmarks. It is often used to analyse shape variations within an evolutionary context (e.g., Black & Berendzen, 2020), to aid in taxon identification (e.g., Santos *et al.*, 2019) and can even distinguish between populations (e.g., Ibañez *et al.*, 2007). Some studies have applied GMM on scutes, scales, and otoliths of other fish groups, indicating the possibility to use these skeletal elements for species identifications (e.g., Ponton, 2006; Ibañez *et al.*, 2007; Thieren & Van Neer, 2014). No study of flatfish vertebrae using GMM has been performed so far, and the number of studies applying this technique on vertebrae of other fish taxa is also limited. Guillaud *et al.* (2016) used three to seven landmarks and sliding semi-landmarks to identify modern and archaeological Salmonidae vertebrae to species relatively easily. GMM has also been applied to identify the habitat of archaeological fish remains by comparing the shape of the anterior and posterior sides of precaudal and caudal vertebrae of archaeological remains to a collection of samples from a known habitat (Samper Carro *et al.*, 2018). These studies indicate the potential for this technique to differentiate flatfish by the shape of their vertebra.

As *P. flesus* can be both left-eyed and right-eyed, this has an impact on the shape of the bones, especially the cranial bones, with both forms showing different characteristics in homologous bones. Both forms are in general each other's mirror image, although slight differences might be present (e.g., Wouters *et al.*, 2007). This could mean that both forms could potentially also show slight shape differences in their vertebrae due to the asymmetry causing a mirror-image effect, which could be detected using GMM.

In this paper, we measure the morphology of a modern and an archaeological sample collection of flatfish vertebrae by acquiring 2D pictures in anterior and left-lateral (sinistral) views. In detail, we tested the following research questions: i) can GMM be used to determine the position along the spinal column of a flatfish vertebra; ii) can the taxonomic level of archaeological flatfish vertebrae be identified by using a modern sample as a reference? We initially describe the morphological variation present in modern flatfish vertebra using GMM. We then test the classification system by classifying modern flatfish vertebra to taxa using GMM on an ideal dataset before finally exploring the classification of archaeological flatfish vertebra to taxa using GMM to test the accuracy of species assignment.

4.2 Materials and methods

4.2.1 Sample selection

4.2.1.1 Modern sample collection

Modern Pleuronectiformes specimens were selected from the fish bone collections housed at the Royal Belgian Institute of Natural Sciences (RBINS) and University of York (YZL). 73 flatfish from five different families and 19 species were sampled. From each specimen the atlas, a few cervical vertebrae, a few precaudal vertebrae and some caudal vertebrae were selected. Each specimen was laid out with the vertebrae in the correct order. One or more vertebrae were skipped between each sample, as consecutive vertebrae show little morphological differences, depending on fragmentation and warping of the bones. If possible, a minimum of 10 complete vertebrae per specimen were photographed. Table 4.1 provides an overview of the species used and details can be found in table C1 in the appendix.

Table 4.1. Overview of the specimens used in this study. Details can be found in table C1.

Family	**Genus**	**Species**	**Author**	**Number of specimens**	**Remarks**
Bothidae	Arnoglossus	laterna	(Walbaum 1792)	3	
Citharidae	*Citharus*	*linguatula*	(Linnaeus 1758)	2	
Pleuronectidae	*Glyptocephalus*	*cynoglossus*	(Linnaeus 1758)	5	
Pleuronectidae	*Hippoglossoides*	*platessoides*	(Fabricius 1780)	7	
Pleuronectidae	*hippoglossus*	*hippoglossus*	(Linnaeus 1758)	5	
Pleuronectidae	*Limanda*	*limanda*	(Linnaeus 1758)	6	
Pleuronectidae	*Microstomus*	*kitt*	(Walbaum 1792)	7	
Pleuronectidae	*Platichthys*	*flesus*	(Linnaeus 1758)	6	Right-eyed
Pleuronectidae	*Platichthys*	*flesus*	(Linnaeus 1758)	4	Left-eyed
Pleuronectidae	*Pleuronectes*	*platessa*	Linnaeus 1758	6	
Scophthalmidae	*Lepidorhombus*	*boscii*	(Risso 1810)	1	
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	(Walbaum 1792)	3	

Table 4.1 continued

Family	Genus	Species	Author	Number of specimens	Remarks
Scophthalmidae	*Scophthalmus*	*maximus*	(Linnaeus 1758)	4	
Scophthalmidae	*Scophthalmus*	*rhombus*	(Linnaeus 1758)	3	
Scophthalmidae	*Zeugopterus*	*punctatus*	(Bloch 1787)	1	
Scophthalmidae	*Zeugopterus*	*regius*	(Bonnaterre 1788)	1	
Soleidae	*Buglossidium*	*luteum*	(Risso 1810)	1	
Soleidae	*Dicologlossa*	*hexophthalma*	(Bennett 1831)	1	
Soleidae	*Pegusa*	*lascaris*	(Risso 1810)	2	
Soleidae	*Solea*	*solea*	(Linnaeus 1758)	5	

4.2.1.2 Archaeological sample collection

A total of 105 archaeological samples were analysed from two archaeological sites (figure 4.1). These two sites were selected as the material was available at the time when this part of the analysis was appropriate and the initial results were sufficient to interpret the success of the methodology, thus not requiring to expand to other, later available, archaeological sites. Sixty one samples derived from Barreau Saint-George-Desserte ferroviaire in northern France (50° 58' 27.8" N, 2° 10' 7.6" E) dating from the end of the 10th century to the beginning of the 11th century CE. Most remains from this site were identified as Pleuronectidae and also a single *Solea solea* bone was uncovered (Oueslati, 2019). Forty-four were samples from 16-22 Coppergate in the United Kingdom (53° 57' 27.4" N, 1° 4' 51.5" W), a site in the walled city center of York in northern England. This site dates from the Roman period (1st - 4th century CE) to the Late Medieval period (13th - 14th century CE). A large diversity of fish bones from many different families, including Pleuronectidae and Scophthalmidae, have been identified from this site (Harland *et al.*, 2016).

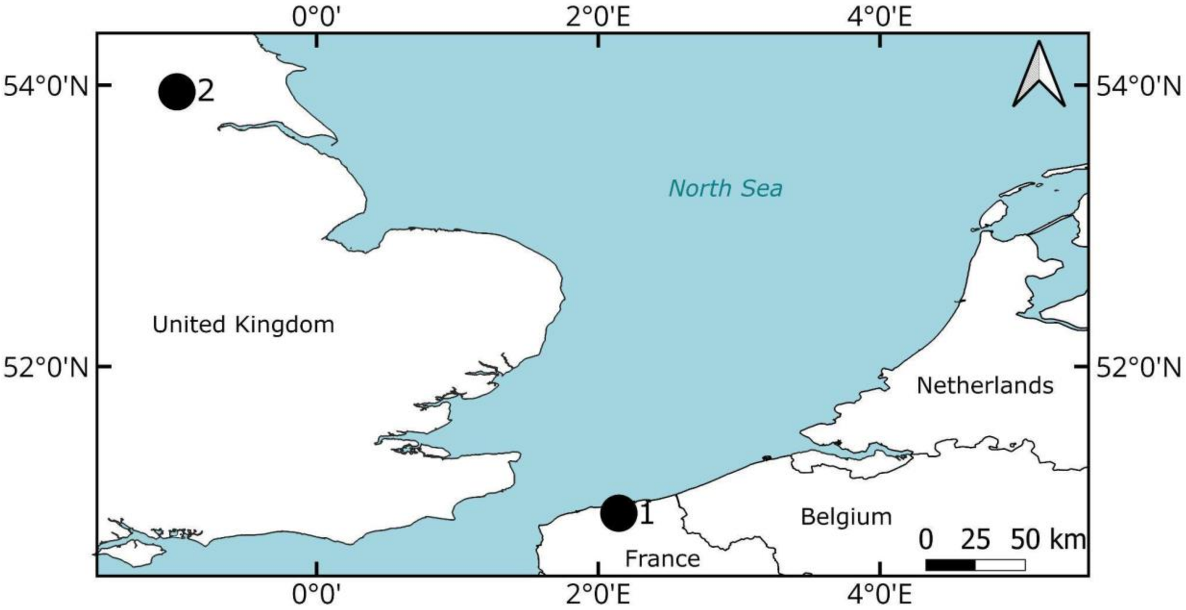

Figure 4.1. Map with the locations of the two analysed archaeological sites. 1: Barreau Saint-George-Desserte ferroviaire; 2: 16-22 Coppergate.

The samples were identified morphologically as flatfish following diagnostic criteria published in Watt *et al.* (1997) and Wouters *et al.* (2007) and with comparison to modern reference specimens housed at the University of York. An overview of the samples can be found in appendix part C2.

4.2.2 Photography

Digital images were taken from each selected sample. Vertebrae were photographed from two views, anterior and sinistral. The dextral and posterior side were not included in this study as these do not provide much more morphological information than is not already available from the anterior and sinistral views. See table C1 in the appendix for details on the number of photos taken for each specimen.

For photography, a NIKON D5600 with an EX Sigma 105mm 1:2.8 DG macro HSM lens with 62 mm diameter was used. The following settings of the camera were applied: ISO 200, F22, shutter 1’’, manual mode, highest resolution JPEG, no zoom. The camera was mounted on an arm that could be moved to position the camera in an angle perpendicular to the surface on which the vertebrae were lying. The camera was placed at a distance of the bone to allow the whole vertebra, including the arches, to be in the image, usually 10-30 cm. A 10-second timer allowed the camera to stabilise after pushing the shutter button, to get as sharp an image as possible. To support the vertebrae in the correct place, a piece of kneadable plasticine was used. By manually adjusting the lens, the image was focused on the structures important for landmarking. In every photo, a scale bar was placed at the same height as the focused structures, and a label indicating the species and collection number was added as well. A black, non-shiny background, such as black cotton cloth, provided good contrast with the lightly coloured bones.

4.2.3 Landmark configurations

Landmarking of the photographs was carried out using TPSdig232 Version 2.31 (Rohlf, 2017). Landmarks of type 1, 2, and 3 were used (Bookstein, 1991). All landmarks were placed on predetermined structures present in all taxa as illustrated and described in figure 4.2 and table 4.2. Cervical, precaudal, and caudal vertebrae were all landmarked in the same way using 25 landmarks in the anterior view and 12 in sinistral view, including missing landmarks in some cases. Several other initially selected landmarks were part of the landmark configuration but during the analysis they were found to be inconsistent and were thus further removed from the analysis (table C1 and figure C26 in appendix; also see discussion). Cervical vertebrae have fewer landmarks available (see LM with an * in table 4.2) and these were labelled as missing landmarks using TPSdig232, while caudal vertebrae have lateral spina present (see LM with an † in table 4.2). Atlas vertebrae followed a different landmark configuration with 13 landmarks in anterior view and 9 in sinistral view. Using the scale bar on the photographs, all photographs could be scaled, using 1 cm. All TPS files received a unique name, with their order number, sample identifier, type of vertebra, view, family, genus and species code.

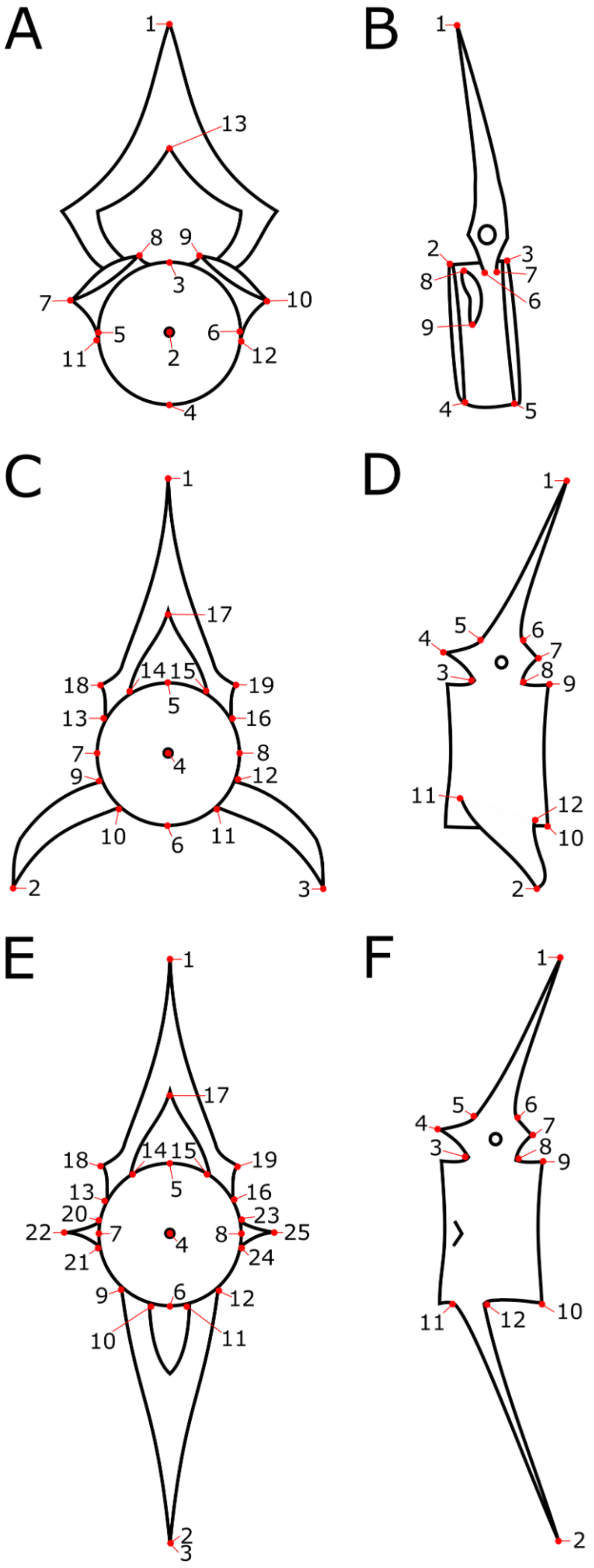

Figure 4.2. Landmark configurations. A. anterior view of atlas vertebra; B. sinistral view of atlas; C. anterior view of precaudal vertebra; D. sinistral view of a precaudal vertebra; E. anterior view of caudal vertebra; F. sinistral view of a caudal vertebra. Numbers are explained in table 4.2.

Table 4.2. Definition of landmarks used per view and vertebra type, i.e. atlas and other (cervical, precaudal, and caudal). Landmarks indicated with * are absent in cervical vertebrae, but present in precaudal and caudal vertebrae. Landmarks indicated with † are only present in some caudal vertebrae.

Nr.	Anterior atlas	Anterior other	Sinistral atlas	Sinistral other
1	Tip of neural arch	Tip of neural arch	Tip of neural arch	Tip of neural arch
2	Notochord of center	Tip of dextral haemal arch	Dorsal edge of anterior side of center	Tip of haemal arch or sinistral haemal processus
3	Most dorsal part of the edge of the center	Tip of sinistral haemal arch	Dorsal edge of posterior side of center	Ventral implant of sinistral anterior dorsal spina
4	Most ventral part of the edge of the center	Notochord of center	Ventral most part of anterior part of center	Tip of sinistral anterior dorsal spina
5	Dextral part of the edge of the center, at the same height as LM4 and perpendicular to LM5-LM6	Most dorsal part of the edge of the center	Ventral most part of posterior part of center	Dorsal implant of sinistral anterior dorsal spina
6	Sinistral part of the edge of the center, at the same height as LM4 and perpendicular to LM5-LM6	Most ventral part of the edge of the center	Anterior implant of neural arch	Dorsal implant of sinistral posterior dorsal spina
7	Lateral edge of dextral condylus	Dextral part of the edge of the center, at the same height as LM4 and perpendicular to LM5-LM6	Posterior implant of neural arch	Tip of sinistral posterior dorsal spina
8	Medial edge of dextral condylus	Sinistral part of the edge of the center, at the same height as LM4 and perpendicular to LM5-LM6	Dorsal most edge of condylus	Ventral implant of sinistral posterior dorsal spina
9	Medial edge of sinistral condylus	Lateral implant of the dextral haemal processus*	Ventral most edge of condylus	Dorsal edge of posterior side of center
10	Lateral edge of sinistral condylus	Medial implant of the dextral haemal processus*		Ventral edge of posterior side of center
11	Lateral implant at center of dextral condylus	Medial implant of the sinistral haemal processus*		Anterior implant of haemal arch or sinistral haemal processus*
12	Lateral implant at center of sinistral condylus	Lateral implant of the sinistral haemal processus*		Posterior implant of haemal arch or sinistral haemal processus*
13	Dorsal most part of the neural canal	Lateral implant of the dextral neural processus		
14		Medial implant of the dextral neural processus		
15		Medial implant of the sinistral neural processus		
16		Lateral implant of the sinistral neural processus		
17		Dorsal most part of the neural canal		
18		Dorsal tip of the dextral anterior dorsal spina		

Table 4.2 continued

Nr.	Anterior atlas	Anterior other	Sinistral atlas	Sinistral other
19		Dorsal tip of the sinistral anterior dorsal spina		
20		Dorsal implant of the dextral anterior lateral spina†		
21		Ventral implant of the dextral anterior lateral spina†		
22		Tip of the dextral anterior lateral spina†		
23		Dorsal implant of the sinistral anterior lateral spina†		
24		Ventral implant of the sinistral anterior lateral spina†		
25		Tip of the sinistral anterior lateral spina†		

4.2.4 Analysis

4.2.4.1 Description of shape variation in modern samples

TPS files were analysed with R (R Core Team (2022), version 4.1.1 (2021-08-10) -- "Kick Things") using the following packages: MASS, caret (Kuhn, 2008), geomorph (Adams & Castillo, 2013), Arothron (Profico *et al.*, 2017), and Morpho (Schlager, 2017).

Two types of analyses were carried out, one set on the atlas vertebrae (n=69), and the other set on the cervical, precaudal and caudal vertebrae (n=1067) as these vertebra types differ in their morphological structures. Subsets were created to allow for particular comparisons between groups or taxa using specific sets of landmarks. Missing landmarks in the modern dataset were estimated using the *estimate.missing()* function in geomorph (also see Arbour *et al.*, 2014). Outliers could be identified and removed from the dataset by calculating the Riemannian distance between two landmark sets using the *kendalldist()* function on the loadings of PCAs obtained with the *procSym()* function of the sinistral and anterior views. Any sample outside of the range provided by the interquartile range method was removed from the dataset.

The anterior and sinistral views were analysed by performing a PCA using the *procSym()* function. Afterwards, both views were analysed combined using the *twodviews()* function in Arothron following Profico *et al.* (2019).

A plot of the PC scores visualised the morphological variation between groups. Convex hulls were added using the *chull()* function of the grDevices package. The minimal and maximum deformation for each principal component axis were also visualised using *twodvarshape()* and *deformGrid2d()* functions from Arothron and Morpho packages respectively.

4.2.4.2 Classification test using modern samples

A linear discriminant analysis (LDA) was performed to classify the specimens to vertebra types and taxonomic groups (family and species) and to assess the success rate of this classification. The analysis was run using all specimens to classify the vertebra types, families, and species excluding LM 9 to 12 in the anterior view and LM 11 and 12 in the sinistral view. The analysis was also run for each vertebra type separately to classify families and species using the whole available landmark configuration for each vertebra type. Species with only one specimen were removed from the dataset for the analysis.

The linear discriminant analysis was performed 100 times for each subset of the modern dataset and the mean of the accuracy rate of all 100 runs was calculated. The analysis was performed on the anterior, sinistral, and combined views. For each linear discriminant analysis, the modern samples were divided into two groups, a training set and a testing set, with a 70:30 ratio respectively. A GPA and PCA were performed using *procSym()* on the training set for individual views. To condense the data for ease of analysis and to reduce the computational time, a PCA using the *prcomp()* function on the PC scores of the first PCA was performed. Only the PC scores from this second PCA explaining cumulatively less than 99% of the variance were taken to create a training model with the *train()* function using a LDA. The testing set was then standardised using the mean shape of the first PCA of the training set, as the testing set is proportionally large and would otherwise influence the mean shape of both sets combined too much. Using the *predict()* function the landmark data after standardisation of the testing set is converted into PC scores. Using these PC scores the vertebra type or taxonomy of each sample is calculated using the LDA training model. Based on the specimen data, the accuracy of the classification was then determined. To analyse and classify using the combined view, the PC scores of the training dataset of the individual views using *procSym()* were combined into one dataframe to create the training model. The landmark configurations of the testing sets of the individual views were transformed individually using the corresponding mean shape of the first PCAs for the individual views and were combined afterwards to convert the landmark data into PC scores of the testing sets to classify the samples.

4.2.4.3 Identification of archaeological samples

Each archaeological sample was analysed individually against the modern reference dataset using LDA to try to identify the most probable vertebra type, family and species.

Landmarks, that were not present in the archaeological sample, were also removed from the reference dataset. A GPA and PCA were performed using *procSym()* combining the archaeological sample and a selected subset of the reference dataset for individual views. The subset was determined by the identification level required. The first step was to identify the vertebra type of each sample, for which all cervical, precaudal and caudal reference samples were included, though using the reduced landmarks configuration, excluding LM 9 to 12 in the anterior view and LM 11 and 12 in the sinistral view. From this subset, the most probable family could be identified, after which only the reference samples from this most probable family were used to identify the most probable species. The analysis was also run with the vertebra type given, as this could be identified visually, to identify the family and subsequently the species of each archaeological sample. This was also the approach used for the atlas vertebrae.

To condense the data for ease of analysis and to reduce the computational time, a PCA using the *prcomp()* function on the PC scores of the first PCA was performed using only those of the reference subset. Only the PC scores from this second PCA explaining cumulatively less than 99% of the variance were taken to create a training model with the *train()* function using a LDA. The landmark configuration of the archaeological sample did not need to be standardised

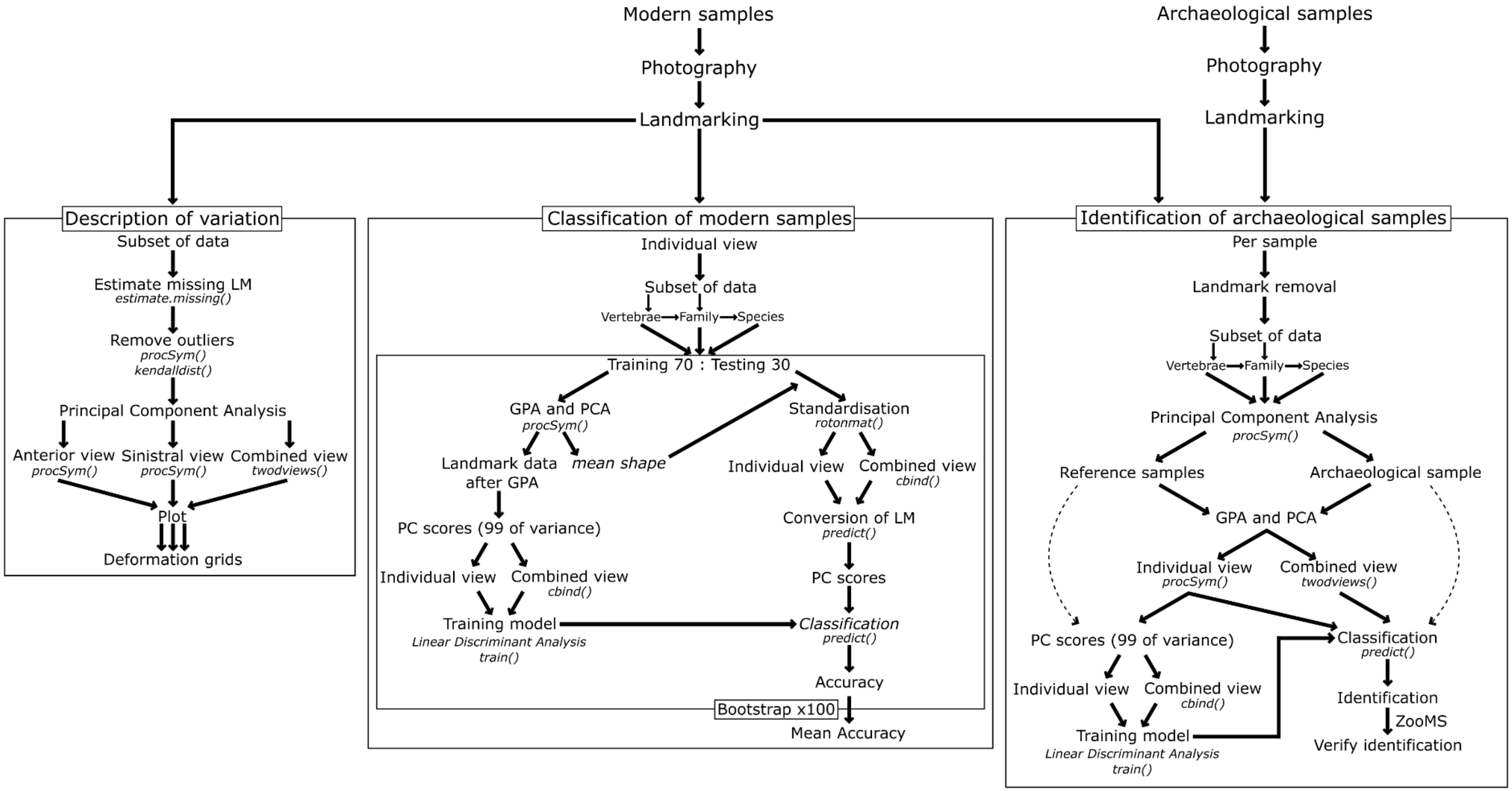

Figure 4.3. Workflow of methodology.

using the mean shape of the first PCA of the reference set as the subset consists mostly of the reference samples and only one archaeological sample, causing the mean shape to be based mostly on the data from the reference subset. The PC scores of the archaeological sample after the initial GPA and PCA were used to calculate the vertebra type or taxonomy using the LDA training model. To analyse and classify using the combined view, the PC scores of the reference dataset of the individual views were combined into one dataframe to create the training model. The PC scores for the combined view of the archaeological sample were obtained by using the *twodviews()* function.

For each sample the most probable family and species were noted as well as the probability score for the classification. The accuracy of GMM on archaeological samples was confirmed by identifying the samples using collagen peptide mass fingerprinting (ZooMS), following Dierickx *et al.* (2022).

Figure 4.3 provides a schematic workflow of the analysis

4.2.5 Data deposition

The script of the analysis is provided in the appendix part C3.

4.3 Results

4.3.1 Morphological shape variation in modern samples

Initially, the variation of the modern samples is described using PCA (figure 4.4-5, table 4.3 and figures C1-C25 in appendix part C1) to determine the potential for GMM to be used for classification purposes.

Some landmarks that were initially selected were later removed from the analysis when it turned out that they were difficult to place consistently between taxa (see table C2, figure C26 in appendix).

We first checked what appropriate morphological information was carried by the tips of the neural and haemal arches is, as these are often broken off in archaeological samples (also see table 4.9), but might hold valuable morphological information for taxonomic purposes.

In the atlas, the landmark configuration including the arch tips (LM 1 to 13 anterior view and 1 to 9 sinistral view) was checked against the landmark configuration without the arch tip (LM 2 to 13 anterior view and 2 to 9 sinistral view) to see if the separation between taxa was better with or without the top of the neural arch. It seems that the presence of the tip of the neural arch can slightly improve the separation on the PCA plots between families (figure C21), especially in the sinistral view, but within families the change seems minimal (figure C22-24). Within Pleuronectidae, the separation is not improved (figure C22).

For the precaudal vertebrae (LM 1 to 19 anterior view and 1 to 12 sinistral view versus 4 to 19 anterior view and 3 to 12 sinistral view), the loss of the arch tips also did not provide a large change in separation between taxa, and it even improved the separation between taxa in the sinistral view in some cases. In the caudal vertebra, the loss of the arch tips improved the separation between families and between species in the Scophthalmidae and Pleuronectidae families.

This indicates that the loss of the neural and haemal arches only results in minimal change regarding the separation between taxa. It was therefore decided to not further include the arch tips in the rest of the analysis (LM 1 in anterior view and LM 1 in sinistral view for the atlas and LM 1, 2, and 3 in anterior view and LM 1 and 2 in sinistral view for other vertebrae).

In most cases, the distinction between vertebrae types can be easily done visually by the researcher themselves, as is the case for the atlas vertebra, but also often for the other vertebrae types. GMM can also be used to distinguish between the other types of vertebrae. When all taxa are included in the analysis (LM 4 to 8 and 13 to 19 anterior view and 3 to 10 sinistral view) there seems to be a slight separation between the vertebrae types, i.e. cervical, precaudal and caudal, on PC1 in all views, which explains 64.92% of the variance in anterior view, 39.49% in sinistral view and 49.12% in combined views (figure 4.4). This distinction allows for the remainder of the analysis to be conducted for each vertebra type separately.

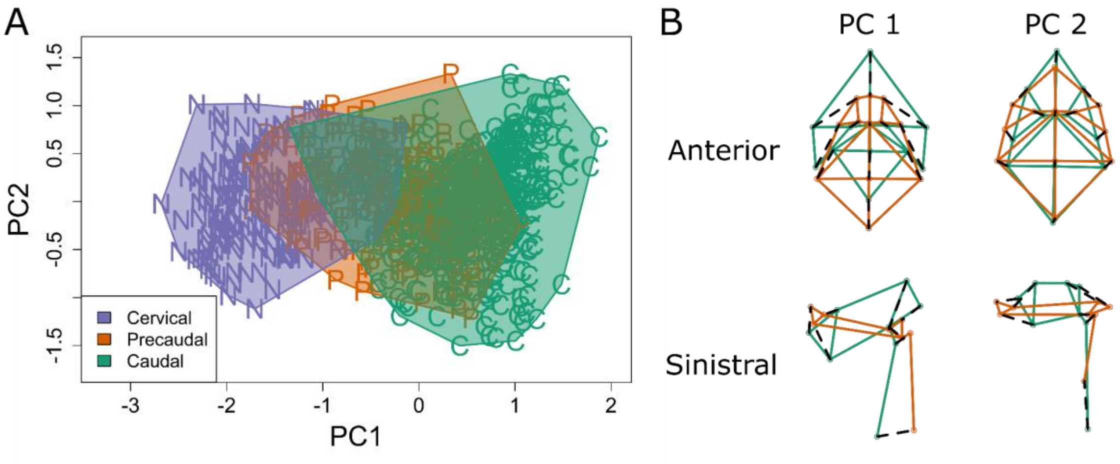

Figure 4.4. A. Scatterplot of PC1 against PC2 for a principal component analysis of all cervical, precaudal and caudal samples (n=1067) grouped by vertebra type using the combined view; B. Deformation grids of anterior (upper) and sinistral (lower) views for both PC1 (left) and PC2 (right) comparing the minimal deformation (green) with the maximum deformation (red).

Using the atlas (figure 4.5) the five families can be well separated in anterior view and combined view on PC1 (32.17% anterior, 20.38% sinistral, 25.04% combined) and PC2 (20.84% anterior, 19.75% sinistral, 13.98% combined), but Pleuronectidae and Scophthalmidae do not clearly separate in sinistral view.
Within Pleuronectidae, the species seem to be slightly separated in PC1, PC2 and PC3 in the combined view and somewhat in anterior and sinistral view, except for *H. hippoglossus* and *P. flesus* (figure A2). *Pleuronectes platessa* and *Platichthys flesus* can be slightly separated from each other on PC2 and PC3 in the combined view (figure C2).
Scophthalmidae species separate strongly in PC1 and PC2 in all views (figure C4).
Soleidae species separate clearly on PC1, PC2, and PC3 in all views (figure C5), but there are only a few specimens. The two *S. solea* specimens seem to show relatively large differences in shape.

For the cervical vertebrae (figure 4.5), there doesn't seem to be a clear distinction between the families (figure C6) and within the Pleuronectidae (figures C7 and C8) and Soleidae (figure A10) in any view. Within Scophthalmidae there seems to be a slight separation on PC2 and PC3 in combined view, PC1 and PC2 in anterior view, and PC3 in sinistral view (figure C9).

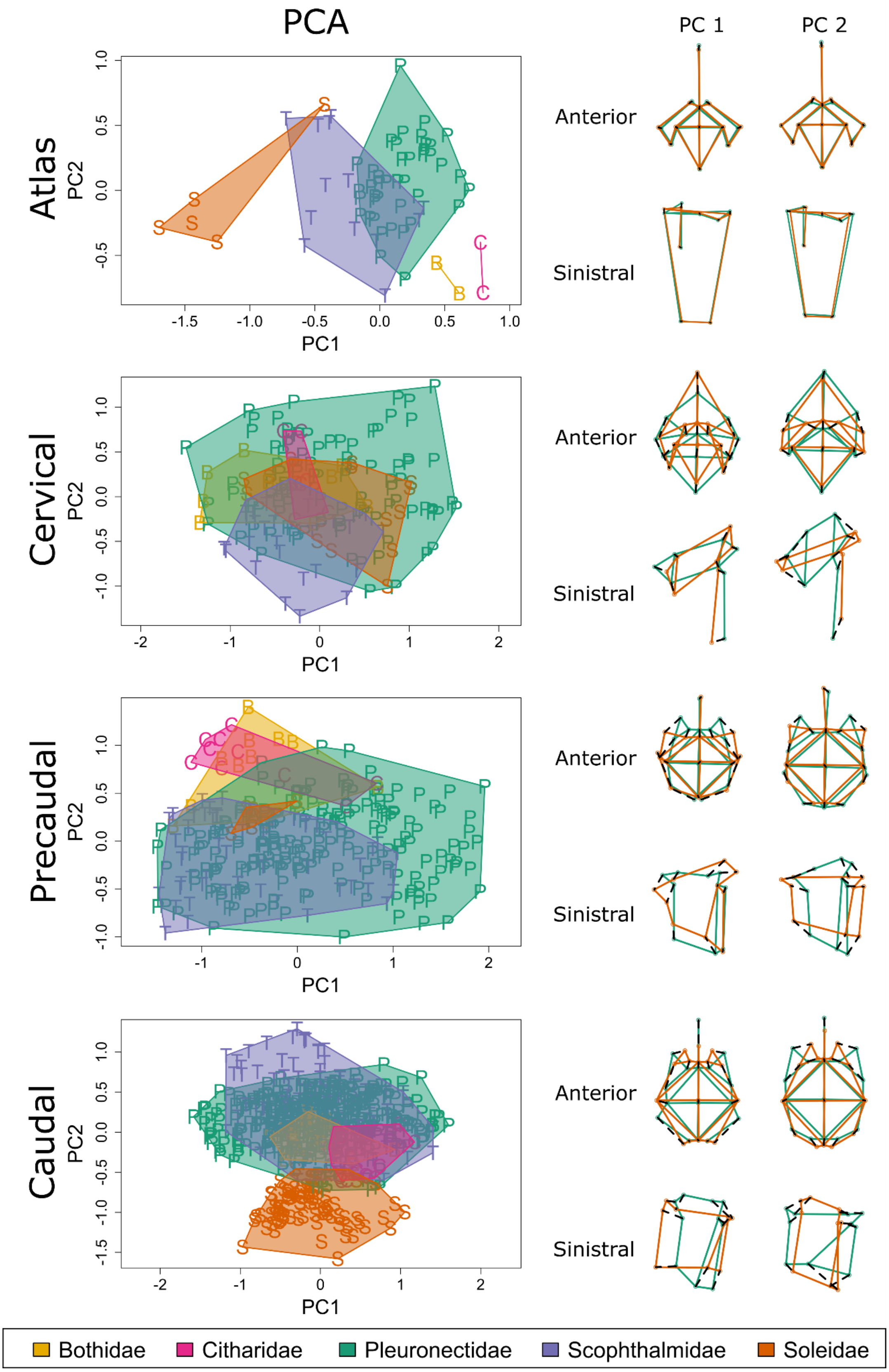

Figure 4.5. Principal component analysis plots and shape variation plots of PC1 and PC2 for combined view for each vertebra type; convex hulls by family level. Minimal deformation of the shape variation is green and the maximum deformation is red.

In the precaudal vertebrae (figure 4.5) Bothidae, Citharidae and Soleidae are separated from the other families on PC2 and PC3 in combined view and anterior view (figure C11). Pleuronectidae and Scophthalmidae seem to overlap completely on all axes and in all views. Within Pleuronectidae there are slight differences noticeable on PC2 and PC3 between the species, but all species still overlap largely (figure C12). *Pleuronectes platessa* and *Platichthys flesus* seem to differ on PC2 and PC3 in the combined and anterior views (figure C13). Within Scophthalmidae there is a clear separation between the species on PC2 and PC3 in combined and anterior view and also a slight separation on PC1 in sinistral view (figure C14). As Soleidae only have 0-2 morphologically well distinct precaudal vertebrae, there were only a few samples available (figure C15). These are not discussed further.

Table 4.3. PCA variance explained by the first three PC axes for different subsets and vertebrae types.

		Combined view			**Anterior view**			**Sinistral view**		
Vertebrae type	**Group**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
All	vertebra type	49.12	12.7	5.74	64.92	9.93	6.59	39.49	25.33	7.99
Atlas	Family	25.04	13.98	11.68	32.17	20.84	14.98	20.38	19.75	17.81
Atlas	Pleuronectidae	21.01	15.87	11.54	24.22	19.54	14.54	26.7	23.26	17.38
Atlas	Scophthalmidae	43.24	16.41	13.34	51.63	18.78	10.42	39.79	28.44	15.16
Atlas	Soleidae	53.45	22.7	9.85	61.68	19.46	11.27	54.4	24.87	8.86
Atlas	*P. platessa/P.flesus*	24.74	21.88	13.52	38.22	19.34	15.68	35.02	20.23	14.76
Cervical	Family	27.25	14.92	10.21	44.92	16.43	10.66	29.56	22.07	13.84
Cervical	Pleuronectidae	29.5	15.24	12.87	50.78	17.64	7.36	32.83	25.35	12.37
Cervical	Scophthalmidae	30.58	20.59	11.37	48.05	18.53	10.26	40.98	18.27	10.78
Cervical	Soleidae	36.66	17.44	12.09	45.57	19.42	13.33	41.42	25.54	11.87
Cervical	*P. platessa/P.flesus*	31.29	18.64	13.1	46.13	18.65	12.66	45.97	23.01	12.88
Precaudal	Family	40.12	11.53	8.53	52.2	13.99	7.7	31.67	21.87	10.46
Precaudal	Pleuronectidae	43.57	11.31	7.64	54.15	11.96	8.45	35.4	21.2	10.97
Precaudal	Scophthalmidae	43.83	17.75	6.95	61.5	10.72	8.05	39.19	23.6	9.5
Precaudal	Soleidae	46.31	26.81	16.73	48.17	29.41	14.49	45.32	25.43	22.22
Precaudal	*P. platessa/P.flesus*	36.66	11.85	8.33	43.69	14.75	8.78	34.76	16.3	12.1
Caudal	Family	30.18	20.68	10.32	46.02	13.7	8.84	40.72	22.72	11.21
Caudal	Pleuronectidae	39.1	12.04	8.68	47.96	12.88	8.06	42.18	15.07	13.84
Caudal	Scophthalmidae	37.65	22.75	7.92	46.73	18.73	9.86	48.33	23.65	6.22
Caudal	Soleidae	43.79	12.23	7.14	52.12	10.38	9.44	51.73	13.93	9.17
Caudal	*P. platessa/P.flesus*	44.51	10.71	9.43	54.98	10.23	7.74	46.03	18.79	11.58

For the caudal vertebrae (figure 4.5), there is the option of adding the landmarks from the lateral spines in the anterior view (LM 20 to 25) or excluding these. Many specimens do not have these landmarks present, and there is not a clear taxonomic reason for this. There seems to be some variability within a specimen whether these landmarks are present. For this reason, these landmarks are not further included.

The caudal vertebrae show a slight separation for Soleidae from the other families on PC2 in combined view (figure C16). The other families largely overlap in all views.

Within Pleuronectidae, there is a slight separation between the species on PC2 and PC3 in combined and anterior views, while only on PC3 in sinistral view (figure C17). *Pleuronectes platessa* and *P. flesus* largely overlap in all views (C18).
Within Scophthalmidae there is a separation between species on PC2 and PC3 in combined and anterior views. In the sinistral view there is only a slight separation on PC2, but the species mostly overlap (figure C19).
Within Soleidae the species largely overlap in all views and all axes (figure C20).

Between right-eyed and left-eyed *P. flesus* there seems to be a slight difference in morphology as seen in the anterior views in precaudal vertebrae along PC2 (figure C25), but no clustering was observed in the other views or in the caudal vertebra. Atlas and cervical vertebrae were not analysed as there are only a handful of samples available.

4.3.2 Classification of modern samples

Five species were removed from the dataset when classifying modern samples, as these only had one specimen in the dataset with a limited number of TPS files: *D. hexophthalma, B. luteum, Z. punctatus, Z. regius,* and *L. boscii*. Citharidae and Bothidae were retained for family level classification, but as there was only one species in each of these families in the dataset, no further analysis was performed. Table 4.4 summarises the mean accuracies for the bootstrap classification of vertebra types, families and species using all specimens. Table 4.5 summarises the mean accuracies for the bootstrap classification per vertebra type for family level or species level identifications. The sample size was too small for the atlas and precaudal of Soleidae to analyse for species level.

Tables 4.4 and 4.5 show that the combined view allows for higher accuracies for almost all subset analyses, ranging from small increases to quite significant improvements, except for the atlas vertebrae. Therefore, it is recommended to apply the combined view for classification of flatfish taxa, unless dealing with atlas vertebrae. For the atlas vertebra, family level identifications seem to work best on the anterior and combined views, while species level identifications within each family seem to work best using the sinistral view. Only *P. platessa and P. flesus* seem to be better distinguished using the combined view with 79.4% mean accuracy.

Table 4.4. Average accuracy and standard deviation of bootstrapped (n=100) classification to vertebra type and species for modern samples per view, considering all cervical, precaudal and caudal vertebrae.

Group	**Anterior**	**Sinistral**	**Combined**
Vertebra type	0.8202±0.02	0.8281±0.02	0.8953±0.02
Family	0.6936±0.73	0.7347±0.02	0.8015±0.02
Species	0.3803±0.02	0.4082±0.02	0.5729±0.02

The classification to vertebra type using all specimens is largely successful, especially for the combined view with an average accuracy of 89.5% to identify the specimen to the correct vertebra type. To identify the family level using all specimens, the accuracy is slightly lower, 80.15%, while the accuracy is inadequate to use for species level identifications with only 57.29%. For the precaudal vertebrae, it is better to identify the specimens using a hierarchical system, with first classification to vertebra type and then family level

(89.53%*95.69%=85.67%), as the probability of classifying the specimens correctly is higher than using a non-hierarchical system (80.15%). For the cervical and caudal vertebrae, the probability of classifying the correct family is higher when using a non-hierarchical classification. Of course, when the vertebra type is known, it is best to directly classify to family or species. For species identifications, the best result is obtained by first identifying to family and then to species.

Precaudal and caudal vertebrae have a higher mean accuracy for species level classification than atlas and cervical vertebrae, which could be related to the larger sample size for these subsets.

Table 4.5. Average accuracy and standard deviation of bootstrapped (n=100) classification to taxa for modern samples per view and vertebra type.

	Family level	**Species level**			
Vertebra type	**Pleuronectiformes**	**Pleuronectidae**	**plaice/flounder**	**Scophthalmidae**	**Soleidae**
Atlas					
Anterior	0.8478±0.07	0.4435±0.13	0.774±0.14	0.55±0.24	/
Sinistral	0.7102±0.08	0.4375±0.11	0.74±0.17	0.845±0.22	/
Combined	0.8232±0.07	0.4275±0.15	0.794±0.15	0.7475±0.20	/
Cervical					
Anterior	0.7247±0.06	0.5122±0.07	0.704±0.15	0.5636±0.14	0.492±0.18
Sinistral	0.7916±0.05	0.5584±0.07	0.7578±0.12	0.4799±0.20	0.804±0.14
Combined	0.8441±0.04	0.7752±0.07	0.8129±0.13	0.6065±0.20	0.664±0.15
Precaudal					
Anterior	0.9229±0.03	0.6195±0.06	0.7946±0.08	0.6341±0.11	/
Sinistral	0.8826±0.04	0.6871±0.05	0.8684±0.06	0.9061±0.07	/
Combined	0.9569±0.02	0.8179±0.05	0.9126±0.05	0.9011±0.07	/
Caudal					
Anterior	0.7538±0.02	0.627±0.04	0.7746±0.06	0.8175±0.07	0.8183±0.08
Sinistral	0.7858±0.03	0.652±0.04	0.8535±0.05	0.7268±0.07	0.829±0.07
Combined	0.8401±0.02	0.7809±0.03	0.9282±0.04	0.8425±0.07	0.9132±0.06

Remarkably, there is a high classification accuracy for *P. platessa and P. flesus*, two species that are osteologically very similar. Using the atlas and cervical vertebrae, these two species can be distinguished from each other with ca. 80% (note large standard deviation, ca. 0.14) success rate, and using the precaudal and caudal vertebrae ca. 91% (small standard deviation, ca. 0.05), which is much higher than what is possible using morphological observation by eye alone (1-15% of all flatfish bones (e.g., Ervynck & Van Neer, 1992; Enghoff, 1999; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019). As no diagnostic features on the bones have been found so far to visually distinguish these two species (Wouters *et al.*, 2007; chapter 3 thesis), this would be a meaningful result if it is replicated on archaeological material.

Classification of the modern dataset to right-eyed or left-eyed *P. flesus* was relatively accurate (see table 4.6). The mean accuracy is highest for the anterior and combined view of the caudal vertebrae. The mean accuracy is quite low for the cervical vertebrae, and the anterior view of the precaudal vertebrae.

Table 4.6. Average accuracy and standard deviation of bootstrapped (n=100) classification for right- and left-eyed *P. flesus* per view and vertebra type.

View	Cervical (n=18)	Precaudal (n=40)	Caudal (n=84)
Anterior	0.5217±0.18	0.4544±0.11	0.6866±0.08
Sinistral	0.4937±0.19	0.588±0.14	0.6259±0.09
Combined	0.5314±0.17	0.573±0.12	0.6904±0.08

4.3.3 Identification of archaeological samples

Using the classification developed in the previous step, archaeological samples were attempted to be identified to family and species level. Table 4.7 summarises the identification success rate for each vertebra type per view. Details of the analysis for the archaeological samples can be found in tables C3-C8 in the appendix part C.

Table 4.7. Percentage of correctly identified archaeological samples to vertebra type using GMM by view. Vertebra type verified by visual identification.

Vertebra types	Anterior	Sinistral	Combined
Cervical (n=11)	5 (45.45%)	5 (45.45%)	6 (54.55%)
Precaudal (n=28)	16 (57.14%)	9 (32.14%)	15 (53.57%)
Caudal (n=58)	52 (89.66%)	54 (93.10%)	49 (84.48%)
Overall (n=97)	**73 (75.26%)**	**68 (70.10%)**	**70 (72.16%)**

Compared to the modern dataset, the classification of vertebra type of the archaeological dataset is much less accurate (68-73% versus 82-89%). A few vertebrae (2 precaudal and 2 caudal vertebrae) could not be identified as these had too few landmarks remaining (only 1 or 2), which were not sufficient to be run by the linear discriminant analysis. Even if these four samples would have been correctly identified, the success rate of the application on archaeological remains is lower compared to the accuracy obtained from the modern dataset.

When the vertebra type was able to be classified visually, the success rate for the family and species level identifications were checked for the archaeological samples (table 4.8).
The success rate for family level identification is rather high for the archaeological samples and is not much lower than the average success rate for the modern dataset. For the caudal vertebrae, there is even a clearly higher success rate for the archaeological samples. Due to the absence of other families in the archaeological dataset, however, this success rate should be treated with caution, as this wouldn’t necessarily reflect a real classification test.
When looking at the success rate of the species identifications, there is a clear difference between the archaeological dataset and the modern dataset. In most cases, less than 50% of the archaeological samples are correctly identified to species. Furthermore, the analysis identified the samples to a variety of different species, which were mostly not recorded from the archaeological sites.
Overall the sinistral view seems to be the most successful view to identify the archaeological material to species (40.00%). The combined view (35.24%) and the anterior view perform much worse (26.67%).

Table 4.8. Percentage of correctly identified archaeological samples to taxon using GMM when vertebra type is provided. Species verified by collagen peptide mass fingerprinting.

Species (ZooMS)	Species (GMM) Anterior	 Sinistral	 Combined
Atlas vertebra			
Pleuronectidae (n=8)	7 (87.5%)	7 (87.5%)	8 (100.00%)
P. flesus (n=4)	1 (25.00%)	2 (50.00%)	2 (50.00%)
P. platessa (n=4)	1 (25.00%)	2 (50.00%)	1 (25.00%)
Cervical vertebra			
Pleuronectidae (n=11)	9 (81.82%)	9 (81.82%)	9 (81.82%)
P. flesus (n=9)	0 (0.00%)	5 (55.55%)	2 (22.22%)
P. platessa (n=2)	0 (0.00%)	1 (50.00%)	1 (50.00%)
Precaudal vertebra			
Pleuronectidae (n=28)	26 (92.86%)	27 (96.43%)	25 (89.29%)
P. flesus (n=16)	3 (18.75%)	9 (56.25%)	4 (25.00%)
P. platessa (n=11)	2 (18.18%)	3 (27.27%)	4 (36.36%)
L. limanda (n=1)	1 (100.00%)	0 (0.00%)	1 (100.00%)
Caudal vertebra			
Pleuronectidae (n=58)	54 (93.10%)	55 (94.83%)	55 (94.83%)
P. flesus (n=29)	8 (27.59%)	13 (44.83%)	13 (44.83%)
P. platessa (n=27)	10 (37.04%)	7 (25.93%)	8 (29.63%)
L. limanda (n=2)	1 (50.00%)	0 (0.00%)	1 (50.00%)

The main cause for the overall reduced accuracy of the classification method on the archaeological samples is fragmentation. Archaeological samples are often fragmented due to preservation, which causes structures of the bones to have been broken off or damaged. This makes it difficult to place landmarks in some cases, reducing the morphological information available for a sample. Figure 4.6 shows an archaeological sample that is clearly missing some landmarks. Table 4.9 provides an overview of the frequency a landmark is present in archaeological samples; details per archaeological sample can be found in table C7 in the appendix. In four cases, the few numbers of landmarks present, even hindered the analysis, as the analysis could not be run on samples with only two or fewer landmarks present.

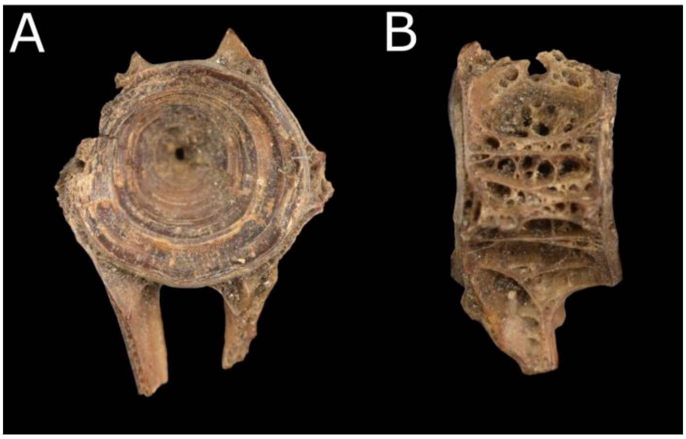

Figure 4.6. Example of an archaeological sample analysed in this study (COP0339), showing the preservation and lack of landmarks. A. anterior view; B. sinistral view.

Table 4.9. The frequency (% of number of samples) of a landmark present in the archaeological dataset.

	Atlas		**Cervical**		**Precaudal**		**Caudal**	
LM nr	**anterior**	**sinistral**	**anterior**	**sinistral**	**anterior**	**sinistral**	**anterior**	**sinistral**
1	0.00	0.00	27.27	9.09	3.57	7.14	3.45	1.72
2	100.00	100.00	NA	36.36	28.57	35.71	1.72	1.72
3	100.00	100.00	NA	90.91	53.57	85.71	1.72	91.38
4	100.00	100.00	100.00	72.73	100.00	71.43	100.00	82.76
5	100.00	100.00	100.00	90.91	100.00	78.57	100.00	82.76
6	100.00	100.00	90.91	81.82	96.43	78.57	96.55	82.76
7	100.00	100.00	100.00	81.82	96.43	71.43	100.00	75.86
8	100.00	100.00	100.00	81.82	100.00	85.71	100.00	91.38
9	87.50	100.00	NA	100.00	92.86	100.00	100.00	100.00
10	100.00		NA	100.00	92.86	100.00	100.00	100.00
11	100.00		NA	NA	100.00	96.43	100.00	98.28
12	100.00		NA	NA	100.00	100.00	100.00	100.00
13	0.00		100.00		100.00		96.55	
14			100.00		100.00		98.28	
15			100.00		100.00		98.28	
16			90.91		100.00		98.28	
17			81.82		75.00		72.41	
18			81.82		85.71		82.76	
19			90.91		96.43		87.93	
20			0.00		0.00		72.41	
21			0.00		0.00		70.69	
22			0.00		0.00		63.79	
23			0.00		0.00		65.52	
24			0.00		0.00		65.52	
25			0.00		0.00		63.79	

As there is no way of verifying the sidedness of archaeological *P. flesus* samples confidently, the classification of right- and left-eyed *P. flesus* is not further discussed. Several samples were classified as left-eyed specimens for at least one view using this classification method per vertebra type and only one sample was classified as left-eyed by all three views (table C6 in appendix).

4.4 Discussion

4.4.1 Morphological variation between modern samples

Geometric morphometrics allows some distinction between vertebrae type and taxa of modern flatfish vertebrae via analysis of 2D landmark configurations of two views.

Of the landmarks initially selected, some were discarded during the analysis, as it became clear they were either difficult to use consistently (see table C2 and figure C26) or were often missing in archaeological remains and contributed little to morphological variation, such as the arch tips (figures C22-C24). Loss of the arch tips improved the differentiation between taxa in a PCA slightly in some cases, which was most obvious in the sinistral view and the caudal

vertebrae. This might be explained by the fact that the relative position of the arch tips changes strongly with vertebra number, which is especially apparent in the sinistral view and in the caudal vertebrae. Loss of the arch tips reduces the morphological variation caused by the vertebra number and makes the variation related to taxonomy relatively more important.
Furthermore, as vertebra types can differ in their landmark configuration, it is important to have the option in the analysis to change the landmark subsets depending on the vertebra types included. This also allows for comparisons between different landmarks sets for the same vertebra type. This is easily done through the use of R rather than premade geometric morphometric software.

Distinction between vertebra types is easily carried out with GMM, especially in the anterior view, although not perfect as seen in figure 4.4. This view is also the most useful for visual classification of vertebra type by zooarchaeologists as vertebra types differ strongly in the implantation of the haemal arches, which shows best in the anterior view.

One of the easiest ways to visually distinguish between vertebrae of different Pleuronectiformes taxa is the general shape of the vertebra, but also the surface of the lateral side of the center of the vertebra, which often consists of several ridges running anteroposteriorly along the center. These ridges, however, could not be landmarked as there don't seem to be any clear homologous structures present between the taxa, losing potentially very diagnostic features for the GMM analysis and resulting in limited separation in the PCA between the vertebrae types.

From the analysis on the modern reference samples, it seems that the anterior and combined views are best to distinguish between taxa using the atlas vertebrae. The cervical vertebrae cannot be used to distinguish taxa using PCA. This is partly due to the reduced number of landmarks available, as the haemal processes are absent, but could also be due to the limited morphological variation between taxa. Precaudal and caudal vertebrae can be used in several cases to distinguish between taxa, although in most cases the separation is not clear and there remains some overlap between the taxa on the principal component plot. This could mean that the vertebrae between and within families are rather similar and only show slight morphological differences that are being picked up by this GMM approach.

The atlas vertebra seems to allow for much better distinction between taxa than the other vertebrae types, which could be due to the more distinct shape of the center and the presence of the condyli. These articulate with the neurocranium, which provides more morphological shape variation and is more taxon specific compared with vertebrae (e.g., Wouters *et al.*, 2007).
With cervical vertebrae being in the transition zone from the neurocranium to the body, the size and shape of structures such as the onset of the haemal arch and the implantation of the neural arch, differ strongly between these few vertebrae at the beginning of the spinal column. This could create a greater morphological difference between vertebrae from the same individual than between vertebrae from different species. Also along the caudal vertebra series, this could explain the lack of distinction between taxa seen in the PCA, as especially in the sinistral view, the stronger inclination of the arches, even at their bases, could create more variation within an individual than between taxa. The precaudal vertebrae in general seems to show the best distinction for all taxa and all views, but also here a slight effect of the changes along the spinal column could create noise in the analysis. As PC1 seems to barely

show a distinction between taxa using the cervical, precaudal and caudal vertebrae, it is assumed that this axis carries the variation caused by the changes along the spinal column.

In this dataset it seems that precaudal vertebrae - and potentially atlas and cervical, although more samples are needed to verify this - do show a slight morphological distinction between right- and left-eyed *P. flesus* as seen in the PCA using the anterior view, where the asymmetry can be best detected.
By applying this technique on archaeological bones, this could potentially reveal the presence of many reversed flounder in assemblages, as there are not many reversed flounder bones reported so far from archaeological sites. Distinguishing between these two forms could reveal more about the populations and ecology of exploited flounder, as the abundance of reversed flounder is geographically dependent and could impact the ecology of the individual fish (Fornbacke *et al.*, 2002; Russo *et al.*, 2012).

Although the distinction between taxa is limited, there does seem to be slight differences in shape between vertebra types and taxa in specific subsets, meaning it could potentially be possible to identify vertebrae by comparing their shape with this modern reference dataset.

4.4.2 Classification of modern samples

A high mean accuracy was obtained using the bootstrap classification test on modern specimens showing the potential to use GMM to identify species of flatfish using vertebrae.

From the analyses it is clear that the combined view in general allows for higher classification accuracies compared to the anterior and sinistral views individually. It is therefore recommended to use the combined view approach for identification analyses. The improved accuracies can easily be explained by the increased amount of morphological information present in the dataset when combining different views together. This approach can be used to simulate a 3D methodology and can be of use when 3D modelling is not possible due to time constraints, issues with accessibility to scanning material or analysing software, or when two separate landmark datasets are required when dealing with non-spatially linked objects or living organisms. When available, however, a 3D approach is preferable (Profico *et al.*, 2019). Only for atlas vertebrae does the anterior seem to be better at classifying families and Pleuronectidae than the combined view. This might be due to the presence of the condyli in the anterior view, providing crucial diagnostic shape information, without the noise from the sinistral view.

The mean accuracies are rather high for most subsets, indicating that the little morphological distinction between taxa is enough for the analysis to work in most cases, albeit not perfect. The high accuracy for *P. platessa* and *P. flesus* is remarkable, which shows that there is ample morphological distinction between these two species. This contrasts with the lack of clear diagnostic features found between these two species so far using conventional visual morphological identification (Wouters *et al.*, 2007; Chapter 3 this thesis). The landmark configuration should be explored in more detail to see if any morphological difference between the two species can also be detected visually; although none was observed during a short study after obtaining the GMM results. The lowest mean accuracies were consistently noticed for Pleuronectidae. The mean accuracy to distinguish between species in this family was even lower than 0.5 for the atlas vertebrae. This family contains many species with similar morphology of the vertebrae. The lower accuracy could be due to the lack of distinction between the taxa, as noticed during the first part of the analysis, and potentially also due to the inadequate number of specimens per species included in this study compared to the number of species in this family. The lack of distinction between Pleuronectidae species was noticed early on in this research and even adding more specimens for these species during the analysis did not improve distinction. It is therefore more likely that there is simply not enough morphological differentiation that would allow a successful classification of these osteologically similar species.

Contrary to what was expected is the low accuracy of determining the sidedness of *P. flesus* for cervical and precaudal samples. This can however be explained by the small sample size of these two subsets. For the caudal vertebra, the success rate is rather high with a mean accuracy of 0.69 for the combined view and 0.68 for the anterior view. Asymmetry can be best detected from the anterior view. Therefore, as expected, the anterior and combined views give the highest accuracy. As there is some distinction between both forms on the PCA plot (see figure C25) for the precaudal vertebrae, it can be expected that the accuracy can be increased if more samples are available to use as reference material to allow for a comparative classification.

This classification method could be used in the future to look for any diagnostic features that would allow visual identification of flatfish vertebrae, as mentioned above for *P. flesus* and *P. platessa*. It would be possible to assess which landmarks contribute the most to the differentiation of taxa, which would mean that there are morphological differences between taxa. Potentially, these could be used to describe a visual identification method as well. This was not attempted in-depth in this study due to both time constraints and the morphological analysis carried out in Chapter 3 (this thesis) not resulting in useful diagnostic criteria. Furthermore, assessing which landmarks are required for successful and accurate classification could help to select vertebrae for analysis that minimally have these essential landmarks present, which can avoid unnecessary analyses.

4.4.3 Identification of archaeological samples

The identification success of vertebra type, family level and species level on archaeological samples is much lower than for the modern dataset as expected due to the generally poor preservation of archaeological remains which reduces the number of available landmarks for analysis. This results in a lower accuracy of the classification system, meaning only well-preserved samples might be able to be identified using GMM. As was noticed during the analysis, however, even archaeological samples that were not severely fragmented, occasionally had low identification success. In addition to fragmentation, preserved archaeological bones can also become deformed during taphonomic processes, which may alter the shape of bones. No sample analysed in this study showed clear deformation visually and it is therefore thought that this has only minimally affected this analysis.

The type of a vertebra is only correctly identified in around 70-75% of cases using GMM, whereas this can easily be done visually by a trained zooarchaeologist as long as there is some preservation of the haemal arches. As can be expected, the anterior view works best overall to classify the vertebra type using GMM, as this view allows the best interpretation of the presence and shape of haemal arches. The sinistral view seems to work well with caudal vertebrae, which can be explained by the stronger inclination of the base of the arches in these vertebrae, which can be detected by GMM. Even with the bases of the haemal arches present, GMM still classifies some vertebrae incorrectly, making GMM potentially less reliable than a visual classification to vertebra type.

Family level identifications are relatively successful on archaeological material compared to modern specimens, while species level identifications are much less accurate. As fragmentation usually occurs on the arches and spina, it could be that these structures are more important for species level identifications than for the family level identifications. Furthermore, identification is somewhat difficult due the small shape variation observed between species, which is more apparent within a family than between families. This is especially a limiting factor for Pleuronectidae which affects the applicability of the method. When only considering *P. platessa and P. flesus* in the dataset, there are clear improvements for the species identification compared to the situation where all species are included in the analysis (see table C2 in appendix), although the species identifications are still much less accurate than in the modern dataset. Contrary to what was found during the classification test on modern material, the sinistral view has the highest success rate on archaeological material to identify a sample to the correct species. It may be that the fragmentation of landmarks in the anterior view has a larger effect on the success rate than the fragmentation of landmarks in the sinistral view.

As no other landmarks could be defined other than the ones used and trialled here, alternative shape analysis approaches could potentially be applied to see if these have a higher success rate of identifying archaeological samples. One possible approach is the addition of semi-sliding landmarks, which can capture the curvature of the centrum of the vertebrae in anterior view, as has been done by Guillaud *et al.* (2016). Also, 3D approaches (e.g., Sztencel-Jabłonka *et al.*, 2009; Gabelaia *et al.*, 2018; Caro *et al.*, 2019) and neural networks (e.g., Storbeck & Daan, 2001; Rauf *et al.*, 2019) are other alternative approaches, of which the latter can be used potentially to include some of the more nuanced and non-landmarkable features in the analysis, such as the ridges running along the lateral side of the vertebrae.

The combination of a limited shape variation and fragmentation of the archaeological samples is the most likely reason why geometric morphometrics is not a reliable tool for species identification of archaeological remains of flatfish, as less than 50% of the samples are correctly identified. Alternative identification methods, such as collagen peptide mass fingerprinting (e.g., Dierickx *et al.*, 2022) and DNA (e.g., Kijewska *et al.*, 2009; Pappalardo & Ferrito, 2015), are required to differentiate between vertebrae of different species of archaeological flatfish in the North Sea area.

4.5 Conclusion

Landmark-based geometric morphometric analysis on 105 flatfish vertebrae from the North Sea revealed that this technique is unreliable to identify archaeological material of Pleuronectiformes to species as fewer than 50% of analysed samples are correctly identified. This is most likely due to the combination of a lack of morphological shape variation between taxonomic groups and the fragmentation of archaeological material. The technique however does show promising results on modern flatfish vertebrae and it could be used for other datasets as well, thanks to the flexibility of the software written.

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Chapter 5. Peptide mass fingerprinting of preserved collagen in archaeological fish bones for the identification of flatfish in European waters

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The majority of Chapter 5 is formed of a paper recently published in *Royal Society Open Science* (Dierickx, K., Presslee, S., Hagan, R., Oueslati, T., Harland J., Orton, D., Alexander, M., Hendy, J., Harvey. V. (2022). Peptide mass fingerprinting of preserved collagen in archaeological fish bones for the identification of flatfish in European waters. *Royal Society Open Science,* 9(7), 220149.). Katrien Dierickx has been responsible for conceiving the idea for this study, sample collection, lab work, data analysis, interpretation of the zooarchaeological results and drafting the paper. Tarek Oueslati (University of Lille), the York Archaeological Trust and Cecily Spall (Field Archaeology Specialists) provided the archaeological samples. Lab work and analyses was done with the training by and support of Samantha Presslee (University of York, UoY), Richard Hagen (UoY), Jessica Hendy (UoY), and Virginia Harvey (UoY; University of Chester). Results of the archaeological analysis were analysed and discussed with the help of Tarek Oueslati and Jen Harland (UoY; University of the Highlands and Islands). Michelle Alexander (UoY) and David Orton (UoY) provided feedback on the manuscript. The general archaeological application of collagen peptide mass fingerprinting has not yet been published and it is intended to include these results in the same publication as the isotope results (Chapter 6).

Abstract

Bones of Pleuronectiformes (flatfish) are often not identified to species due to the lack of diagnostic features on bones that allow adequate distinction between taxa. This hinders in-depth understanding of archaeological fish assemblages and particularly flatfish fisheries throughout history. This is especially true for the North Sea region, where several commercially significant species have been exploited for centuries, yet their archaeological remains continue to be understudied. In this research, 8 peptide biomarkers for 18 different species of Pleuronectiformes from European waters are described using MALDI-TOF MS and LC-MS/MS data obtained from modern reference specimens. Bone samples (n=610) from thirteen archaeological sites dating to the Medieval period (c. 6th–16th century CE) were analysed using ZooMS. Of the 609 that produced good quality spectra, 467 were identified as flatfish species, revealing a switch in targeted species through time and indicating that ZooMS offers a more reliable and informative approach for species identification than osteological methods alone. We recommend this approach for future studies of archaeological flatfish remains as the precise species uncovered from a site can tell much about the origin of the fish, where people fished and whether they traded between regions.

Key words: ZooMS; Zooarchaeology; Ichthyoarchaeology; Fish remains; Mass spectrometry; Pleuronectiformes

5.1 Introduction

The North Sea is part of the Atlantic Ocean and is a shelf sea located for the most part on the European continental shelf with a surface area of around 575 000 km^2. This shallow and sandy/muddy sea is an ideal habitat for flatfish (Pleuronectiformes). Over 20 species of flatfish are reported from the North Sea, with around 12 species of modern-day commercial interest (Heessen *et al.*, 2015).

Flatfish remains are difficult to identify to species using morphological analyses due to the lack of diagnostic criteria between taxa in many bones (e.g., Ervynck & Van Neer, 1992; Enghoff, 1999; Wouters *et al.*, 2007; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019), which become even less useful when dealing with badly preserved archaeological bones. For example, since the 1990s only 1–15% of all Pleuronectidae bones have been identified to species, while the remaining samples were categorised at family level (Pleuronectidae) or the *Pleuronectes platessa* Linnaeus 1758*/Platichthys flesus* (Linnaeus 1758)*/Limanda limanda* (Linnaeus 1758)-complex (plaice/flounder/dab respectively) in some major zooarchaeological reports (e.g., Ervynck & Van Neer, 1992; Enghoff, 1999; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019). This issue is more significant for vertebrae than cranial bones as there are even fewer diagnostic morphological features present in these elements that allow distinction between taxa (e.g. Clavel, 1997; Wouters *et al.*, 2007). A similar problem is present within the Scophthalmidae family, whereby species rarely get identified (e.g., Nicholson, 2009; Harland *et al.*, 2016). Within Soleidae *Solea solea* (Linnaeus 1758) (Dover sole) resembles *Pegusa lascaris* (Risso 1810) (sand sole), which are both present in the English Channel and the southern part of the North Sea (Heessen *et al.*, 2015).

Studying flatfish bones from archaeological sites around the North Sea area can help to better understand shifts in the environment, economy, fisheries, human diet and social status throughout history. Since these species complexes are difficult to identify, many questions remain unanswered about their exploitation and how it might have changed throughout time. Identifying species that are known from the more northern or southern areas from the North Sea, such as for example *Hippoglossus hippoglossus* (Linnaeus 1758) (halibut) and *S. solea* respectively, can help to uncover historical environmental changes in the North Sea as well as potentially revealing trade in fish through time (Ervynck *et al.*, 2004). Differentiating species that can occur in freshwater environments, such as *P. flesus*, from marine species (such as *P. platessa* and *L. limanda*) can uncover changes in fisheries and the onset of intensive marine fish exploitation in Europe, the so-called “marine fish-event horizon” which occurred during the Medieval period (e.g., Barrett *et al.*, 2004a). It is therefore important to identify archaeological remains of these fish to species wherever possible in order to understand the history of their exploitation. As flatfish fisheries continue to be of economic importance in modern times (e.g., Marine Management Organisation, 2020; Statbel, 2021), insight into modern exploitation can help the management of the flatfish stocks. Species identification is therefore also of utmost importance when evaluating modern fisheries, and it has been shown that flatfish in the commercial food chain are often misidentified or mislabeled (e.g., Crego-Prieto *et al.*, 2012; Kappel & Schröder, 2016; Christiansen *et al.*, 2018; Deconinck *et al.*, 2020).

ZooMS (Zooarchaeology by Mass Spectrometry) uses peptide mass fingerprinting of collagen ‘Type I’ (hereafter ‘collagen’) preserved in bone tissue to help assign taxonomic identification

(Collins *et al.,* 2009; Buckley *et al.*, 2009; Collins *et al.*, 2010). ZooMS has been used to identify bones, teeth, skin, and antlers of a wide variety of taxa (e.g., Buckley *et al.*, 2009; Buckley *et al.*, 2010; van der Sluis *et al.,* 2014; Charlton *et al.*, 2016; Buckley *et al.*, 2017; Brandt *et al.*, 2018; Buckley *et al.*, 2018; Desmon *et al.*, 2018; Hofman *et al.*, 2018; Amsgaard Ebsen *et al.*, 2019; Harvey *et al.*, 2019; Culley *et al.*, 2021; Marković *et al.*, 2021; Peters *et al.*, 2021), but also eggshells (e.g., Stewart *et al.*, 2013; Presslee *et al.*, 2018) and to identify human remains (e.g., Brown *et al.*, 2016; McGrath *et al.*, 2019; Brown *et al.*, 2021b). There is a growing number of publications applying ZooMS to fish remains (e.g., Collins *et al.*, 2009; Korzow Richter *et al.*, 2011; Buckley, 2018; Harvey *et al.*, 2018). The latest publications describing markers for Xiphiidae, Scombridae and Salmonidae, show the increasing utility of this technique to identify archaeological fish remains to genus and even species level (Rick *et al.*, 2019; Korzow Richter *et al.*, 2020; Buckley *et al.*, 2021). Collagen of certain fish taxa consists of three collagen chains forming a triple helix: α1, α2, and α3. All these three chains differ from each in their amino acid sequence, since all three are coded by different genes (*COL1A1, COL1A2, COL1A3*). This makes certain fish collagen more diverse and more prone to show diagnostic markers between taxa, compared to that of all other vertebrates, which have only two different types of collagen chain (α1, α2) (Korzow Richter *et al.*, 2011; Harvey *et al.*, 2021).

This study aims to improve flatfish identification through the use of a fast and affordable molecular alternative to traditional osteological methods by defining diagnostic peptide biomarkers in extracted flatfish collagen.

5.2 Material and methods

5.2.1 Collagen fingerprinting of Pleuronectiformes

5.2.1.1 Sample selection

Modern Pleuronectiformes bones were sampled from museum and fresh specimens caught in the North Sea and surrounding areas and the Mediterranean Sea since the 1990s. The museum specimens (less than 31 years old) were taken from the collections held at the Royal Belgian Institute of Natural Sciences (RBINS) and the University of York Zooarchaeology Laboratory (YZL). Fresh fish from UK and Belgian shops were water macerated in an oven at 40 ºC for 2–3 days to retrieve their bones. Museum specimens preferably came from untreated bones, although warm-water maceration and cooking does not seem to have a large impact on the collagen quality (Korzow Richter *et al.*, 2011). Bones known to be treated with chemicals were avoided since the collagen could be damaged (Korzow Richter *et al.*, 2011). When sampling museum collections, vertebrae, branchial rays, and fin rays were selected, as these are numerous in fish and contain little morphological information, reducing the impact of destructive analysis.

Eighteen flatfish species from five different families were sampled: Bothidae (*Arnoglossus laterna* (Walbaum 1792)), Citharidae (*Citharus linguatula* (Linnaeus 1758)), Pleuronectidae (*Glyptocephalus cynoglossus* (Linnaeus 1758), *Hippoglossoides platessoides* (Fabricius 1780), *Hippoglossus hippoglossus* (Linnaeus 1758), *Limanda limanda* (Linnaeus 1758), *Microstomus kitt* (Walbaum 1792)*, Platichthys flesus* (Linnaeus 1758)*, Pleuronectes platessa* Linnaeus 1758), Scophthalmidae (*Lepidorhombus boscii* (Risso 1810)*, Lepidorhombus* *whiffiagonis* (Walbaum 1792), *Scophthalmus maximus* (Linnaeus 1758), *Scophthalmus rhombus* (Linnaeus 1758), *Zeugopterus regius* (Bonnaterre 1788)), and Soleidae (*Buglossidium luteum* (Risso 1810), *Pegusa impar* (Bennett 1831), *Pegusa lascaris* (Risso 1810), *Solea solea* (Linnaeus 1758)). Table 5.1 provides an overview and details of the specimens used for each species. Figure 5.1 shows a cladogram with the relations between the included species.

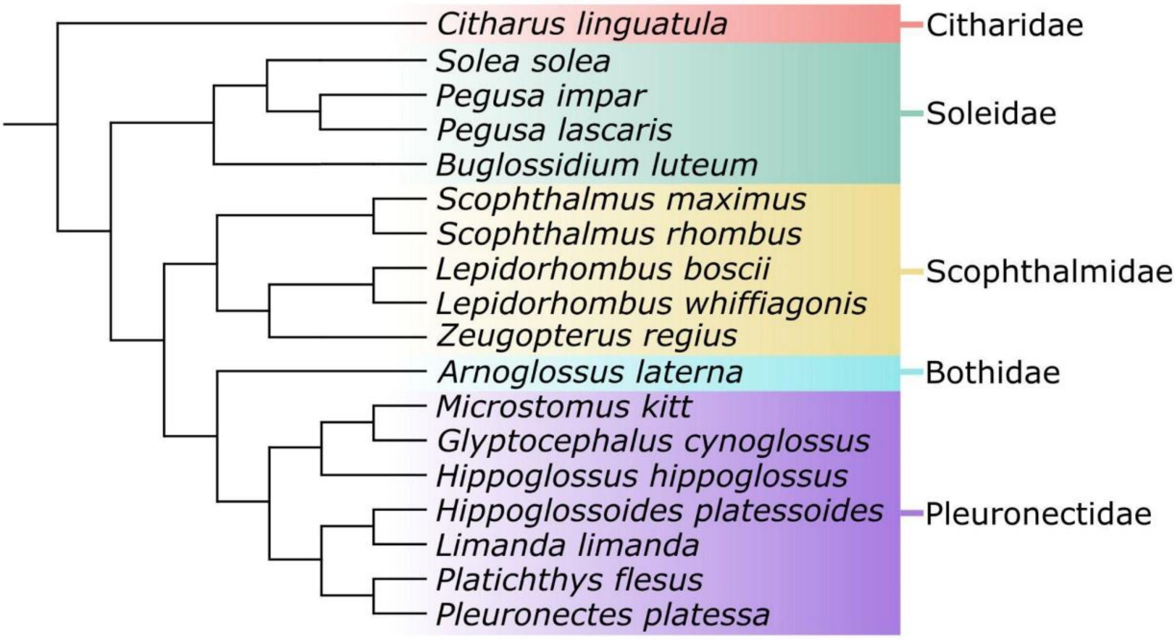

Figure 5.1. Cladogram showing the relations between the 18 species of Pleuronectiformes included in this study, based on Tinti *et al.* (2000), Chanet (2003), and Betancur-R *et al.* (2017).

5.2.1.2 Collagen extraction

All laboratory analysis was undertaken at the University of York. Collagen was extracted from the fish bones using the acid insoluble protocol, adapted from Buckley *et al.* (2009), which consists of the following steps: demineralisation of the bone, gelatinisation, digestion, and purification. Demineralisation of a small piece of bone, between 5 and 35 mg, occurred by adding 250 µl 0.6 M hydrochloric acid to the bone and leaving it at 4 ºC until the bone became demineralised and pliable, usually within 1 or 2 days. The acid was then removed and discarded. To remove any possible contaminants, such as humic acids, the remaining bone was rinsed once with 250 µl 0.1 M sodium hydroxide and three times with a 200 µl 50 mM ammonium bicarbonate (NH_4HCO_3) buffer of pH 8.0 (Ambic). The bone was then gelatinized in a heating block at 65 ºC in 100 µl Ambic for one hour. A 50 µl aliquot of the supernatant was transferred to a new tube, to which 1 µl of 0.5 µg/µl trypsin was added and the solution left overnight in a heating block at 37ºC. Trypsin digests the collagen into strands of peptide at the C-terminal to arginine and lysine residues. After stopping the digestion by trypsin by adding 1 µl of 5% trifluoroacetic acid (TFA), the peptides were extracted and purified using 100 µl Pierce™ C18 ZipTips® with washing (0.1% TFA and UHQ water) and conditioning (0.1% TFA in 50:50 acetonitrile and UHQ water) solutions, as per manufacturer's protocol.

Table 5.1. List of modern specimens used for the ZooMS reference library. All samples were analysed using MALDI-TOF MS and a selection using LC-MS/MS.

Genus	Species	Common name	Museum collection	Skeletal element	Weight (mg)	LC-MS/MS
Arnoglossus	*laterna*	Med. scaldfish	RBINS A2-038-P-17	caudal vertebra	15.3	
Arnoglossus	*laterna*	Med. scaldfish	RBINS A2-038-P-18	caudal vertebra	20.4	x
Arnoglossus	*laterna*	Med. scaldfish	RBINS A4-020-P-02	caudal vertebra	21.3	
Citharus	*linguatula*	Spotted flounder	RBINS 24630	caudal vertebra	16.7	
Citharus	*linguatula*	Spotted flounder	RBINS 24631	caudal vertebra	20.3	x
Citharus	*linguatula*	Spotted flounder	RBINS 24632	caudal vertebra	18	
Citharus	*linguatula*	Spotted flounder	RBINS DCB842	caudal vertebra	28.5	
Glyptocephalus	*cynoglossus*	Witch	RBINS 91-017-P-55	caudal vertebra	27.7	
Glyptocephalus	*cynoglossus*	Witch	RBINS 91-017-P-56	caudal vertebra	21.8	
Glyptocephalus	*cynoglossus*	Witch	RBINS DCB359	fin ray	22.1	x
Glyptocephalus	*cynoglossus*	Witch	YZL 0902	caudal vertebra	15.3	
Hippoglossoides	*platessoides*	Long rough dab	RBINS 91-017-P-142	fin ray	25	x
Hippoglossoides	*platessoides*	Long rough dab	RBINS DCB767	caudal vertebra	26.4	
Hippoglossoides	*platessoides*	Long rough dab	RBINS DCB849	caudal vertebra	20.6	
Hippoglossoides	*platessoides*	Long rough dab	RBINS DCB850	caudal vertebra	31.6	
Hippoglossus	*hippoglossus*	Halibut	RBINS 91-017-P-2	caudal vertebra	31.5	x
Hippoglossus	*hippoglossus*	Halibut	RBINS 91-017-P-78	caudal vertebra	26.8	
Hippoglossus	*hippoglossus*	Halibut	RBINS A4-022-P-0005	fin ray	30.7	
Hippoglossus	*hippoglossus*	Halibut	RBINS DCB844	caudal vertebra	22.1	
Hippoglossus	*hippoglossus*	Halibut	YZL1970	branchiostegal ray	24.8	
Hippoglossus	*hippoglossus*	Halibut	YZL1970	part vertebra	35.1	
Limanda	*limanda*	Dab	RBINS 23876	fin ray	17.6	
Limanda	*limanda*	Dab	RBINS A2-028-P-0041	caudal vertebra	23.2	
Limanda	*limanda*	Dab	RBINS A4-002-P-0061	caudal vertebra	28.6	x
Limanda	*limanda*	Dab	YZL 0853	caudal vertebra	15.7	
Microstomus	*kitt*	Lemon sole	RBINS 23882	fin ray	22.4	
Microstomus	*kitt*	Lemon sole	RBINS A3-001-P-0062	caudal vertebra	34	
Microstomus	*kitt*	Lemon sole	RBINS A4-001-P-0088	caudal vertebra	24.6	
Microstomus	*kitt*	Lemon sole	RBINS A4-001-P-0091	fin ray	19.5	
Microstomus	*kitt*	Lemon sole	YZL 1963	caudal vertebra	31.2	x
Platichthys	*flesus*	Flounder	RBINS A2-028-P-61	caudal vertebra	29.5	
Platichthys	*flesus*	Flounder	RBINS A2-038-P-22	fin ray	16.7	
Platichthys	*flesus*	Flounder	RBINS A4-001-P-36	caudal vertebra	21.4	x
Platichthys	*flesus*	Flounder	YZL 1973	caudal vertebra	18.3	
Platichthys	*flesus*	Flounder	YZL 1974	caudal vertebra	18.8	
Pleuronectes	*platessa*	Plaice	RBINS 23806	fin ray	17.3	x
Pleuronectes	*platessa*	Plaice	RBINS 96-87-P-5	caudal vertebra	25.5	
Pleuronectes	*platessa*	Plaice	RBINS A2-057-P-27	caudal vertebra	19.6	
Pleuronectes	*platessa*	Plaice	YZL 1966	caudal vertebra	15.1	
Pleuronectes	*platessa*	Plaice	YZL 1967	fin ray	16.2	
Pleuronectes	*platessa*	Plaice	YZL 1968	caudal vertebra	24.9	
Lepidorhombus	*boscii*	Four-spot megrim	RBINS DCB773	caudal vertebra	9.7	x
Lepidorhombus	*whiffiagonis*	Megrim	RBINS 91-017-P-14	caudal vertebra	30.8	x
Lepidorhombus	*whiffiagonis*	Megrim	RBINS 91-017-P-26	caudal vertebra	20.4	
Lepidorhombus	*whiffiagonis*	Megrim	RBINS 91-017-P-59	fin ray	29.9	

Table 5.1 continued

Genus	**Species**	**Common name**	**Museum collection**	**Skeletal element**	**Weight (mg)**	**LC-MS/MS**
Lepidorhombus	*whiffiagonis*	Megrim	RBINS A4-001-P-94	caudal vertebra	22	
Scophthalmus	*maximus*	Turbot	RBINS 91-017-P-98	caudal vertebra	30.5	
Scophthalmus	*maximus*	Turbot	RBINS A2-019-P-0047	caudal vertebra	33.3	
Scophthalmus	*maximus*	Turbot	RBINS A2-023-P-0002	fin ray	19.9	
Scophthalmus	*maximus*	Turbot	RBINS A2-052-P-0012	fin ray	26.1	x
Scophthalmus	*maximus*	Turbot	YZL 1962	caudal vertebra	24.3	
Scophthalmus	*maximus*	Turbot	YZL 1964	caudal vertebra	21.8	
Scophthalmus	*maximus*	Turbot	YZL 1965	caudal vertebra	19.4	
Scophthalmus	*maximus*	Turbot	YZL 1969	branchiostegal ray	27	
Scophthalmus	*maximus*	Turbot	YZL 1969	caudal vertebra	22.1	
Scophthalmus	*maximus*	Turbot	YZL 1969	fin ray	21.9	
Scophthalmus	*rhombus*	Brill	RBINS 23664	caudal vertebra	23	
Scophthalmus	*rhombus*	Brill	RBINS 23771	fin ray	25.8	x
Scophthalmus	*rhombus*	Brill	RBINS 24823	fin ray	31.9	
Scophthalmus	*rhombus*	Brill	RBINS A3-004-P-0016	caudal vertebra	19.6	
Scophthalmus	*rhombus*	Brill	YZL 1960	caudal vertebra	27.3	
Scophthalmus	*rhombus*	Brill	YZL 1961	caudal vertebra	20.4	
Zeugopterus	*regius*	Eckström's topknot	RBINS A2-019-P-0030	caudal vertebra	11	x
Buglossidium	*luteum*	Solenette	RBINS 23080	caudal vertebra	20.3	
Buglossidium	*luteum*	Solenette	RBINS 91-017-P-138	caudal vertebra	5.4	x
Buglossidium	*luteum*	Solenette	RBINS A4-020-P-03	caudal vertebra	6.7	
Pegusa	*impar*	Adriatic sole	RBINS DCB915	caudal vertebra	14.9	x
Pegusa	*lascaris*	Sand sole	RBINS A2-057-P-0049	caudal vertebra	20	
Pegusa	*lascaris*	Sand sole	RBINS A2-057-P-0051	caudal vertebra, fin ray	27.8	x
Pegusa	*lascaris*	Sand sole	RBINS A2-057P-0050	caudal vertebra	29.3	
Pegusa	*lascaris*	Sand sole	RBINS A3-004-P-0003	caudal vertebra	29.5	
Solea	*solea*	Dover sole	RBINS 91-017-P-90	caudal vertebra	21.1	
Solea	*solea*	Dover sole	RBINS 24857	fin ray	22.7	x
Solea	*solea*	Dover sole	RBINS A2-019-P-48	caudal vertebra	18.8	
Solea	*solea*	Dover sole	RBINS A2-036-P-28	fin ray	24.2	
Solea	*solea*	Dover sole	RBINS A4-001-P-133	caudal vertebra	27.3	
Solea	*solea*	Dover sole	YZL 1972	caudal vertebra	25.1	

5.2.1.3 MALDI-TOF MS

Extracted collagen was spotted on a 384 steel target plate in triplicate. A 1 µl aliquot of every sample was spotted together with 1 µl of matrix solution (α-cyano-4-hydroxycinnamic acid). Each sample was externally calibrated against an adjacent spot containing a mixture of six peptides (des-Arg1-bradykinin *m/z* = 904.681, angiotensin I *m/z* = 1295.685, Glu1-fibrinopeptide B *m/z* = 1750.677, ACTH (1–17 clip) *m/z* = 2093.086, ACTH (18–39 clip) *m/z* = 2465.198 and ACTH (7–38 clip) *m/z* = 3657.929). The spots were air dried at room temperature. The samples were analysed using a Bruker Ultraflex III MALDI-TOF (matrix assisted laser desorption ionization-time of flight) mass spectrometer at the Bioscience Technology Facility, University of York, with the following settings: ion source 25 kV; ion source 21.4 kV; lens voltage 9 kV; laser intensity 40–55%; and mass range 800–4000 Da. Peptide masses below 650 Da were suppressed.

5.2.1.4 LC-MS/MS

Liquid chromatography tandem mass spectrometry (LC-MS/MS) was performed using a Thermo Scientific Orbitrap Fusion™ Tribrid™ housed at the Centre of Excellence in Mass Spectrometry, Chemistry Department, University of York on one specimen for each species (see table 5.1). Data were acquired over 1 h acquisitions, with elution from a 50 cm PepMap and high resolution MS2 in DDA mode with top12 peaks selected for MS2 per scan.

Peptides were re-suspended in aqueous 0.1% trifluoroacetic acid (v/v) then loaded onto an mClass nanoflow UPLC system (Waters) equipped with a nanoEaze M/Z Symmetry 100 Å C18, 5 µm trap column (180 µm x 20 mm, Waters) and a PepMap, 2 µm, 100 Å, C18 EasyNano nanocapillary column (75 µm x 500 mm, Thermo). The trap wash solvent was aqueous 0.05% (v:v) trifluoroacetic acid and the trapping flow rate was 15 µL/min. The trap was washed for 5 min before switching flow to the capillary column. Separation used gradient elution of two solvents: solvent A, aqueous 0.1% (v:v) formic acid; solvent B, acetonitrile containing 0.1% (v:v) formic acid. The flow rate for the capillary column was 300 nL/min and the column temperature was 40°C. The linear multi-step gradient profile was: 3-10% B over 7 mins, 10-35% B over 30 mins, 35-99% B over 5 mins and then proceeded to wash with 99% solvent B for 4 min. The column was returned to initial conditions and re-equilibrated for 15 min before subsequent injections.

The nanoLC system was interfaced with an Orbitrap Fusion Tribrid mass spectrometer (Thermo) with an EasyNano ionisation source (Thermo). Positive ESI-MS and MS2 spectra were acquired using Xcalibur software (version 4.0, Thermo). Instrument source settings were: ion spray voltage, 1,900 V; sweep gas, 0 Arb; ion transfer tube temperature; 275 °C. MS1 spectra were acquired in the Orbitrap with: 120,000 resolution, scan range: *m/z* 375-1,500; AGC target, 4e5; max fill time, 100 ms. Data dependent acquisition was performed in topN mode using a selection of the 12 most intense precursors with charge states >1. Easy-IC was used for internal calibration. Dynamic exclusion was performed for 50 s post precursor selection and a minimum threshold for fragmentation was set at 5e3. MS2 spectra were acquired in the Orbitrap with: 30,000 resolution, max fill time, 100 ms., HCD; activation energy: 32 NCE.

5.2.1.5 Analysis

All spectra obtained from the MALDI-TOF MS were analysed using mMass software v5.5.0 (Niedermeyer & Strohalm, 2012). The averaged spectrum was cropped between 800–4000 *m/z*. Data from the LC-MS/MS were searched against a local database with 151 published teleost fish collagen sequences obtained from NCBI Blast (Madden, 2002) using Mascot search engine (Perkins *et al.*, 1999; version 2.8.0) as follows: error tolerant; up to 1 missed cleavage; ±3 ppm peptide tolerance; ±0.01 Da MS/MS tolerance; 2+, 3+, and 4+ peptide charge; monoisotopic; Carbamidomethyl (C) as fixed modification; Oxidation (K) and Oxidation (P) as variable modifications. After the initial search, a decoy search was performed to verify the obtained amino acid sequences using the following settings: decoy; up to 2 missed cleavages; ±3 ppm peptide tolerance; ±0.01 Da MS/MS tolerance; 2+, 3+, and 4+ peptide charge; monoisotopic; Carbamidomethyl (C) as fixed modification; Oxidation (K), Oxidation (M), Oxidation (P), and Deamidation (NQ) as variable modifications. The terminology used follows Unimod (Creasy & Cottrell, 2004).

Mass peaks present in the MALDI-TOF MS data that differed between taxa were searched specifically in Mascot. If the score of the peptide given by Mascot was higher than the score for a false-positive match, the peptide was noted as a potential biomarker. Each high-scoring mass peak was checked for quality using the ion spectra given by Mascot. The criteria for a good quality fragment ion spectrum were: 1) many y- and b-ions and/or 2) clear spectrum with high and isolated peaks (figure 5.2). Using the aligned collagen fish database with 151 sequences from NCBI Blast, the locus of the peptide from the LC-MS/MS could be found using BioEdit v7.2 (Hall, 2011). The nomenclature used follows Brown *et al.* (2021a). α1 and α3 collagen chains were differentiated following Harvey *et al.* (2021). The final selection of peptide biomarkers was made by choosing the minimum number of markers needed to distinguish between all species.

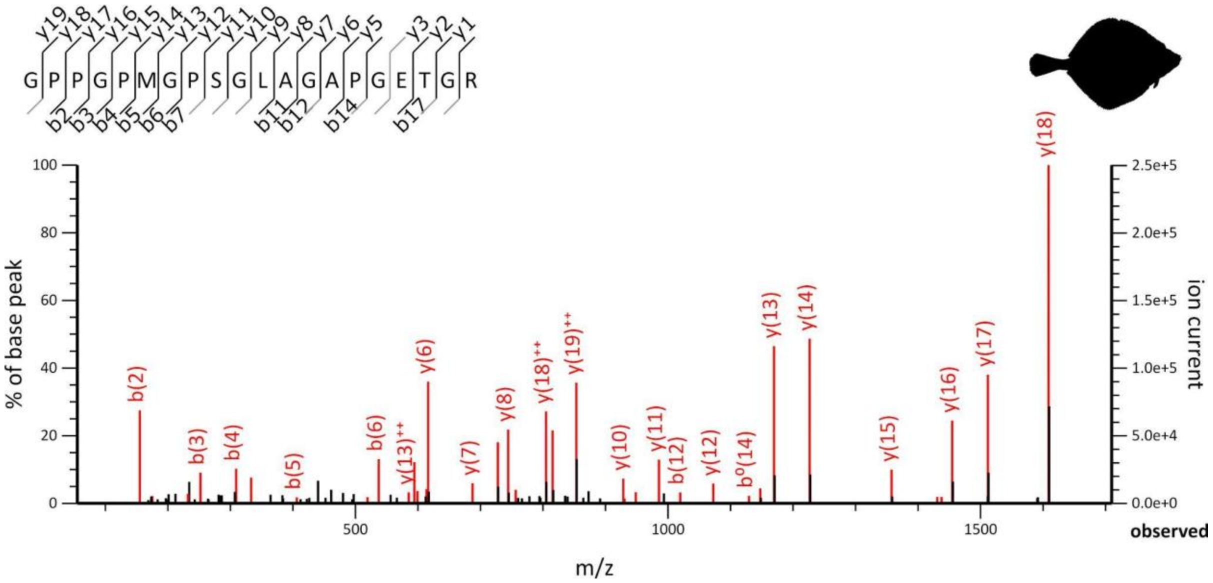

Figure 5.2. Example of a high-quality ion spectrum of the COL1α1 817 - 836 peptide marker of *Pleuronectes platessa* with many y- and b-ions and high and isolated peaks as result of the Mascot search.

Flatfish collagen sequences were obtained *de novo* by scaffolding the peptide sequences obtained via Mascot. For each flatfish species, the whole collagen sequence of the best-matching database sample was cleaned up by removing all the peptides that did not have a score above the homology threshold provided by Mascot and copied into BioEdit. Using the predicted amino acid substitutions from Mascot, each peptide in the alignment was modified to match the most likely substitution. The non-matched part of the sequences were filled with the amino acid sequence of the taxonomically closest available species in NCBI Blast.

As all amino acid sequences of the biomarkers are obtained via LC-MS/MS and Mascot searches, no distinction could be made between isoleucine (Ile) and leucine (Leu) as these amino acids are isobaric (having the same mass). All possible Ile/Leu substitutions predicted by Mascot searches were therefore reported as leucine substitutions as standard. Substitutions between alanine (Ala) and serine (Ser) and between proline (Pro) and Ile/Leu result in a +16 Da mass shift, which is the same as when an amino acid oxidises. As Mascot cannot distinguish between these cases, the most likely amino acid sequence was selected out of the options Mascot provided, based on the probability scores of the different amino acids, the quality of the ion spectra, and the principle of parsimony using the sequence of the most closely related species.

5.2.2 Archaeological application

A total of 202 archaeological flatfish bones were selected from three archaeological sites from the North Sea basin for an initial case study: Barreau Saint-George-Desserte ferroviaire in northern France (n=92); 16-22 Coppergate (n=96), and Blue Bridge Lane (n=14), both from York in the United Kingdom (figure 5.3). These three sites were selected as the material was available at the time when this part of the analysis was appropriate, and the initial results were sufficient to interpret the success of the methodology, thus not requiring to expand to other, later available, archaeological sites. The samples were morphologically identified to family level according to diagnostic morphological criteria for each element as published in Wouters *et al.* (2007) for Pleuronectidae and following comparisons with reference specimens of Pleuronectidae and Scophthalmidae using the fishbone collection at the University of York. From each context one sample from each potentially different individual was selected, which was determined by the species identification, element representation and the estimated size of the individual fish. A substantial quantity of fish bones were uncovered at each of these sites which have been well reported in the literature: Oueslati (2019) for Barreau Saint-George and Harland *et al.* (2016) for both York sites. Table 5.2 summarises the reported flatfish remains from each of the three sites per taxon and period. Original morphological identifications were available for 75 of the Coppergate bones and all (n=14) of those from Blue Bridge Lane.

Barreau Saint-George-Desserte ferroviaire (50° 58' 27.8'' N, 2° 10' 7.6'' E) is located in the city of Saint-George-sur-L'Aa in northern France, close to the coast and connected to the sea by the river Aa. The site dates from the end of the 10th century to the beginning of the 11th century CE. The abundant fish remains from this site were identified as mostly of Pleuronectidae, a single *S. solea*, and some Gadidae (Oueslati, 2019). 16-22 Coppergate (53° 57' 27.4'' N, 1° 4' 51.5'' W) is situated in the city center of inland York, UK, between the rivers Ouse and Foss. A large diversity of fish species have been reported (Harland *et al.*, 2016) with *Anguilla anguilla* (Linnaeus 1758), Clupeidae, Cyprinidae, *Esox lucius* Linnaeus 1758 and Salmonidae being the more common species in the Anglo-Scandinavian periods (7th - 11th century CE), while Gadidae and Pleuronectidae become more abundant during the High and Late Medieval periods (11th - 15th century CE) (Harland *et al.,* 2016). The selected samples from this site date from the Roman period (1st - 4th century CE) to the Late Medieval period (13th - 14th century CE). Blue Bridge Lane (53° 57' 5.6'' N, 1° 4' 34.5'' W) lies south of the walled city center of York at Blue Bridge Lane on the east bank of the river Ouse, at its confluence with the river Foss. *Clupea harengus* Linnaeus 1758 is the most abundant species in this site, but also *A. anguilla*, *E. lucius*, Cyprinidae, and Gadidae are common in certain phases (Harland *et al.,* 2016). The selected samples from Blue Bridge Lane date from the 7th century to the 16th century CE.

More than half (n=113) of the archaeological samples were analysed following the same protocol as described above for the modern reference samples (see table D9 in appendix for details). The remaining samples (n=89) were analysed following a different protocol so that the extracted protein from these selected samples was also available for stable isotope analysis, which requires a greater amount of collagen. Here, 50–500 mg bone was demineralised with 0.4 M HCl at 4°C until the hydroxyapatite was dissolved. The remaining bone was rinsed with ultra-pure water and gelatinised by adding 8 ml of 0.001 M HCl to each sample and placing them in a heating block at 70 °C for 24-48 hours. An Ezee-filter^{TM} was used to remove insoluble debris from the samples before freeze drying for 48 h. ZooMS was performed by dissolving ~1 mg of extracted collagen in Ambic solution, adding 1 µl trypsin and leaving the samples overnight at 37 °C. The samples were then filtered using ZipTips®, plated and analysed on the MALDI-TOF MS following the procedure described above. Each sample was identified by searching for the diagnostic masses from the selected peptide biomarkers on the mass spectra and by matching them to the mass spectra from the reference samples.

In a second part, fish bone samples from 10 other sites (n=408) were also analysed (see Chapter 2 in this thesis for details of the sites) following the dissolving collagen protocol.

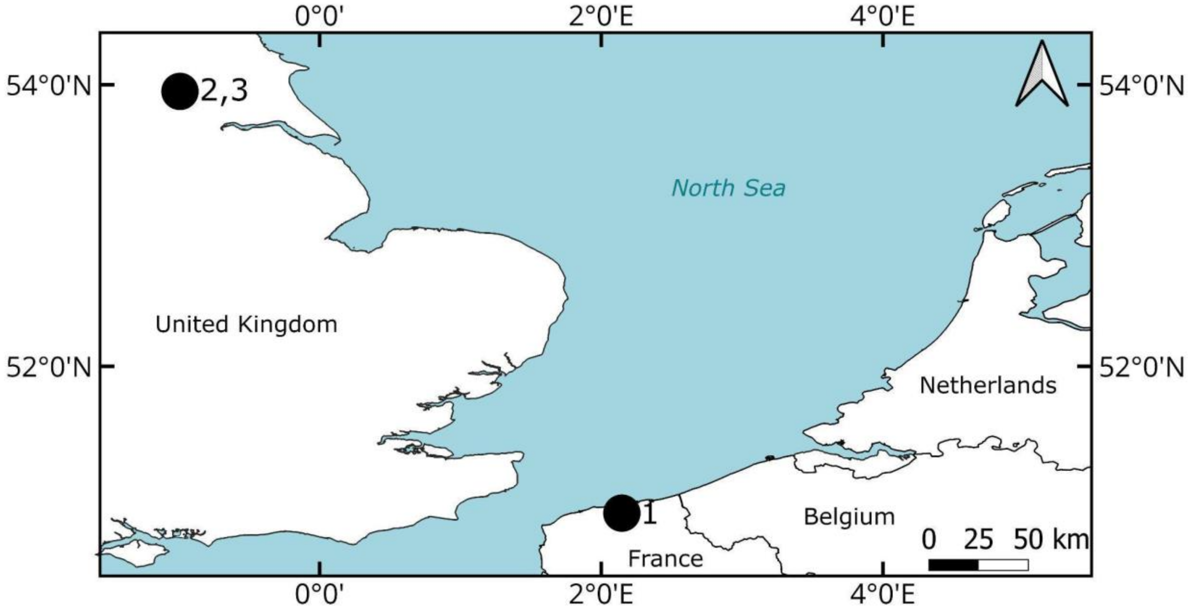

Figure 5.3. Map of the southern North Sea basin with the location of the three archaeological sites. 1: Barreau Saint-George-Desserte ferroviaire; 2: 16-22 Coppergate; 3: Blue Bridge Lane.

5.2.3 Data deposition

Datafiles of the MALDI-TOF MS spectra, LC-MS/MS raw and mgf files, and MZID files of the Mascot query against the collagen database of the reference samples and the MALDI-TOF MS spectra of the archaeological samples from Barreau Saint-George, Coppergate and Blue Bridge Lane were deposited on Dryad and can be accessed by following this link: https://doi.org/10.5061/dryad.5qfttdz7f.

5.3 Results

5.3.1 Taxon resolution

Each of the 18 species included in this study were found to have a unique combination of peptide biomarkers, confirming that European flatfish can be identified to species using collagen peptide fingerprinting. All species can be identified using only 8 different peptide biomarkers: COL1α1 817–836, COL1α1 934–963, COL1α2 625–648, COL1α2 658–687, COL1α2 688–704, and COL1α2 757–789 for all species, and additionally COL1α3 889–909 for Scophthalmidae and COL1α2 991–1027 for *Pegusa* sp. The peptide markers and their corresponding masses are summarised in table 5.3 and the differences between the homologous sequences are detailed in appendices tables D1-8. Each time, *Pleuronectes platessa* is used as the base sequence whenever possible as this is the taxonomic type species of the order. In one case, *Platichthys flesus* is used as the base sequence, as this is the closest related species to *P. platessa*. No sequences were recovered for peptide α1 934 in *Z. regius* and *C. linguatula*, for α2 658 in *G. cynoglossus* and *A. laterna*, for α2 688 in *P. platessa,* and for α2 757 in *A. laterna,* possibly because their sequences did not match any of the sequences in the custom database. Several peptide biomarkers did not show on the MALDI-TOF spectra, but did provide a result when searching using the LC-MS/MS data, probably because not all peptides are charged and detected by the MALDI-TOF MS; these are put between brackets in table 5.3. In several peptide biomarkers, oxidations of proline or other post-translational modifications were noticed for some species, resulting in a mass shift compared with the expected mass based on the amino acid substitutions for that species. Oxidations were also noted if they were seen in the MALDI-TOF MS spectra and uncovered using the Mascot search. The collagen mass fingerprint spectra of each species (figures D1-D18), the ion spectra of each peptide biomarker for each species (figures D19-D127), and the collagen amino acid sequences for each species can be found in the appendix.

5.3.1.1 Pleuronectiformes

All flatfish share a peptide peak at *m/z* 1878 (GFPGTPGLPGIKGHR) of COL1α1 76–90, but this mass peak also seems to be shared with other common species from the eastern Atlantic area such as *E. lucius*, *Melanogrammus aeglefinus* (Linnaeus 1758), Cyprinidae and *Gadus morhua* Linnaeus 1758*.* No single distinct peptide marker was found that is unique to flatfish, but rather it is the combination of multiple biomarkers that distinguishes a particular species. All flatfish species analysed here can also be easily distinguished from other published fish species using the peptide biomarkers described in Harvey *et al.* (2018), Rick *et al.* (2019), Korzow Richter *et al.* (2020), and Buckley *et al.* (2021), as these show different combinations of mass peaks, which match with none of the flatfish.

5.3.1.2 Pleuronectidae

No distinct peptide was found that is unique to the Pleuronectidae. Several Pleuronectidae species share the same sequence and mass for some of the selected peptide biomarkers. Interestingly, *Microstomus kitt* whose placement as a Pleuronectid genus is confirmed by mtDNA and nDNA studies (e.g., Betancur-R., *et al.*, 2013; Vinnikov *et al.,* 2018), has no mass or sequence shared with any of the other Pleuronectidae, indicating that this species is more differentiated and therefore likely to be more evolutionary diverged from the other Pleuronectidae. This case confirms the potential of using the amino acid sequence of collagen as a tool for the phylogenetic mapping of species, as described in Harvey *et al.* (2021). The other Pleuronectidae can be distinguished from each other by combining several of the selected biomarkers. Crucially, the osteologically-similar species *P. platessa* and *P. flesus* can be distinguished by just two peptide biomarkers, illustrated in figure 5.4.

Table 5.2. Reported flatfish remains per taxon as identified morphologically and per period (CE) from Barreau Saint-George-Desserte ferroviaire (BSG) by Oueslati (2019) and 16-22 Coppergate and Blue Bridge Lane by Harland *et al.* (2016). ‘a’ indicates that the species might be present, but identification wasn’t confirmed.

	BSG	Coppergate													Blue Bridge Lane					
	end 10th - beginning of 11th	mid-late 800/early900	c930/935 to 955/6	c955/6	c955/6 to early mid 1000	mid-later1000	mid 1000 to mid 1100	mid 1000 to early 1200	mid 1100 to 1200	1200to late 1200	1275 to mid 1300	1300 to late 1300	1360 to 1500	other	late 7th - mid9th	late 11th-late 12th	late 12th-mid 14th	early-mid14th	late 14th - early 16th	unphased
Pleuronectidae		7	13	5	6	11	9	5	1	24	7		9	5	14	48	3	3	7	1
P. platessa	35				1		2	a		7	a	1	a	1		13	1		1	
P. flesus	56			a	a		1			2				1	1					
plaice or flounder	756														3					
H. hippoglossus						1														
Scophthalmidae							1									2				
S. maximus								a												
Soleidae																2				
S. solea	1																			
Pleuronectiformes															2	1				

Table 5.3. List of the selected peptide biomarkers with corresponding mass peaks (*m/z*) per Pleuronectiformes species. Mass peaks that are not or not always visible in the mass spectra are noted between brackets.

	α1 817	**α1 817 (+16 Da)**	**α1 817 (+32 Da)**	**α1 817 (+48 Da)**	**α1 934**	**α1 934 (+16 Da)**	**α1 934 (+3216 Da)**	**α2 625**	**α2 625 (+16 Da)**	**α2 625 (+32 Da)**	**α2 625 (+48 Da)**	**α2 658**	**α2 658 (+16 Da)**	**α2 688**	**α2 688 (+16 Da)**	**α2 757**	**α2 757 (+16 Da)**	**α2 757 (+32 Da)**	**α2 757 (+48 Da)**	**α3 889 (additional)**	**α2 991 (additional)**	**α2 991 (additional) (+16 Da)**
Pleuronectidae																						
Pleuronectes platessa	1762	1778	1794	1810	2649	2665	2681	2169				2499				2893	2909					
Glyptocephalus cynoglossus	1795	1811	1827		2632			2153	2169					1588	1604	2879	2895					
Hippoglossoides platessoides	(1778)	1794			2629	2645		2173				(2515)		1572		2893						
Hippoglossus hippoglossus	1779	1795			2645			2169				2541	(2557)	1588		2873	2889	2905	2921			
Limanda limanda	(1778)	1794	1810	1826	(2629)	2613		2169				2499		1630		2863	2879					
Microstomus kitt	(1791)	1807	1823		2641	2657		2127	2143			2543		1602		(2867)	(2883)					
Platichthys flesus	(1762)	(1778)	(1794)		(2649)	(2665)	(2681)	2169				2499		1572		(2903)	2919	2935	2951			
Bothidae																						
Arnoglossus laterna	(1778)	1794	1810		(2679)	(2695)	2711	2111						1545								
Citharidae																						
Citharus linguatula	1770	1786						2121	2137			2426		1573		2931	2947	2963				
Scophthalmidae																						
Lepidorhombus boscii	1774	1790			(2655)			2157				2528	2544	1544		2901	2917	2933	2949	1520		
Lepidorhombus whiffiagonis	1760	1776			2655	2671		(2137)	2153			2528		(1560)		(2889)	2905	2921	(2937)	1520		
Zeugopterus regius	(1758)	1774	1790					2137	2153			2528		(1574)		(2911)	2927	2943	(2959)	1534		
Scophthalmus maximus	(1758)	1774	1790		2665	2681	2697	2121	2137	2153	2169	2512		1600		2885	2901	2917	2933	1520		
Scophthalmus rhombus	(1758)	(1774)	1790		2665	2681	(2697)	2121	2137	2153		2512		1556	1572	(2859)	(2875)	(2891)		1520		
Soleidae																						
Buglossidium luteum	1774	1790			2681	2697		2121	2137			(2462)		(1547)		(2955)	2971	2987	(3003)			
Pegusa impar	1784	1800	1816	1832	2723	2739	2755	2095	2111	2127		2468		1517		2955	2971	2987	3003		3490	3506
Pegusa lascaris	1784	1800			(2707)	(2723)	(2739)	2095	2111	2127		2468		1517		2955	2971	2987	3003		3522	
Solea solea	(1784)	1800	1816	1832	(2681)	2697		(2095)	2111	2127		2484		1517		2888	2904					

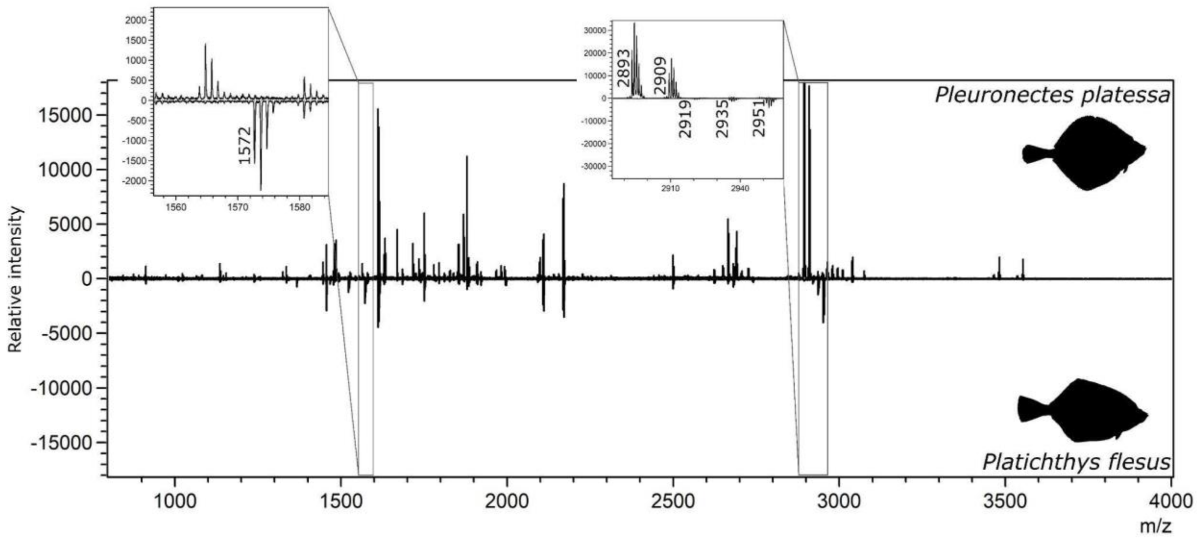

Figure 5.4. Collagen fingerprint comparison between *Pleuronectes platessa* (top) and *Platichthys flesus* (bottom) with details of the peptide markers α2 688 – 704 (left) and α2 757 – 789 (right).

5.3.1.3 Scophthalmidae

All Scophthalmidae share the same sequence for α2 658, although *Scophthalmus* sp. have a lower mass than *Zeugopterus* and *Lepidorhombus* sp. due to the lack of an oxidative modification. Each Scophthalmidae species has a unique sequence for α2 757. Additionally, α1 817, α1 934, α2 625, α2 688, and α3 889 provide diagnostic information for this family. Several masses described in the *Scophthalmus* sp. here, were already noted by Harvey *et al.* (2018) for these species: *m/z* 1600, *m/z* 1774/1790, *m/z* 2137, and *m/z* 2665/2681. For *S. rhombus*, however, no peak at *m/z* 1600 was observed in this study and the peak at *m/z* 1223 described by Harvey *et al.* (2018) for *S. maximus* was not observed in the specimens used for this study, while most *Scophthalmus* sp. showed a peak at *m/z* 1239. One *S. rhombus* did show a peak at *m/z* 1223. The osteologically similar *S. maximus* and *S. rhombus* can be distinguished by two peptide biomarkers, illustrated in figure 5.5.

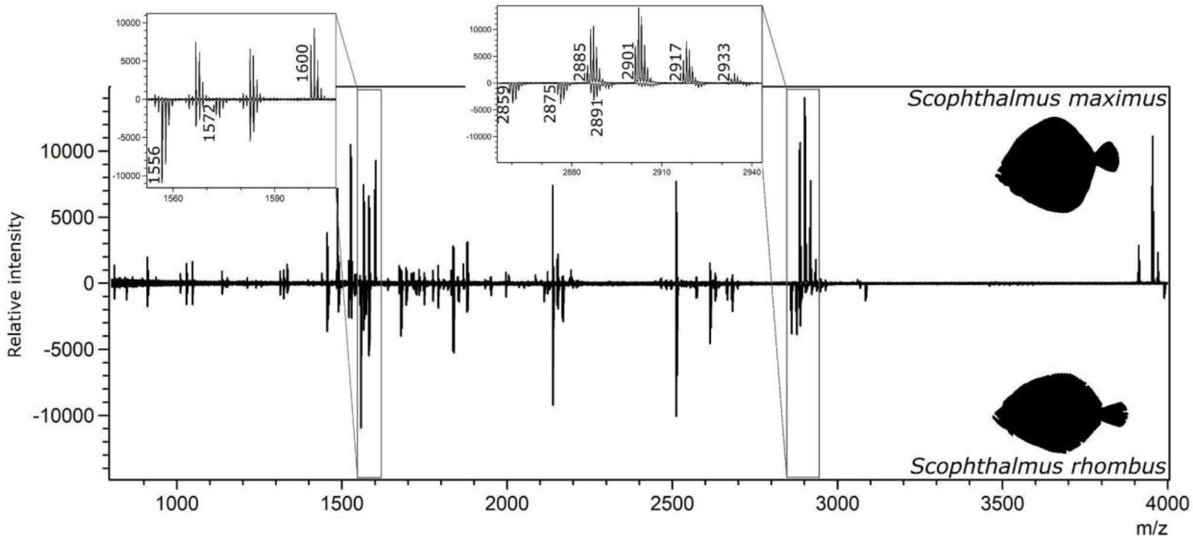

Figure 5.5. Collagen fingerprint comparison between *Scophthalmus maximus* (top) and *S. rhombus* (bottom) with details of the peptide markers α2 688 – 704 (left) and α2 757 – 789 (right).

5.3.1.4 Soleidae

Pegusa sp. and *S. solea* share the same sequence for five of the seven selected biomarkers. *Buglossidium luteum* often has a unique amino acid sequence for the markers. *Pegusa* sp. and *S. solea* can be distinguished using α1 934, and α2 757. *Pegusa impar* shows a peak at 1517 *m/z* from α2 688 in the mass spectrum, but in the reference sample from this study it also showed a slight peak at 1516 *m/z* from COL1α1 076–090 and COL1α1 889–906. *Pegusa impar* and *P. lascaris* do not have different peptide biomarker sequences but do however show differences in their mass spectra, albeit for two markers (α1 934 and α2 991) only with a ±16 Da difference, possibly caused by oxidation, of which only the latter marker distinguishes the species (figure 5.6).

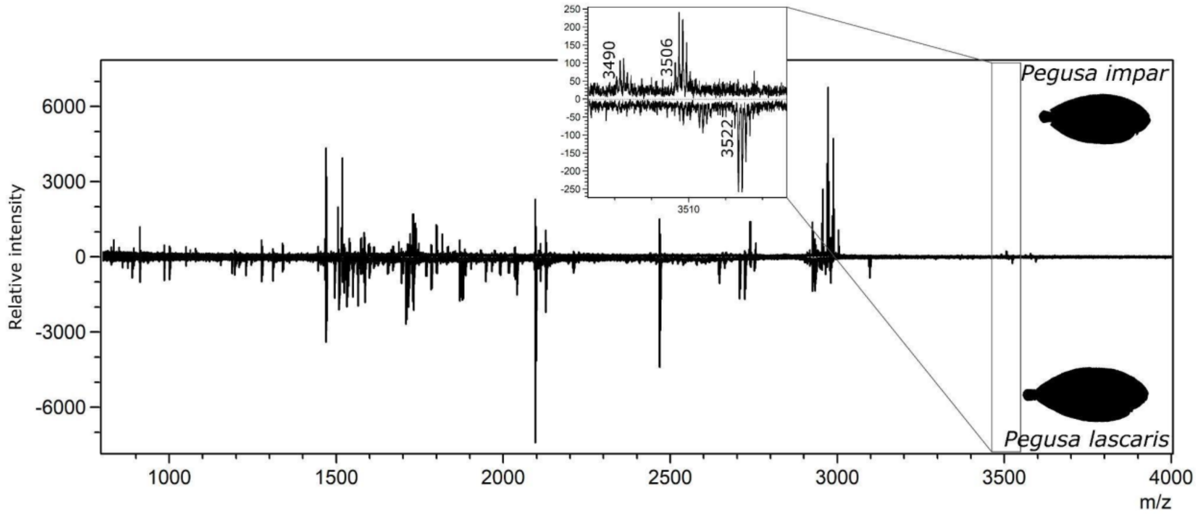

Figure 5.6. Collagen fingerprint comparison between *Pegusa impar* (top) and *P. lascaris* (bottom) with details of the peptide markers α2 991 – 1027.

5.3.1.5 Other taxa

Arnoglossus laterna and *Citharus linguatula*, both being the only representatives of their families in this study, have distinct masses and sequences for several of the markers, which are not shared by any of the other species.

5.3.1.6 Possible issues in data analysis

In some cases, there are overlapping mass peaks visible in the peptide mass fingerprints, which can cause potential confusion when using the selected peptide biomarkers to identify species. For some of the diagnostic masses, another species can show a peak at the same mass (isobaric). In these cases, this peak originates from a different collagen peptide than the diagnostic one (table 5.4).

Table 5.4. List of isobaric masses and peptide markers found with their sequences and the peptide biomarkers with the same masses.

Species	Mass	Sequence	Locus	Confusion with locus	Confusion with species	Remarks
C. linguatula	1534	R.GNPGAAGAAGAQGPIGPR.G	a2 502	a3 889	*Z. regius*	
S. rhombus	2111	K.GSPGAEGPSGASGLPGPQGIAGSR.G	a1 757	a2 625	*S. solea, A. laterna, Pegusa impar, Pegusa lascaris*	
M. kitt	2665	?	?	a1 934	*S. maximus, S. rhombus, P. flesus, P. platessa*	only in 2 samples, no match in Mascot
G. cynoglossus	2863	R.GLTGPIGLPGSAGSTGDKGEPGAAGPVGPGGAR.G	a1 586	a2 757	*L. limanda*	
P. platessa	2947	R.GVMGPTGPVGAPGKDGDVGAQGQSGPAGPAGER.G	a1 421	a2 757	*P. lascaris*	
S. rhombus	2947	R.GPPGPAGSSGPQGFTGPPGEPGEAGASGPMGPR.G	a1 010	a2 757	*P. lascaris*	
S. maximus	2947	R.GPPGSPGSSGPQGFTGPPGEPGEPGASGPMGSR.G	a3 010	a2 757	*P. lascaris*	
S. solea	2947	R.GPPGPAGSSGPQGFTGPPGEPGEAGAAGPMGPR.G	a1 010	a2 757	*P. lascaris*	
P. platessa	2947	R.GPPGPSGSSGPQGFTGPSGEPGEPGAAGPMGPR.G	a1 010	a2 757	*P. lascaris*	

5.3.2 Archaeological sample identification

5.3.2.1 Case studies

Out of the 202 analysed archaeological flatfish bones, 99.5% (201 of 202) of the samples provided a clear mass spectrum suitable for species identification. Out of these 201 successful spectra, 196 were identified as a flatfish species. Only one sample failed to provide a mass spectrum of adequate quality to allow taxonomic identification, most likely due to a lack of preserved collagen. Most of the samples analysed were identified to *P. platessa* and *P. flesus*, with a few examples each of *L. limanda* and *S. maximus* (table 5.5; figures S128-131). Detailed information on the context, dating, estimated size of the fish, skeletal element, original identification, protocol, and ID markers used for each sample can be found in appendix table D9. Due to the lack of labelling, it was not possible to match any ZooMS samples from Barreau Saint-George and 21 from Coppergate to osteologically identified samples from previous reports.

Table 5.5. Overview of the number of samples identified to species by ZooMS from the three archaeological sites.

Species	**Barreau-Saint George (FR)**	**Coppergate, York (UK)**	**Blue Bridge Lane, York (UK)**	**Total**
Pleuronectes platessa	34	57	10	101
Platichthys flesus	58	24	3	85
Limanda limanda	0	5	1	6
Scophthalmus maximus	0	4	0	4
Total identified species	**92**	**90**	**14**	**196**
Failed	0	1	0	1
Unknown species	0	5	0	5
Total per site	**92**	**96**	**14**	**202**

Table 5.6 compares the success ratio of ZooMS with the osteological identifications performed previously on these sites by other authors. Analysis through ZooMS resulted in species identifications for between 93.8% to 100% of the flatfish bones from each site, where only 10.9% to 15.7% of flatfish bones could be identified to species using traditional methods (Harland *et al.*, 2016; Oueslati, 2019). The ratio between *P. platessa* and *P. flesus* was similar for both ZooMS and the zooarchaeological report on Barreau Saint-George (Oueslati, 2019), while the amount of *P. flesus* found using ZooMS was higher than was reported from both York sites (Harland *et al.*, 2016) (appendix table D10). Somewhat unexpectedly, the *L. limanda* and *S. maximus* that were identified through ZooMS were not reported in the previous morphological assessments.

A total of 74 Coppergate and 14 Blue Bridge Lane specimens were available for direct comparison of the original attributions with those derived from ZooMS (appendix table D11). Of the 19 samples identified to species osteologically, only three were misidentified according to the ZooMS identifications. Approximately a fifth of specimens were successfully identified to species osteologically, and most of these were cranial elements, which naturally have more variation between species and are thus easier to identify by morphology. Most of the morphological family level identifications were successful: 69%; with ZooMS then providing further refinement to species level. These were mostly vertebrae, as they are morphologically very difficult to distinguish to species. Six Coppergate bones were morphologically misidentified in some way: 3 cranial elements were incorrectly identified as *P. platessa* when they were *P. flesus* or vice versa; 1 was incorrectly identified as Pleuronectidae when it was Scophthalmidae; and 2 were identified as Pleuronectidae but ZooMS identified them as an unknown fish from the Perciformes order. One vomer was morphologically identified as Scophthalmidae, with a note that the specimen was unusually large and difficult to identify; ZooMS identified this as *P. platessa*. One originally identified bone failed to provide a usable spectrum for ZooMS identification.

Table 5.6. Comparison of the identification success rate of ZooMS applied to the selected samples compared with the success rate of osteological analyses as published in the zooarchaeological reports for the three sites. Data from the zooarchaeological reports taken from Harland *et al.* (2016) and Oueslati (2019). Higher taxon level means any osteological identification to genus, family or order.

	Identified using osteology		**Identified using ZooMS**	
	number	**percentage**	**number**	**percentage**
Barreau Saint-George				
NISP	848		92	
Higher taxon level	756	89.16%		
Species level	92	10.85%	92	100%
Coppergate				
NISP	120		96	
Higher taxon	103	85.83%		
Species	17	14.17%	90	93.75%
Blue Bridge Lane				
NISP	102		14	
Higher taxon	86	84.31%		
Species	16	15.69%	14	100%

Table 5.7. Distribution of *Pleuronectes platessa* and *Platichthys flesus* samples per larger time period of Coppergate and Blue Bridge Lane.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***
7th - mid 10th	2	15
Mid 10th - mid/late 11th	2	4
Mid 11th - late 12th/early 13th	18	3
12th - 16th	45	3

Within the York sites, there is a clear switch in dominant flatfish species throughout the Medieval period (table 5.7). During the Early Medieval period/Anglo-Scandinavian period (7th–mid/late 11th century CE), *Platichthys flesus* is the dominant species within the samples analysed for both case studies in York, while during the High and Late Medieval periods (mid 11th–late 12th/early 13th and 12th–16th century CE) *Pleuronectes platessa* becomes the most abundant flatfish species.

One bone, initially selected for analysis as it resembled *S. solea*, turned out to be a *C. harengus* after matching it with the spectra published by Harvey *et al.* (2018). Three samples were similar to each other in their mass spectrum and morphologically resembled *Perca fluviatilis*, matching tentatively with the published spectrum from this species by Harvey *et al.* (2018). COP0133 could not be identified to species. Its mass spectrum does resemble the reference sample of *P. flesus* from Buckley *et al.* (2022) analysis, but as this sample does not match our reference mass spectra for *P. flesus*, we are unsure which species this COP0133 is. One possibility is that this sample was simply contaminated in the lab with another sample, causing several peaks typical for Pleuronectidae to appear, but without matching exactly to one species. Another option could be that this sample belongs to another (sub)species of flatfish (e.g. *P. solemdali* from the Baltic region (Momigliano *et al.*, 2018) that might perhaps show a slightly altered mass spectrum compared with the congenerics from the North Sea. As this vertebra sample dates from the 13th century and previous research showed that cod from the Baltic Sea was being imported to York at that time (Barrett *et al.*, 2011), this could be a valid possibility. Another option could be hybridisation of two species of Pleuronectidae. Without access to a well-identified modern sample with known geographical or genetic origins, this is difficult to assess further.

5.3.2.2 General archaeological analysis across the southern North Sea

408 additional samples were analysed from 10 other sites (see chapter 2 for detailed descriptions). Out of the 610 samples analysed using ZooMS in total, 19 samples had to be reanalysed a second or even third time as the first result was inconclusive or the sample did not provide a quality mass spectrum. After reanalysis, all these samples produced a high quality mass spectrum. In total, 467 samples were identified as Pleuronectiformes. The remaining samples were identified as other fish taxa using published mass spectra and markers (Harvey *et al.*, 2018; Rick *et al.*, 2019; Korzow Richter *et al.*, 2020; Buckley *et al.,* 2021). However, as there was no general synthesis of collagen peptide mass fingerprinting on Cypriniformes available at the time of this study, all Cypriniformes were not further identified to species. Osteological identification to this order is quite straightforward, and therefore these samples are noted as cf. Cyprinidae for their ZooMS identification. By comparing the mass spectra from these Cypriniformes, it seems that there are at least 6 different species of this order in the dataset.

Taking into consideration that sampling occurred with the intention to analyse a varied selection of flatfish for stable isotope analysis and that only bones large enough for this analysis were considered, we can have a look at the flatfish species presences through time and compare them between regions (table 5.8). Other fish groups are not further considered, as only a few samples of each main group were selected and analysed to serve as a habitat baseline for stable isotope analysis. Therefore, their presence cannot be used to infer changes in fish exploitation. The identifications and further details of all samples can be found in the appendix table D9.

Table 5.8. Flatfish species identified using ZooMS per archaeological site.

Site	***P. platessa***	***P. flesus***	***L. limanda***	***S. maximus***	***S. rhombus***	***S. solea***	**Total**
COP	57	24	5	4			**90**
BBL	10	3	1				**14**
CAO	11						**11**
GSJ	13	8					**21**
SGA	10	5					**15**
SOT	3	4					**7**
CAN	25	6			2	8	**41**
BSG	34	58		1			**93**
KOK	36	8		5	1		**50**
GEN	33	17		2			**52**
VLA	24	12		1			**37**
KAS	2	2					**4**
PLA	13	20					**33**
Total	**271**	**167**	**6**	**13**	**3**	**8**	**467**

Solea solea was only sampled from Tradescent Lane in Canterbury, a High/Late Medieval monastic site. Scophthalmidae were found in a handful of sites, but only in low quantities, from the Early Medieval period in Koksijde to the High/Late Medieval period in Barreau Saint-George, Canterbury, Coppergate, Gent, and Vlaardingen. *Limanda limanda* has only been found in the two York sites from the High and Late Medieval periods. *Platichthys flesus* was found in all sites, except one Early/High Medieval site in London and *Pleuronectes platessa* was found in all sites. In most sites, *P. platessa* is the most abundant species overall, but in Barreau Saint-George and Plantage Leiderdorp *P. flesus* is slightly more abundant.

When looking at the abundances of each flatfish species through time combining all sites (figure 5.7), a slight relative decrease is noticed throughout the Medieval period of *P. flesus,* while *P. platessa* increases relatively. When comparing the frequency of *P. flesus* and *P. platessa* between time periods (excluding the Roman and unknown categories), they seem to significantly differ from each other, as found by a Chi-squared test ($p=0.0005059$, $X^2=22.078$). This indicates that the observed differences in abundance of these two species is dependent on the time period.
Scophthalmus maximus is present throughout most of the Medieval period, but only in very low numbers, while *S. rhombus* is only identified from the High Medieval period. *Limanda limanda* is identified in the High and Late Medieval periods and *S. solea* in the High Medieval period, but each only from one settlement.

To test for any nuanced changes in species abundance through time, each site is individually explored (tables 5.9-17). All samples from the sites Barreau Saint-George, GSJ06, SGA89, SOT89, and Kastanjelaan were dated from the same phases in each site.
In Coppergate in York a clear transition from a dominance of *P. flesus* to a dominance of *P. platessa* is noticed around the 11th century CE, as is mentioned earlier. The other flatfish species identified in York only appear during the second half of the Medieval period.
Blue Bridge Lane has only a few *P. flesus* samples present in the Early Medieval period, but none in the Late Medieval Period, while *P. platessa* is present in all time periods in this site. Although the numbers are low, this matches the situation in Coppergate.
In London, only the site CAO has multiple phases but the only flatfish species identified from that site is *P. platessa*. When comparing the four London sites, it does seem that *P. flesus* is also abundant in the Early and Early/High Medieval period in GSJ, SGA and SOT, and is not present in the High/Late and Late Medieval period in CAO, but this could just be a site effect, and does not necessarily reflect a general economic effect through time.
The site in Canterbury shows a strong dominance of *P. platessa* during the High and early Late Medieval period.
In Barreau Saint-George, *P. flesus* is the most abundant species in the 11th century CE.
In Koksijde both *P. flesus* and *P. platessa* are present, with the latter being dominant in both the Early and High Medieval periods.
In Gent also both species are present throughout the Early and High Medieval periods and both *P. flesus* and *P. platessa* are almost equally abundant in the 12th century.
Pleuronectes platessa seems to be a continuous presence in Vlaardingen from the Early till the Late Medieval period, while *P. flesus* only appears in this site during the Late Medieval period.
In Plantage in Leiderdorp *P. flesus* is the most abundant species in the Early Medieval period, but *P. platessa* also appears in high quantities during the 9th century.

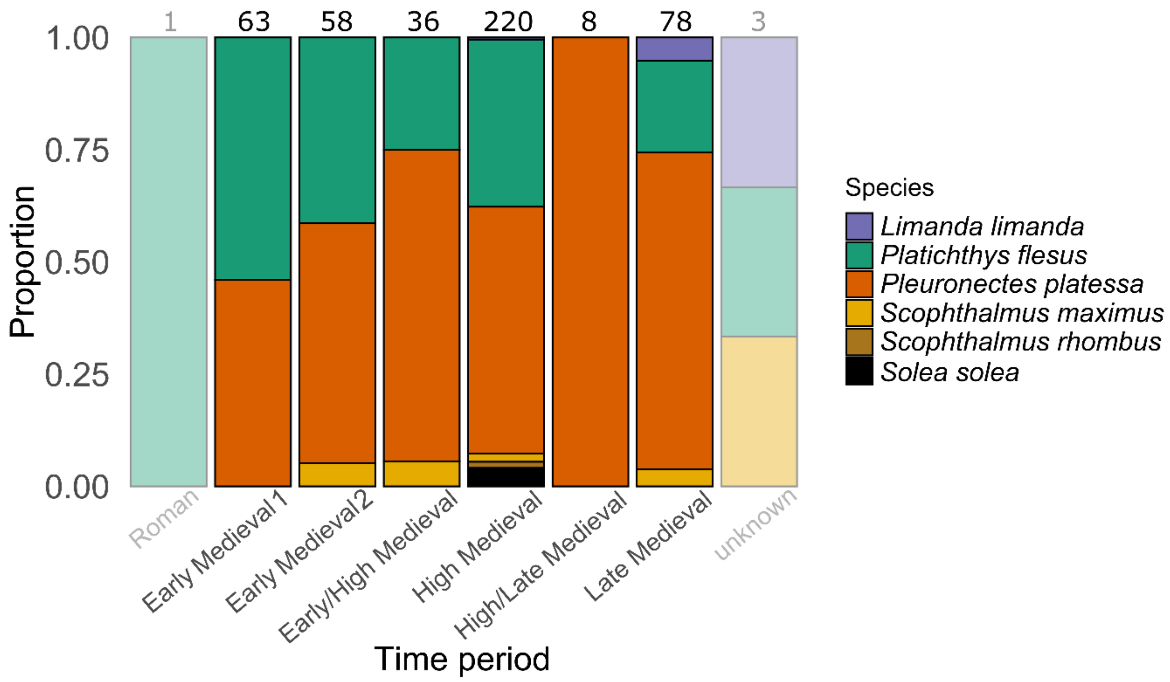

Figure 5.7. Proportions of ZooMS identifications of flatfish species per time period from all archaeological sites. The number on each bar indicates the frequency. The Roman and unknown periods are greyed out for methodological reasons mentioned above.

Table 5.9. Frequency of flatfish samples per larger time period of Coppergate, York.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Limanda limanda***	***Scophthalmus maximus***
late 1st - late 4th or later		1		
7th - mid 10th	1	12		
Mid 10th - mid/late 11th	2	1		
Mid 11th - late 12th/early 13th	18	6	1	1
12th - 14th	36	3	3	2

Table 5.10. Frequency of flatfish samples per time period of Blue Bridge Lane, York.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Limanda limanda***
7th - 8th	1	3	
Late 12th - mid 14th	8		
Late 14th - early 16th	1		1

Table 5.11. Frequency of flatfish samples per time period of the four sites in London.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***
7th - 9th	13	9
900 - 1150	2	
10th - 12th	11	8
1150 - 1270	5	
1240 - 1380	4	

Table 5.12. Frequency of flatfish samples per time period of Tradescent Lane, Canterbury.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Scophthalmus maximus***	***Solea solea***
Early 12th - mid 13th	22	5	2	9
Post 1275	3	1		

Table 5.13. Frequency of flatfish samples per time period of Barreau Saint-George.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Scophthalmus maximus***
11th	34	58	1

Table 5.14. Frequency of flatfish samples per time period of Hof ter Hille, Koksijde.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Scophthalmus maximus***
770 - 1000	10	1	
880 - 1030	4	5	3
890 - 1150	12	1	2
1020 - 1150	10	1	

Table 5.15. Frequency of flatfish samples per time period Zwarte Laag, Gent.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Scophthalmus maximus***	***Scophthalmus rhombus***
10th - first half 11th	12	5		
first half 11th - mid 11th	8	1		
12th	13	11	2	1

Table 5.16. Frequency of flatfish samples per time period Gat in de Markt, Vlaardingen.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***	***Scophthalmus maximus***
891 - 933	2		
1000 - 1050	4		
1050 - 1170	6		
1180 - 1217	1		
1217 - 1250	3	4	
1250 - 1300	6	4	
1300 - 1350	2	4	1

Table 5.17. Frequency of flatfish samples per time period Plantage, Leiderdorp.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***
650 - 760		9
800 - 850	13	11

Table 5.18. Frequency of flatfish samples per time period Kastanjelaan, Leiderdorp.

Period (century CE)	***Pleuronectes platessa***	***Platichthys flesus***
8th - 10th	2	2

5.4 Discussion

5.4.1 Species identification of flatfish using ZooMS

Collagen fingerprinting by mass spectrometry allows straightforward distinction between multiple species of flatfish (Pleuronectiformes) from European waters, especially those of the North Sea. Flatfish species that are frequently reported at archaeological sites and that are able to reach sizes larger than 20 cm SL (standard length), making them interesting for commercial purposes, were included in this study. As not all of the smaller Pleuronectiformes species in European waters were included, mostly due to a lack of access to samples during the coronavirus pandemic, caution is advised when applying this technique to bones from smaller sized fish. Additional species from the North Sea and surrounding areas, such as *Microchirus variegatus* (Donovan 1808), *Zeugopterus norvegicus* (Günther 1862) and *Z. punctatus* (Bonnaterre 1788) from the North Sea and *Reinhardtius hippoglossoides* (Walbaum 1792) from the North Atlantic, should be included in future studies to make more definitive conclusions, especially when trade from more southern or northern Atlantic areas or even the West-Atlantic and Mediterranean is suspected. Based on the results presented here, it can be expected that different genera of flatfish can easily be distinguished using several peptide markers. Within the same genus, however, there might be more difficulties to differentiate between species, depending on the time passed since the divergence of the species, which is correlated to the number of amino acid substitutions of collagen (Buckley, 2018).

Notably, six of the eight selected biomarkers for flatfish were used in previous studies as good markers to distinguish between other fish taxa: α1 688, α1 817, α1 934, α2 625, α2 658, α2 688, and α2 757 (Harvey *et al.*, 2018; Rick *et al.*, 2019; Korzow Richter *et al.*, 2020; Buckley *et al.,* 2021). This could indicate that these specific locations in the collagen sequence are more prone to amino acid substitutions than other regions of the protein, resulting in clear differences between taxa as they evolutionary diverge from each other. The proposed biomarker for *Scophthalmus* sp. at *m/z* 1223/1239 found by Harvey *et al.* (2018), however, was not found consistently in this data set. Both masses can occur in both species as well as in other flatfish, but are just as often absent from *Scophthalmus* sp. Searching for these masses using Mascot did not return any sequences for *S. maximus* and *S. rhombus*. These peptide peaks were therefore not selected as diagnostic biomarkers for flatfish species.

The one available sample of *Z. regius* provided low quality MALDI-TOF and LC-MS/MS data. Since there is only one sample for this species, as for *P. impar* and *L. boscii*, the presence of mass peaks in fingerprints could not be verified and must be used cautiously until more samples are analysed that show the observed biomarkers to be species-specific and to occur consistently in all conspecifics.

Pegusa impar and *P. lascaris* only differ in their mass spectra by a mass shift caused by oxidation, which is not a reliable discriminator, meaning that archaeological samples cannot be identified to the correct species with certainty using ZooMS. As *P. impar* occurs only in the Mediterranean and the southern eastern Atlantic (Quéro *et al.*, 1986), this species could be excluded in some cases when dealing with fish remains from the Atlantic region. However, we cannot exclude the potential of fish being traded between regions. In the Mediterranean region, however, both *Pegusa* sp. can occur as well as many other Soleidae (Quéro *et al.*, 1986).

As some species show isobaric peptides with some of the selected peptide biomarkers of other species, there could potentially be some confusion when trying to identify species using MALDI-TOF MS spectra. For each species for which confusion with another species can happen due to isobaric peptides, only one diagnostic mass seems to be involved, meaning that the other diagnostic masses should not be affected by this. It is therefore advised to use as many of the selected peptide biomarkers as possible when identifying and not to rely on solely one biomarker for each species. Furthermore, it is important to know that some of the proposed biomarkers can be of low intensity in the mass spectra, but that their presence/absence is more important than their intensity for identification purposes. The use of a reference mass spectrum, such as those provided in the appendix, to compare against a sample's mass spectrum is also advised.

With certain Actinopterygii species having a diversified α3 collagen chain, the gene for which originates from the gene coding for the α1 chain, the sequences and therefore the mass from the corresponding locus in both chains could be either the same or different (Korzow Richter *et al.*, 2011; Harvey *et al.*, 2018). This was noted for COL1α1 76–90, which has the same sequence and mass in Pleuronectiformes as COL1α3 76–90. *Esox lucius* and *Gadus morhua,* two European species for which sequence data from the collagen database on Blast was available for the isobaric mass peak, did not have the same sequence for COL1α3 76–90 due to amino acid substitutions. The α3 can therefore provide more variability in certain taxa as it can be diversified, but could potentially also cause some issues interpreting the mass peaks of peptides when they are isobaric.

As the used methodology differs from the one used in Buckley *et al.* (2022), it is difficult to directly compare the peptide mass peaks obtained with theirs and the differences in methodology could explain the different results obtained. When searching for peptide markers proposed by Buckley *et al.* (2022) in our MALDI-TOF MS and LC-MS/MS data, only a few peaks were found, while the majority was not seen consistently in the mass spectra, not found as a collagen peptide, or both.

5.4.2 Archaeological identification and interpretation

5.4.2.1 Case studies

As shown by the three archaeological case studies presented here, ZooMS provides objective, reliable and high-resolution identification of the species assemblage of flatfish remains compared with traditional osteological methods. As such it has the potential to uncover the hidden diversity of flatfish in archaeological assemblages that would otherwise go undetected. The low diversity and relative frequencies of flatfish species found in these three case studies from two different geographical regions confirms the general conclusions from zooarchaeological studies of flatfish around the North Sea area. These indicate that the majority of flatfish remains uncovered represent only a few species, dominated by *P. platessa* and *P. flesus* with occasional finds of *L. limanda*, *H. hippoglossus*, *M. kitt*, *S. solea*, *S. maximus* and *S. rhombus*. A surprising number of *L. limanda* and *S. maximus* were, however, uncovered using ZooMS. At both sites in York the presence of *L. limanda* was not mentioned in the zooarchaeological report by Harland *et al.* (2016). This suggests that some of the less frequently reported species might be more common in the zooarchaeological assemblages than previously understood. With collagen mass fingerprinting, these species might become more visible than relying solely on osteological methods.

Platichthys flesus and *Pleuronectes platessa* are common flatfish species found in the northeast Atlantic. Both species use shallow coastal or estuarine environments for spawning, but when the fish get larger, *P. flesus* is more likely to remain in the estuary or coastal regions, while *P. platessa* moves out to more open marine environments (Russo *et al.*, 2008). Adult *Platichthys flesus* is also found in estuaries, rivers and seas that have a lower salinity than the North Sea and Atlantic Ocean, while adult *P. platessa* seems to be absent or much less common in these habitats (e.g., Aarnio *et al.*, 1996; Selleslagh & Amara, 2008; Selleslagh & Amara, 2015). *Platichthys flesus* also appears to have a preference for specific locations in an estuarine and riverine environment based on its size, with the smaller *P. flesus* more common upstream, while larger *P. flesus* are more common downstream (e.g., Souza *et al.*, 2013; Amorim *et al.*, 2018).

The large proportion of *P. flesus* in Barreau Saint-George is therefore noticeable. Given the small estimated size of these fish (see table D9 in appendix), this would suggest that the juvenile *P. flesus* were exploited in estuaries. As it is thought that flatfish were mostly targeted for local consumption in this site (Oueslati, 2019), a nearby exploitation of small flounder would be practical. Samples from *P. platessa* on the other hand, seem to have come from both small and larger individuals, which are more likely to have been captured in more coastal waters.

At both York sites a dominance of *P. flesus* within the ZooMS samples is apparent in the Anglo-Scandinavian periods (c. 7th–11th century CE), while *P. platessa* became the most abundant species in the High and Late Medieval periods (c. 11th–16th CE). A slight dominance of *P. platessa* during the 12th–14th century CE in Coppergate and Blue Bridge Lane was noticed by Harland *et al.* (2016), but the dominance of *P. flesus* during the Early Medieval period and the timing of the transition between the species has only now been revealed by applying collagen fingerprinting on these fish remains. This chronological shift between flatfish species is significant for mirroring the gradual transition from freshwater and estuarine exploitation to marine fishing seen more generally during the Medieval period. This so-called fish event horizon, is characterised by a relative decrease in freshwater fish exploitation and an increased focus on marine species, such as Gadidae and Clupeidae, probably caused by a multitude of factors such as socio-economic changes, warmer climate, and pollution (Barrett *et al.*, 2004a). The results here show that the transition from the more estuarine and riverine living species *P. flesus* to the more marine *P. platessa* during the 11th century in York coincided with the general intensification of marine fishing in northwest Europe.

The five misidentified samples were thought to be flatfish during the initial selection using osteological methods. These misidentifications show that traditional zooarchaeology can be prone to mistakes even at higher taxonomic levels and that ZooMS is a more reliable and objective method. It also highlights a limitation of this technique however, where at the moment ZooMS is hampered by a lack of good published reference spectra for many fish species and a limited number of species for which peptide biomarkers have been published. By comparing the initial osteological identifications with the results from ZooMS, it seems that traditional morphological methods need to remain at a family level for vertebrae, but selected cranial elements can be (cautiously) identified successfully to species as long as good reference collections are available for consultation. ZooMS can make an important contribution to identify elements for which there are no diagnostic criteria, such as vertebrae (Wouters *et al.*, 2007) and fragmented bones, and to clarify cranial elements that are of uncertain species-level attribution.

5.4.2.2 General archaeological analysis

With ZooMS, species identification of flatfish remains is now possible on a large scale allowing for comparisons between regions and time periods.

There is a clear difference in frequency of *P. flesus* and *P. platessa* between time periods, indicating that there is indeed a relative decrease in consumption of *P. flesus* and a relative increase in consumption of *P. platessa* throughout the Medieval period around the North Sea. This shift is especially noticeable between the High and Late Medieval periods, when marine fishing increased around the North Sea. This would match the species ecologies, with *P. flesus* known to be a more close-coastal and estuarine living species, while *P. platessa* is more associated with open marine environments. It is therefore likely that, as people moved more to the open seas for fisheries, such as those of herring and cod, they also fished more on *P. platessa*. Close coastal fisheries might have become less important economically, therefore reducing the amount of *P. flesus* exploited. Whether this is indeed a correct hypothesis, has to be verified by applying stable isotope analysis, as this could potentially reveal the catch habitat of these samples (see Chapter 6).

Most sites individually follow the same trend, with *P. flesus* being more abundant and often being the most abundant flatfish in the Early Medieval period, while *P. platessa* often is the most abundant species in the High or Late Medieval period. Also the high amount of *P. flesus* in the 11th century site of Barreau Saint-George and the high amount of *P. platessa* in the 12th-13th century Canterbury could be following this trend, although site specific circumstances could also explain these amounts. Both sites are coastal and lie both in the southernmost part of the North Sea, although Canterbury is a monastic site, while Barreau Saint-George is thought to be a fish processing site with potentially important exploitation of *P. flesus* from the nearby estuaries.

Some other sites, however, do not follow the same trend, and show that it is important to look at both the general trends in a region (i.e. North Sea) and trends within a site or settlement, as these would otherwise go unnoticed.

In Leiderdorp *P. platessa* is absent from the 7th-8th century contexts, while it shows up in the 9th century CE and is just as abundant as *P. flesus*. In the initial report from the site excavation it was mentioned that no changes in fish consumption were noticed between the Merovingian and Carolingian period (Dijkstra *et al.*, 2016), but with ZooMS this has changed. The skeletal element distribution also changes in this site around the 8-9th century, with a higher proportion of postcranial bones in the 9th century. In this site the transition between the two species thus seemed to have happened earlier compared to the other sites and based on the element distribution, it might indicate an increase of imported processed fish. One reason for this might be the changing water bodies around the site. During the Carolingian period, the trench was not connected to the Rhine river and probably held still freshwater, whereas during previous periods it was connected to the main river and had a tidal regime. This might have increased the need to import fish that could have been processed (Dijkstra *et al.*, 2016). Furthermore, the long-distance trade across the Rhine with inland and coastal sites increased during the Carolingian period as proven by the import of metal and wood objects for example (Dijkstra *et al.*, 2016), showing that trading and import of fish from other regions should not be excluded.

In London *P. platessa* is abundant early on from the 7th century, although *P. flesus* remains high in abundance as well. It is possible that, with London already trading with the continent via marine routes (Loveluck & Tys, 2006), that marine fishing of flatfish was already ongoing in this settlement early on as people had easy access to the North Sea. This has to be confirmed with the stable isotope analysis of these samples. The larger cities on the continent, with whom London could have been trading, would also have had easy access to the sea. Therefore, it can be expected that larger cities on the continent also would show an abundance of marine fish during the Early Medieval period. As none of the larger trading cities, such as Dorestad in the Netherlands and Paris in France, were analysed here, this cannot be confirmed yet.

Also in Koksijde *P. platessa* is the most abundant species starting from the 8th century, while *P. flesus* seems to be a species of minor importance in this site. Although Koksijde is a coastal site, the lack of a large river and nearby estuaries in this site contrary to Barreau Saint-George, might have favoured the early exploitation of *P. platessa*.

In Zwarte Laag, Gent, both species seem to be present in the High Medieval period, with *P. platessa* seemingly slightly more abundant than *P. flesus*. During the Late Medieval period, both species become equally abundant. Gent's connection to both local estuaries and the open sea could mean that flatfish were exploited from multiple habitats throughout the Medieval period.

In Vlaardingen no *P. flesus* is identified from the Early or High Medieval period, but this species seems to be just as abundant as *P. platessa* in the Late Medieval period. It is possible that the environment around this settlement changed throughout the Medieval period (Van Loon & de Ridder, 2006), favouring *P. flesus* to become more abundant in estuaries. There is archaeological and historical evidence of severe flooding events at the end of the 12th century, after which dikes were put in place, and during later periods (Van Loon & de Ridder, 2006). The type of usage of the site also changed during this period, and the record might contain more domestic refuse, compared to older phases in the site (Van Loon & de Ridder, 2006). It is, however, also possible that in Vlaardingen, *P. flesus* became an economically or culinary interesting choice for people as well to consume, perhaps.

The other flatfish species (*S. maximus, S. rhombus, S. solea,* and *L. limanda*) have only been identified from a handful of samples. This low abundance matches osteological reports on fish remains from around the North Sea, in which *P. flesus* and *P. platessa* are usually mentioned to be the most abundant species, although many osteological identifications remain at a higher taxon level, such as the plaice/flounder/dab complex or Pleuronectidae.

The presence of *S. solea* in Tradescent Lane in Canterbury could be linked either to the location of the site, it being a close-coastal settlement in the southern part of the North Sea, or to the type of occupation, as *S. solea* has been linked to more elite occupations, such as monasteries (Ervynck & Van Neer, 1992).

Scophthalmus species seem to only be present in sites close to the coast and/or in the High and Late Medieval period, when and where marine fishing is ongoing.

None of the other Pleuronectidae, Scophthalmidae or Soleidae or other families found in the North Sea have been identified using ZooMS or traditional zooarchaeological methods on the selected sites. Most of these are either quite small and therefore less interesting for fisheries and consumption or their remains could simply be overlooked during excavations. Further, some of these species occur more in the northern part of the North Sea or in neighbouring waters, making it less likely that these were exploited on a regular basis in the selected sites.

5.4.3 Other applications

This is only one of a few in-depth studies focusing on a single order of Actinopterygii that have found diagnostic biomarkers for all individual species considered. This shows that ZooMS has much potential in this often overlooked group of animals to identify different taxa. In addition to archaeological applications, these peptide biomarkers provide a cheaper alternative to DNA barcoding approaches used in fisheries management to verify the taxon of fish intended for consumption. Recent studies have indicated that modern day fisheries are still troubled by misidentifications in the food chain of wild-caught fish, including flatfish (e.g., Crego-Prieto *et al.*, 2012; Kappel & Schröder, 2016; Christiansen *et al.*, 2018; Deconinck *et al.*, 2020). ZooMS could potentially also be applied to answer other ecological questions such as the trophic food webs of flatfish and the ecology of their predators and indeed those of many other species through, for example, gut content analysis (e.g., Berg *et al.,* 2002; Albania *et al.*, 2012).

5.5 Conclusion

Collagen fingerprinting enables greater depth in the analysis of flatfish remains from European archaeological sites and can improve interpretations of past fisheries, trade, and consumption behaviour. Eight collagen peptide markers, described using MALDI-TOF MS and LC-MS/MS, suffice to identify at least 18 different species of flatfish found in European waters. By analysing 202 fish bones from the three archaeological case studies, species previously unreported from the sites became apparent, which showed that there is still an unknown diversity of flatfish in archaeological assemblages. Furthermore, providing a better understanding of species presences through time, major shifts of fisheries can be detected at a detail level that was not possible previously without ZooMS. Analysis of 13 archaeological sites show a clear trend, switching from *P. flesus* to *P. platessa* throughout the Medieval period around the North Sea, which could be related to environmental changes and socio-economic changes in societies.

ZooMS collagen fingerprinting continues to be of crucial importance to fully understand fish assemblages, and the increasing number of markers available for species identification, will contribute to a more detailed understanding of historical fisheries.

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Chapter 6. Finding the right plaice at the right time: Multi-isotope analysis and collagen peptide mass fingerprinting of flatfish remains reveal historical catch habitats

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This chapter is a draft of a paper that will be submitted for publication in a peer-reviewed journal. Some elements from other chapters in this thesis will also be included for the final paper, such as parts of the introduction (Chapter 1), the major findings of ZooMS identifications (Chapter 5), and the conclusion (Chapter 7). Katrien Dierickx is responsible for sample selection, lab work, data analysis, making figures, interpreting the zooarchaeological results, and drafting the paper. It has received input from David Orton (University of York) and Michelle Alexander (University of York), who provided feedback on the study and draft of the paper. Matt Von Tersch (University of York) assisted with the lab analysis and Peter Schauer (University of York) advised on the statistical data analysis.

Abstract

Flatfish are ecologically diverse species that commonly occur in marine environments, but also in estuarine and riverine habitats. This complicates the examination of the potential role of flatfish in the marine ‘fish event horizon’, an economic shift in human exploitation from freshwater to marine fish species during the 10-11th centuries CE around the North Sea. A multi-isotope analysis of carbon (δ^{13}C), nitrogen (δ^{15}N) and sulfur (δ^{34}S) was performed on collagen from 356 archaeological flatfish and 120 comparative archaeological marine or freshwater species to explore the catch habitat of flatfish between 600 and 1600 CE from the North Sea area. All samples were identified to species using collagen peptide mass fingerprinting. *Platichthys flesus* were captured in both freshwater and marine environments, while other flatfish were derived from marine habitats. No clear transitions are observed, but a subtle shift towards more marine exploitation towards the end of the period is identified. Sites show slight differences in δ^{13}C and δ^{34}S within the same species, related to the local environments. Remarkable is the high abundance of marine *P. platessa* and *P. flesus* during the Early Medieval period, which shows a clear marine or coastal exploitation of flatfish early on, well before the onset of the marine fish event horizon. A minority of human populations continued to rely on freshwater exploitation of *P. flesus* until at least the High/Late Medieval period. This study represents the first multi-disciplinary investigation of flatfish remains to make species-specific interpretations of flatfish exploitation.

Key words: Stable isotopes, Zooarchaeology, North Sea, Medieval, Pleuronectiformes, Fish remains

6.1 Introduction

Archaeological sites around the southern part of the North Sea show a clear increase in marine fisheries in western Europe around the 10-11th century AD, the so-called “fish event horizon” (Barrett *et al.*, 2004a). The most marked increases are seen for Gadidae (e.g., cod (*Gadus morhua* Linnaeus 1758), haddock (*Melanogrammus aeglefinus* (Linnaeus 1758)), whiting (*Merlangius merlangus* (Linnaeus 1758)), which were much less common in inland sites prior to this period. Meanwhile freshwater species, such as Cyprinidae and Salmoniformes became relatively less abundant in later periods (Barrett *et al.*, 2004a; Van Neer & Ervynck, 2007). Flatfish are significant within this dynamic, as certain species commonly caught by humans can reside in both marine and freshwater habitats. The dynamics of flatfish (Pleuronectiformes) exploitation through time hasn't been well understood until now. Flatfish have been uncovered from sites well before the marine fish event, but the representation of the whole order of Pleuronectiformes becomes more abundant in general during and after the marine fish event (Barrett *et al.*, 2004a; Van Neer & Ervynck, 2007).

Pleuronectiformes are regarded as being primarily marine species. Some species, however, are known to occur, at least during a part of their lives, in brackish and freshwater systems, such as for example *Platichthys flesus* (Linnaeus 1758), or European flounder (e.g. van Beek *et al.*, 1989; Elliott *et al.*, 1990; McGoran & Morritt, 2017). Other common species found in the North Sea area, such as *Pleuronectes platessa* Linnaeus 1758 (plaice), *Limanda limanda* (Linnaeus 1758) (dab), *Scophthalmus maximus* (Linnaeus 1758) (turbot), *S. rhombus* (Linnaeus 1758) (brill), *and Solea solea* (Linnaeus 1758) (Dover sole), are generally found in coastal or open marine environments. The spawning season for flatfish varies per species and per location. During this season, they can migrate to specific spawning sites, which could therefore have an impact when and where certain species are available for fisheries (Wimpenny, 1953, cited by Metcalfe *et al.*, 2006). The eggs or larvae can be transported to inshore waters or estuarine nurseries, where the larvae continue to grow (e.g., Jager, 1999; Ramos *et al.*, 2010; Primos *et al.*, 2013). Larvae of flatfish are symmetrical, resembling other teleosts more than their adult conspecifics. At one point during their development, they start to grow asymmetrical and changes in their physiology occur. It is during this orbital migration that flatfish commence their benthic lifestyle and most move out to more marine habitats, but species such as *P. flesus*, are more likely to remain in the estuary or coastal regions (Russo *et al.*, 2008).

There are three main groups of flatfish species based on diet: crustacean-feeders, fish-feeders, and polychaete/mollusc-feeders (De Groot, 1971). The precise diet composition (i.e. relative abundances of prey species), might depend on the locality of a flatfish, the availability of food, and the competition from other species (Livingston, 1987; Darnaude *et al.*, 2001; Guedes & Araújo, 2008), and can impact the isotope composition for individual fish. *Pleuronectes platessa* feeds on small meiobenthos and crustaceans when they are in the postlarval stadium, and switches to feeding mainly on polychaete worms as juveniles to mainly large molluscs, crustaceans and echinoids (Braber & De Groot, 1973; Ameczua *et al.*, 2003). The diet of *Platichthys flesus* consists of crustaceans, molluscs, polychaetes and fish (De Groot, 1971). *Limanda limanda* also feeds on polychaetes, crustaceans and molluscs, and also on bryozoa, echinoids, sponges, fish and fish eggs. There is a shift in the preferred species throughout the life of *L. limanda* towards a wider diversity of crustaceans (Braber & De Groot, 1973). They do not feed on hard shells of molluscs, but rather seem to eat only the soft siphon of bivalves (Braber & De Groot, 1973). *Scophthalmus maximus* and *S. rhombus* feed mainly on fish, such as *Ammodytes* sp., *Clupea* sp., *Gobius* sp., and Gadidae, and also on crustaceans, molluscs and polychaetes. Juvenile *S. maximus* additionally feeds on small crustaceans like shrimps (De Groot, 1971; Braber & De Groot, 1973). *Solea solea* feeds mainly on polychaetes throughout its life (Braber & De Groot, 1973), but is found to also eat a large quantity of bivalves and amphipods in the Mediterranean Sea (Darnaude *et al.*, 2001) and also echinoids, crustaceans, and molluscs (De Groot, 1971).

Due to the changes in habitat choice and diet throughout the life cycle of flatfish, simple species identification of flatfish remains from archaeological sites is not sufficient to tackle the question of where they have been feeding and might have been caught (freshwater, marine, estuarine environments). Bulk stable isotope analysis of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$), of fish collagen can aid in differentiating between fish residing in different aquatic environments and potentially geographic regions (e.g., Fuller *et al.*, 2012; Robson *et al.*, 2016). Furthermore, visual and morphological identification of certain flatfish species, such as *P. flesus* and *P. platessa*, can be very difficult and molecular techniques are required to distinguish between these (Dierickx *et al.*, 2022).

Many studies have analysed fish isotopes from western and northern Europe and the number of dedicated European fish isotope studies is increasing (e.g., Barrett *et al.*, 2008, 2011; Fuller *et al.*, 2012; Hutchinson *et al.*, 2015; Häberle *et al.*, 2016; Robson *et al.*, 2016; Ervynck *et al.*, 2018; Olafsdottir *et al.*, 2021). Most work so far has focused on Gadidae, specifically *G. morhua*, to uncover trade across Europe (e.g., Barrett *et al.*, 2008, 2011; Orton *et al.*, 2011; Nehlich *et al.*, 2013; Hutchinson *et al.*, 2015; Olafsdottir *et al.*, 2021).

Only a handful of isotope studies, however, have included flatfish (figure 6.1 and table E1 in the appendix). Of these, Fuller *et al.* (2012, Belgium), Robson *et al.* (2016, Baltic Sea), and Ervynck *et al.* (2018, Belgium) attempted to determine the catch environment. All flastfish analysed from Mesolithic/Neolithic Denmark (n=6) have remarkably lower $\delta^{15}N$ values and higher $\delta^{13}C$ values than samples from Roman to Postmedieval Germany, Belgium and the UK from the North Sea (n=23). It is possible that this is caused by the presence of seagrass in the Baltic Sea, which is enriched in ^{13}C (Robson *et al.*, 2016; Röhr *et al.*, 2016; Guiry *et al.*, 2021), while the influence of freshwater systems in the Baltic Sea creates an environment lower in ^{15}N compared to the North Sea. *Pleuronectes platessa* (plaice, n=3)*, Hippoglossus hippoglossus* (Linnaeus 1758) (halibut, n=1) and about half of *Platichthys flesus* (flounder, n=7) from Belgium, Germany and the UK seem to have been captured from marine environments, characterised by both high $\delta^{15}N$ and $\delta^{13}C$ values, whereas the remaining half of *P. flesus* (n=5), especially the smaller individuals, were feeding in a freshwater environment and might have been captured there as well (Müldner & Richards, 2005; Fischer *et al.*, 2007; Müldner & Richards, 2007; Antanaitis-Jacobs *et al.*, 2009; Fuller *et al.*, 2012; Göhring *et al.*, 2016; Dahliwal *et al.*, 2019; Ervynck *et al.*, 2018). The small freshwater *P. flesus* are more enriched in ^{15}N than the larger *P. flesus* and *P. platessa*, which could reflect the change in diet throughout the life of this species and dietary differences compared to *P. platessa* (Fuller *et al.*, 2012; Ervynck *et al.*, 2018). No isotope data is available from archaeological non-Pleuronectid flatfish species e.g. *Scophthalmus maximus, S. rhombus, or Solea solea*.

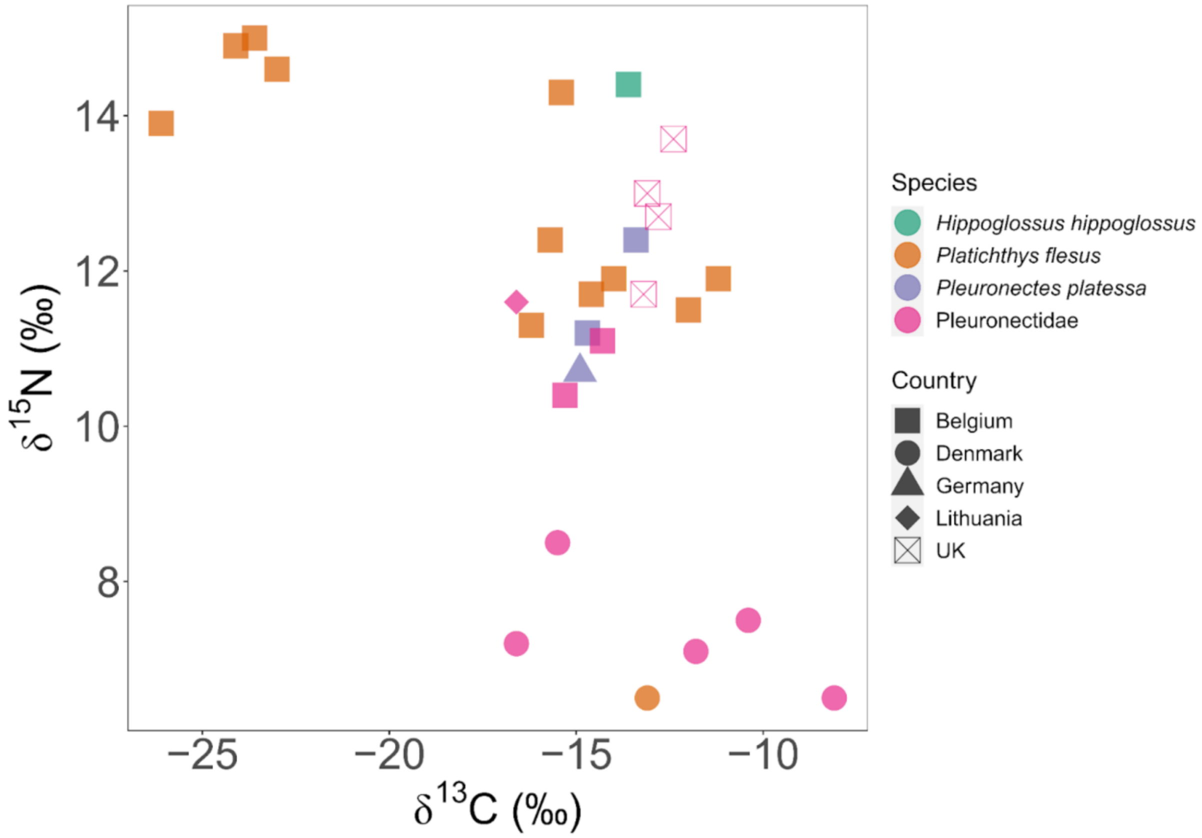

Figure 6.1. Plot of δ^{15}N against δ^{13}C of published archaeological isotope data on Pleuronectidae species from different countries and periods (for details and references see table E1). Green: *H. hippoglossus*; Red: *P. flesus;* Purple: *P. platessa*; Pink: unknown Pleuronectidae; Circle: Belgium; Triangle: Denmark; Square: Germany; Diamond: Lithuania; Crossed square: UK.

In this study, a large body of archaeological remains of multiple species within Pleuronectiformes (n=356) and comparative samples of marine and freshwater fish (n=120) are analysed. An integrated biomolecular approach utilising multi-isotopic (δ^{13}C, δ^{15}N, δ^{34}S) and proteomic species identification (ZooMS) techniques is used to investigate thirteen sites from around the southern North Sea dating to the Medieval period (6th century - 16th century CE) and reveals changes in flatfish fisheries in terms of targeted habitats and species. This will be done by exploring the stable isotope values using various statistical analyses (descriptive, ANOVA, generalised linear model, and principal component analysis) and visualisations (scatterplots, raincloud plots, rKIN niche space, and Isomemo maps) and identifying the species using collagen peptide mass fingerprinting. For each of these approaches the dataset for carbon and nitrogen isotope values is shown first and secondly the sulfur isotope value dataset. ANOVA and generalised linear modelling (GLM) will be evaluated for their applicability on archaeological isotopic data with this dataset and to provide more insight into the results. ANOVA can be used to detect differences between the means of isotope values of categories (such as time periods and sites), while generalised linear models allow for a better understanding of the relationship between variables (i.e. isotopes and independent variables).

6.2 Material and methods

6.2.1 Archaeological sites

The sites were selected based on their location, dating, and reported number of Pleuronectiformes bones. A detailed summary of each site is provided in Chapter 2 (appendix for publication). Figures 6.2 and 6.3 indicate the geographical location and the chronology of the sites respectively (also see figure E1 in the appendix for radiocarbon dating results for Barreau Saint-George).

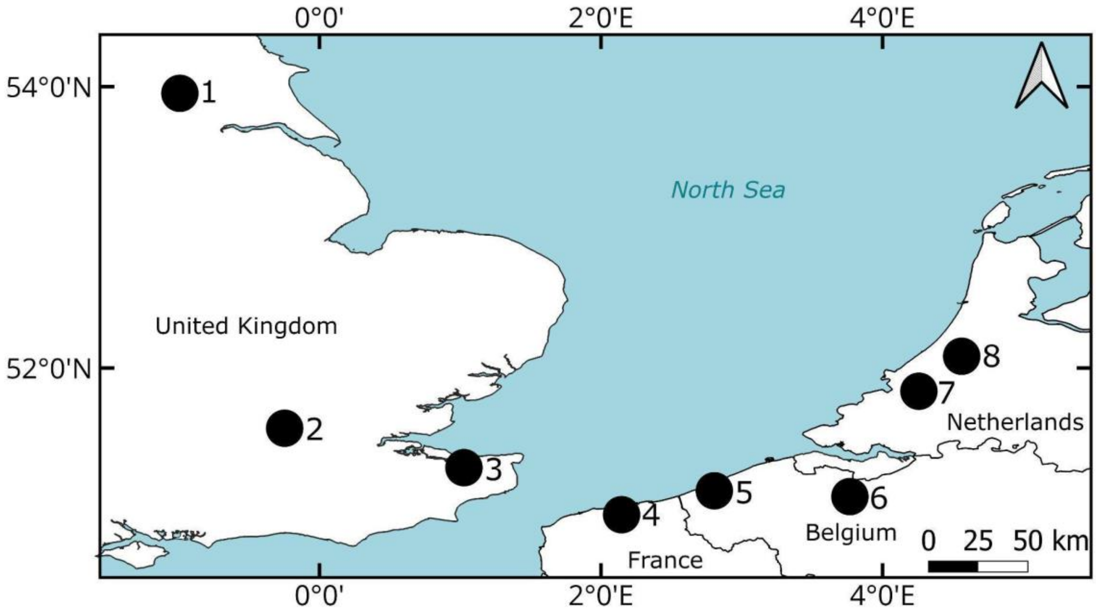

Figure 6.2. Map of the southern North Sea basin with the 13 archaeological sites in eight locations. 1. York with *16-22 Coppergate* (COP) and *Blue Bridge Lane* (BBL); 2. London with *CAO96* (CAO), *GSJ06* (GSJ), *SGA89* (SGA), and *SOT89* (SOT); 3. Canterbury with *Tradescent Lane* (CAN); 4. Saint-George-sur-l'Aa with *Barreau Saint-George-Desserte ferroviaire* (BSG); 5. Koksijde with *Hof ter Hille* (KOK); 6. Gent with *Zwarte Laag* (GEN); 7. Vlaardingen with *Gat in de Markt* (VLA); 8. Leiderdorp with *Kastanjelaan* (KAS) and *Plantage* (PLA).

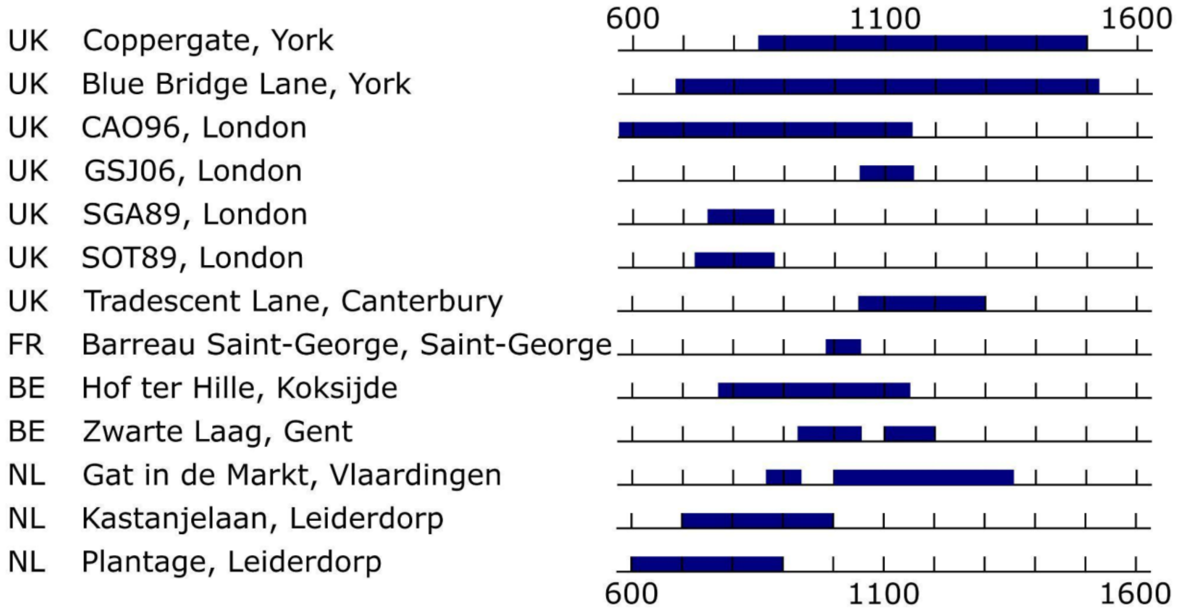

Figure 6.3. Chronological overview of selected sites.

6.2.2 Sample selection and preparation

From each site, a subset of flatfish samples was selected for stable isotope analysis (table E13 in the appendix). Every medieval phase/period (6th - 16th century CE) from each site was sampled. Where available only one sample per preliminary identified taxon, context, estimated size, and certain elements was selected to avoid repetition of the same individual fish. Whenever available, selected samples from freshwater and marine living species were also analysed to provide a comparative dataset for both habitats for each major period within each site. For freshwater species, mostly Esocidae and Cyprinidae were sampled. For marine species, mostly Gadidae, such as *G. morhua*, *M. merlangus*, and *M. aeglefinus*, were selected.

For every fish bone, the following characteristics were noted:

- Site (name (variable *Site*), year of excavation, geographical coordinates);
- Context/pit (phase, dating, depth);
- Collecting method and sieving mesh size if known;
- Taxon: every identified taxonomic level with notes of diagnostic criteria;
- Skeletal element: which bone, left or right, and which fragment, based on zonation system used by Harland and Barrett (2003);
- Size of the bone (maximum length);
- Size estimation to a size class (variable *Size_class*; in cm SL);
- Measurements following Morales and Rosenlund (1979);
- Pathologies and cut marks (e.g., Harland & Van Neer, 2018);
- Colour using the Munsell colour charts.

Size was estimated by comparing the archaeological bone to the equivalent element of modern reference specimens of known size. As precise estimations are difficult to achieve, a size estimation class (in cm SL) was noted for each specimen (mostly for flatfish).

Phasings of the sites were categorised into time periods to discuss results (table 6.1). For each published period a start and end date were also provided, in bins of 25 years. Terms such as “early xth century” were interpreted as the first quarter of the xth century (e.g., 800-825) and “late xth century” as the fourth quarter of the xth century (e.g., 875-900), following Orton *et al.* (2014). For example, this results in a phasing as “mid to late 800s/early 900s” to be interpreted as “850-925“. Based on these start and end dates a mid date was calculated (variable *Mid*) and used as a continuous numerical proxy for time periods, making it easier to numerically compare different phases.

Table 6.1. Overview of the time periods used.

Period	Abbreviation	Start (CE)	End (CE)
Roman period	R	0	500
Early Medieval 1	EM1	600	900
Early Medieval 2	EM2	850	1050
Early/High Medieval	E/HM	875	1150
High Medieval	HM	1000	1300
High/Late Medieval	H/LM	1025	1500
Late Medieval	LM	1200	1600
Post-Medieval	PM	1550	1800

Seven modern commercially acquired flatfish samples were analysed alongside the archaeological samples as references and to see if baselines have shifted through time.

6.2.3 Collagen extraction

Every sample was cleaned prior to collagen extraction using a sandblaster to remove soil and dirt on the outer surface. Sand of 25-50 μm was used at a pressure between 20-50 psi, depending on the bone size and preservation, minimising damage.

At least 100 mg and maximum 800 mg of bone of each sample was taken, but for a few samples less material was available. Control samples (n=18) of 100 mg ground homogenised bovine bone were also added to each batch.

Eight ml of 0.4 M HCl was added to each bone for demineralisation and the samples were placed on a rocker at 4°C until demineralisation was complete. If required, the acid was replaced every 48h. Once the bones were demineralised, the acid was removed and the bones were rinsed three times with ultra-pure water. Next, 8 ml pH3 HCl was added to each sample which were then placed in a heating block at 70°C for 24-48 hours until the collagen had gelatinised. To remove larger pieces remaining after gelatinisation, the samples were filtered using an Ezee-Filter^{TM} Separator (Elkay Laboratory Products). The samples were frozen at 20°C overnight before being placed in a freeze-drier at -55°C for 48h. The resulting collagen was weighed to calculate the yield.

6.2.4 Humic acid and lipid content contamination test

(In appendix for publication)

Humic acids may be present in certain burial environments which can impact stable isotope values. These may be removed by treating archaeological bones with NaOH prior to gelatinisation (Lowry *et al.*, 1941) which does not impact the stable isotope values of archaeological samples (Kennedy, 1988; Katzenberg, 1989; Ambrose, 1990; Guiry & Szpak, 2020). Samples from different archaeological sites were compared in this study, of which some came from deposits that are prone to the presence of humic acids (e.g. waterlogged Coppergate in York). We therefore explored whether humic acids were present and what the effect was on the isotopic values after a NaOH treatment.

Most flatfish species are not regarded as fatty fish, however, some species can have quite a high lipid content, depending on the tissue. *Pleuronectes platessa* and other Pleuronectidae have a rather low lipid content (e.g., 0.8-4.3% mean (Karl *et al.*, 2013)), while *H. hippoglossus* can have a lipid content of up to 8% mean value in its muscle tissue (Zeng *et al.*, 2010). These higher lipid contents can have a significant impact on stable isotope values if lipids are not removed prior to analysis. One study reported that lipid extraction should not have a significant effect on the values if the collagen yield of the extraction is sufficient (>3.5% yield) (Tsutaya *et al.*, 2018).

To explore the potential impact of humic acids and lipids five samples from Coppergate that were large enough to provide enough material for four separate experiments, were selected from 2 different taxa: 2 *Scophthalmus maximus* and 3 *Pleuronectes platessa*. Each sample was divided into four parts, one for each test protocol. (1) One test protocol consisted of not treating the bone and analysing it using the standard collagen extraction protocol, as described above. (2) Another test protocol consisted of a normal demineralisation procedure, followed by removal of humic acids. To each demineralised sample 8ml of 0.01 M NaOH was added and the samples were placed in a water bath in a sonicator for 15 minutes. If there was a colour change visible after the bath, the NaOH was replaced and the samples were again put in the sonicator for another 15 minutes. This continued until there was no more colour change in the NaOH. After this, the samples were rinsed with demineralised water, and further gelatinised and extracted as described above. (3,4) Two of the test protocols consisted of each sample being treated with dichloromethane (DCM) to remove any potential lipid in the bones prior to demineralisation. About 8 ml of DCM was added to the samples and the samples were placed in a sonicator for 15 minutes. After this, the DCM was replaced and the samples were placed in the sonicator again for 15 minutes twice. After lipid extraction, (3) one of these two parts was extracted following the standard protocol, while (4) the other part was extracted and washed with NaOH, similar to protocol 2. After analysis, the isotope values of these samples were compared to see the effect of each treatment.

6.2.5 Isotopic analysis

0.4-0.6 mg of collagen was weighed out in duplicate for mass spectrometry. Prior to demineralisation, a treatment with DCM was carried out to remove lipids (following treatment 3 described in section 6.2.4) from the seven modern flatfish samples; not for the archaeological samples.

Stable carbon and nitrogen isotopic compositions were determined using a Sercon 20-22 continuous flow isotope ratio mass spectrometer coupled to a Universal Sercon gas solid liquid elemental analyser at the University of York. Samples were usually analysed in duplicates, unless otherwise stated in table E13 in the appendix. Accuracy was determined by measurements of international standard reference materials within each analytical run. These were International Atomic Energy Agency (IAEA) 600 $\delta^{13}C_{raw} = -27.72 \pm 0.148$ ‰, $\delta^{13}C_{true} = -27.77 \pm 0.043$ ‰, $\delta^{15}N_{raw} = 0.82 \pm 0.2$ ‰, $\delta^{15}N_{true} = 1 \pm 0.2$ ‰; IAEA N_2 $\delta^{15}N_{raw} = 20.45 \pm 0.3$ ‰, $\delta^{15}N_{true} = 20.3 \pm 0.2$ ‰; IA Cane, $\delta^{13}C_{raw} = -11.73 \pm 0.12$ ‰; $\delta^{13}C_{true} = -11.64 \pm 0.03$ ‰.

The overall uncertainties on the measurements of each sample were calculated based on the method of Kragten (1994) by combining uncertainties in the values of the international reference materials and those determined from repeated measurements of samples and reference materials. These are expressed as one standard deviation. The maximum uncertainty for all samples across all runs was <0.33 ‰ for $\delta^{13}C$ and <0.92 ‰ for $\delta^{15}N$.

In addition, a homogenised bovine bone extracted and analysed within the same batch as the samples produced the following average values; $\delta^{13}C$ = -23.13 ± 0.13 ‰; $\delta^{15}N$ = 6.03 ± 0.28 ‰. This was within the overall mean value from 89 separate extracts of this bone sample, which produced values of $\delta^{13}C$ = -23.14 ± 0.16 ‰ and $\delta^{15}N$ = 6.07 ± 0.23 ‰.

Stable sulfur isotopic composition, alongside stable carbon and nitrogen isotopic compositions, for a subset of the samples were determined using a Delta V Advantage continuous-flow isotope ratio mass spectrometer coupled via a ConfloIV to an IsoLink elemental analyser (Thermo Scientific, Bremen) at SUERC, East Kilbride as described in Sayle *et al.* (2019). Twenty percent of the samples were run in duplicate (see table E14 in the appendix).

The International Atomic Energy Agency (IAEA) reference materials USGS40 (L-glutamic acid, $\delta^{13}C_{VPDB}$ = –26.39 ± 0.04 ‰, $\delta^{15}N_{AIR}$ = –4.52 ± 0.06 ‰) and USGS41a (L-glutamic acid, $\delta^{13}C_{VPDB}$ = 36.55 ± 0.08 ‰, $\delta^{15}N_{AIR}$ = 47.55 ± 0.15 ‰) were used to normalise $\delta^{13}C$ and $\delta^{15}N$ values. Two in-house standards (GS2, $\delta^{34}S_{VCTD}$ = –10.28 ± 0.18 ‰ and GAS2, $\delta^{34}S_{VCTD}$ = 18.56 ± 0.10 ‰) that are calibrated to the International Atomic Energy Agency (IAEA) reference materials IAEA-S-2 (silver sulfide, $\delta^{34}S_{VCTD}$ = 22.62 ± 0.08 ‰) and IAEA-S-3 (silver sulfide, $\delta^{34}S_{VCTD}$ = –32.49 ± 0.08 ‰) were used to normalise $\delta^{34}S$ values. Results are reported as per mil (‰) relative to the internationally accepted standards VPDB, AIR and VCDT.

Normalisation was checked using the marine collagen USGS88 ($\delta^{13}C_{VPDB}$ = –16.06 ± 0.07 ‰, $\delta^{15}N_{AIR}$ = 14.96 ± 0.14 ‰, and $\delta^{34}S_{VCTD}$ = 17.10 ± 0.44 ‰), the porcine collagen USGS89 ($\delta^{13}C_{VPDB}$ = –18.13 ± 0.11 ‰, $\delta^{15}N_{AIR}$ = 6.25 ± 0.12 ‰, and $\delta^{34}S_{VCTD}$ = 3.86 ± 0.56 ‰), and the well characterised Elemental Microanalysis IRMS fish gelatine standard B2215 ($\delta^{13}C_{VPDB}$ = –22.92 ± 0.10 ‰, $\delta^{15}N_{AIR}$ = 4.26 ± 0.12 ‰, and $\delta^{34}S_{VCTD}$ = 1.21 ± 0.24 ‰), which gave the values noted in table 6.2.

Table 6.2. International standards used to normalise the sulfur isotope analysis data.

Standard/Run date	**$\delta^{13}C_{VPDB}$ (‰)**	**$\delta^{15}N_{AIR}$ (‰)**	**$\delta^{34}S_{VCTD}$ (‰)**
USGS88			
25/01/2022	–16.42 ± 0.12 (n=6)	15.19 ± 0.27 (n=6)	17.27 ± 0.53 (n=6)
27/01/2022	–16.40 ± 0.07 (n=6)	15.15 ± 0.09 (n=6)	17.39 ± 0.41 (n=4)
22/07/2022	–16.26 ± 0.01 (n=7)	15.14 ± 0.06 (n=7)	17.59 ± 0.42 (n=5)
26/07/2022	–16.24 ± 0.09 (n=7)	15.15 ± 0.24 (n=7)	17.40 ± 0.30 (n=5)
28/07/2022	–16.24 ± 0.05 (n=7)	15.19 ± 0.06 (n=7)	16.97 ± 0.29 (n=5)
09/08/2022	-16.25 ± 0.06 (n=7)	15.33 ± 0.06 (n=7)	17.63 ± 0.21 (n=5)
USGS89			
25/01/2022	–18.06 ± 0.12 (n=6)	6.54 ± 0.10 (n=6)	4.81 ± 0.62 (n=6)
27/01/2022	–18.13 ± 0.13 (n=6)	6.41 ± 0.03 (n=6)	4.97 ± 0.34 (n=5)
B2215			
25/01/2022	–23.03 ± 0.11 (n=4)	4.39 ± 0.08 (n=4)	1.22 ± 0.23 (n=4)
27/01/2022	–23.23 ± 0.15 (n=4)	4.18 ± 0.07 (n=4)	1.70 ± 0.23 (n=4)
22/07/2022	–22.88 ± 0.10 (n=4)	4.30 ± 0.12 (n=4)	1.07 ± 0.30 (n=4)
26/07/2022	–22.83 ± 0.13 (n=4)	4.34 ± 0.10 (n=4)	1.48 ± 0.20 (n=4)
28/07/2022	–22.99 ± 0.08 (n=4)	4.26 ± 0.07 (n=4)	1.10 ± 0.29 (n=4)
09/08/2022	-22.93 ± 0.05 (n=4)	4.31 ± 0.07 (n=4)	1.38 ± 0.40 (n=4)

6.2.6 Species identification

Each selected sample was identified to family level and species level where possible using available identification keys (e.g., Watt *et al.*, 1997; Wouters *et al.*, 2007). As morphological approaches are not sufficient to distinguish between species of Pleuronectidae, collagen peptide mass fingerprinting was carried out. Around 1 mg of the extracted collagen was dissolved in 50 mM ammonium bicarbonate (NH_4HCO_3) buffer of pH 8.0 and 1 µl trypsin was added. The samples were left overnight at 37 °C for digestion. The samples were then filtered using ZipTips®, plated and analysed on the MALDI-TOF MS. Extracted collagen was spotted on a 384 steel target plate in triplicate. A 1 µl aliquot of every sample was spotted together with 1 µl of matrix solution (α-cyano-4-hydroxycinnamic acid). Each sample was externally calibrated against an adjacent spot containing a mixture of six peptides (des-Arg1-bradykinin m/z = 904.681, angiotensin I m/z = 1295.685, Glu1-fibrinopeptide B m/z = 1750.677, ACTH (1–17 clip) m/z = 2093.086, ACTH (18–39 clip) m/z = 2465.198 and ACTH (7–38 clip) m/z = 3657.929). The spots were air dried at room temperature. The samples were analysed using a Bruker Ultraflex III MALDI-TOF (matrix assisted laser desorption ionization-time of flight) mass spectrometer at the Bioscience Technology Facility, University of York, with the following settings: ion source 25 kV; ion source 21.4 kV; lens voltage 9 kV; laser intensity 40–55%; and mass range 800–4000 Da. Peptide masses below 650 Da were suppressed. All samples were identified by following the biomarkers and methodology described in Dierickx *et al.* (2022) for flatfish and Harvey *et al.* (2018) for other fish taxa.

6.2.7 Data analysis

Data was analysed using R (R Core Team (2022), version 4.1.1 (2021-08-10) -- "Kick Things"). Poor quality collagen was removed from the dataset. Samples that did not match the quality criteria were also removed (see results).

Data was visualised using *ggplot()* (ggplot2 package; Wickham, 2016) in R. Normality was tested using Shapiro-Wilk test for whole groups and subgroups. Homoscedasticity was verified using a Levene's test (carr package). To test for significant differences between categories within a variable ANOVA (*aov()* from stats package) was used. The following are assumptions for an ANOVA:

- The population must be close to a normal distribution. This is tested using the Shapiro-Wilk test.
- Samples must be independent. This is valid for our dataset.
- Population variances must be homogeneous (i.e. homoscedastic). This is tested using a Levene's test.
- Groups must have equal sample sizes. In most cases this is met. Occasionally there are smaller groups.

Due to the combination of numerical and categorical variables in the ANOVA, no post hoc analysis was performed. Using this dataset, the applicability of this statistical analysis on archaeological isotopic data will be evaluated.

To visualise the isotope values for both geographical location and chronology, the Isomemo app (Fernandes *et al.*, 2017; https://isomemoapp.com/app/iso-memo-app) was used. To generate a general average geographical distribution per isotope variable, the AverageR model is applied. The TimeR model is used to visualise geographical distributions through time. These models use Generalized Additive Models. The following settings were applied: linear extrapolation behaviour; aquatic; mean estimation type; convex hull applied; and 100km radius for AverageR; and additionally, 150 spatial basis functions; planar smooth type; and time-sliced spatial convex for TimeR.

A generalised linear model (GLM) was applied firstly to evaluate the applicability of this approach to archaeological isotope data, and secondly to test which variables are good predictors of isotopic values. Using the Akaike Information Criterion, the model with the fewest independent variables without a significant loss of fit was selected. Using the variance inflation factor (*vif()* in car package) collinearity between variables in a model could be determined. Correlation between variables was checked using Fisher's exact test for categorical variables and an Ancova for a continuous and a categorical variable. A Shapiro-Wilk test was used to test for normality of the residuals of a model and a plot of the fitted values against the residuals was made to evaluate the goodness of fit of the model on the data.

Principal component analysis (PCA) was performed on data from the three isotopes, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, to see which contributed most to the variation seen in the data. The PCA was carried out using the *prcomp()* function in R and the PCA plots of PC1 and PC2 and the biplot were visualised using *fvid_pca_ind()* and *fvid_pca_biplot()* functions from the factoextra package.

6.2.8 Collagen quality criteria

Collagen can degrade over time due to taphonomic processes, and contaminants that can seep in, such as the above-mentioned humic acids and lipids (Guiry & Szpak, 2021). Both processes can cause a change in the isotopic composition, either by the (potentially differential) loss of specific amino acids or by the influx of other molecules with a different isotope composition. It is therefore crucial to understand what the impact of these processes are on the isotopic values of archaeological samples.

With lipids and humic acids being rich in carbon, the C:N ratios and particularly $\delta^{13}C$ can be altered. This could especially affect fish bones from marine species buried in a C3 plant-rich environment (Guiry & Szpak, 2021). To evaluate the degradation and contamination of collagen, quality criteria have been proposed, which were mostly based on observed values. DeNiro (1985) proposed to use C:N as a quality criteria for contamination and set the range between 2.9 and 3.6, although the isotope values could still be altered within this range. Ambrose (1990) defined alternative criteria with yield of collagen > 0.5-2.0%, %C > 13%, and %N > 4.8% (also see DeNiro & Weiner, 1988; Van Klinken, 1999; Dobberstein *et al.*, 2009). Guiry and Szpak (2020) reduced the range of C:N to 3.00-3.33 based on expected collagen compositions and observed data. They also noticed a difference between a few fish taxa, depending on the environment where they live (Guiry & Szpak, 2020).
However, as each species has a different composition of collagen due to evolution and species divergence (Buckley, 2018), the baseline of the collagen quality criteria could potentially differ between species, meaning that quality criteria should be defined for each species separately based on the collagen composition (as was also noted by Guiry & Szpak, 2021). The collagen composition and species-specific quality criteria has been defined for cod (*G. morhua*), as well as for a seal (*Phoca* sp.), cattle (*Bos taurus*) and human (*Homo sapiens*) by Guiry and Szpak

(2021). For cod[1] the expected C:N ratio, calculated from the collagen amino acid sequence, is 3.1. From this collagen composition, the effects of degradation (loss of collagen) and contamination (relative increase in the amount of one element or isotope versus another) can be assessed, leading to upper range limits for each species (Guiry & Szpak, 2021). Modelled cod samples that had a C:N of 3.6 had a -1.85‰ shift in $\delta^{13}C$ while only a -0.21‰ shift in $\delta^{15}N$ compared with samples with a C:N of 3.1. A similar negative correlation was found in observed data from archaeological samples. Guiry and Szpak therefore propose to use quality criteria depending on the C:N ratios observed in archaeological fish samples and the expected C:N and $\delta^{13}C$ of that species. The criteria can either be conservative with a lower upper limit of C:N that only allows a slight shift (0.5‰) in $\delta^{13}C$ or liberal with a higher upper limit allowing for a larger shift in (1.0‰) in $\delta^{13}C$ (Guiry & Szpak, 2021).

Similar quality criteria have been proposed for sulfur isotope analysis. Privat *et al.* (2007) stated that any sample with %S above 0.6%, C:S below 200, and N:S below 60 should not be included in the analysis. Richards *et al.* (2001) reduced the range for C:S and put 494 ± 128 as the limit. For marine mammals, Craig *et al.* (2006) defined the range for C:S between 457-535, and 136-160 for N:S. The sulfur content for many species was defined by Nehlich and Richards (2009) using either DNA sequences, amino acid sequences or mass spectrometry analysis of bone collagen samples. The former method, however, might not be the best approach, as unknown posttranslational processes of proteins can be overlooked, underestimating the amount of sulfur in collagen. Mass spectrometry approaches might be the best approach if any contaminants or presence of other proteins of a sample can be excluded. Fish samples must follow the criteria defined by Nehlich and Richards (2009): C:S between 125-225 and N:S between 40-80. Modern fish samples tend to have a %S of 0.52-0.83wt%, while archaeological fish samples might have a lower %S due to degradation of collagen, but should still be above 0.4wt% and below 0.85%wt to not be excluded.

Following the same principle as Guiry and Szpak (2021), we analysed the collagen composition of flatfish, which was constructed de novo by using LC-MS/MS data obtained from the same samples used for collagen peptide mass fingerprinting marker development (Dierickx *et al.*, 2022; also see appendix D). By calculating the amount of each amino acid in the sequence and the number of chemical elements (i.e. C., N., and S), the expected weight percentages of each element and the expected abundance and atomic mass ratios of C:N, C:S, and N:S could be calculated for each flatfish species, accounting for the removal of one H_2O molecule per peptide bound. As all amino acids consist of both C and N, the effect of a missed amino acid substitution is minimal on the expected/calculated %C, %N, and C:N. However, a missed amino acid substitution involving methionine could dramatically change the expected %S, C:S and N:S if only relying on amino acids sequences obtained through LC-MS/MS analysis as methionine, the only sulfur-containing amino acid in collagen is not a very common amino acid.

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[1] For fish this might all be more complex than for mammals and birds. Fish have continuous growth and bone growth might change throughout its life, which can also affect preservation of the bone in burial environments. Big fish, which also often have a different diet (usually more piscivorous and thus higher $\delta^{15}N$ values and potentially slightly different habitat, thus different $\delta^{13}C$ values) might preserve worse or better than smaller fish from the same species. Correlations found might thus not solely depend on contaminations?

6.3 Results

6.3.1 Overview

476 archaeological samples in total were analysed for carbon and nitrogen isotope values, including 356 flatfish (2 *L. limanda*, 91 *P. flesus*, 237 *P. platessa*, 13 *S. maximus*, 3 *S. rhombus*, 7 *S. solea*, and 3 Pleuronectidae), and 120 other fish samples (30 Cypriniformes, 19 *Esox lucius* Linnaeus 1758, 2 *Conger conger* (Linnaeus 1758), 1 cf. *Salmo trutta trutta* Linnaeus 1758, 33 *Gadus morhua*, 34 *Melanogrammus aeglefinus*, 1 *Merlangius merlangus*), as identified by ZooMS following Harvey *et al.* (2018) and Dierickx *et al.* (2022). Of these, only four samples failed to provide enough collagen for analysis (3 Pleuronectidae and 1 Cypriniformes) (see table E13 in the appendix).

Sulfur isotope analysis was performed on a subset of samples, which showed high quality collagen and represented a good overall distribution of species, size, time period and site. In total, 166 archaeological samples were analysed across three species: *P. platessa* (n=106), *P. flesus* (n=59; 51 marine and 8 freshwater), and *L. limanda* (n=1).

Seven modern samples (3 *P. platessa* and 4 *P. flesus*) were also analysed to verify the isotopic quality criteria for sulfur and to provide a modern reference for ecosystems.

6.3.2 Lipid extraction and NaOH treatment test

The isotopic values of each treatment only show slight differences from the control treatment, and there are no clear directional effects of each treatment on the values (figure 6.4 and table E2 in the appendix). The C:N ratio remains rather constant at 3.19 ± 0.07. The combined treatment of lipid and NaOH seems to slightly increase the C:N values in three out of five samples. It was therefore decided to not do any treatments prior to the initial analysis of the samples.

6.3.3 Quality criteria

6.3.3.1 Expected criteria

The collagen amino acid sequences were obtained for each of the flatfish species considered here, namely *P. platessa, P. flesus, L. limanda, S. rhombus, S. maximus* and *S. solea* by LC-MS/MS analysis of collagen (see Dierickx *et al.*, 2022; appendix part D). The calculated %C ranges between 46.6-47.2%, %N 14.8-15.0%, %S 0.4%, C:N 3.1-3.2, C:S 117.9-125.8, and N:S 37.0-40.6 (table 6.3).

These calculated ranges fall within the quality criteria proposed by Guiry and Szpak (2020; 2021) for Actinopterygii. It is noticeable, however, that the three Pleuronectidae have a remarkably higher C:N ratio than the Scophthalmidae and Soleidae species, which is also much higher (up to Δ0.09) than the 3.1 C:N ratio observed for *G. morhua* by Guiry and Szpak (2021). It has to be noted that the majority of these sequences were obtained from published sequences on NCBI and that for each family the most closely related sequence was used, which could also explain the family differences observed here. Based on the calculated C:N ratio, the conservative upper limit defined by Guiry and Szpak (2021) for (coldwater) fish does

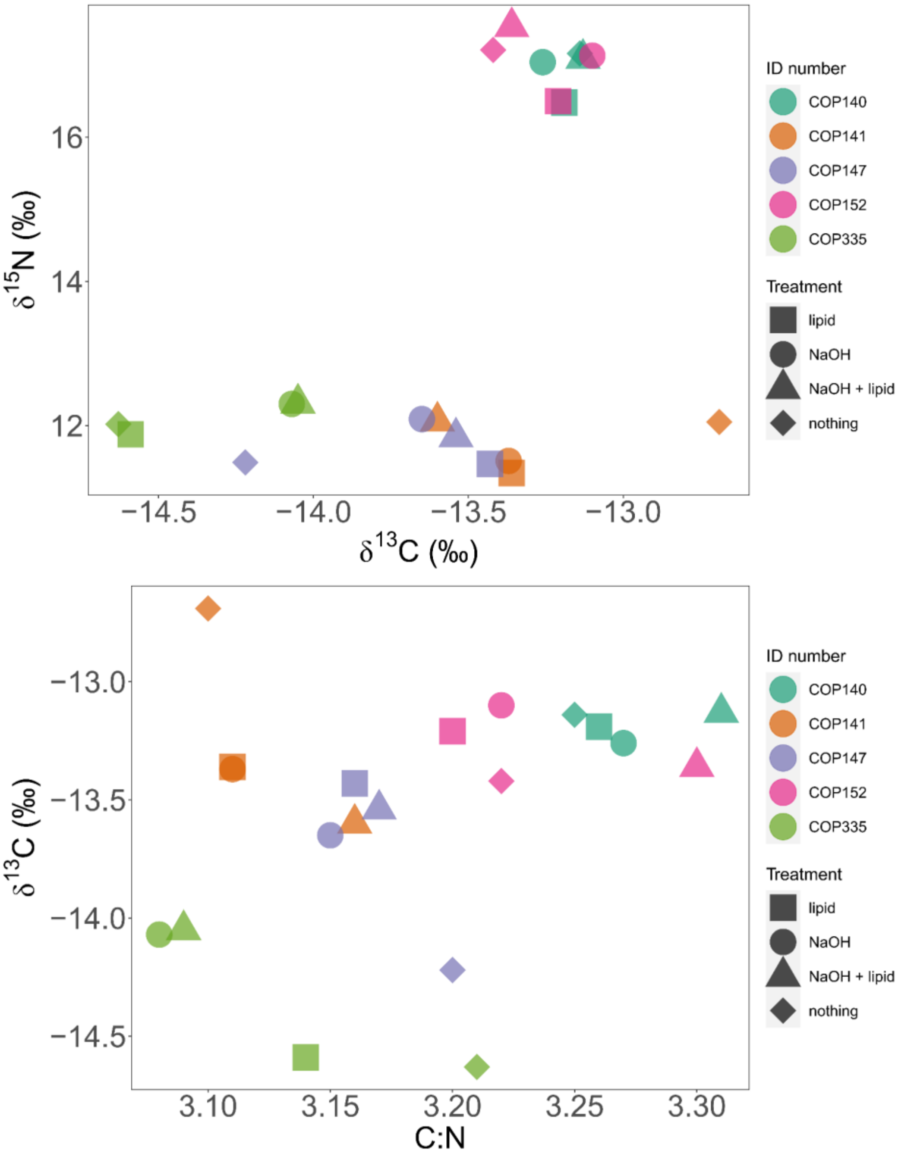


Figure 6.4. Plot of $\delta^{15}N$ against $\delta^{13}C$ (upper) and $\delta^{13}C$ against C:N (bottom) of the test protocols, coloured by sample and shaped by treatment. The details of each sample can be found in table E2.

Table 6.3. Estimated collagen composition for each species based on amino acid sequences obtained from LC-MS/MS analysis.

Species	**%C**	**%N**	**%S**	**C:N**	**C:S**	**N:S**
Pleuronectes platessa	55.64	17.44	0.47	3.19	118.18	37.04
Platichthys flesus	55.60	17.46	0.47	3.18	117.94	37.04
Limanda limanda	55.56	17.47	0.46	3.18	120.49	37.88
Scophthalmus rhombus	55.33	17.65	0.47	3.14	118.72	37.86
Scophthalmus maximus	55.27	17.67	0.47	3.13	118.48	37.89
Solea solea	55.21	17.81	0.44	3.10	125.76	40.56

not make sense for flatfish. The trend observed for *G. morhua* by Guiry and Szpak (2021) indicates a potential alteration of values beyond a C:N of 3.2. But as this is the expected composition for flatfish, a value close to 3.2 for C:N in this study does not indicate strong contamination or degradation. However, Pleuronectiformes (especially Pleuronectidae) seem to have similar expected C:N values to the warm water fish species analysed in Guiry and

Szpak (2021). We will therefore use the liberal upper limit proposed by Guiry and Szpak (2021) as quality criteria for the samples from this study, which is 3.5, considering the range of our flatfish samples have a δ^{13}C range from -23.56‰ to -10.37‰, and mean of -14.17‰. This upper limit also follows more generally applied criteria such as those proposed by van Klinken (1999). The lower limit applied on the dataset is 3.0 C:N.

6.3.3.2 Observed quality criteria

In the archaeological dataset after removal of poor-quality samples (C:N<2.5 or >4.0), only some samples from *P. platessa* and *P. flesus* have slightly elevated C:N values, which could be a result of contamination. There seems to be a slight negative correlation for *P. platessa* and the marine *P. flesus* as seen on figure 6.5 and in table 6.4, which is significant for *P. platessa*. Due to this, it was decided to remove samples with a C:N value above 3.5 (n=7), based on the quality criteria as discussed above.

Table 6.4. Observed ranges for C:N values per species of all archaeological samples, slope of the simple linear regression, and Pearson correlation test coefficient and p-value between δ^{13}C and C:N. Marine *P. flesus* are samples from this species with a δ^{13}C higher than -20‰ and freshwater *P. flesus* lower than -20‰. Bold results indicate significant differences.

Species	**N**	**C:N min**	**C:N max**	**Slope**	**Correlation coefficient (Pearson)**	**P-value**
Pleuronectes platessa	236	3.01	3.64	-4.427	-0.4215753	**1.383e-11**
Platichthys flesus	89	3.10	3.79	-4.8649	-0.1813515	0.08898
Marine *P. flesus*	81	3.11	3.79	-7.765	-0.4087811	**0.0001514**
(Freshwater *P. flesus)*	8	3.1	3.23	-16.12	-0.7303657	**0.03963**
(Limanda limanda)	2	3.15	3.18	-59.33	/	/
(Scophthalmus rhombus)	3	3.13	3.23	-10.25	-0.9589496	0.183
Scophthalmus maximus	13	3.10	3.34	-3.091	-0.2578749	0.395
(Solea solea)	7	3.12	3.18	2.385	0.07724616	0.8693

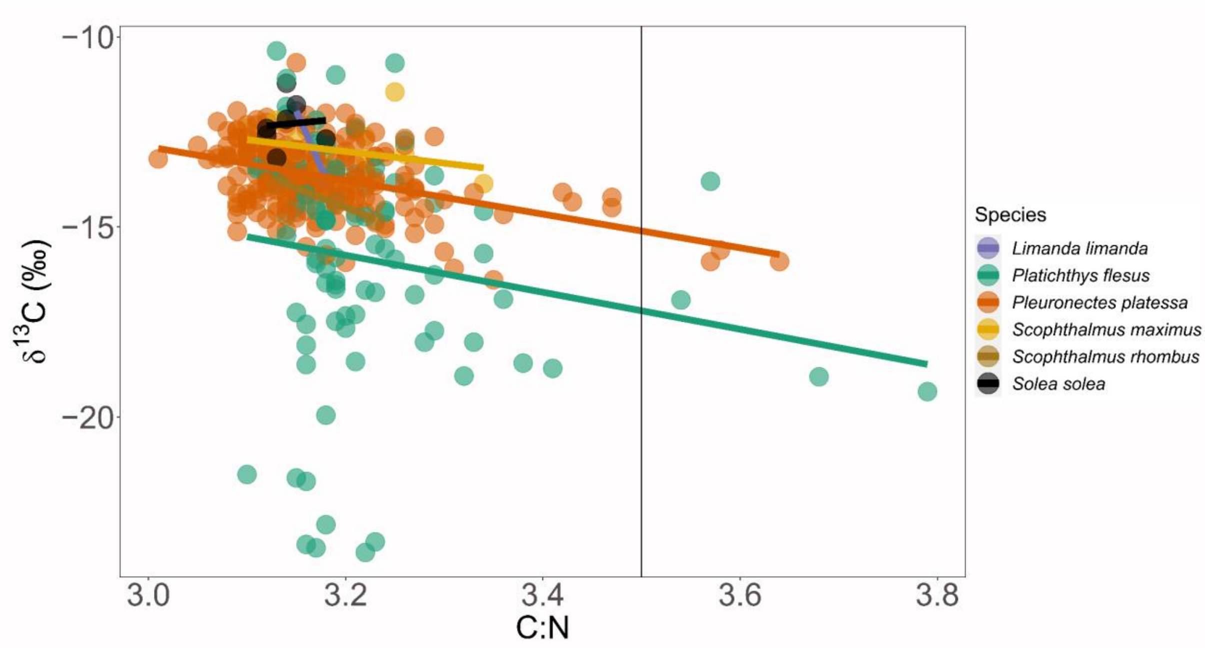


Figure 6.5. Archaeological Pleuronectiformes showing δ^{13}C against C:N. Coloured by species. The regression line per species was added using a simple linear regression. The quality criteria cut-off value of 3.5 is indicated by the vertical black line.

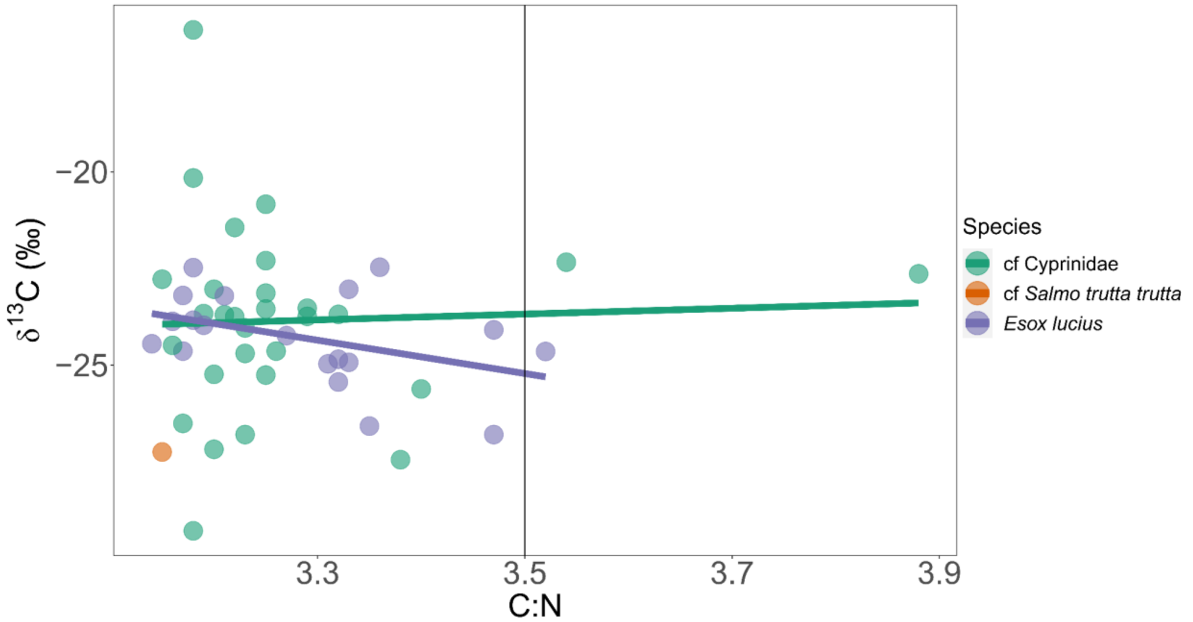


Figure 6.6. Archaeological freshwater species showing δ^{13}C against C:N. Coloured by taxon as identified using ZooMS. The regression line per species was added using a linear model. The quality criteria cut-off value of 3.5 is indicated by the vertical black line.

For the freshwater species (figure 6.6) there is no significant correlation noticed for *E. lucius* (r = -0.4198953, p-value = 0.07348, slope = -4.311), with only one sample with a C:N above the cut-off value of 3.5. This sample was removed from the dataset for the next steps of the analysis. Although no significant correlation was found for Cypriniformes (r = 0.04361173, p-value = 0.8223, slope = 0.7547), it is possible that there might be a significant correlation for one individual species. It was also decided to remove the two samples with C:N > 3.5 from further analysis.

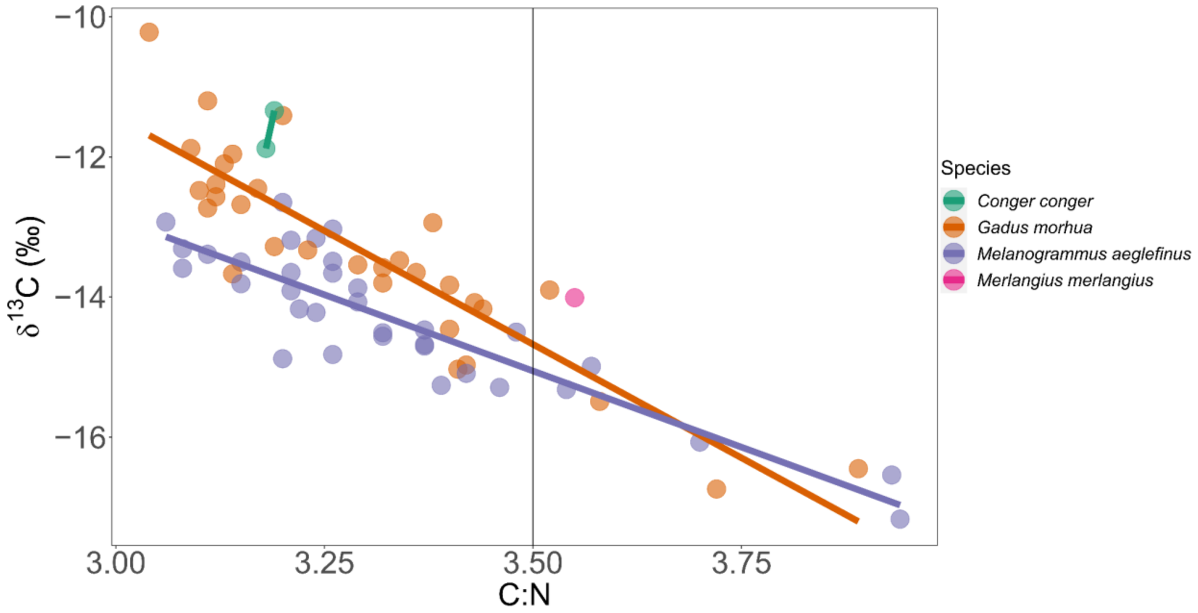


Figure 6.7. Archaeological marine species showing δ^{13}C against C:N. Coloured by species. The regression line per species was added using a linear model. The quality criteria cut-off value of 3.5 is indicated by the vertical black line.

There is a strong correlation between C:N and δ^{13}C for Gadidae (figure 6.7), i.e. *G. morhua* and *M. aeglefinus* (r = -0.8909792, p-value = **4.166e-11**, slope = -6.484 and r = -0.8854754, p-value = **7.656e-12**, slope = -4.3519 respectively). It was decided to remove only the ten samples above the cut-off value, including the one sample of *M. merlangus*, as there seems to be a strong indication of contamination/degradation. Although the criteria according to Guiry and Szpak (2021) suggest removing any samples with a C:N>3.3, it was decided to follow the same criteria for all taxa in this study, acknowledging that those fish with higher C:N values might possess δ^{13}C values that may be shifted by up to 1‰, but this is not of significance to this study as they are serving as a marine comparator.

In figure 6.8 a clear correlation can be seen between δ^{13}C and δ^{34}S for *P. flesus* (r=0.4985, p-value=**5.856e-05**). There is no significant correlation between δ^{13}C and δ^{34}S for *P. platessa* or between δ^{15}N and δ^{34}S for both species (p-value>0.05).

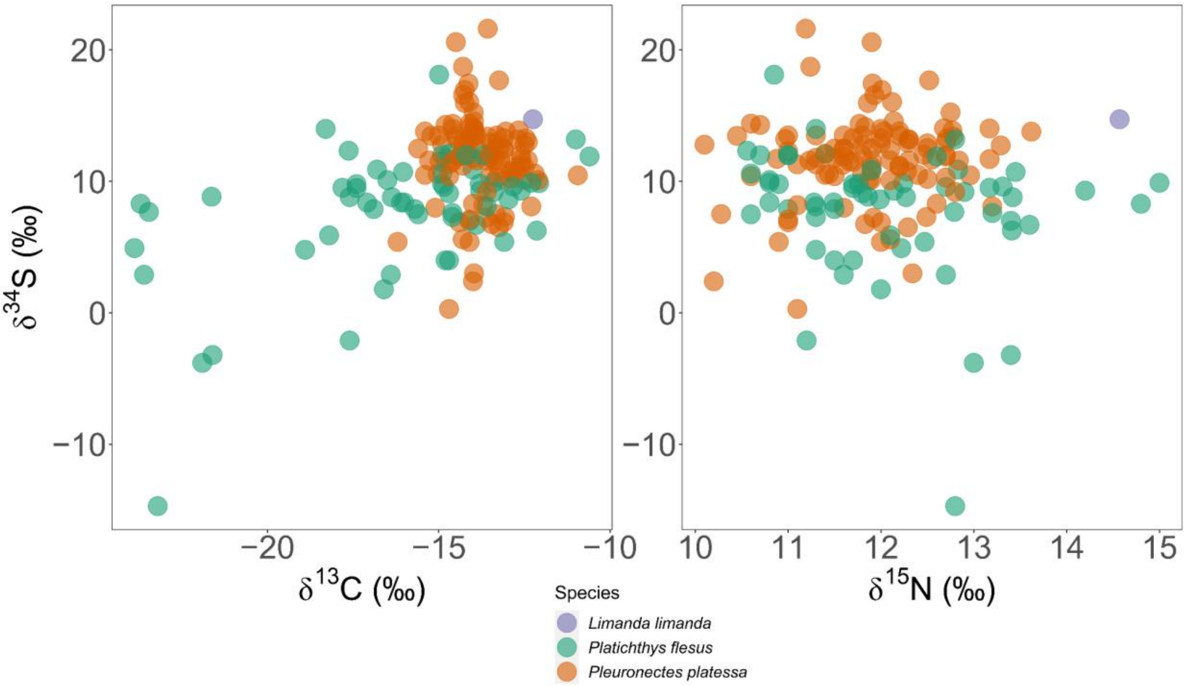


Figure 6.8. δ^{13}C and δ^{34}S (left) and δ^{15}N and δ^{34}S (right) of all analysed samples per species.

For %S the majority of the samples fall between the limits proposed by Nehlich and Richards (2009) (figure 6.9). Thirty-seven samples (22%) from the sites Coppergate, Zwarte Laag, Gat in de Markt and Plantage fall above the upper limit of 0.85% and could potentially contain exogenous sulfur. These are therefore excluded from further analysis. Seven additional samples (from Coppergate, Koksijde, Gat in de Markt, and Plantage) do not meet the criteria by Nehlich and Richards (2009) for C:S (figure 6.10) and N:S (figure 6.11) and also have %S close to the range limits. For this reason, these samples were also excluded. After removing the samples that do not meet the quality criteria by Nehlich and Richards (2009), 122 samples are analysed in more detail.

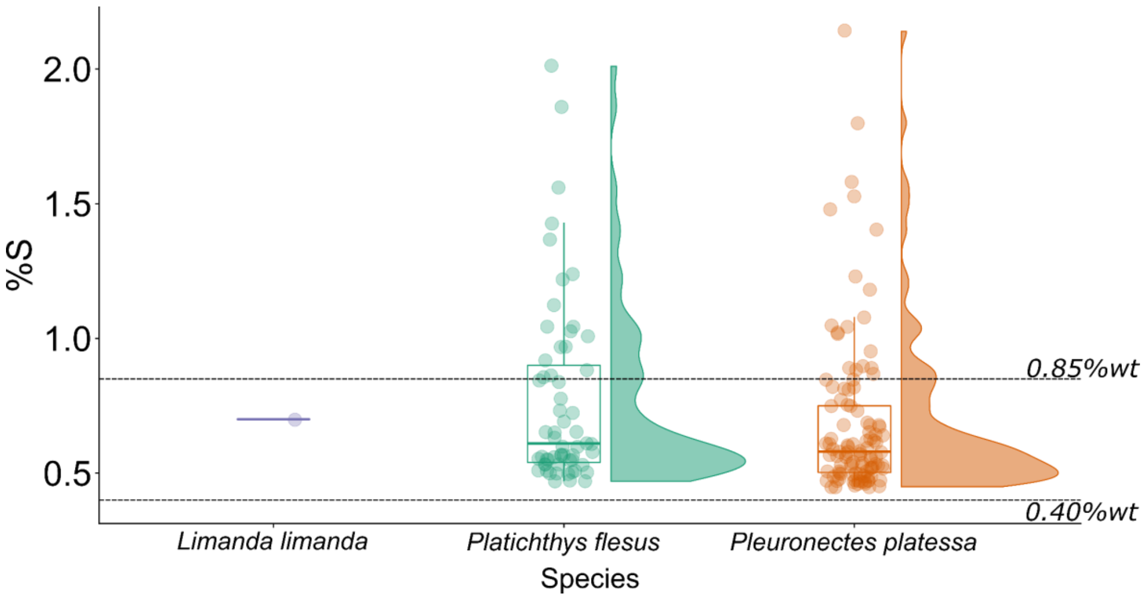


Figure 6.9. %S of all analysed archaeological samples per species. The horizontal lines indicate the recommended upper and lower limit for quality criteria proposed by Nehlich and Richards (2009).

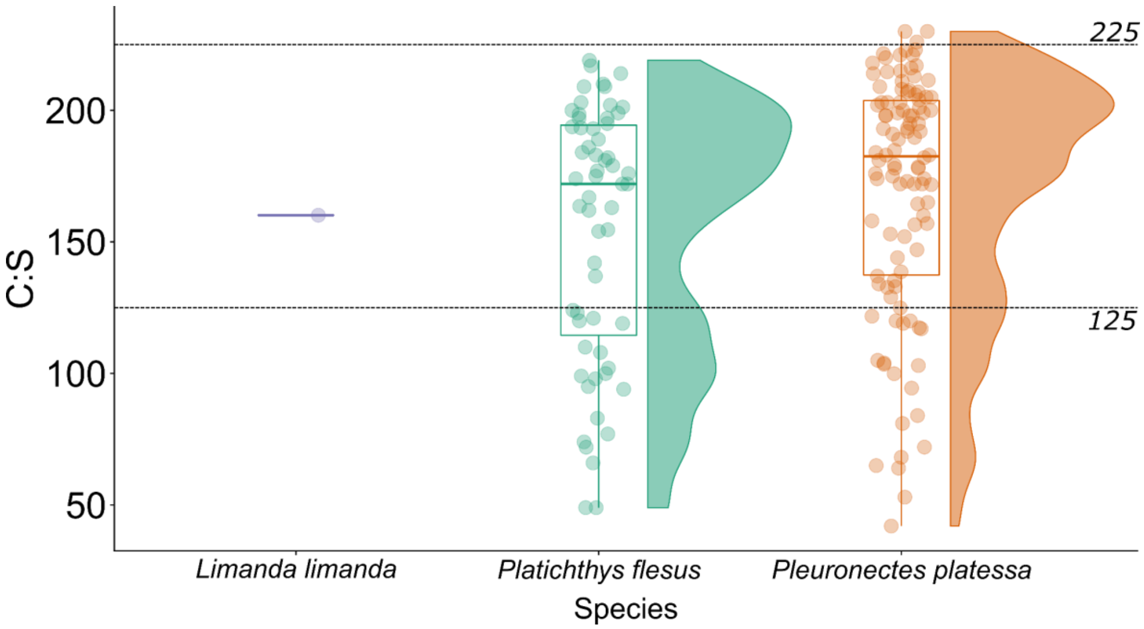


Figure 6.10. C:S of all analysed archaeological samples per species. The horizontal lines indicate the recommended upper and lower limit for quality criteria proposed by Nehlich and Richards (2009).

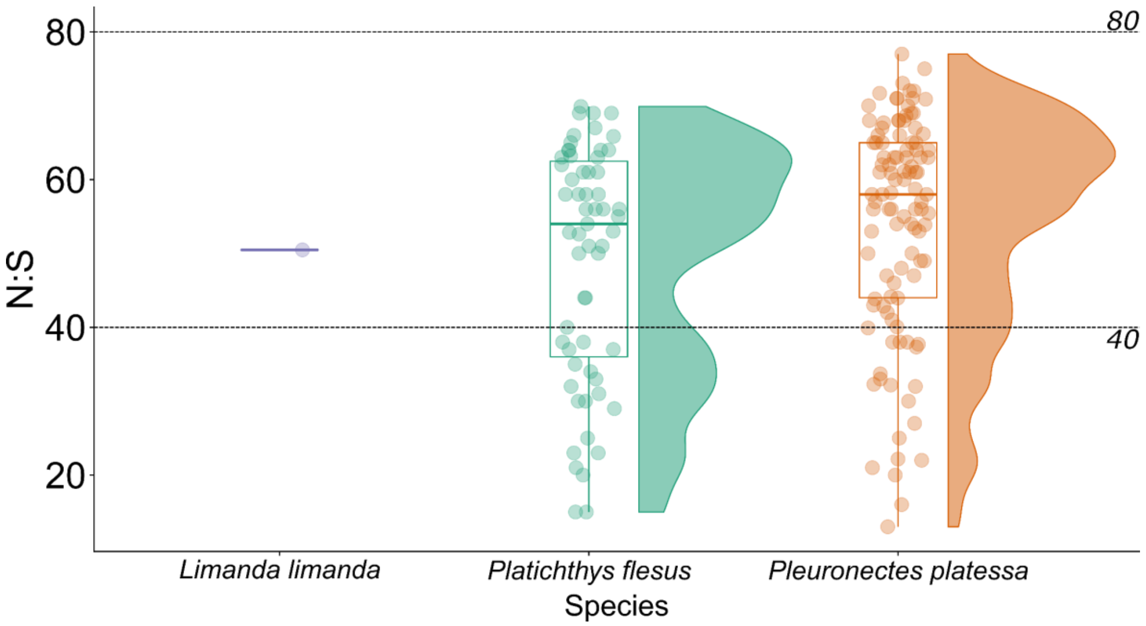


Figure 6.11. N:S of all analysed archaeological samples per species. The horizontal lines indicate the recommended upper and lower limit for quality criteria proposed by Nehlich and Richards (2009).

All modern samples matched the quality criteria for carbon and nitrogen as applied above and for sulfur as defined by Nehlich and Richards (2009) (table 6.9).

6.3.4 Data description

An overview of descriptive statistics is provided in table 6.5. Boxplots for each flatfish species are provided in figure 6.12. The information for the other species can be found in the table E3 in the appendix. A Shapiro-Wilk test was performed to test normality for the isotope values. No flatfish species possesses a distribution of δ^{13}C and δ^{15}N that is significantly different from normal distribution, except for *P. flesus*. In this species, there is a bimodal distribution with some samples below -20‰ and the majority above -20‰ for δ^{13}C. Of these two groups, the former group – termed freshwater *P. flesus* while the latter group is termed marine *P. flesus* – has a distribution for δ^{13}C that is significantly different from normal distribution, although the W-statistic is high (figure 6.13; table 6.6). For *S. maximus, S. rhombus* and *S. solea* the sample sizes are rather small and, although we can't reject the null hypothesis (i.e. the distribution follows normal distribution), the density plots in figure 6.12 don't seem to follow a normal distribution for δ^{13}C and δ^{15}N. Samples that fall outside of the ranges of the boxplots on figure 6.12 are regarded as statistical outliers. These are not removed from the dataset, as they could still be biologically meaningful as little is known about the ranges for isotopic values for these species, although interpretation of these samples was done carefully.

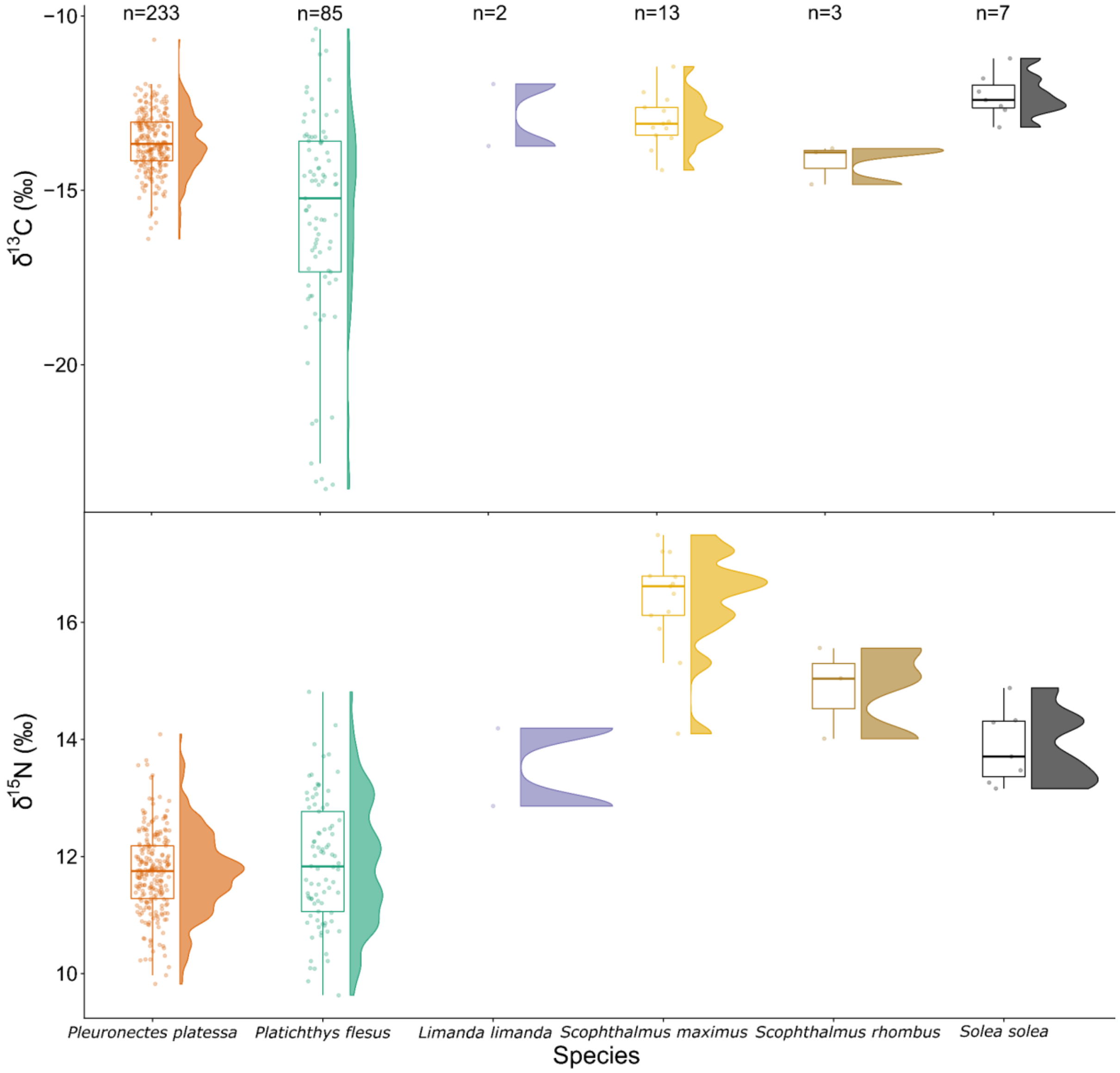


Figure 6.12. Boxplots and density plots of δ^{13}C (top) and δ^{15}N (bottom) of each flatfish species.

Table 6.5. Descriptive statistics for each flatfish species.

	P. platessa		***P. flesus***		***L. limanda***	***S. maximus***	***S. rhombus***	***S. solea***
		all	freshwater	marine				
N	233	85	8	77	2	13	3	7
δ^{13}C								
min	-16.39	-23.56	-23.56	-19.95	-13.73	-14.42	-14.83	-13.19
max	-10.68	-10.37	-21.51	-10.37	-11.95	-11.45	-13.8	-11.22
mean	-13.63	-15.79	-22.66	-15.08	-12.84	-13.01	-14.18	-12.29
median	-13.67	-15.23	-23.05	-14.74	-12.84	-13.09	-13.91	-12.41
sd	0.85	3.03	0.9	2.15	1.26	0.76	0.57	0.64
variance	0.72	9.2	0.81	4.62	1.58	0.58	0.32	0.41
δ^{15}N								
min	9.82	9.63	11.52	9.63	12.86	14.1	14.01	13.16
max	14.09	14.81	14.24	14.81	14.19	17.49	15.56	14.88
mean	11.73	11.9	12.6	11.82	13.53	16.37	14.87	13.87
median	11.75	11.83	12.36	11.78	13.53	16.62	15.04	13.71
sd	0.7	1.08	0.84	1.08	0.94	0.9	0.79	0.64
variance	0.49	1.18	0.71	1.18	0.88	0.81	0.62	0.41
C:N								
min	3.01	3.1	3.1	3.11	3.15	3.1	3.13	3.12
max	3.47	3.41	3.23	3.41	3.18	3.34	3.23	3.18
mean	3.17	3.2	3.17	3.21	3.17	3.2	3.17	3.14
median	3.15	3.19	3.17	3.19	3.17	3.19	3.15	3.14
sd	0.69	0.06	0.04	0.06	0.02	0.06	0.053	0.02
variance	0.0048	0.0039	0.0017	0.0041	0.0005	0.004	0.0028	0.0004

Table 6.6. Shapiro-Wilk test for isotope values of each flatfish species. Bold results indicate significant results.

	δ^{13}C		**δ^{15}N**	
Species	**W-statistic**	**p-value**	**W-statistic**	**p-value**
Pleuronectes platessa (n=233)	0.99116	0.1706	0.99288	0.3269
Platichthys flesus (n=85)	0.93804	**0.0004972**	0.9883	0.6452
Freshwater *P. flesus* (n=8)	0.93115	**0.0004809**	0.92091	**0.0001566**
Marine *P. flesus* (n=77)	0.98634	0.5829	0.98347	0.4176
Limanda limanda (n=2)	/	/	/	/
Scophthalmus maximus (n=13)	0.98647	0.9975	0.89389	0.1103
Scophthalmus rhombus (n=3)	0.82909	0.186	0.96517	0.6415
Solea solea (n=7)	0.97979	0.9585	0.92524	0.5112

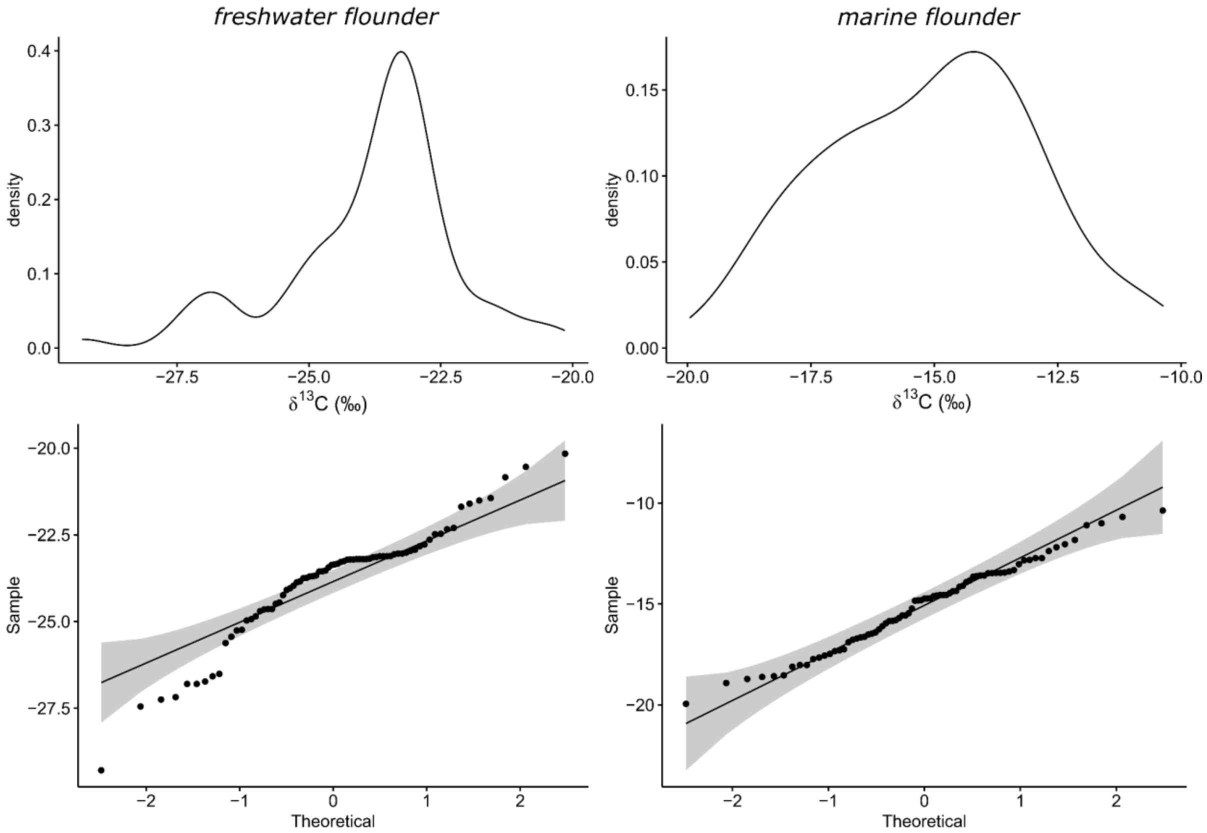


Figure 6.13. Density plot (top) and qqplot (bottom) for freshwater *P. flesus* (left; $\delta^{13}C < -20‰$) and marine *P. flesus* (right; $\delta^{13}C > -20‰$).

On figure 6.14 it can be seen that *P. platessa* and *P. flesus* have a different distribution of $\delta^{34}S$ (table 6.7). For the samples analysed, only *P. flesus* seems to have samples that have low $\delta^{34}S$ values compared to the majority of samples. A few samples of *P. platessa* have slightly higher $\delta^{34}S$ values. For both *P. platessa* and *P. flesus* $\delta^{34}S$ is not normally distributed (table 6.8; figure 6.14), due to a slight bimodal distribution of the former and the presence of freshwater samples for the latter species. $\delta^{34}S$ of marine *P. flesus* on the other hand shows no significant difference from normal distribution.

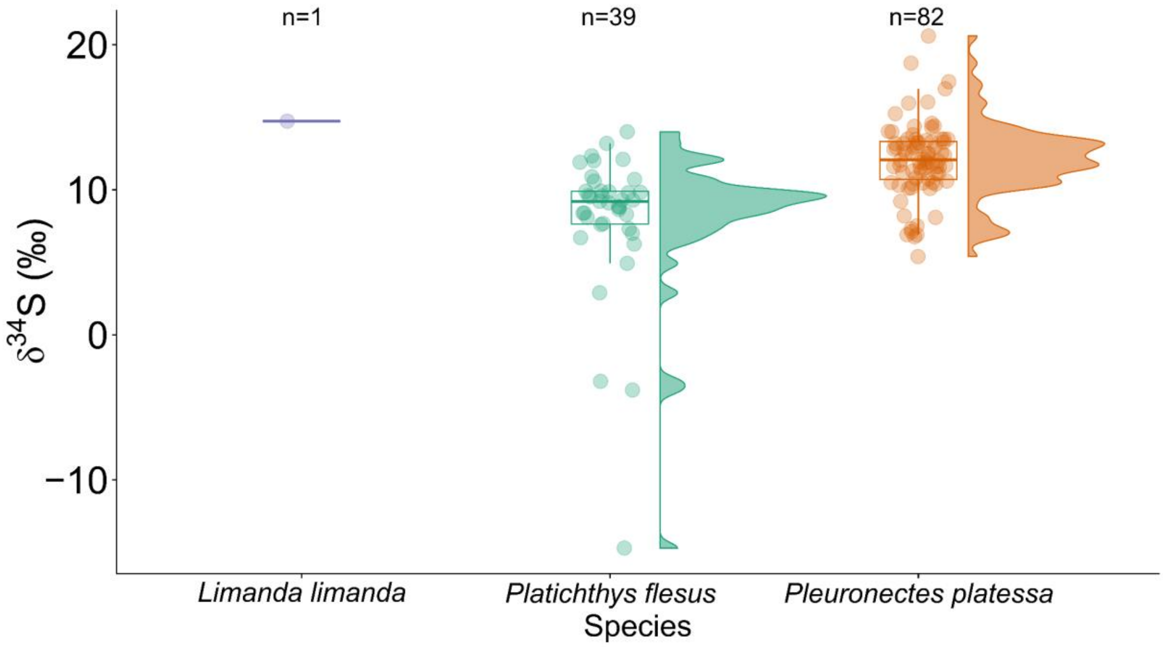


Figure 6.14. $\delta^{34}S$ of criteria-matched samples per species.

Table 6.7. Descriptive statistics for $\delta^{34}S$ for each flatfish species of the archaeological samples.

	P. platessa	*P. flesus*			*L. limanda*
		all	freshwater	marine	
N	82	39	8	31	1
$\delta^{34}S$					
min	5.40	-14.700	-14.700	6.260	14.73
max	20.60	14.00	8.840	14.00	
mean	12.07	7.969	1.369	9.673	
median	12.06	9.200	3.915	9.590	
sd	2.592497	5.148353	8.146122	1.863572	
variance	6.721038	26.50554	66.3593	3.472901	
C:S					
min	129.0	137.0	154.0	137.0	160.1
max	223.0	219.0	219.0	216.9	
mean	187.7	186.6	179.2	188.3	
median	193.2	191.0	178.0	193.0	
sd	25.32148	19.89799	22.22213	19.27832	
variance	641.1774	395.9299	493.823	371.6538	
N:S					
min	41.00	44.00	50.02	44.00	50.49
max	73.05	69.90	69.00	69.90	
mean	59.83	59.27	57.33	59.71	
median	61.11	61.00	59.00	61.00	
sd	8.301657	6.459054	6.269319	6.508434	
variance	68.91751	41.71938	39.30436	42.35972	

Table 6.8. Shapiro-Wilk test for $\delta^{34}S$ of each flatfish species. Bold results indicate significant results.

Species	**W-statistics**	**p-value**
Pleuronectes platessa (n=82)	0.95681	**0.00757**
Platichthys flesus (n=39)	0.69004	**8.751e-08**
Marine *P. flesus* (n=31)	0.97303	0.6059
Freshwater *P. flesus* (n=8)	0.8689	0.147

A scatterplot showing the results from the seven modern samples of *P. platessa* and *P. flesus* can be seen in figure 6.15. The samples from the North Sea have a similar distribution, albeit with less variation between them, as conspecific archaeological samples for all three isotope values. The one sample from the Norwegian coast, however, has higher $\delta^{13}C$ and $\delta^{15}N$ and lower $\delta^{34}S$ values compared to its archaeological conspecifics.

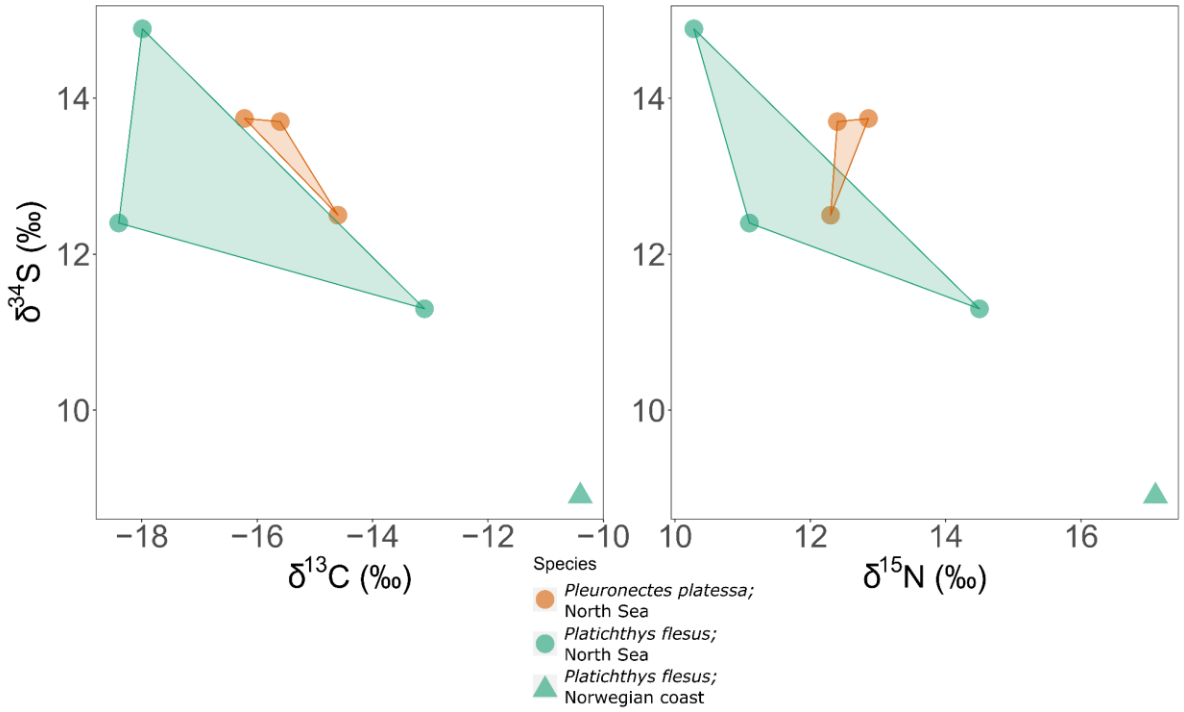


Figure 6.15. $\delta^{13}C$ and $\delta^{34}S$ (left) and $\delta^{15}N$ and $\delta^{34}S$ (right) of modern samples, coloured according to species and shape to catch location.

Table 6.9. Isotope values of modern samples.

Species	Location	Sample	%C	%N	%S	C:N	C:S	N:S	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
P. platessa	North Sea	1966	41.6	15.1	0.53	3.2	210	65	-15.6	12.4	13.7
P. platessa	North Sea	1967	40.4	15	0.52	3.1	208	66	-14.6	12.3	12.5
P. platessa	North Sea	1968	40.9	14.1	0.5	3.4	219	65	-16.22	12.86	13.74
P. flesus	North Sea	1973	41.8	14.6	0.52	3.3	215	64	-18.4	11.1	12.4
P. flesus	North Sea	1974	41.4	14.7	0.58	3.3	191	58	-17.99	10.28	14.89
P. flesus	North Sea	1979	41.6	14.8	0.55	3.3	201	61	-13.1	14.5	11.3
P. flesus	Norwegian coast	1984	40.6	15.1	0.56	3.1	192	61	-10.4	17.1	8.9

6.3.5 Ecological visualisation

6.3.5.1 Habitat distinctions

Based on $\delta^{13}C$ and $\delta^{15}N$ and the species identifications, all of our archaeological fish samples can be easily separated into three large groups: freshwater species, marine Gadidae and flatfish (figure 6.16). A clear distinction between the freshwater and marine group is visible. Most flatfish have higher $\delta^{13}C$ values than the freshwater samples, being more similar to the marine Gadidae for $\delta^{13}C$, but a few have $\delta^{13}C$ values below -20‰, falling within the freshwater group. These samples could originate from fish that have lived in estuarine or freshwater environments. One freshwater sample (Cypriniformes from High Medieval Vlaardingen) possesses an unusually high $\delta^{13}C$ value. Flatfish have a rather restricted range for $\delta^{15}N$. Only a few samples have higher δ^{15}N values, identified as the more piscivorous species such as *S. maximus* and *S. rhombus*. The marine Gadidae also have elevated δ^{15}N values. The freshwater species have a wide range of δ^{15}N.

Within flatfish (figure 6.17), there is a clear differentiation between some taxa. Scophthalmidae have elevated δ^{15}N values compared to Pleuronectidae. All flatfish samples with δ^{13}C<-17‰ have been identified as *P. flesus*, which is the species known to occur in riverine and estuarine environments.

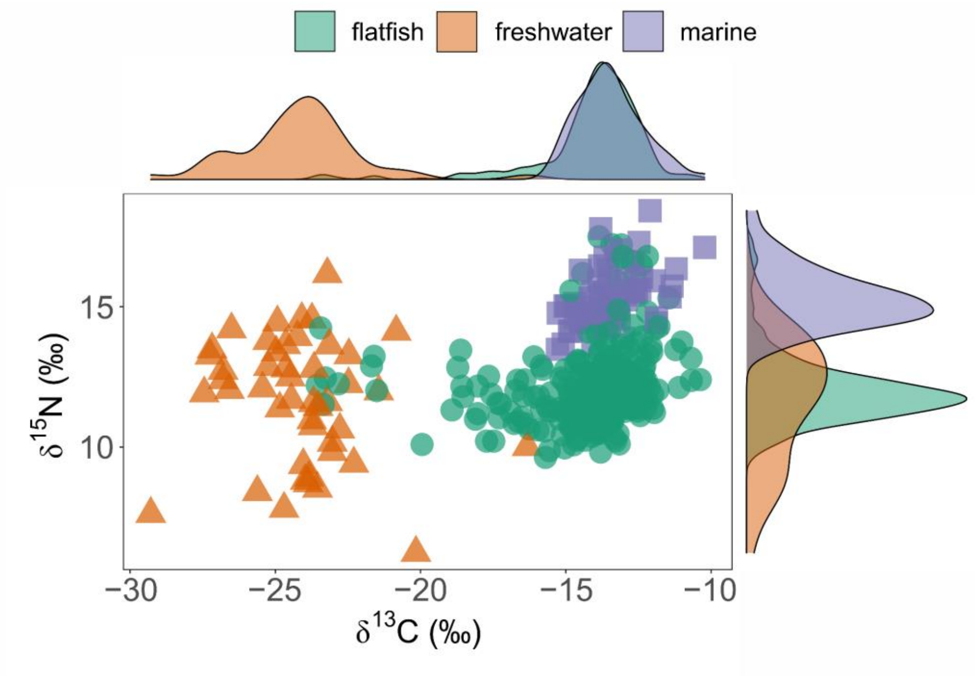


Figure 6.16. Scatterplot of δ^{13}C and δ^{15}N of all archaeological fish samples, with density plots for both variables. Colour and shape according to the broad ecological group.

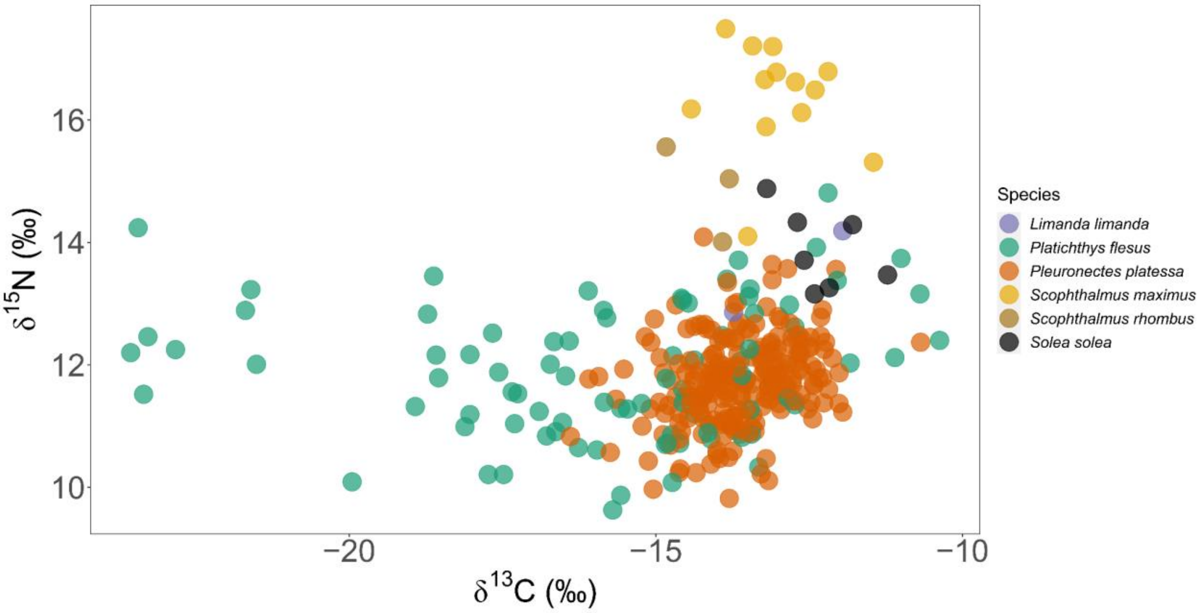


Figure 6.17. Scatterplot of δ^{13}C and δ^{15}N of all archaeological flatfish samples, coloured by species identification through ZooMS.

On figure 6.18 it can be seen that the lower $\delta^{13}C$ values of a sample are, the lower $\delta^{34}S$ values are as well. The intermediary samples of *P. flesus*, with $\delta^{13}C$ between -20‰ and -15‰, which are thought to be 'estuarine' samples, do not show a difference in $\delta^{34}S$ compared to the 'marine' samples of this species. The marine samples of both species with a $\delta^{13}C$ between -15‰ and -10‰, have a $\delta^{34}S$ range of 5.4-20.6‰. This matches with the marine and freshwater influenced groups described in Nehlich (2015). No clear relationship between $\delta^{15}N$ and $\delta^{34}S$ is noticed.

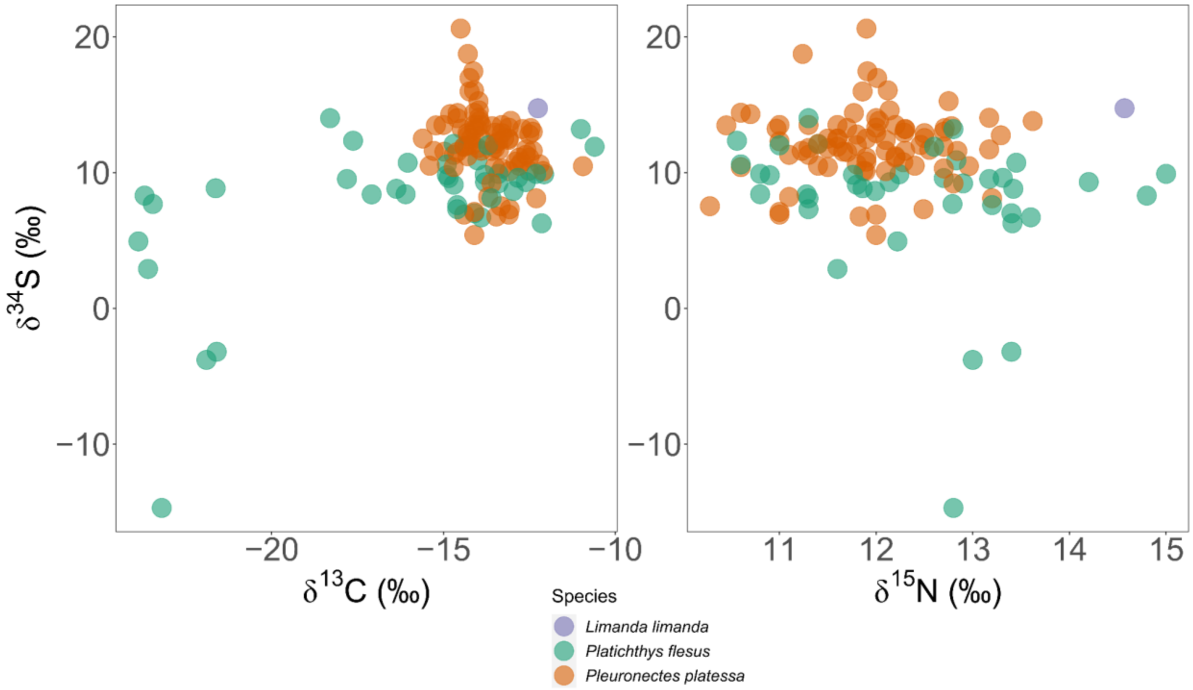


Figure 6.18. $\delta^{13}C$ and $\delta^{34}S$ (left) and $\delta^{15}N$ and $\delta^{34}S$ (right) of criteria-matched samples per species.

Detailed figures on marine, freshwater and other flatfish species can be found in the appendix (figures E5-13 and table E6).

6.3.5.2 Isotopic niche space

Using the rKIN package (Ekrich *et al.*, 2020; Robinson, 2021), the isotopic niche space can be analysed for each of the most abundant species (sample size > 10). This was possible for *P. flesus, P. platessa* and *S. maximus* for $\delta^{13}C$ and $\delta^{15}N$, and only the first two for $\delta^{34}S$. As can be seen in figures 6.19 and 6.20 and in table 6.10*, Pleuronectes platessa* is almost completely overlapped by *P. flesus*, which has an incredibly large isotopic niche space due to samples coming from different habitats. These two species consume similar prey, and while *P. flesus* can occur in different habitats, both species are well known to live in similar marine environments. Only for $\delta^{34}S$ is *P. platessa* slightly not overlapped by *P. flesus* Both Pleuronectidae species only have limited overlap with *S. maximus*, due to the higher trophic level of the latter species. For analysis of freshwater and marine species, see figures E3-4 and tables E4-5 in the appendix.

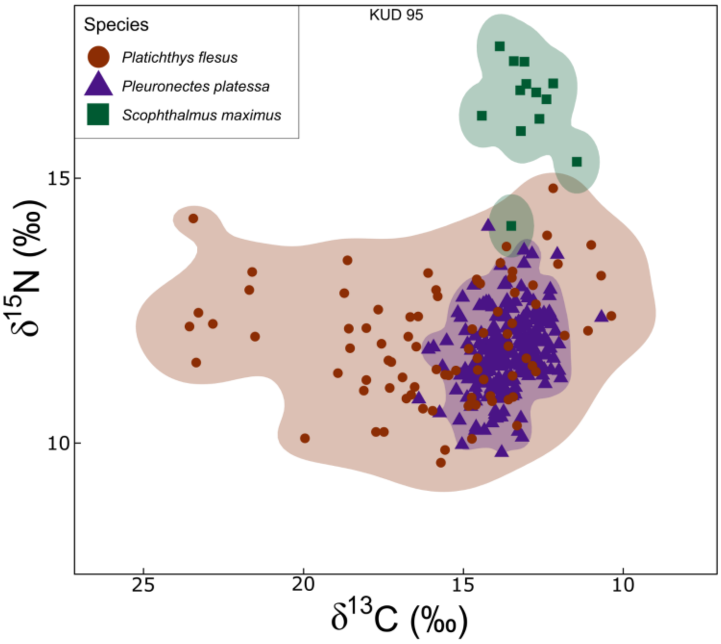


Figure 6.19. rKIN plot using KUD at 95% for *P. flesus, P. platessa* and *S. maximus.*

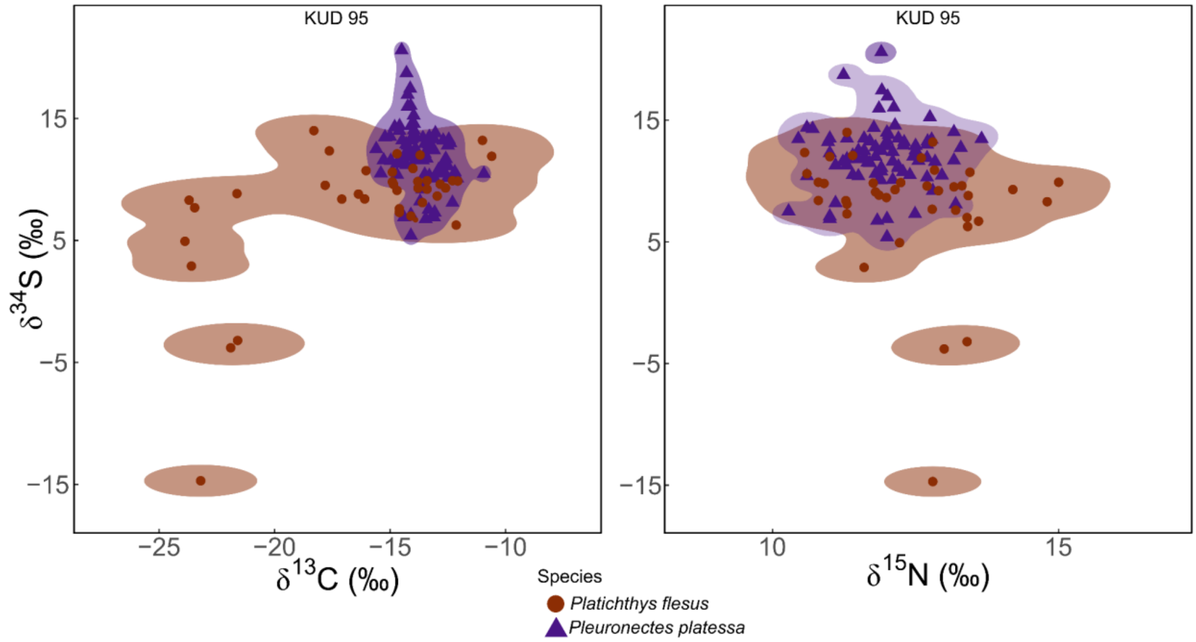


Figure 6.20. rKIN plot using KUD at 95% of $\delta^{13}C$ and $\delta^{34}S$ (left) and $\delta^{15}N$ and $\delta^{34}S$ (right) for *P. flesus* and *P. platessa.*

Table 6.10. Shape area of the isotope niche space and overlap of polygons of the isotope niche space of each flatfish species at 95% KUD.

	Shape area	**Overlap of polygons**		
Species		*P. platessa*	*P. flesus*	*S. maximus*
$\delta^{15}N \sim \delta^{13}C$				
P. platessa	12.19703	1	1	0.010
P. flesus	62.01640	0.197	1	0.025
S. maximus	10.06518	0.012	0.151	1
$\delta^{34}S \sim \delta^{13}C$				
P. platessa	41.09942	1	0.754	
P. flesus	173.59837	0.179	1	
$\delta^{34}S \sim \delta^{15}N$				
P. platessa	36.20443	1	0.777	
P. flesus	62.17553	0.452	1	

6.3.6 Comparing regions

In the following sections, only *P. platessa* and *P. flesus* will be discussed in detail. The results for the other species are provided in the appendix, but will not be part of the larger discussion as the small sample sizes prevent meaningful interpretations. In the appendix, plots for $\delta^{34}S$ without the freshwater samples from *P. flesus* can be found.

When comparing the different sites for *P. platessa* (figure 6.21), clear differences can be observed for carbon isotope values. The Dutch sites, Gent, and Coppergate all contain samples with slightly lower $\delta^{13}C$ values (<15.5‰), which are not found at the coastal sites, the sites in London, or Blue Bridge Lane. No major difference between the sites were found for nitrogen isotope values.

Comparing sites of *P. platessa* for $\delta^{34}S$ (figure 6.22) shows a clear difference in geographical distribution. Some sites have a very small range of $\delta^{34}S$ (e.g., SOT89, Blue Bridge Lane), while others have a very large range (e.g., Coppergate, Vlaardingen). Remarkable are the two extreme values for Vlaardingen, while the majority of samples all have a rather similar distribution. GSJ06 and SGA89 have on average lower $\delta^{34}S$ values compared to the other sites and samples with similar low values are also present in Barreau Saint-George, Koksijde, Gent, and Vlaardingen. Based on Nehlich *et al.* (2013) these samples could be classified as freshwater fish, but $\delta^{13}C$ shows these are all freshwater influenced marine samples. Coppergate and one sample from Vlaardingen have samples with very high $\delta^{34}S$ values (15‰ or more), which would correspond to the strongly marine category as used by Nehlich *et al.* (2013).

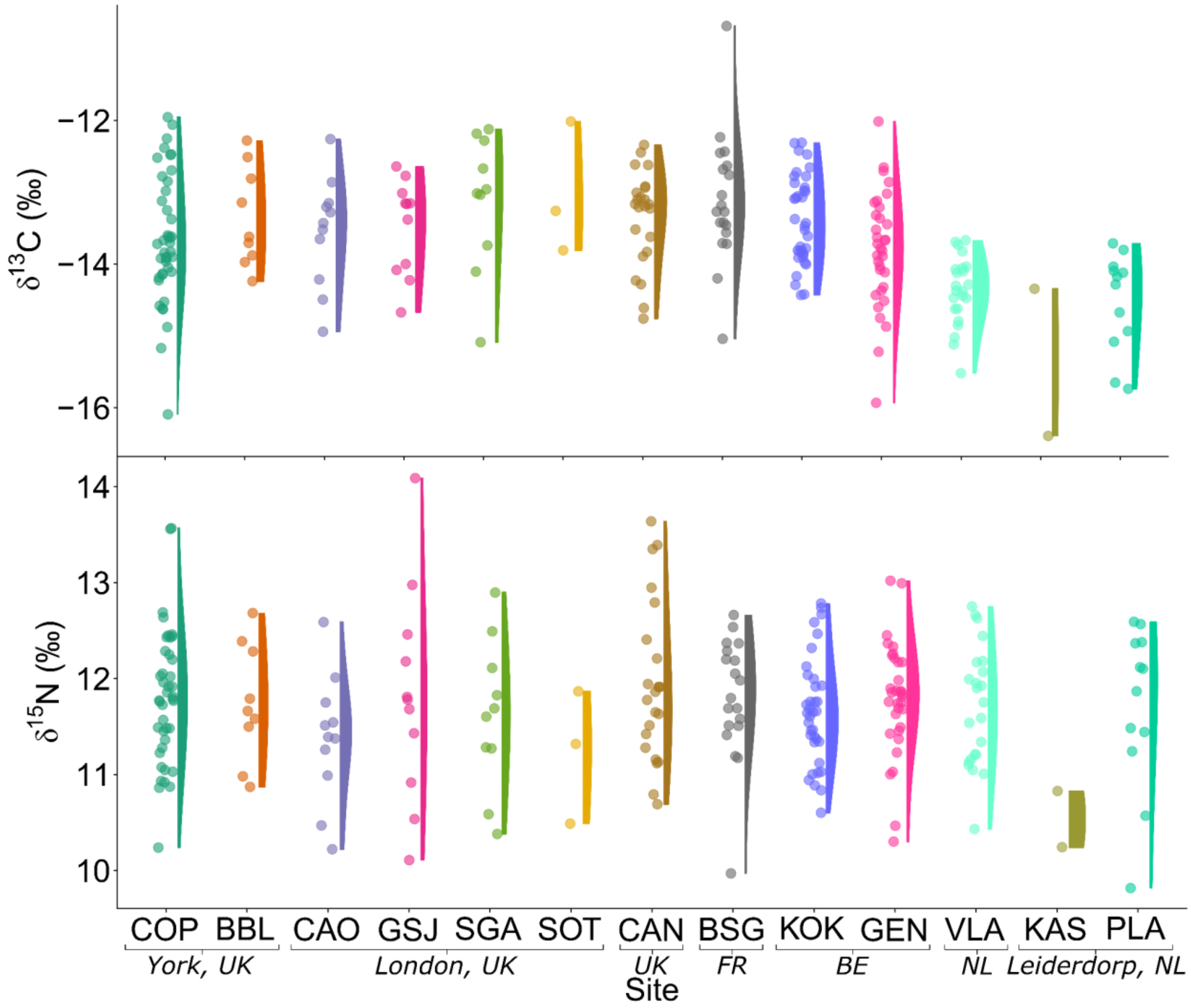


Figure 6.21. $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) per site of *P. platessa*.

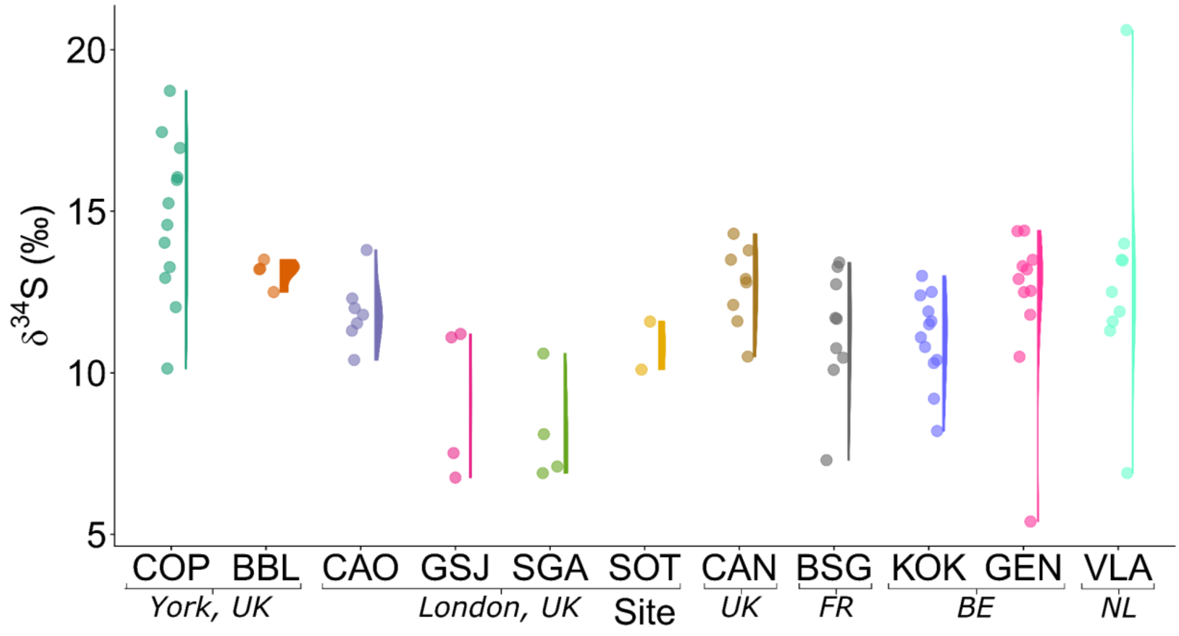


Figure 6.22. $\delta^{34}S$ per site of *P. platessa.*

For *P. flesus* there are large differences between the sites for carbon and to some extent for nitrogen isotope values (figure 6.23). The three coastal sites, Barreau Saint-George, Canterbury and Koksijde do not have any samples with very low $\delta^{13}C$ ($\delta^{13}C<-20‰$; minimum for these three sites is -18‰); only *P. flesus* with a strong marine signal is present in these sites. The samples from Gent and the Dutch sites also show mostly a marine signal but two samples (one from Gent and one from Vlaardingen) have lower $\delta^{13}C$ values, indicating more coastal and estuarine signals. Most freshwater samples originate from England from both York and London, with only a handful of samples in these sites showing a clear marine signal. In general, the continental sites seem to have slightly lower $\delta^{15}N$ values compared to the English sites for *P. flesus*, especially those from London and Canterbury.

For *P. flesus*, there are clear differences between the sites for $\delta^{34}S$ (figure 6.24). When only looking at marine *P. flesus* (see figure E38 in the appendix), the continental sites (Barreau Saint-George, Koksijde, and Gent) and Canterbury seem to have higher $\delta^{34}S$ values than the sites in York and London. Especially Canterbury and Gent have on average higher $\delta^{34}S$ values. The freshwater *P. flesus* all have $\delta^{34}S<10‰$. The samples from London have negative $\delta^{34}S$ values, while the samples from York and Vlaardingen have positive $\delta^{34}S$ values.

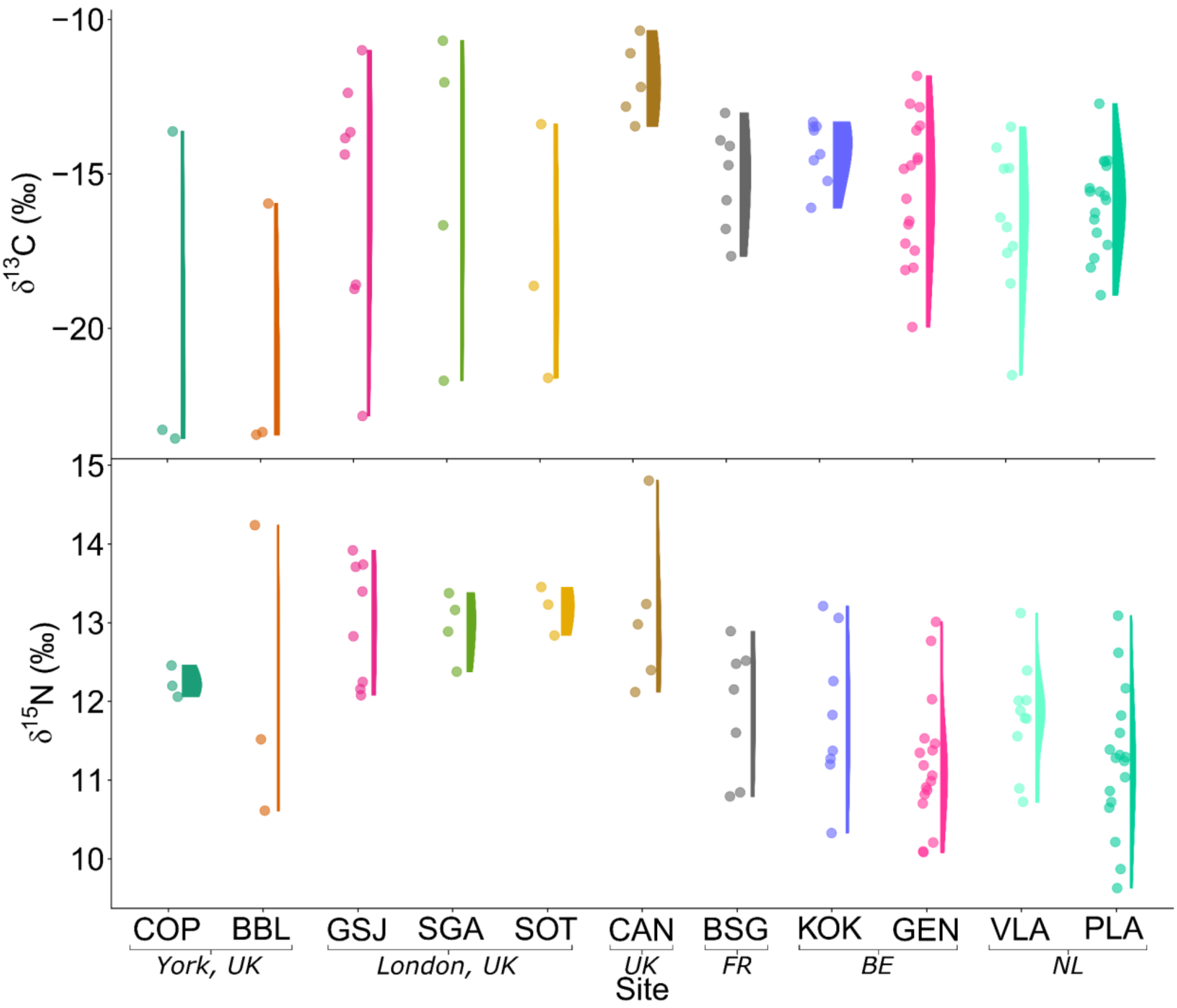


Figure 6.23. $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) per site of *P. flesus*.

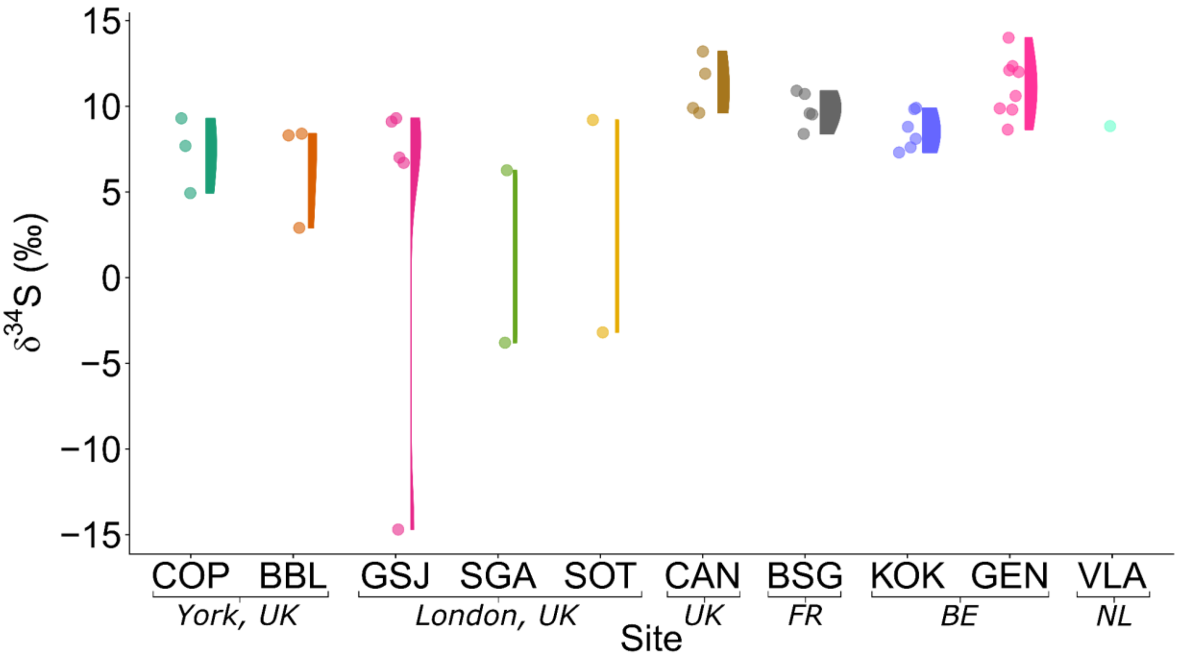


Figure 6.24. δ^{34}S per site of *P. flesus.*

There is a significant difference from normal distribution for Coppergate and Blue Bridge Lane for δ^{13}C of *P. flesus*, due to the presence of freshwater samples and the small sample size (table E7 in the appendix). No significant difference from homogeneity of variance was found using the Levene's test for sites for δ^{13}C of *P. platessa* (p-value = 0.6724), δ^{15}N of *P. platessa* (p-value = 0.5334), δ^{13}C of *P. flesus* (p-value = 0.1014), and δ^{15}N of *P. flesus* (p-value = 0.4623). This matches the assumptions necessary for ANOVA (section 6.2.7).

There is a significant difference from normal distribution for Gent for δ^{34}S of *P. platessa*, and for Blue Bridge Lane and GSJ06 of *P. flesus.* This is most likely due to the small sample sizes for most of these groups and the presence of samples with low δ^{34}S values (table E8 in the appendix). No significant difference from homogeneity of variance was found using the Levene's test for site for δ^{34}S of *P. platessa* (p-value = 0.4073). No significant difference from homogeneity of variance was found using the Levene's test for site for δ^{34}S of *P. flesus* (p-value = 0.3786).

There is little observed difference between the sites for the other species of flatfish, although δ^{15}N of *S. maximus* is higher in Coppergate compared to the other sites this species was found in (see figure E9 in the appendix). For freshwater species there is little difference between the sites for *E. lucius* and slight differences for Cypriniformes, which might be species related. For δ^{15}N it is noticeable that the sites on the west coast of the North Sea have higher values for *E. lucius* and Cypriniformes compared to the east coast (see figure E7 in the appendix). Within each marine species there is little difference between the sites for both δ^{13}C and δ^{15}N (see figure E8 in the appendix).

6.3.7 Comparing time periods

To compare changes through time, samples from all sites are grouped together per time period, as defined in the method section (table 6.1), per species. This of course could create biases in the chronological analysis as not every site is equally represented through time. The abbreviations for the sites included for each time period per species are mentioned in the text. Plots for δ^{13}C and δ^{15}N values per time period for each individual site can be found in the appendix (figures E14-37).

When comparing carbon and nitrogen isotope values through time periods for *P. platessa*, no clear differences could be observed between the time periods (figure 6.25). There are seemingly fewer samples with low δ^{13}C values during the second part of the Early (COP, BBL, SGA, SOT, KOK, GEN, VLA, PLA, KAS) and Early/High Medieval (CAO, GSJ, KOK) periods. The Late Medieval period (COP, BBL, CAO, CAN, VLA) seems to have on average slightly lower values for δ^{13}C than the other time periods. There are samples from the Early/High till the Late Medieval period (COP, BBL, CAO, GSJ, CAN, BSG, KOK, GEN, VLA) with slightly higher δ^{15}N values, which do not appear during the Early Medieval period; these are not related to size (see below).

A large proportion of samples from *P. platessa* from the Early Medieval to the High Medieval period (all sites) have lower δ^{34}S values, compared to those from the High/Late (COP, BBL, VLA) and Late Medieval period (COP, BBL, CAO, CAN, VLA). All samples from the High/Late and Late Medieval period clearly originate from a marine habitat (figure 6.26).

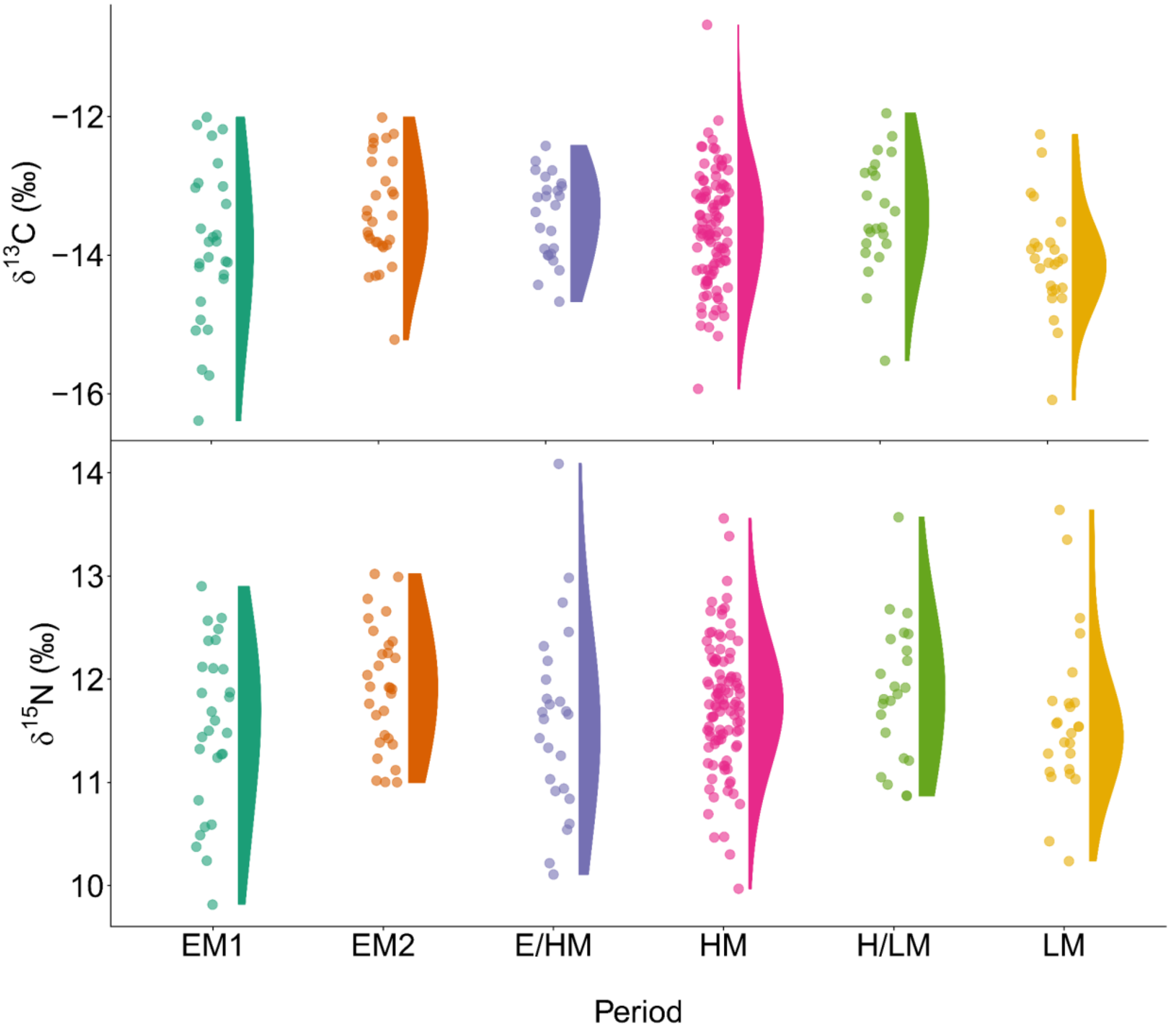


Figure 6.25. δ^{13}C (top) and δ^{15}N (bottom) per period of *P. platessa*.

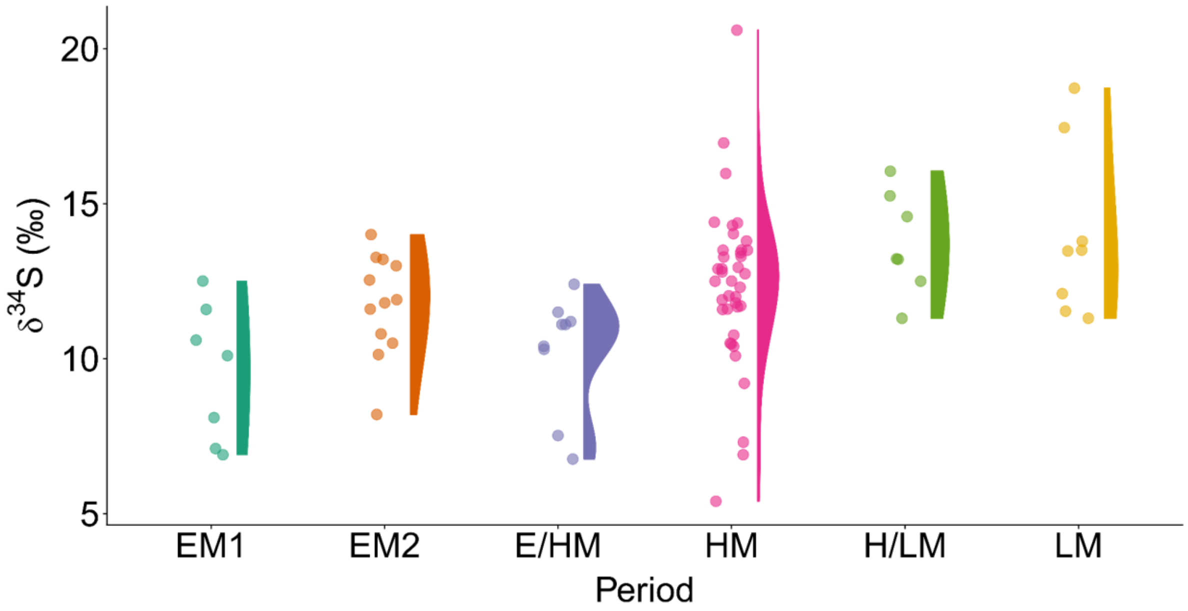


Figure 6.26. δ^{34}S per period of *P. platessa*.

For *P. flesus* there also do not seem to be any clear differences between the time periods (figure 6.27). The second half of the Early Medieval period (9-11th centuries CE; COP, KOK, GEN) doesn't show an increase in samples with higher δ^{13}C values, which are present in most other time periods, including samples from the same sites. The freshwater individuals appear in most time periods, although they are more abundant in the first half of the Early Medieval period. No differences between the time periods for δ^{15}N values are observed.

For marine *P. flesus* there is also a slight increase in δ^{34}S through time, but slightly less clear than for *P. platessa*, as there is only one sample from the Late Medieval period (CAN) and the difference between the Early Medieval (COP, BBL, SGA, SOT, KOK, GEN) and High Medieval (CAN, BSG, KOK, GEN) period is rather small due to the small sample size. The freshwater samples mostly come from the Early Medieval period (COP, BBL, SGA, SOT), but three samples were also observed from the Early/High Medieval (GSJ), High/Late Medieval (COP), and Late Medieval (VLA) period and have low δ^{34}S values (<9‰) (figures 6.28 and E39).

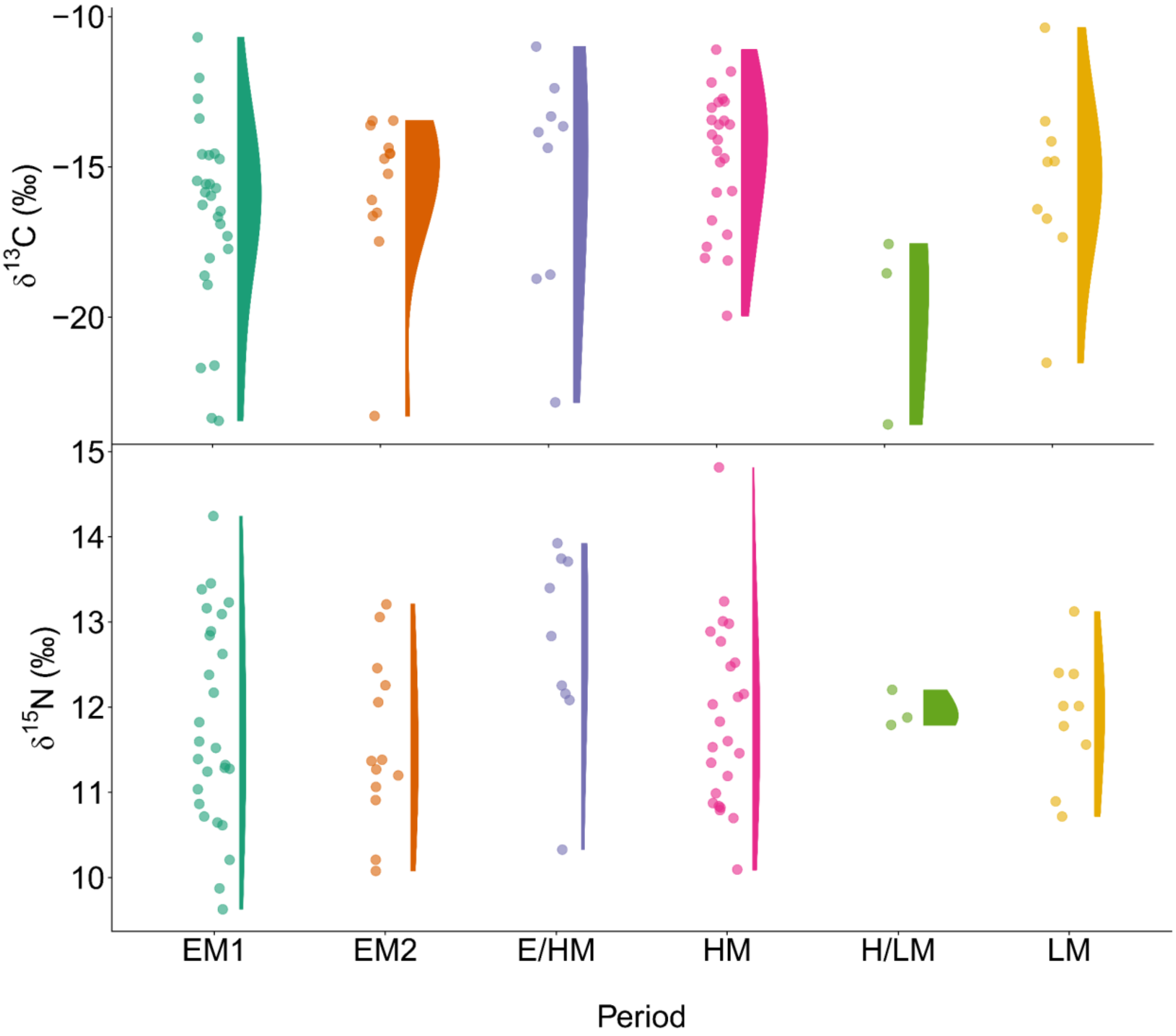


Figure 6.27. δ^{13}C (top) and δ^{15}N (bottom) per period of *P. flesus*.

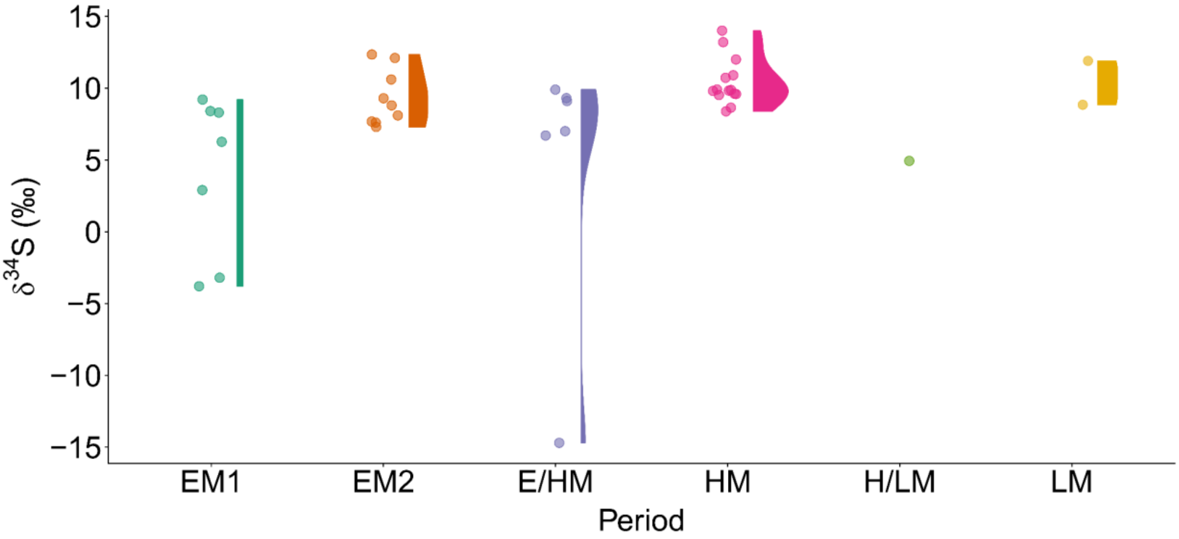


Figure 6.28. δ^{34}S per period of *P. flesus*.

There is a significant difference from normal distribution for EM2 for δ^{13}C of *P. flesus*, due to the presence of one freshwater sample and the small sample size (table E9 in the appendix). No significant difference from homogeneity of variance was found using the Levene's test for periods for δ^{13}C of *P. platessa* (p-value = 0.1508), δ^{15}N of *P. platessa* (p-value = 0.2641), δ^{13}C of *P. flesus* (p-value = 0.8594), and δ^{15}N of *P. flesus* (p-value = 0.2316). This matches the assumptions necessary for ANOVA (section 6.2.7).

There is a significant difference from normal distribution for δ^{34}S for the High Medieval period for *P. platessa*, and Early Medieval period 2, Early/High Medieval, and High Medieval of *P. flesus*. This is most likely due to the small sample sizes for most of these groups and the presence of samples with low δ^{34}S values (table E10 in the appendix). No significant difference from homogeneity of variance was found using the Levene's test for time periods for δ^{34}S of *P. platessa* (p-value = 0.8525). No significant difference from homogeneity of variance was found using the Levene's test for time periods for δ^{34}S of *P. flesus* (p-value = 0.2872).

No clear differences between chronological periods are observed for δ^{13}C values in the other flatfish species (see figure E12 in the appendix). For freshwater species a slight decrease in δ^{13}C values is observed throughout the Medieval period, which is especially clear in the Early and High Medieval periods. No clear difference or trends are observed between chronological periods for δ^{15}N values (see figure E10 in the appendix). No differences between chronological periods were observed for marine species, though a slightly lower mean is observed for δ^{15}N of *M. aeglefinus* in the High Medieval period (see figure E11 in the appendix).

6.3.8 Comparing sizes

To compare the isotope values of different sizes of fish, samples from all sites and time periods are grouped together per size class, as defined in the method section, per species, as separate analysis of size classes per time period and sites (see figures E14-35 in the appendix) did not show any differences between the size classes. This will allow a better insight into changes in the isotope composition throughout a fish's life, which will improve the interpretations for regional and chronological shifts. For size comparisons only certain, clear size classes were retained for these figures as for many fragmented flatfish samples an exact size estimation could not be defined: 10-20 cm SL, 20-30 cm SL, 30-40 cm SL, 40-50 cm SL, and 50-60 cm SL.

For *P. platessa* (figure 6.29) it is noticed that for both δ^{13}C and δ^{15}N there are fewer samples with lower values for the higher size classes, while for *P. flesus* this trend is only clearly visible in δ^{13}C values, but not in δ^{15}N values (figure 6.31). There are fewer samples with higher δ^{15}N values for larger-sized *P. flesus*. All the freshwater *P. flesus* belong to the same rather small size class (10-20 and most from 20-30 cm SL).

For *P. platessa* there is a slight trend visible with more samples with high δ^{34}S values present in 40-50 cm SL than in the smaller size classes, although some samples with lower δ^{34}S values are also still present in 50-60 cm SL (figure 6.30).

No trend of δ^{34}S for the different size classes for marine *P. flesus* was observed (figures 6.32 and E40).

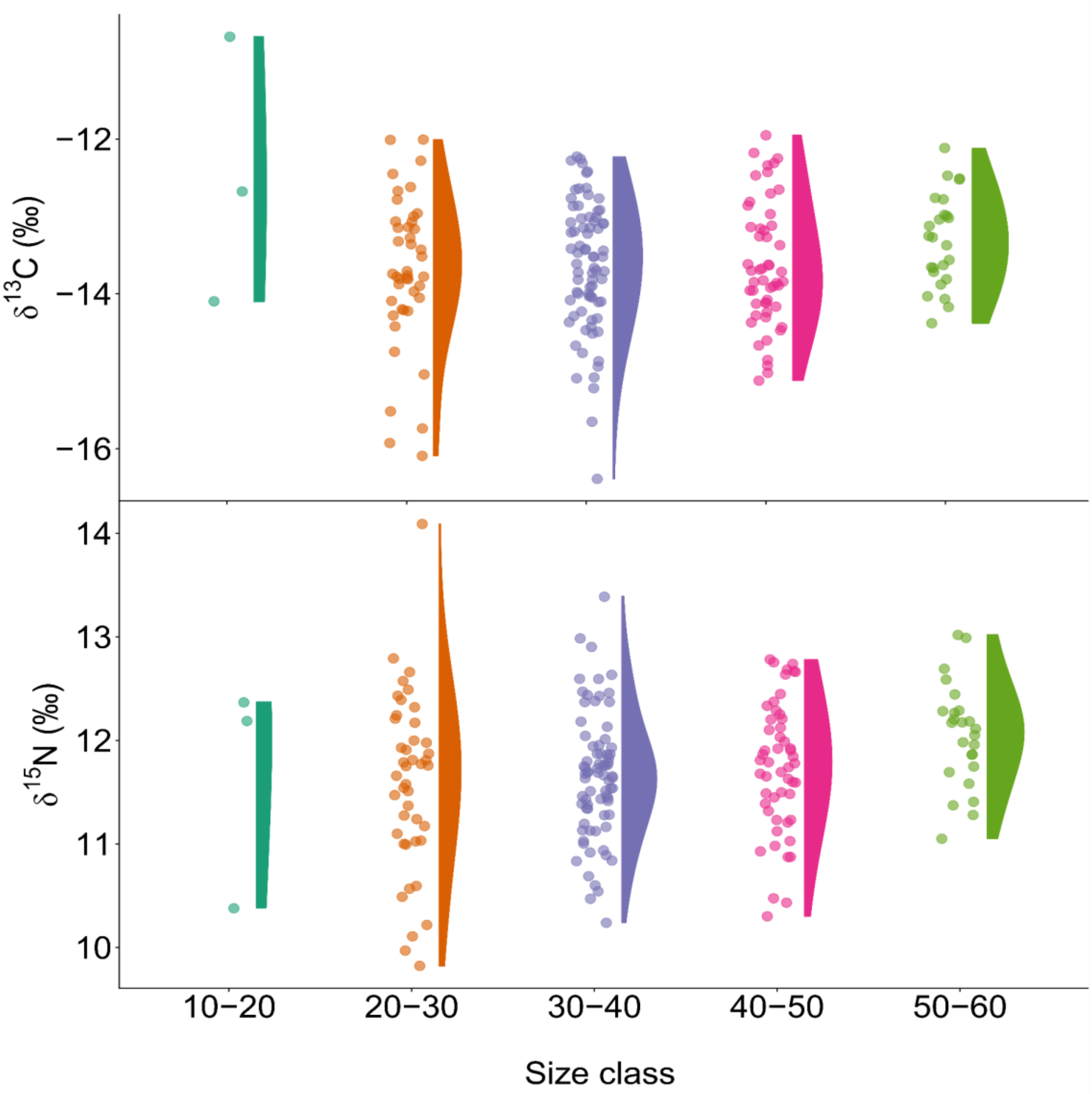


Figure 6.29. δ^{13}C (top) and δ^{15}N (bottom) per size class of *P. platessa*.

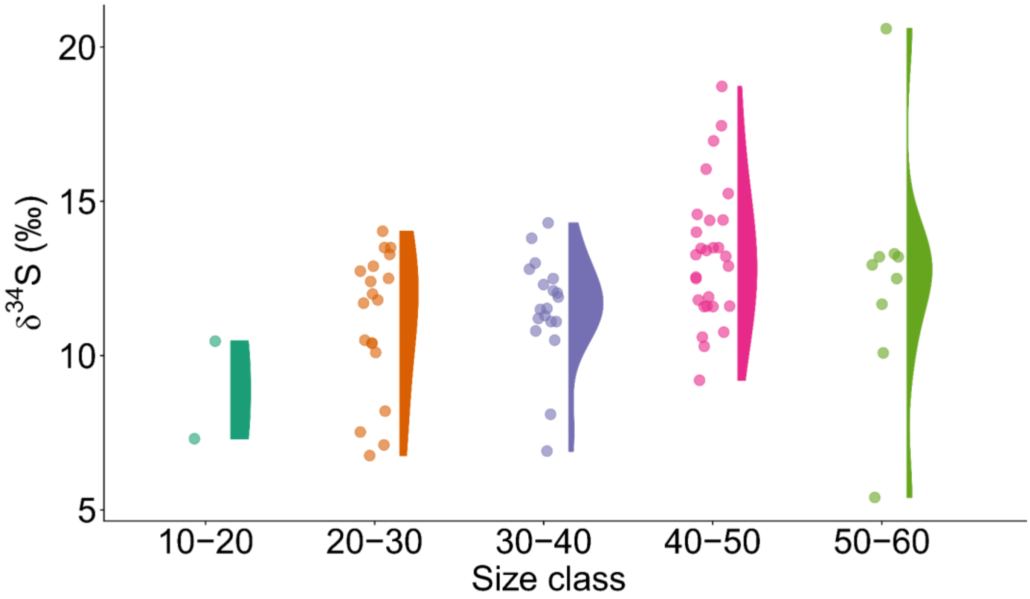


Figure 6.30. δ^{34}S per size class of *P. platessa*.

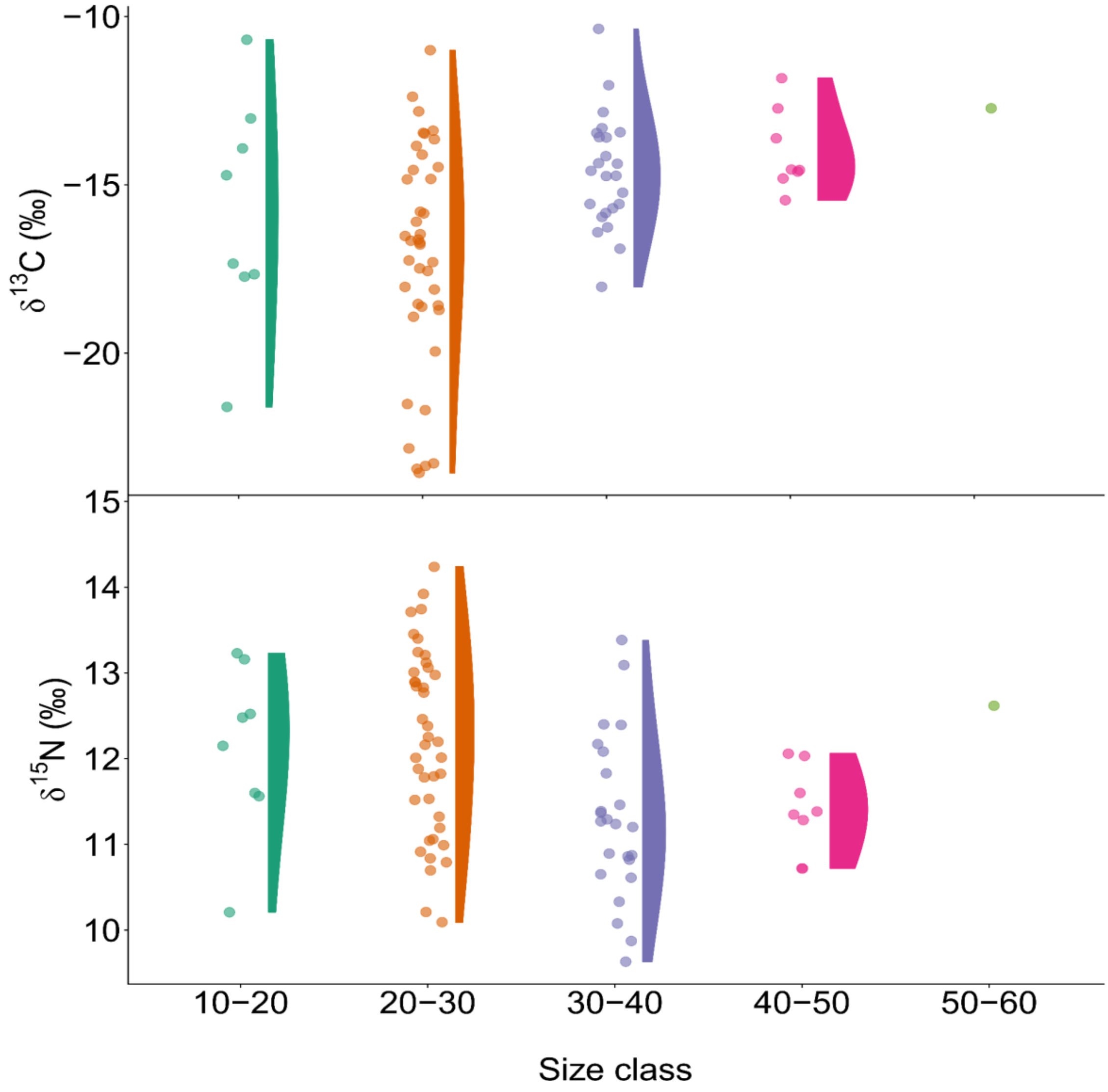


Figure 6.31. δ^{13}C (top) and δ^{15}N (bottom) per size class of *P. flesus*.

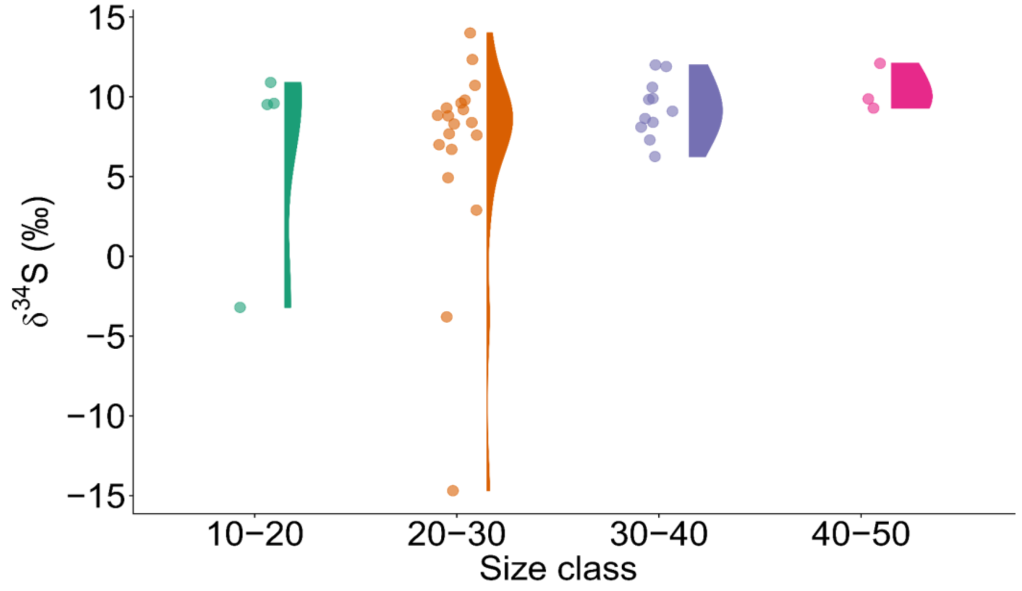


Figure 6.32. δ^{34}S per size class of *P. flesus*.

No size class shows a significant difference from normal distribution for $\delta^{13}C$ and $\delta^{15}N$ (table E11 in the appendix). No significant difference from homogeneity of variance was found using the Levene's test for size class for $\delta^{13}C$ of *P. platessa* (p-value = 0.1147) and $\delta^{15}N$ of *P. flesus* (p-value = 0.07923). Heterogeneity of variance was found for size class for $\delta^{15}N$ of *P. platessa* (p-value = **0.03838**) and $\delta^{13}C$ of *P. flesus* (p-value = **0.01515**). This result doesn't match the assumptions required for ANOVA (see 6.2.7), but as the data is normally distributed, there is no need for a non-parametric test.

There is a significant difference from normal distribution for 20-30 cm SL and 30-40 cm SL of *P. platessa*, and 10-20 cm SL and 20-30 cm SL of *P. flesus* for $\delta^{34}S$. This is most likely due to the small sample sizes for most of these groups and the presence of samples with low $\delta^{34}S$ values (table E12 in the appendix). No significant difference from homogeneity of variance was found using the Levene's test for size class for $\delta^{34}S$ of *P. platessa* (p-value = 0.5556). No significant difference from homogeneity of variance was found using the Levene's test for size class for $\delta^{34}S$ of *P. flesus* (p-value = 0.577).

No clear trends for size classes were observed for the other flatfish species (see figure E13 in the appendix).

6.3.9 Geographical visualisation of isotopic data

6.3.9.1 AverageR maps

The Isomemo app (Fernandes *et al.*, 2017) was used to visualise geographical and chronological variation observed in the data. Only *P. platessa* and *P. flesus* were analysed due to the small sample size for the other species. Using the AverageR model a general geographical pattern of all samples for a species can be visualised, while using TimeR model a geographical pattern through time (from 700 CE to 1300 CE) can be visualised. On the figures, greener shades denote higher $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values, while redder shades denote lower $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values.

For $\delta^{13}C$ a clear north-south gradient can be observed on the AverageR maps (figure 6.33, 6.34, 6.35). For *P. platessa* (figure 6.33) and marine *P. flesus* (figure 6.35) there is a slightly lower value in the northeast compared to the southwest. For all *P. flesus* (figure 6.34) there is a higher value in the north/northwest of the North Sea. For $\delta^{15}N$ a clear west-east gradient is observed on the AverageR maps. The differences between the east and west coasts are however very small for *P. platessa* (Δ0.07‰) and rather large for *P. flesus* (Δ1.10-1.40‰). A clear north-south gradient can be seen in the southern North Sea for $\delta^{34}S$ of *P. platessa*. For *P. flesus*, this $\delta^{34}S$ gradient is also more west-east oriented. For marine *P. flesus* there is a clear increase in $\delta^{34}S$ at the Thames estuary.

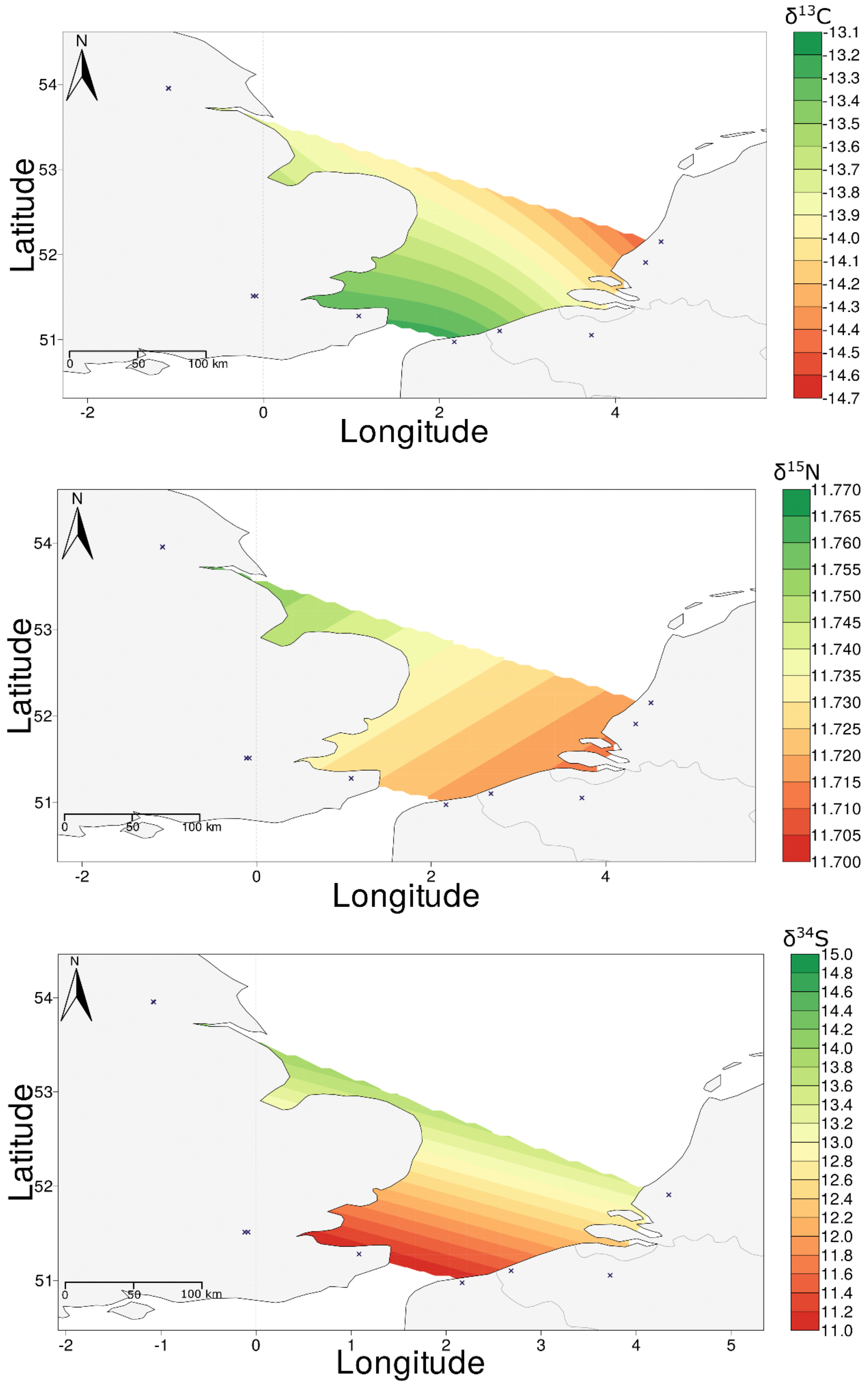


Figure 6.33. AverageR map of $\delta^{13}C$ (n=233, top), $\delta^{15}N$ (n=233, middle), and $\delta^{34}S$ (n=82, bottom) for *P. platessa*.

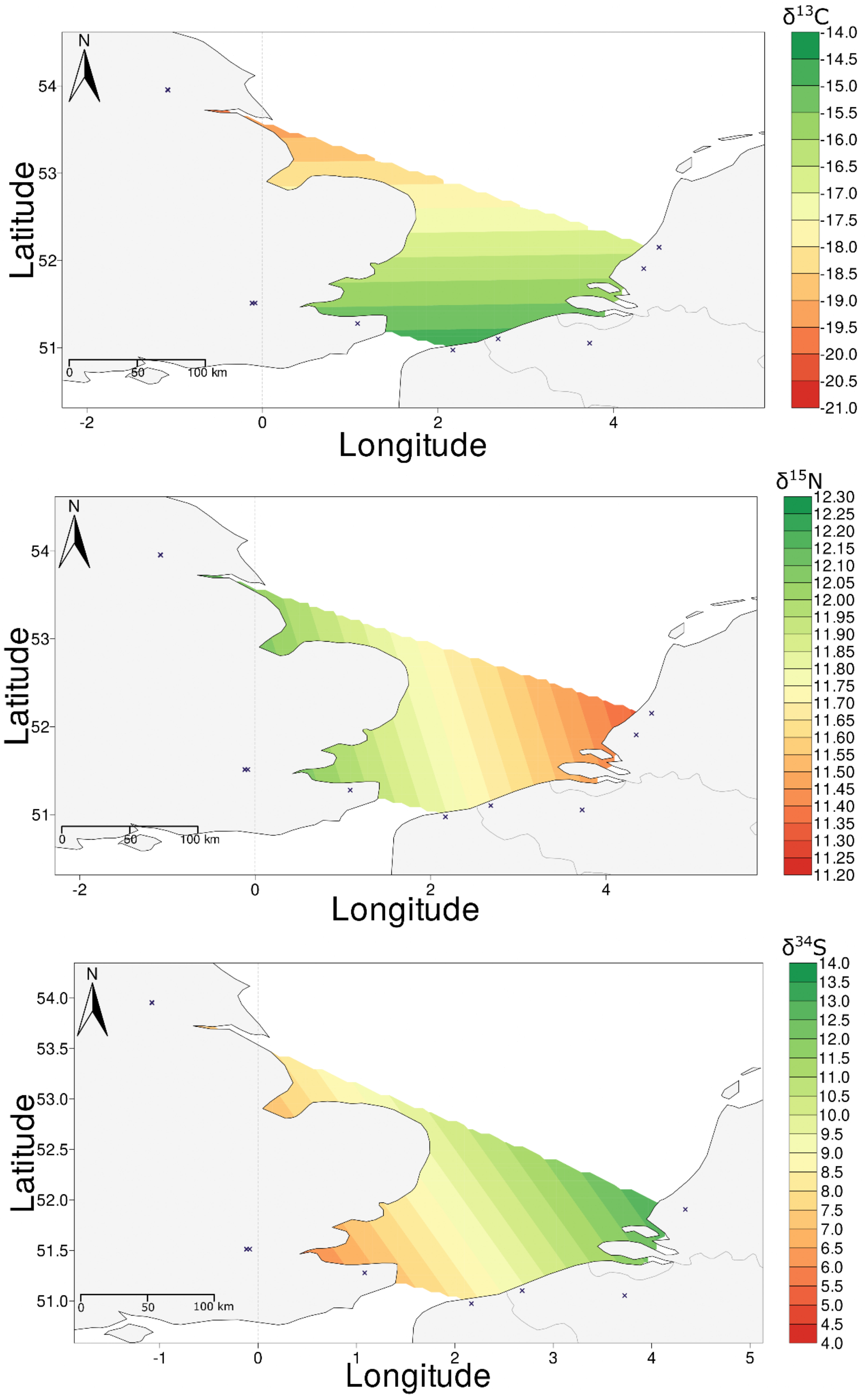


Figure 6.34. AverageR map of δ^{13}C (n=85, top), δ^{15}N (n=85, middle), and δ^{34}S (n=39, bottom) for *P. flesus*.

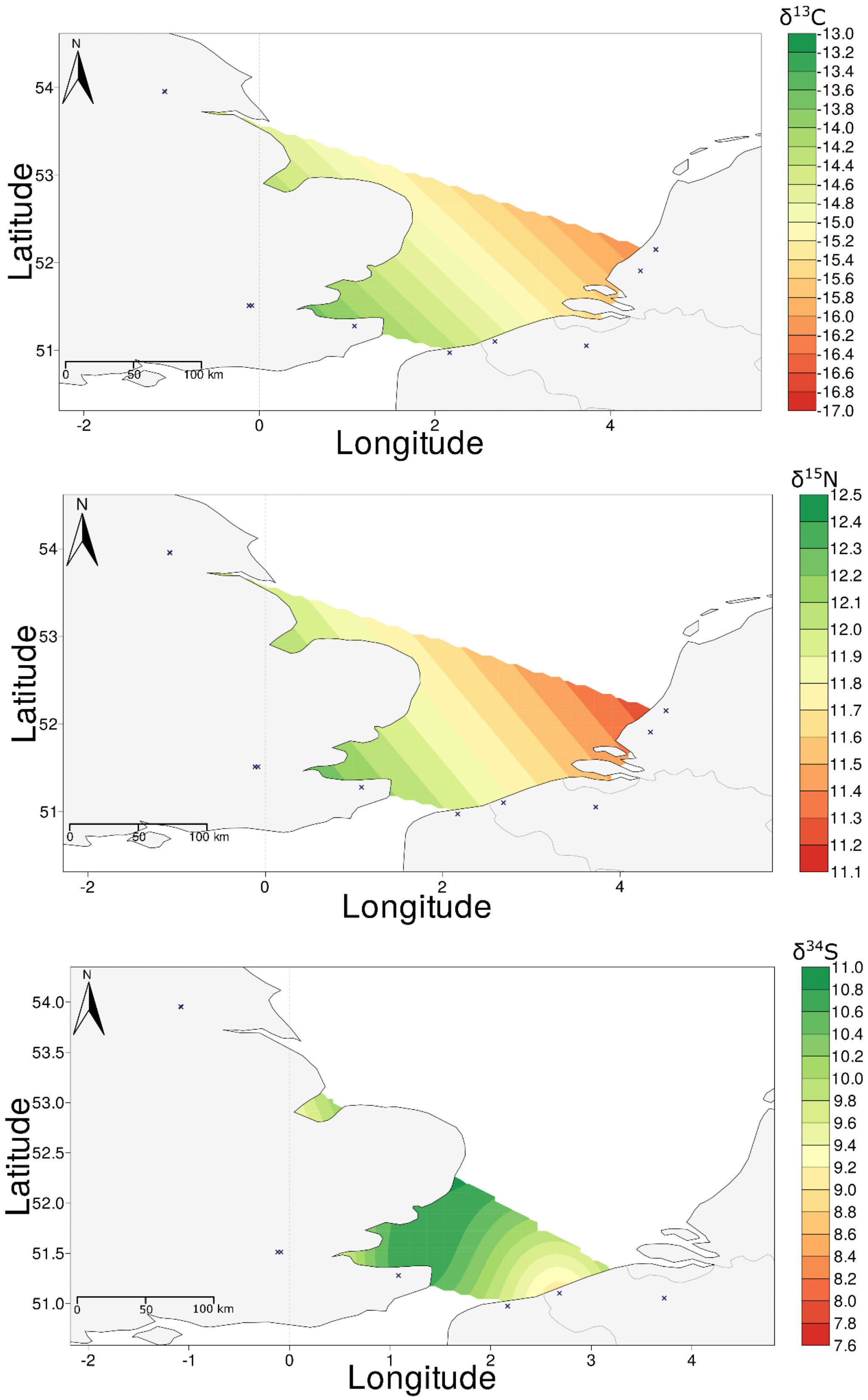


Figure 6.35. AverageR map of $\delta^{13}C$ (n=74, top), $\delta^{15}N$ (n=74, middle), and $\delta^{34}S$ (n=31, bottom) for marine *P. flesus*.

6.3.9.2 TimeR map

Looking through time, no major changes are observed for δ^{13}C for both species (figure 6.36 and E41, E44 in the appendix), with only minor and slight changes in some regions. For δ^{15}N there are clear differences through time for both species with a slight increase (<1-2‰) between 700 CE and 1300 CE (figure 6.37 and E42, E45 in the appendix). Throughout the Medieval period, very little change is observed in δ^{34}S for *P. platessa*, although a slight increase is noticed for the southern part of the sample area (figure 6.38). Due to the smaller number of samples, no clear pattern in δ^{34}S could be visualised for *P. flesus* (figure E43, E46 in the appendix). No difference can be seen between time periods, but this is unsure.

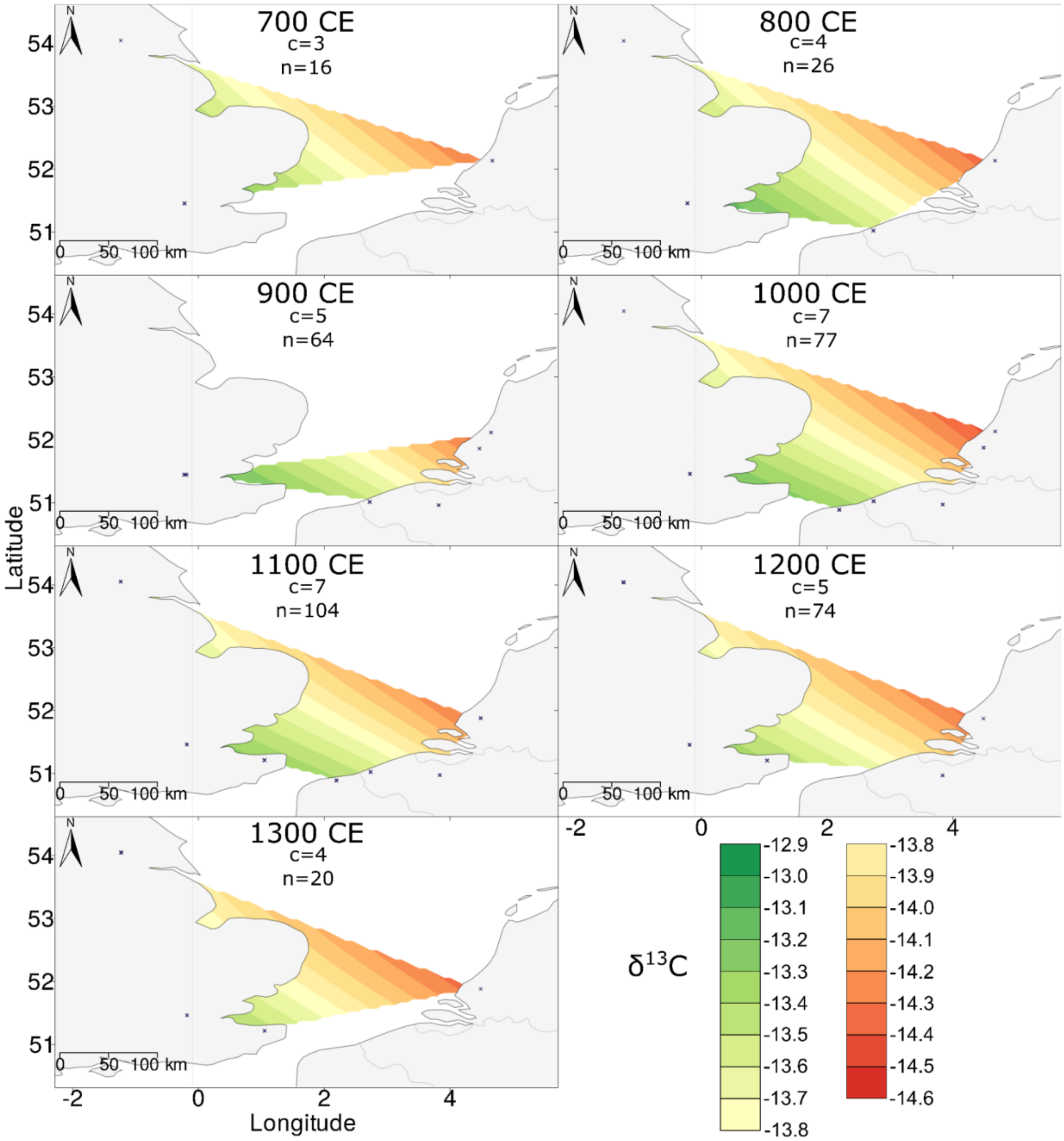


Figure 6.36. TimeR map of δ^{13}C for *P. platessa* per 100-year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

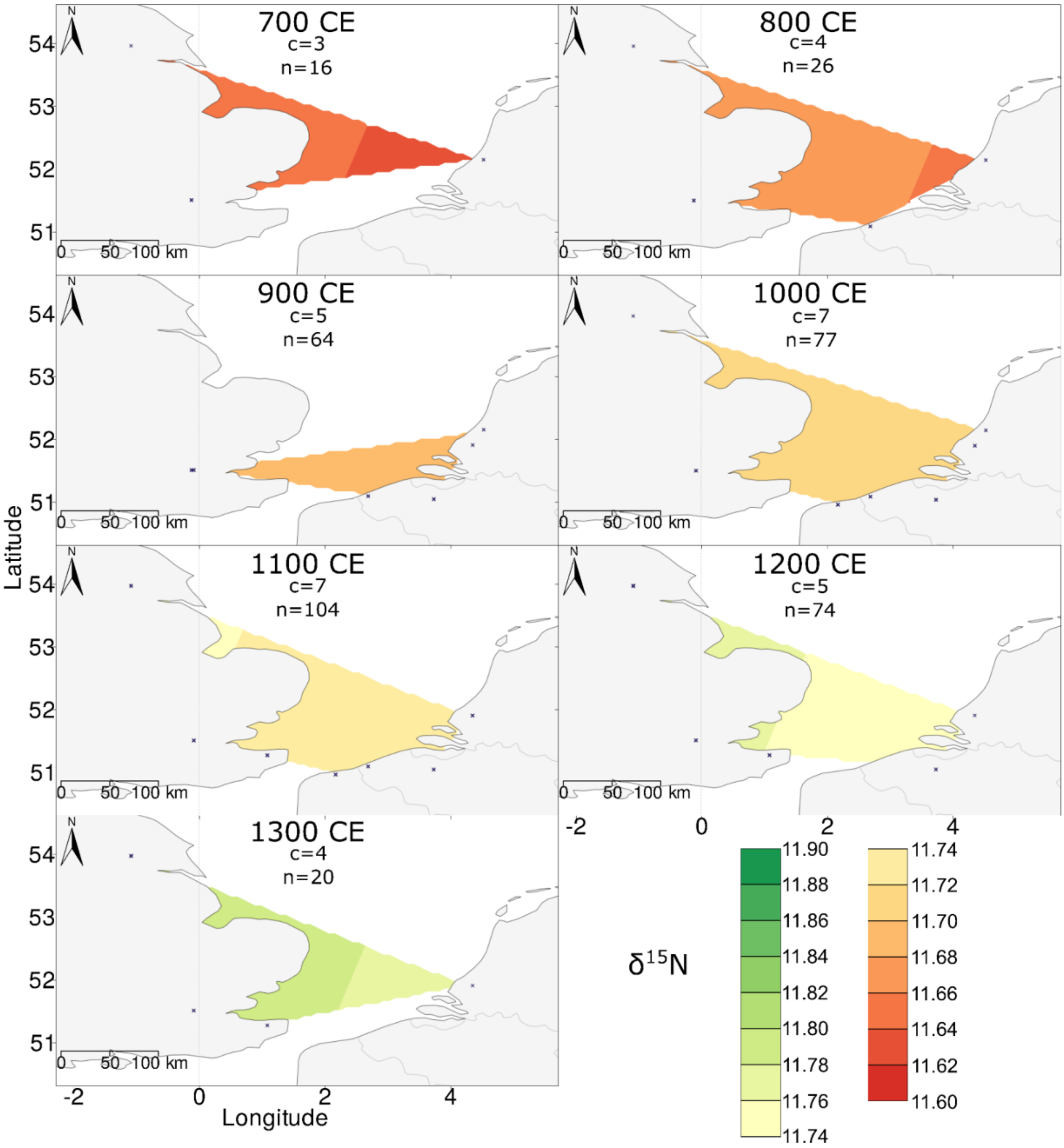


Figure 6.37. TimeR map of $\delta^{15}N$ for *P. platessa* per 100-year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

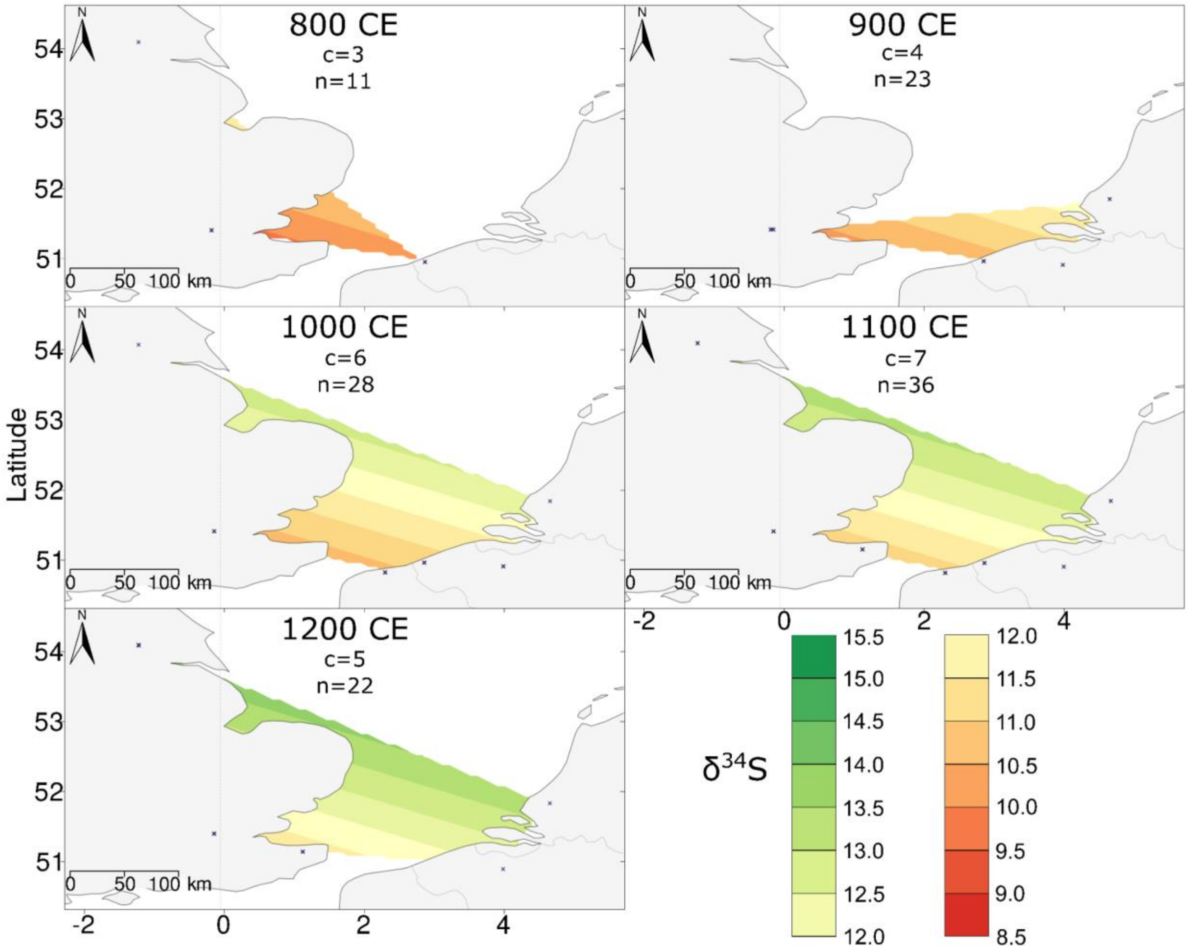


Figure 6.38. TimeR map of δ^{34}S for *P. platessa* per 100-year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

6.3.10 ANOVA

A three-way ANOVA was applied to test if there are significant differences in the mean of the groups within variables for the isotope values. This would indicate if there are effects of size, time, and geography on the isotope values per species. *Size_class*, *Mid*, and *Site* (see methodology section) were used as independent variables as proxies for size, time, and geography respectively and δ^{13}C, δ^{15}N or δ^{34}S as dependent variables separately. This was carried out for *P. platessa* and *P. flesus* separately.

The three-way ANOVA (see table 6.11) revealed that there are significant differences in the mean of δ^{13}C between different sites, sizes and a significant interaction between the effects of time and size for *P. platessa*, which were observed above. There is a significant interaction between the effects of time and site and of time and size in the mean of δ^{15}N for *P. platessa,* which were not observed above and could be related to the reduced ranges for δ^{15}N for some groups within these variables. For *P. flesus*, a significant difference in the mean of δ^{13}C was found between time, site and size, which were also observed above. There are significant differences in the mean of δ^{15}N between sites for *P. flesus,* related to the higher values of δ^{15}N in London and Canterbury. There are significant differences in the mean of δ^{34}S between time, different sites and sizes, and a significant interaction between the effects of site and size for *P. platessa*, which were also observed earlier. There are no significant differences in the mean of $\delta^{34}S$ between sites, size classes or time for *P. flesus,* which is unexpected as strong differences between groups were observed, but the small sample size for some groups might explain this result.

Table 6.11. Summary of output from three-way ANOVA per species and isotope values showing the p-values, and in brackets the degrees of freedom (i.e. df, number of independent values that can vary) and the F-statistic (i.e. variation between sample means). Bold results indicate significant differences.

	P. platessa			***P. flesus***		
Variable	$\delta^{13}C$ (n=233)	$\delta^{15}N$ (n=233)	$\delta^{34}S$ (n=80)	$\delta^{13}C$ (n=85)	$\delta^{15}N$ (n=85)	$\delta^{34}S$ (n=31)
Mid	0.6001 (1: 0.276)	0.36406 (1: 0.829)	**1.10e-06** (1: 36.466)	**0.046738** (1: 4.193)	0.8183 (1: 0.053)	0.133 (1: 2.632)
Site	**1.13e-09** (12: 6.728)	0.24338 (12: 1.267)	**4.94e-05** (10: 6.042)	**0.000553** (10: 4.080)	**2.82e-05** (10: 3.567)	0.559 (9: 0.896)
Size_class	**0.0464** (7: 2.102)	0.14647 (7: 1.575)	**0.00112** (6: 4.985)	**0.000195** (5: 6.242)	0.0972 (5: 2.004)	0.795 (4: 0.415)
Mid x *Site*	0.9512 (6: 0.9512)	**0.02524** (6: 2.486)	0.05089 (6: 2.398)	0.862495 (5: 0.376)	0.4740 (5: 0.925)	0.975 (3: 0.070)
Mid x *Size_class*	**0.0168** (7: 2.540)	**0.00621** (7: 2.953)	0.12932 (4: 1.936)	0.820393 (3: 0.307)	0.9399 (3: 0.133)	0.630 (3: 0.598)
Site x *Size_class*	0.7310 (30: 0.821)	0.54932 (30: 0.948)	**0.00762** (21: 2.605)	0.061820 (12: 1.899)	0.2737 (12: 1.265)	0.866 (5: 0.598)
Mid x *Site* x *Size_class*	0.5348 (12: 0.914)	0.50696 (12: 0.942)	0.92610 (2: 0.077)	0.959205 (3: 0.101)	0.6113 (3: 0.611)	0.932 (1: 0.008)

6.3.11 Generalised linear model

A generalised linear model (GLM) is applied to see how size, species, time, and geography affect the stable isotope values. With these models, predictions of the isotope values could be made based on the known variables of a sample. There are a few assumptions of GLMs:

- Samples and dependent variables are independent; this is met;
- Homogeneity of variance, although not a strict requirement; this is not met for each variable in the different models (see sections 3.6-8);
- Normality of residuals: this will be checked for each model afterwards using a Shapiro-Wilk test.

Although $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values are independent variables, they are analysed separately to better understand the individual factors at play for these variables, as above it is shown that they show different patterns through time and between species, geographical regions and size classes. As $\delta^{15}N$ is normally distributed for each species, a Gaussian link function is applied, resulting in a linear model. $\delta^{13}C$ and $\delta^{34}S$ are not normally distributed for each species according to the Shapiro-Wilk test (see tables 6.6 and 6.8). The density plots of these isotope values, however, seemingly possess a normal distribution. For this reason, a Gaussian link function will be also used for the models of these isotope values and the fit of the model will be verified afterwards. *Size_class*, *Species*, *Mid*, and *Site* were used as independent variables as proxies for size, species, time and geography respectively.

The first models used to explore the data will check if and which effect the flatfish species have on the isotope values. Only marine flatfish were taken into account with a $\delta^{13}C > -20‰$. The following models (figures 6.39) were tested:

- $\delta^{13}C$ ~ *Species*
- $\delta^{15}N$ ~ *Species*
- $\delta^{34}S$ ~ *Species*

For δ^{13}C, the model shows a p-value = **2.2e-16**, F = 23.83 on 5 and 337 df, and adjusted R^2 = 0.2503. A significant effect was found for *P. flesus* for δ^{13}C, which is explained by the presence of some more samples with low δ^{13}C values. For δ^{15}N, the model shows a p-value = **2.2e-16**, F = 95.31 on 5 and 337 df, and adjusted R^2 = 0.5796. A significant effect was found for all species, except *S. solea* and *S. rhombus* for δ^{15}N. For δ^{34}S, the model shows a p-value = **9.476e-06**, F = 21.58 on 1 and 110 df, and adjusted R^2 = 0.1564.

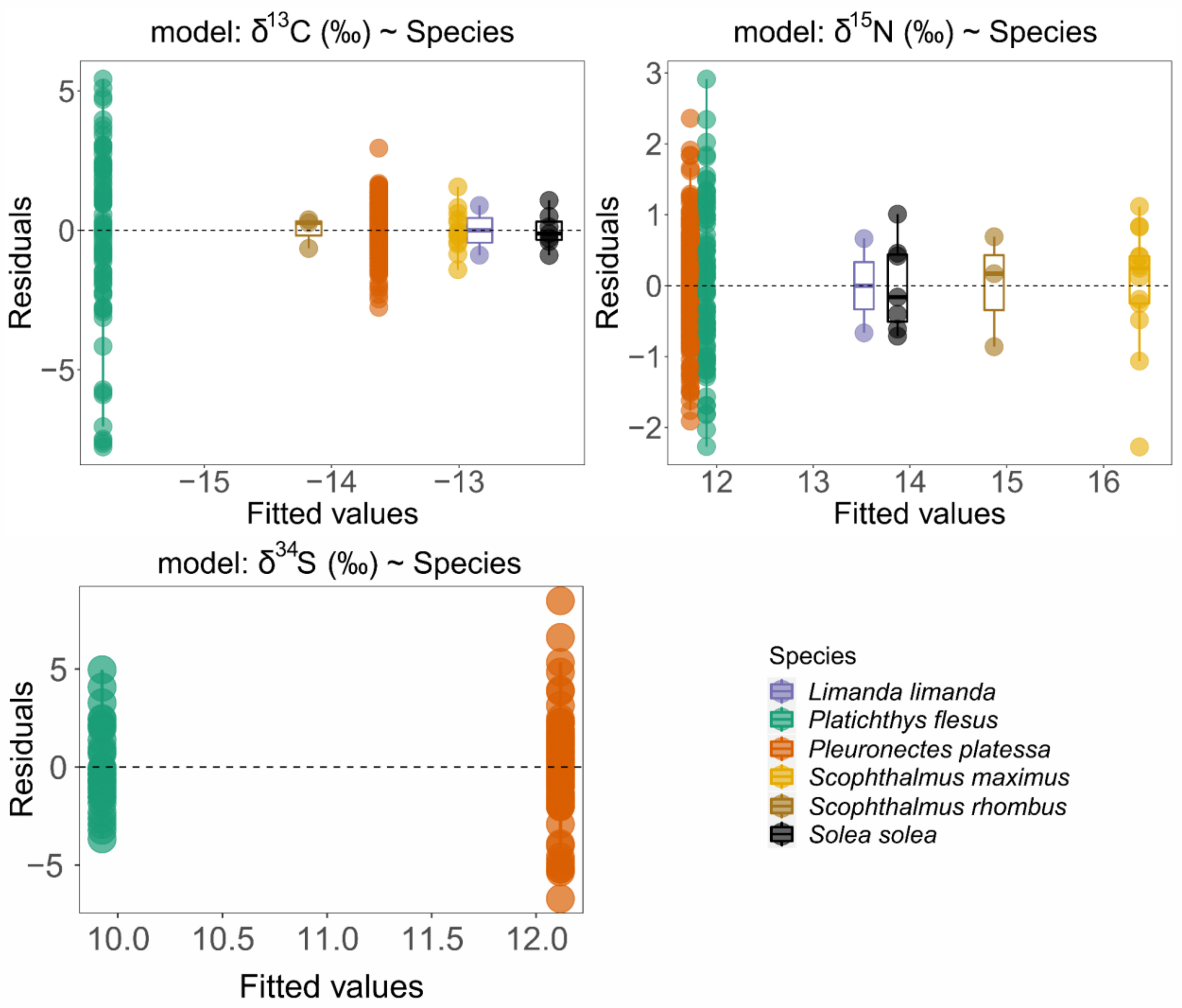


Figure 6.39. Residuals of the models plotted against the fitted values of model δ^{13}C ~ *Species* (upper left), δ^{15}N ~ *Species* (upper right), and δ^{34}S ~ *Species* (bottom left). The different species are clearly separated from each other by the fitted values, indicating that *Species* is a good predicting factor for isotope composition, while the large range of the residual axis shows that the models are not an ideal fit to the data.

These results indicate that *Species* indeed has an effect on all three isotopic values and that it is a good predictor for δ^{13}C, δ^{15}N and δ^{34}S, as was expected since different species show a different distribution for carbon and nitrogen and sulfur isotope compositions (see figures 6.17 and 6.18). Therefore, each species will further be analysed separately. Due to the limited sample size for some species, only models for *P. platessa, P. flesus,* and marine *P. flesus* will be performed. Although several samples for *S. maximus* were available, the small sample size with high variability and the unequal distribution across time and sites made this species subset unsuitable to explore with ANOVA and GLM. For example, a model of δ^{15}N of *S.*

maximus would have been skewed by the presence of one smaller sized individual (figure 6.40). The other flatfish species have an even smaller sample size and a more unequal distribution of the samples, making them even less suitable for further analysis.

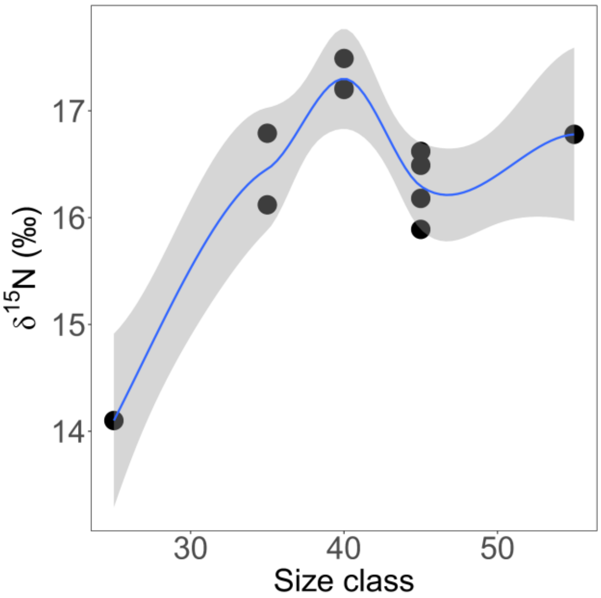


Figure 6.40. $\delta^{15}N$ per size class average value for *S. maximus* with a lowess regression between the two variables, showing the strong effect the one smaller sized sample could have on the model.

As a second part, it was tested what effect time, geography and size have on isotope values for *P. platessa, P. flesus* and marine *P. flesus* separately using the following models:

- $\delta^{13}C_{platessa}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{15}N_{platessa}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{13}C_{flesus}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{15}N_{flesus}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{13}C_{flesus\_marine}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{15}N_{flesus\_marine}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{34}S_{platessa}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{34}S_{flesus\_marine}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)

No interactions between variables were added due to the unequal distribution of samples across the different groups within a variable. The following models (figures 6.41-44) were retained after applying a stepwise AIC:

- $\delta^{13}C_{platessa}$ ~ as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{15}N_{platessa}$ ~ 1
- $\delta^{13}C_{flesus}$ ~ as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{15}N_{flesus}$ ~ as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{13}C_{flesus\_marine}$ ~ as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{15}N_{flesus\_marine}$ ~ as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{34}S_{platessa}$ ~ *Mid* + as.factor(*Site*) + as.factor(*Size_class*)
- $\delta^{34}S_{flesus\_marine}$ ~ as.factor(*Site*)

Based on the stepwise AIC, we removed *Mid* from $\delta^{13}C_{platessa}$, $\delta^{13}C_{flesus}$, $\delta^{13}C_{flesus\_marine}$, $\delta^{15}N_{flesus}$ and $\delta^{15}N_{flesus\_marine}$, and *Mid* and *Size_class* from $\delta^{34}S_{flesus\_marine}$ as removing these variables from the models does not have a significant effect on the goodness of fit. None of the variables seem to have a significant contribution to the model of $\delta^{15}N_{platessa}$.

Correlations between variables can complicate statistical analysis and interpretation. Therefore, it is checked if and which correlations exist between the three independent variables for the carbon/nitrogen dataset and the sulfur dataset.
Fisher's exact test was used to test for significant correlation between the categorical variables in the carbon and nitrogen dataset for *Site* and *Size_class* (df = 84, Chi-squared = 169.84, p-value = **9.185e-08**) and Ancova was used to test for significant correlation between *Mid* and *Site* (df = 12, F-statistics = 43.4, p-value = **<2e-16**) and Mid and *Size_class* (df = 7, F-statistics = 4.447, p-value = **0.000119**) for *P. platessa*. Fisher's exact test was again used to test for significant correlation between the categorical variables *Site* and *Size_class* (df = 50, Chi-squared = 74.882, p-value = **0.01289**) and Ancova was used to test for significant correlation between *Mid* and *Site* (df = 10, F-statistics = 60.66, p-value = **<2e-16**) and Mid and *Size_class* (df = 5, F-statistics = 0.836, p-value = 0.528) for *P. flesus*. Significant correlations were found between all variables for *P. platessa* and *P. flesus* carbon and nitrogen isotope datasets, except between *Mid* and *Size_class* of *P. flesus*. This has to be taken into account when making and interpreting the models.
For the sulfur isotope dataset a Fisher's exact test was used to test for significant correlation between the categorical variables *Site* and *Size_class* (df = 60, Chi-squared = 68.981, p-value = 0.1998) and Ancova was used to test for significant correlation between *Mid* and *Site* (df = 10, F-statistics = 9.191, p-value = **1.5e-09**) and *Mid* and *Size_class* (df = 6, F-statistics = 0.536, p-value = 0.779) for *P. platessa*. Fisher's exact test was used to test for significant correlation between the categorical variables *Site* and *Size_class* (df = 36, Chi-squared = 46.475, p-value = 0.1134) and Ancova was used to test for significant correlation between *Mid* and *Site* (df = 9, F-statistics = 14.29, p-value = **1.86e-08**) and *Mid* and *Size_class* (df = 4, F-statistics = 0.336, p-value = 0.852) for *P. flesus*. Significant correlations were found between *Mid* and *Site* for *P. platessa* and *P. flesus* sulfur isotope datasets. This has to be taken into account when making and interpreting the models.

In the next step, the variance inflation factor (an estimation of multicollinearity) is calculated in each dataset and the normal distribution of residuals is checked for each model. This assesses the quality and goodness of fit of each model. Table 6.12 further summarises details of each model. As all models have a p-value<0.05, there is a significant relationship between the isotope values and the dependent variables.
For the carbon and nitrogen dataset *Site* and *Size_class* have a variance inflation factor of 1.03 and 1.06 respectively for *P. platessa* showing a low collinearity between them. A Shapiro-Wilk test on the residuals of $\delta^{13}C_{platessa}$ doesn't show a significant difference from normality (W = 0.99434, p-value = 0.5372), nor for $\delta^{15}N_{platessa}$ (W = 0.99288, p-value = 0.3269). For $\delta^{13}C$ of *P. platessa* the model is a good fit (figure 6.41), except for the extreme values. This shows that *Site* and *Size_class* are good predictors for $\delta^{13}C$ of *P. platessa*, but do not explain most of the variation seen, as indicated by the low R^2-adjusted, partly due to the uneven sampling across sites.
Site and *Size_class* have a variance inflation factor of 1.05 and 1.11 respectively for *P. flesus* showing a low collinearity between them. A Shapiro-Wilk test on the residuals of $\delta^{13}C_{flesus}$ show a significant difference from normality (W = 0.96666, p-value = **0.02977**), but not for $\delta^{15}N_{flesus}$ (W = 0.97378, p-value = 0.0874). As can be seen from the residue plots for *P. flesus*, the fit of both isotope models is not good, which can be only partially caused by the presence of the

freshwater samples, as the same model excluding these samples is only slightly improved (see below; figure 6.42). The range of the residuals is also quite wide for $\delta^{13}C_{flesus}$. With both the R^2-adjusted being rather low, this would indicate that there are other factors, not included in the model, that explain the variation seen in $\delta^{13}C$ and $\delta^{15}N$. This shows that, despite the significant p-value, *Site* and *Size_class* are not ideal predictors for $\delta^{13}C$ and $\delta^{15}N$ of *P. flesus*. *Site* and *Size_class* have a variance inflation factor of 1.06 and 1.12 respectively for marine *P. flesus* showing a low collinearity between them. A Shapiro-Wilk test on the residuals of $\delta^{13}C_{flesus\_marine}$ doesn't show a significant difference from normality (W = 0.98638, p-value = 0.6035), nor for $\delta^{15}N_{flesus\_marine}$ (W = 0.97851, p-value = 0.2317). As can be seen from the residue plots for marine *P. flesus*, the fit of both isotope models is not ideal (figure 6.43). Even without the freshwater samples, the range of the residuals is quite wide for $\delta^{13}C_{flesus\_marine}$. With both the R^2-adjusted being rather low, this would indicate that there are other factors, not included in the model, that explain the variation seen in $\delta^{13}C$ and $\delta^{15}N$. This shows that, despite the significant p-value, *Site* and *Size_class* are not ideal predictors for $\delta^{13}C$ and $\delta^{15}N$ of marine *P. flesus*.

For the sulfur dataset *Mid, Site* and *Size_class* have a variance inflation factor of 1.55, 1.10 and 1.09 respectively for *P. platessa* showing a low collinearity between them. A Shapiro-Wilk test on the residuals of $\delta^{34}S_{platessa}$ shows a significant difference from normality (W = 0.93007, p-value = 0.0002449), which means the model is not a good fit for the data. This shows that *Mid*, *Site* and *Size_class* are good predictors for $\delta^{34}S$ of *P. platessa*, but do not explain most of the variation seen, as indicated by the R^2-adjusted and the non-normal distribution of residuals, partly due to the uneven sampling across sites (figure 6.44).

A Shapiro-Wilk test on the residuals of $\delta^{34}S_{flesus\_marine}$ doesn't show a significant difference from normality (W = 0.97436, p-value = 0.6639). For $\delta^{34}S$ of marine *P. flesus* the model doesn't seem to be a good fit (figure 6.44). This shows that *Site* is a good predictor for $\delta^{34}S$ of marine *P. flesus*, but does not explain most of the variation seen, as indicated by the R^2-adjusted, and due to the uneven sampling across sites.

Table 6.12. Summary of each model showing the statistics output. Bold results indicate significant results.

Statistics	**$\delta^{13}C_{platessa}$**	**$\delta^{15}N_{platessa}$**	**$\delta^{13}C_{flesus}$**	**$\delta^{15}N_{flesus}$**	**$\delta^{13}C_{flesus\_marine}$**	**$\delta^{15}N_{flesus\_marine}$**	**$\delta^{34}S_{platessa}$**	**$\delta^{34}S_{flesus\_marine}$**
F-statistics	4.955	/	4.939	4.491	3.715	4.289	4.42	3.621
df	212	232	15 and 67	15 and 67	15 and 59	15 and 59	17 and 64	8 and 21
R^2-adjusted	0.2454	/	0.4188	0.3897	0.355	0.4	0.4179	0.4196
p-value	**1.299e-09**	/	**2.3e-06**	**8.922e-06**	**0.0001454**	**2.635e-05**	**6.79e-06**	**0.008515**

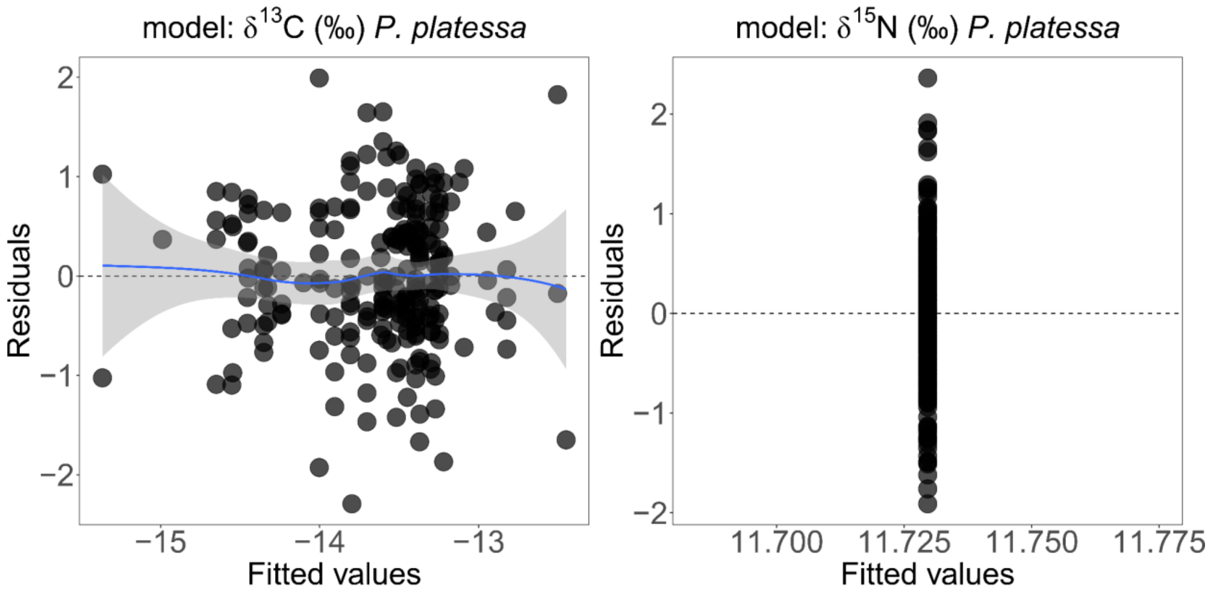


Figure 6.41. Residuals of the models plotted against the fitted values of model δ^{13}C (left) and δ^{15}N (right) for *P. platessa*. The fitted values show the range of the isotope composition, which is a concentrated cloud for the δ^{13}C model, except for some of the more extreme values, while for the δ^{15}N model there is only one point value as there are no variables in the model. The rather small range of the residuals show the model is a rather good fit. The regression line of the δ^{13}C model is relatively flat, which also confirms the model is a good fit of the data.

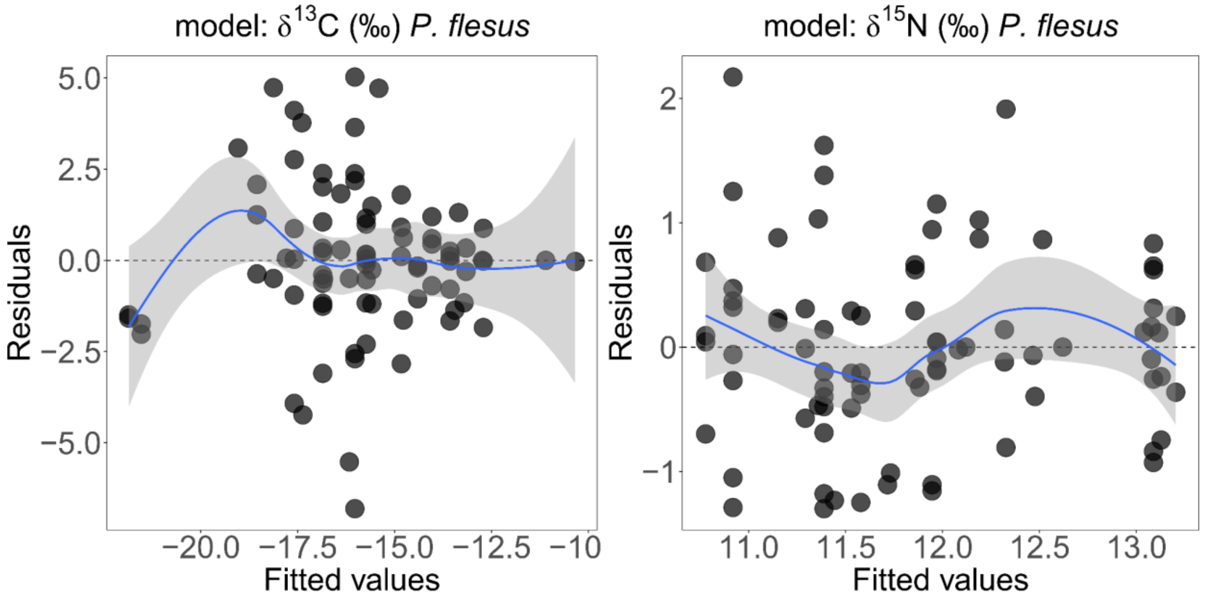
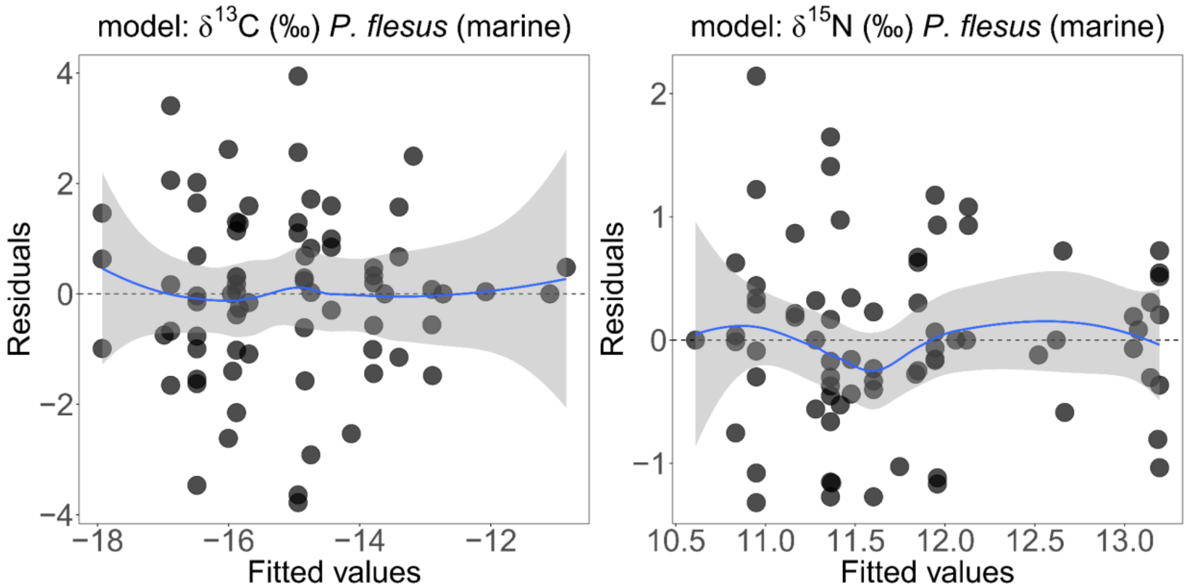
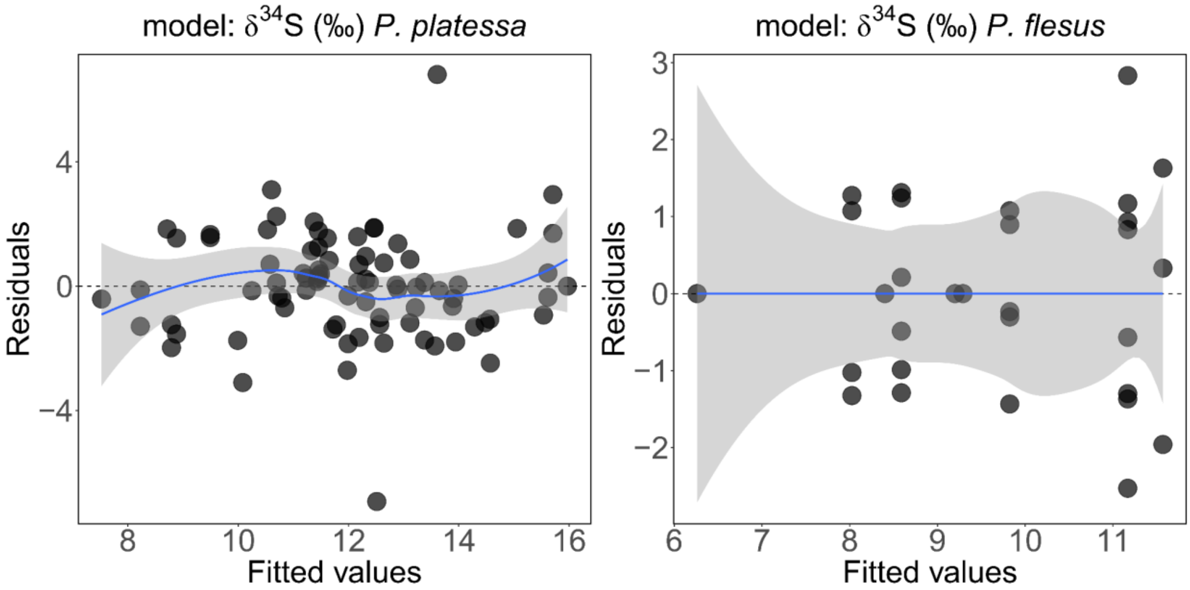


Figure 6.42. Residuals of the models plotted against the fitted values of model δ^{13}C (left) and δ^{15}N (right) for *P. flesus*. The fitted values show the range of the isotope composition, which is a concentrated cloud for the δ^{13}C model and less so for the δ^{15}N model. The range of the residuals is rather large for the δ^{13}C model, which together with the curvature of the regression line for both models, show that the models are not an ideal fit to the data.


model: δ^{13}C (‰) *P. flesus* (marine)

model: δ^{15}N (‰) *P. flesus* (marine)

Figure 6.43. Residuals of the models plotted against the fitted values of model δ^{13}C (left) and δ^{15}N (right) for marine *P. flesus*. The fitted values show the range of the isotope composition, which is a somewhat concentrated cloud for the δ^{13}C model and less so for the δ^{15}N model. The range of the residuals is rather large for the δ^{13}C model and there is some curvature of the regression line for the δ^{15}N model, showing that the models are not an ideal fit to the data.


model: δ^{34}S (‰) *P. platessa*

model: δ^{34}S (‰) *P. flesus*

Figure 6.44. Residuals of the models plotted against the fitted values of model δ^{34}S for *P. platessa* (left) and marine *P. flesus* (right). The fitted values show the range of the isotope composition, which is a concentrated cloud for the *P. platessa* model, except for some of the more extreme values, and not for the *P. flesus* model. The range of the residuals is rather large for the *P. platessa* model and the large uncertainty for the regression line of the *P. flesus* model, showing that the models are not an ideal fit to the data.

GLM's were applied on the data to see which variables can be used to predict stable isotope values, if any. Although site and size classes are good predictors for δ^{13}C and δ^{15}N for *P. platessa* and *P. flesus*, they are not the only factors contributing to the isotope values. The models for $\delta^{34}S$ for both *P. platessa* and marine *P. flesus* are also not ideal. These variables, proxies of time, site and size, only explain the distributions of isotopes partly and will therefore not be enough to accurately predict the isotope values. As seen in the figures in sections 3.6-8, there are indeed differences in distribution visible between groups of different sizes and sites, and time periods for sulfur isotope values, but no major differences are observed.

6.3.12 Principal component analysis

A principal component analysis of the three isotope values shows that for both *P. platessa* and *P. flesus* $\delta^{34}S$ and $\delta^{13}C$ are responsible for explaining the majority (>95%) of the variation (table 6.13 and figure 6.45). For *P. platessa*, the multi-isotope approach results in a separation on PC1 and PC2 between some time periods (figure 6.47), but not clearly between sites (figure 6.46) or size classes (figure E47 in the appendix). For *P. flesus*, sites (figure 6.48) and time periods (figure 6.49) clearly differ from each other by the combination of $\delta^{34}S$ and $\delta^{13}C$, while size classes (figure E48 in the appendix) are barely differentiated.

In figure 6.47, the Early Medieval period 1 and Early Medieval period 2 are clearly distinct from High/Late Medieval and Late Medieval, while High Medieval encompasses all other time periods. This could indicate that there is a clear transition in the isotope values through time for *P. platessa*, as was noticed in figure 6.26 as well.

For *P. flesus* there is no clear shift in the time periods. For this species sites show a better distinction (also see figure 6.48). The sites in York and London seem to be clearly separated from the other sites and from each other, but have a large range in PC1. Canterbury is also slightly distinct from the continental sites.

Table 6.13. Eigenvectors and proportion of variance explained by the principal component analysis axis per species.

Species	***P. platessa***			***P. flesus***		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
$\delta^{13}C$	0.1014247	0.85985091	-0.50036932	-0.52126240	-0.85311553	-0.02189535
$\delta^{15}N$	-0.0106946	0.50387629	0.86370962	0.04233685	-0.05147635	0.99777642
$\delta^{34}S$	-0.9947857	0.08225021	-0.06030125	-0.85234564	0.51917635	0.06295091
Proportion variance	85.26%	10.23%	4.51%	78.41%	19.13%	2.47%

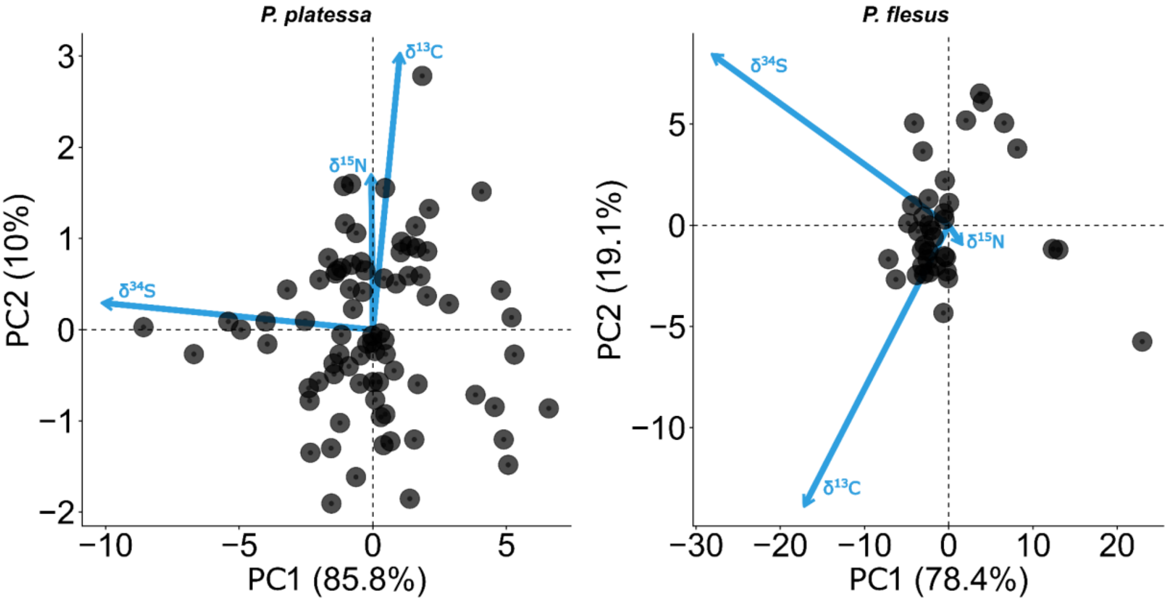


Figure 6.45. Biplot of PCA for PC1 and PC2 of *P. platessa* (left) and *P. flesus* (right).

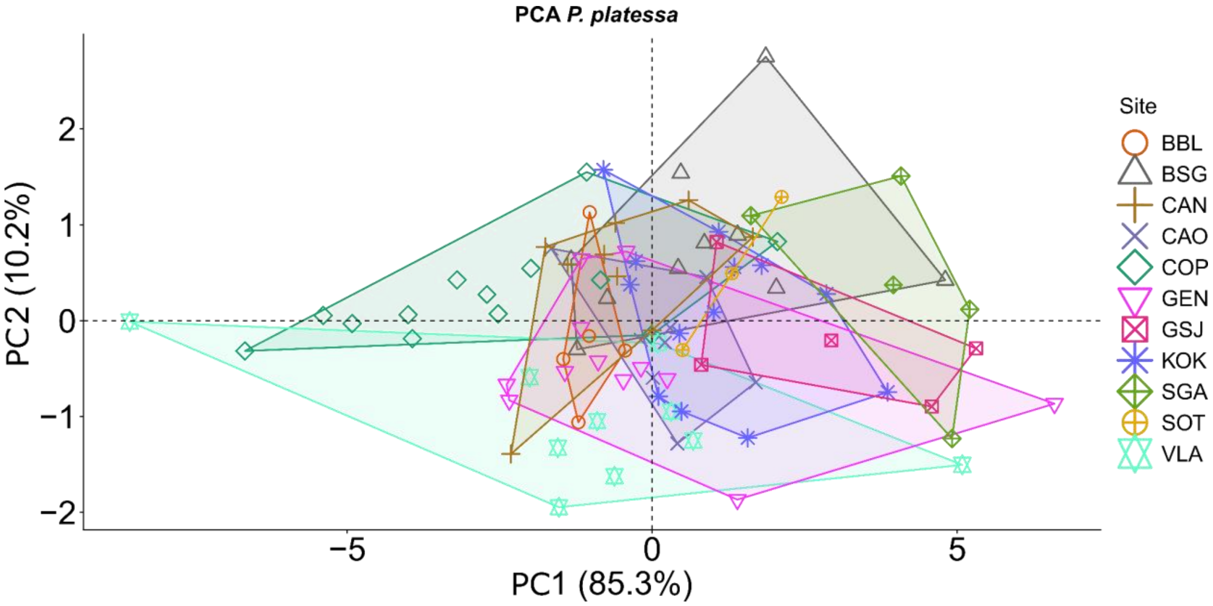


Figure 6.46. Principal component analysis of *P. platessa*, coloured and grouped by site.

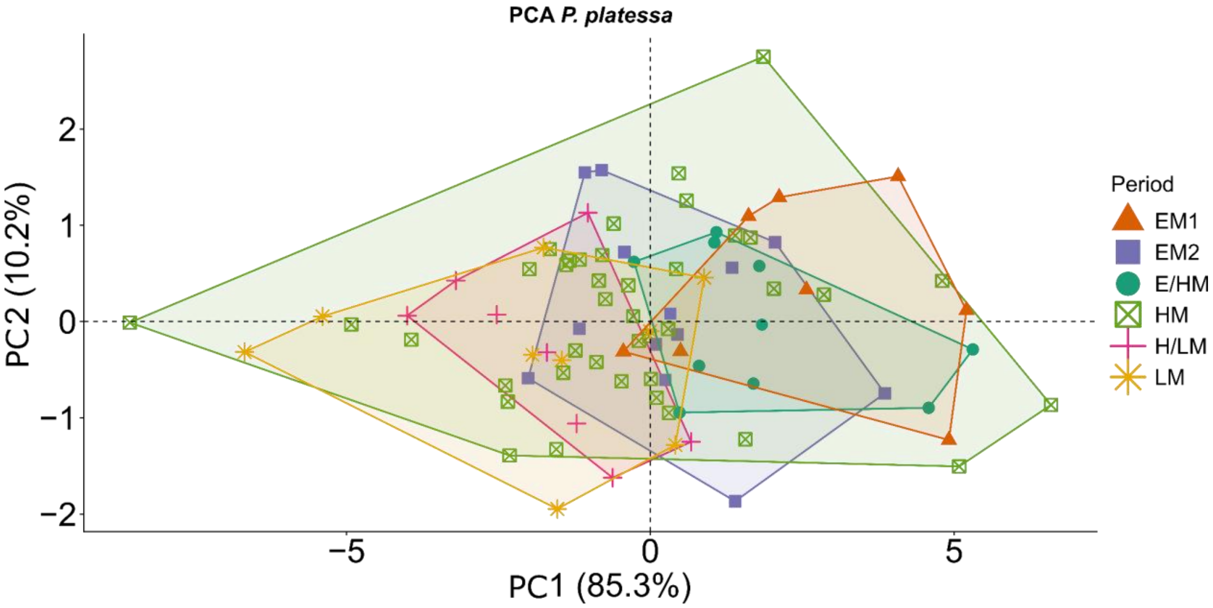


Figure 6.47. Principal component analysis of *P. platessa*, coloured and grouped by period.

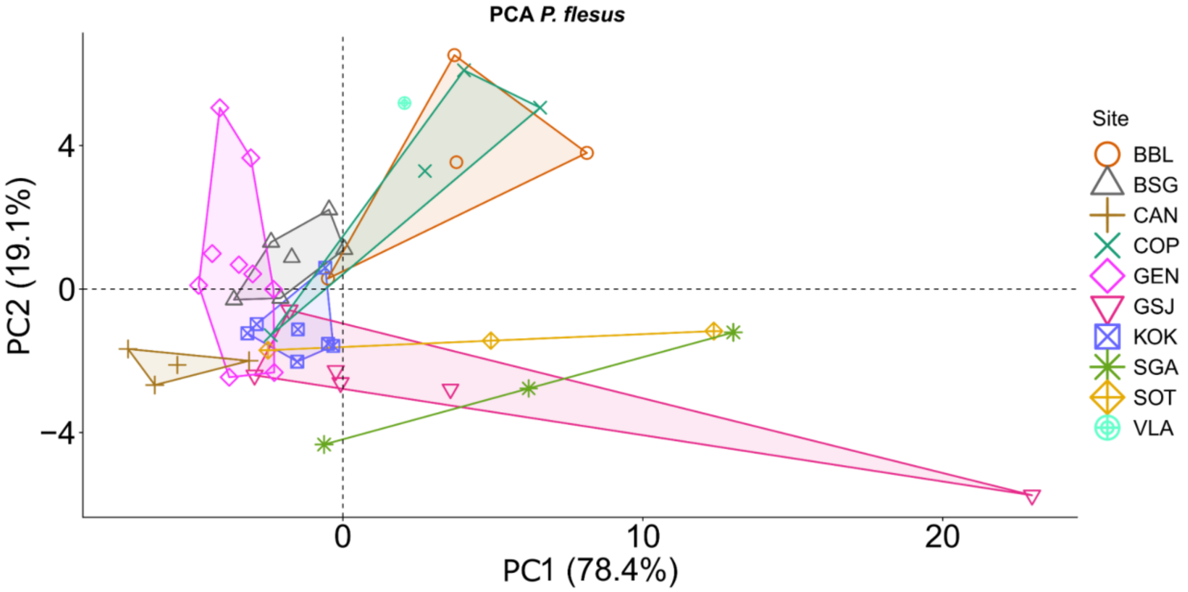


Figure 6.48. Principal component analysis of *P. flesus*, coloured and grouped by site.

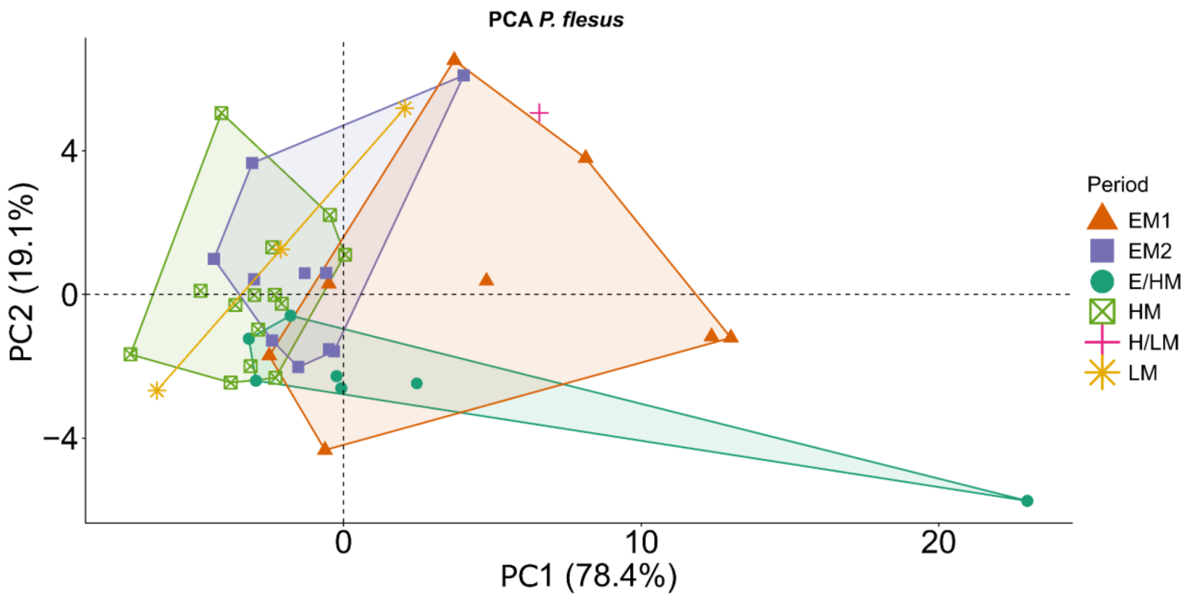


Figure 6.49. Principal component analysis of *P. flesus*, coloured and grouped by period.

6.4 Discussion

6.4.1 Treatments of bone

(In appendix for publication)

Treating archaeological flatfish bones to remove contaminants such as lipids and humic acids with DCM and NaOH did not show any clear improvements on the isotope values and quality criteria. About half of the NaOH- and DCM-treated samples even had a higher C:N ratio compared to the non-treated samples from the same bone. The shifts in nitrogen isotope values are minimal, while for carbon isotope values there could be a difference of Δ0.8‰, which is enough to impact interpretation. These results suggest that in the case of flatfish, it is best not to treat bones with any products to remove contaminants as no consistent effect of the treatments was observed, while taking into account potential contamination when interpreting the results and to verify the quality of the data using predetermined criteria (see below). These findings report a different effect compared to previous studies reporting a clear beneficial change and therefore necessity to remove lipids and humic acids (Guiry *et al.*, 2016b) or no effect at all (Katzenberg, 1989; Kennedy, 1988; Ambrose, 1990; Tsutaya *et al.*, 2018; Guiry & Szpak, 2020). Ofcourse, as the sample size is small and only two species were tested from one site, further research is required to verify the general effect of applying these treatments on archaeological bone.

6.4.2 Quality criteria

Using the collagen amino acid sequences from flatfish, it was shown that the recently proposed quality criteria for carbon and nitrogen isotope values of coldwater species by Guiry and Szpak (2021) was not relevant for flatfish. Therefore, it was determined to follow their proposed criteria based on the C:N ratios matching most with warm water species. This case also confirms the need for species-specific quality criteria, as different species can show large differences in these ratios which can be as high as the shift caused by contaminants. In case of specific species data being unavailable, closely related species phylogenetically should be used as a proxy, rather than ecologically similar species to estimate the expected C:N ratio, as phylogeny is a stronger determinant of the collagen composition than the environment a species is living in, since this protein is coded by several genes (*COL1A1, COL1A2, COL1A3* in the case for fish). The %C and %N analysed using mass spectrometry is lower than what is expected based on the amino acid calculations for all samples. The reason for this is unknown. The loss in weight percentage seems proportionally larger for carbon than for nitrogen. As this is the case for both archaeological and modern samples, degradation due to burial taphonomy can be ruled out.

For sulfur isotope analysis, the quality criteria used followed Nehlich and Richards (2009). About 73% of the archaeological samples matched these criteria. All observed values for %S, C:S, and N:S are much higher than what was calculated based on the collagen amino acid sequences for these species (see tables 6.3 and 6.4). A similar discrepancy was noted by Nehlich and Richards (2009) between mass spectrometry measured and calculated sulfur content. There could be several reasons for this difference. The first possible reason is that there is more sulfur present in collagen than what can be calculated by the amino acid sequence due to the presence of posttranslational modifications, sulfur bridges or other molecules around collagen (such as chondroitin sulphate (Nehlich & Richards, 2009)). This endogenous sulfur could have resulted in a measured %S of about 0.10-0.20% higher than expected, in both the archaeological and modern samples. The other reason could be the presence of exogenous sulfur seeping into the bone during taphonomic processes, resulting in even higher values than expected, as only detected in the archaeological samples. No sample was observed to have a %S lower than the quality criteria, which could indicate degradation, although degradation for carbon and nitrogen was observed. Potentially the differential loss in amino acids impacts methionine, the only sulfur-containing amino acid, less compared to some of the other amino acids in collagen. This study makes it clear that the sulfur compositions calculated using amino acid sequences are not the best proxy to assess the quality when dealing with archaeological samples. We therefore propose to use the criteria set by Nehlich and Richards (2009) until more species-specific criteria are available.

One *P. platessa* sample from Vlaardingen is strongly enriched in ^{34}S and has a δ^{34}S of 20.6‰. Such a high value is uncommon even for open marine fish (see Nehlich *et al.*, 2013, 2015). Although this sample matched the criteria proposed by Nehlich and Richards (2009), the criteria are close to the general criteria range limits. Therefore, no further interpretation for this sample will be done, as it could still potentially be contaminated with exogenous sulfur.

6.4.3 Ecology of species

The isotope values from different species of archaeological fish correspond to the expected isotope niches based on their modern ecologies. *Esox lucius* and Cypriniformes all have rather low δ^{13}C values, which corresponds to freshwater systems. The single Cypriniformes with a higher δ^{13}C value may have lived close to estuaries and fed on food enriched in ^{13}C. Most flatfish and Gadidae indeed match with the δ^{13}C values expected for marine environments. Both δ^{13}C and δ^{15}N for Gadidae match with the isotope data found for central and southern North Sea Gadidae in previous studies (Barrett *et al.*, 2008; Orton *et al.*, 2011). A handful of flatfish samples have δ^{13}C values much lower compared to other samples, which is most likely due to them living and feeding in freshwater systems, such as rivers, or estuaries. For δ^{15}N a clear difference is noticed between Gadidae and Scophthalmidae, and Pleuronectidae, which can be explained by the trophic ecology of these families with the first two consuming more marine fish, while the latter mostly consume marine invertebrates. The wide range in $\delta^{15}N$ observed for the freshwater taxa can be explained by the large taxonomic and thus potentially ecological diversity included in this group.

For sulfur *P. flesus* is more variable than *P. platessa*, as it shows lower $\delta^{34}S$ values for some samples, which corresponds to the freshwater samples as determined by $\delta^{13}C$. No difference in $\delta^{34}S$ was found between the suspected estuarine samples, based on $\delta^{13}C$, and the marine samples of this species.

Platichthys flesus is remarkable for having a large isotope niche space as seen in the very large shape area taken in by this species compared to other species (figures 6.19 and 6.20), especially for $\delta^{13}C$ and $\delta^{34}S$, reflecting the wide variety of habitats this species can be found in.

With the modern samples showing the same (or more restricted range) for carbon, nitrogen and sulfur, this would indicate that the average species ecologies and baselines have not noticeably shifted much since the Medieval period. There is not a clear increase or a decrease in $\delta^{13}C$ or $\delta^{15}N$ compared to the archaeological samples, as would be expected based on the general increase as measured from sediment cores from near the coast in the German Bight since the Medieval period (Serna *et al.*, 2014) or the Suess effect (Keeling, 1979) respectively. The modern sample from the Norwegian coast, however, is clearly isotopically different from the North Sea and archaeological samples, which could be related to the geography and local ecosystem (see Barrett *et al.*, 2011; Mackenzie *et al.*, 2014; St John Glew *et al.*, 2018; Bataille *et al.*, 2021).

Although the sample sizes were small for *L. limanda, S. maximus, S. rhombus* and *S. solea*, this study provides the first archaeological isotope data for these species. As these species are generally found in marine environments, the strong marine signal observed for carbon isotope values matched their modern known habitat selection. The higher $\delta^{15}N$ values observed for these species is related to their diet, which consists on average more of fish and polychaetes compared to the diet of *P. platessa* and *P. flesus*, who feed relatively more on crustaceans and molluscs (De Groot, 1971; Braber & De Groot, 1973; Ameczua *et al.*, 2003). More samples need to be analysed to infer any conclusions related to their ecologies or historic exploitation.

6.4.4 Effect of time, region and size

Stable isotope analysis of carbon and nitrogen has allowed us to identify the catch habitat of flatfish species. As species clearly differ in their collagen composition and ecology, isotopes should be analysed for each species separately, which was possible using collagen peptide mass fingerprinting. The effects of the three variables were checked using a myriad of visual and statistical techniques to explore how isotope values per species differ between sites, time periods, and size classes. The raincloud plots (figures 6.21-32) and ANOVA analysis (table 6.11) have revealed significant differences between time periods, sites, and size classes for the three isotope compositions for both *P. platessa* and *P. flesus.*

With size being an important factor for δ13C and δ34S, it is important to take this into account when comparing different sites and time periods, as different sized fish might obscure other patterns in the dataset present. No apparent differences from the general results were observed in the distribution of individual size classes of P. flesus and P. platessa for their isotope values between sites and time periods in this dataset (see figures E14-37).

6.4.4.1 Geography

A clear trend for isotope values is observed when considering the geographical effect. Sites show clear differences in $\delta^{13}C$ values for flatfish, with the coastal sites relying on typical marine samples, while inland sites occasionally show a sample with lower $\delta^{13}C$ values, which originates from freshwater habitats. Differences were noticed between the different inland sites. Coppergate, Gent and the Dutch sites have some *P. platessa* samples with lower $\delta^{13}C$ values compared to the sites from London and Blue Bridge Lane and the coastal sites. This can be explained by the geographical location of the sites, with the first group being located more inland with access to estuaries to fish, while the second group has easier access to the sea and the Thames estuary, which itself provides easy connection to the sea. For Blue Bridge Lane, which is in York, the same city as Coppergate, however, these values may signify that fish were landed here as part of a larger trading hub focusing on marine fishing during the Early and (High/)Late Medievel periods, while in Coppergate more local and domestic subsistence fishing was taking place throughout the whole Medieval period alongside inland trade of fish, which could explain the higher abundance of samples with relatively lower $\delta^{13}C$ values in the latter, related to a more estuarine or close-coastal exploitation.

Sulfur isotope analysis has mostly been applied to distinguish geographical origins and to differentiate between marine and freshwater origins (e.g, Leakey *et al.*, 2008; Nehlich *et al.*, 2013; Nehlich *et al.*, 2015). This is confirmed in our analysis on flatfish, as there are clear differences between the sites and geographical location for both *P. platessa* and *P. flesus* as seen in the raincloud plots, Isomemo maps, PCA plots, ANOVA and the results from GLM analysis. The correlation observed between $\delta^{13}C$ and $\delta^{34}S$ confirms the use of $\delta^{34}S$ as a proxy for marine-freshwater habitats.

Samples that were identified as freshwater by $\delta^{13}C$ (<-20‰) all have a $\delta^{34}S<9‰$, which corresponds to the delineation of habitat groups by Nehlich *et al.* (2013) and Nehlich *et al.* (2015), in which the freshwater signal for sulfur has an upper limit of around 10‰. Samples defined as marine (>-20‰ $\delta^{13}C$) have $\delta^{34}S$ values between 5 and 20‰. This is a wider range than used by Nehlich *et al.* (2013) and Nehlich *et al.* (2015), which had a lower limit of 7‰.

An important remark has to be made concerning the hydrology of the southern North Sea and $\delta^{34}S$. As many large rivers flow into the southern North Sea, a shallow continental shelf sea, it is possible that this body of water has a baseline of $\delta^{34}S$ that is lower than one would expect for marine environments. The southern North Sea could be regarded as a freshwater-influenced marine environment. This was also noticed by Nehlich *et al.* (2013), who found that locally caught *G. morhua* recovered from sites in this area had on average lower $\delta^{34}S$ values compared to sites which had access to more open marine waters. Furthermore, modern data from jellyfish also show lower $\delta^{34}S$ in the southern part of the North Sea than in the northern part (St John Glew *et al.*, 2018). No clear distinction seems to be possible between fish caught near the coasts or in the open southern North Sea.

In this study, we therefore regard samples with $5‰<\delta^{34}S<10‰$ as freshwater/estuarine, $10‰<\delta^{34}S<15‰$ as estuarine/southern North Sea marine, while samples with $\delta^{34}S>15‰$ as strongly open marine.

The freshwater *P. flesus* samples, which have low δ^{13}C values, mostly originate from England, in York and London, while only two of these originate from the continental side of the North Sea (one has a δ^{13}C=-19.95‰, and was therefore categorised a estuarine). Noticeable are the lower δ^{13}C values on average by Leiderdorp and Vlaardingen in δ^{13}C for both *P. flesus* and *P. platessa*, two settlements close to the estuarine region in the southern Netherlands. This region could be more affected by output from rivers, causing lower δ^{13}C values of flatfish. A pure environmental effect for this seems less likely as Gent, which has a similar environment and accessibility to the North Sea, does show samples with higher δ^{13}C, indicating a stronger marine exploitation, and thus human economic choice. As only one clear freshwater sample was found in the Dutch sites, it is suspected that these sites exploited mostly freshwater influenced estuarine or coastal habitats for flatfish and not freshwater habitats. This is confirmed by δ^{34}S, as only one sample of *P. platessa* and one freshwater sample of *P. flesus* out of ten samples total from Vlaardingen were found to be have lower δ^{34}S values, indicating a brackish and freshwater exploitation respectively. The eight other samples (>10‰ δ^{34}S) from this site showed a clear estuarine or marine signal. Unfortunately, no sample from Leiderdorp matched the quality criteria for sulfur analysis. These samples might have been affected by exogenous sulfur during burial more than samples in other sites.

The English sites in general seem to have proportionally more samples with slightly lower δ^{34}S values than the continental sites. This is particularly the case for London and for *P. flesus*, while some English *P. platessa* samples have higher δ^{34}S values. A large proportion of *P. flesus* samples, especially those from the English sites, originate from estuarine habitats, while southern North Sea samples of *P. flesus* were found in the coastal sites, Canterbury, Saint-George and Koksijde, and in Gent. The high abundance of *P. flesus* in Gent with a high δ^{34}S value is remarkable. Based on the isoscape by Bataille *et al.* (2021) this could be related to a more enriched bedrock present in that area, which can cause the Scheldt river and estuary to show higher δ^{34}S values. These samples could still have been captured in estuaries of the Scheldt despite their higher δ^{34}S values. On the other hand, the *P. platessa* samples with higher δ^{34}S values could also have been captured in more northern waters, where there is more influence of ^{34}S-enriched oceanic water from the Atlantic (e.g., Barrett *et al.*, 2011; Nehlich *et al.*, 2013; St John Glew *et al.*, 2018). Flemish fishers were known to fish in more northern open waters by the end of the Late Medieval period (Ervynck *et al.*, 2004; Van Neer & Ervynck, 2007).

The *P. platessa* samples with very high δ^{34}S values from Coppergate in York date from the 12th-13th century. During this time marine fishing was a common occurrence and York had easy access and potentially trade connections to the northern North Sea (Barrett *et al.*, 2011; Nehlich *et al.*, 2013; St John Glew *et al.*, 2018). On the other hand, the North of England seems to have a more enriched bedrock compared to the bedrock from the other sites (Bataille *et al.*, 2021) and also receives more ocean water from the Atlantic due to the water circulation (Otto, 1983). All three of these reasons could explain the higher δ^{34}S values seen in York compared to other sites (e.g., St John Glew *et al.*, 2018).

The relatively high abundance of freshwater samples in York and London could mean that fishing in the Ouse and the Thames for *P. flesus* was more common practice than it was on the mainland for the inland sites. The isotope results match with what is known from historical reports that fresh plaice (*P. platessa*) was brought inland to London from coastal areas, while flounder (*P. flesus*) was caught in the Thames (Galloway, 2017). Furthermore, in modern times *P. flesus* is also more abundant in the Thames than *P. platessa* (Power *et al.*, 2000), making it more likely that *P. flesus* was locally exploited. As *P. flesus* can also be found in rivers on the continental side of the North Sea, the smaller number of freshwater samples could either be due to sampling, or due to local economic or cultural preferences of people on both sides of the North Sea. Further research, including historical source analysis is needed to better understand the driving factors behind the consumption of marine versus freshwater flatfish.

Both $\delta^{15}N$ and $\delta^{34}S$ isotopic values indicate a different environment in London compared to the other sites, which cannot be attributed to differences in size or time period. One explanation for the lower values for $\delta^{34}S$ is the more depleted bedrock in the area around London and the Thames, which would account for the very low $\delta^{34}S$ observed in fish from this area (Bataille *et al.*, 2021). With London being a large settlement since the Early Medieval period, a first hypothesis for the higher $\delta^{15}N$ values would be pollution or influx of enriched material, such as those originating from fertiliser or the hygienic circumstances in the settlement. However, no correlation between $\delta^{13}C$ and $\delta^{15}N$ was found for the *P. flesus* samples from London and Canterbury, meaning that being deeper inland - or, closer to the center of London - does not lead to an increase in $\delta^{15}N$ values (see Leakey *et al.*, 2008). It is therefore unsure if human-caused pollution is the cause for this increase in $\delta^{15}N$ values. No clear increase in the other large cities or settlements, such as York and Gent, in $\delta^{15}N$ values through time was detected either, showing there is little support for a major influx of anthropogenic enrichment that would impact flatfish isotope values. The diet of *P. flesus* also seems to be quite similar in the Thames as in the other regions in modern times (Doornbos & Twisk, 1984; Hampel *et al.*, 2005; McGoran & Morritt, 2017). The analysed samples from London of this species are also mostly specimens from 20-30 cm SL, similar as in the other sites, excluding a possible size effect in these sites (also see Figure E29-31). It could be that there are other environmental factors that create this clear difference in $\delta^{15}N$ between the Thames estuary and the continental side of the North Sea in *P. flesus*. A similar trend is visible in the cf. Cyprinidae isotope data found in this study. This distinction does not seem apparent in the data for *P. platessa* (figure 6.21), however, nor does it show in studies on other marine fish (e.g., Barrett *et al.*, 2011), which could indicate that the effect is more restricted to the Thames river, impacts the estuary less, and does not affect the flume of the Thames into the North Sea much. Visualising geographical differences using the Isomemo app (figure 6.33-35) does however indicate a slight gradient from east to west as well for both species. This is an opposite gradient as seen in MacKenzie *et al.* (2014) and St John Glew *et al.* (2018) for modern jellyfish data (figure 6.50) and is most likely affected by the presence of samples strongly enriched in ^{15}N present in the Thames basin, as it is less obvious for *P. platessa*. It remains unclear what the precise cause is for the higher $\delta^{15}N$ values observed for fish caught in the Thames and its estuary.

In conclusion, the geography has a significant impact on the isotope composition of flatfish, which can in most cases be explained by the local environment. In a few instances, human economic and dietary choices could be related to the isotopic variations seen. Humans have made conscious choices about which habitat they used to fish flatfish and they could have been trading fish over longer distances.

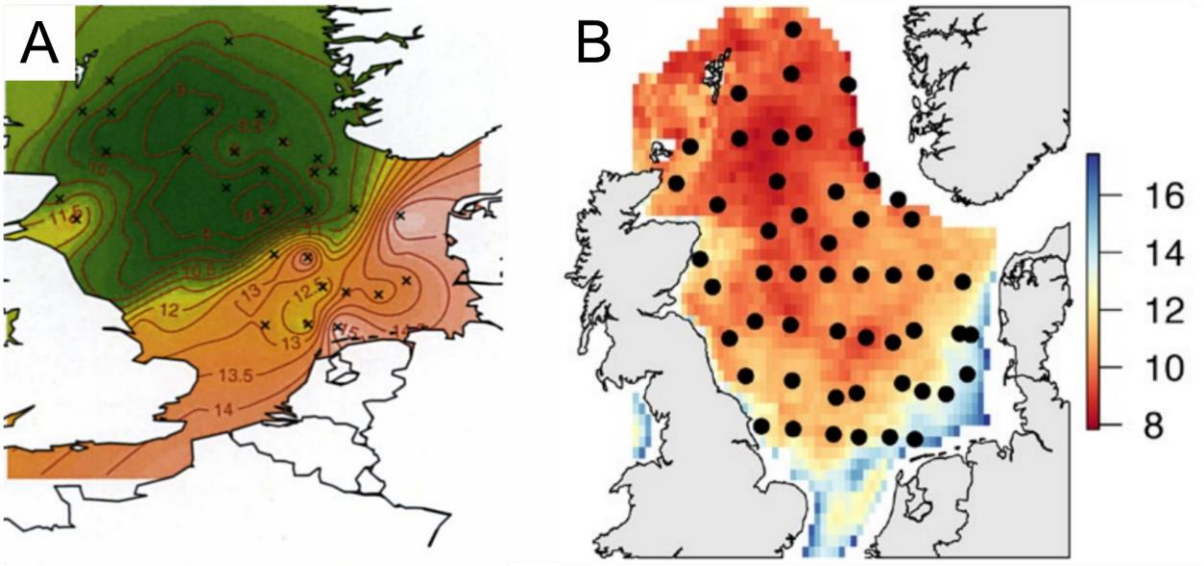


Figure 6.50. Isoscapes of δ^{15}N based on modern jellyfish data (*Cyanea capillata*) adapted from: A. Mackenzie *et al.* (2014), the greener the lower, the redder the higher δ^{15}N values; B. St John Glew *et al.* (2018).

6.4.4.2 Time

Time is not an important variable that influences δ^{13}C and δ^{15}N, but it is slightly for δ^{34}S. The ANOVA and GLM both show that time has a very minor effect on the isotopic values of *P. platessa* and *P. flesus*. Although the ANOVA shows a significant difference between time periods for δ^{13}C of *P. flesus*, the variable is not retained in the GLM models. This lack of a time effect was also noticed in the raincloud plots. No clear trend through time for isotopes of flatfish is noticed for δ^{13}C and δ^{15}N.

What is noticed is a clear presence of freshwater samples of *P. flesus* in the Early Medieval period, and a smaller number of freshwater samples during the High and Late Medieval periods, but the sample sizes are small (5 in EM, 4 in HM and LM). The high abundance of marine *P. platessa* and *P. flesus* is remarkable during the Early Medieval period, with southern North Sea exploitation occurring from as early as the 7th century. This shows a clear estuarine, coastal or marine exploitation of flatfish early on, well before the onset of the marine fish event horizon during the 11th century, as seen in δ^{13}C and δ^{34}S. Therefore, human populations were exploiting and bringing marine fish inland to sites such as those in York, London, Vlaardingen, and Leiderdorp earlier than expected based on data from Gadidae. Similar observations have been made by Ervynck *et al.* (2018), as evidence for marine *P. flesus* dating from as early as the 9th century was found at inland Dendermonde in Belgium using carbon isotope values. Also one marine Clupeidae sample was uncovered from Early Medieval York (Müldner & Richards, 2007). This marine exploitation continued throughout the Medieval period. The freshwater habitat exploitation continued as well to at least the Late Medieval period but to a minor extent.

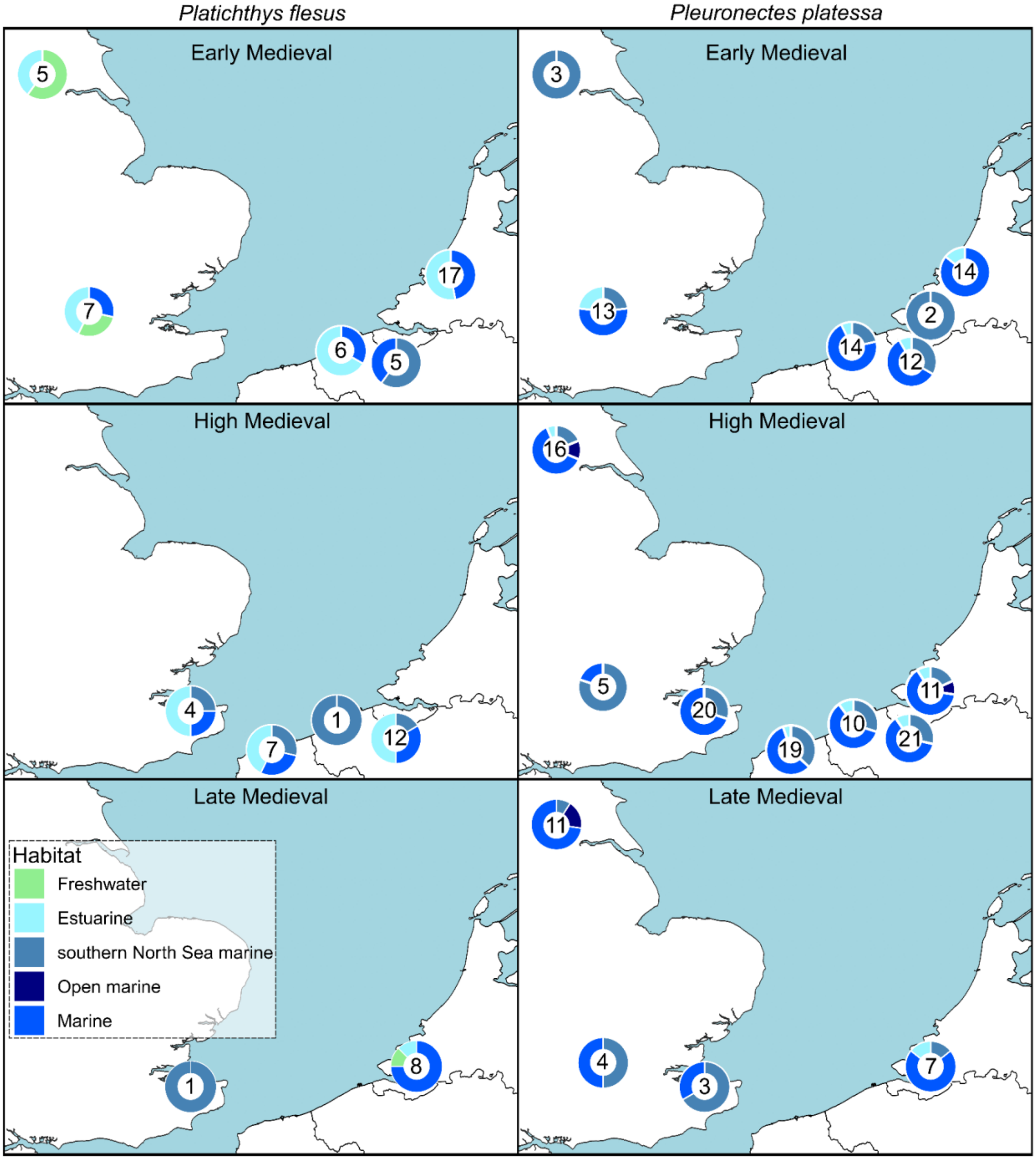


Figure 6.51. Summary of isotope data for *P. flesus* (left) and *P. platessa* (right) for the three main time periods, Early (top), High (mid), and Late (botton) Medieval periods. Samples are categorised into five habitat types based on the isotope data. Freshwater: $\delta^{13}C<-20‰$; Marine: $\delta^{13}C>-20‰$, also encompasses the three following categories; Estuarine: $\delta^{34}S<10‰$ or $-20‰<\delta^{13}C<-17‰$; southern North Sea marine (or freshwater influenced marine): $10‰<\delta^{34}S<15‰$; and Open marine: $\delta^{34}S>15‰$.

A subtle change is detected by Isomemo isoscapes in which a slight increase in average $\delta^{15}N$ is noticed throughout the Medieval period. A similar trend is observed in cranial bones from *G. morhua* for the southern North Sea between the 11th and 16th centuries, in which the mean of the groups slightly increased through time (Barrett *et al.*, 2011). No general increase in $\delta^{15}N$ was, however, observed during the Medieval period based on sediment cores from the German Bight (i.e. the region of the North Sea at the German coast) (Serna *et al.*, 2014). This slight observed increase of $\delta^{15}N$ in fish collagen could be attributed to either anthropogenic factors, such as pollution by farming using animal manure and deforestation (Hansson *et al.*, 1997; Serna *et al.*, 2014; Guiry *et al.*, 2018), or natural variability, such as changes in sea level and a warmer climate during the Medieval period (MacKenzie *et al.*, 2014). However, as there is no clear explanation for this shift and as the shift in $\delta^{15}N$ is minimal, no definitive conclusion can be drawn.

For *P. platessa* the majority of samples with lower $\delta^{34}S$ values date from the Early and High Medieval period, while most samples with higher $\delta^{34}S$ values only appear from the High Medieval period onward. There is also a low abundance of clear estuarine samples during the Late Medieval period for this species. These results could correspond to an increasing outward movement of flatfish fisheries for *P. platessa*. No such pattern is observed for *P. flesus*, which could indicate that *P. flesus* continued to be exploited in near-coastal and brackish waters throughout the whole Medieval period. These habitats are known to have remained important for medieval and post-medieval fisheries (e.g., Müldner & Richards, 2005; Müldner & Richards, 2007; Nehlich *et al.*, 2011; Fuller *et al.*, 2012; Ervynck *et al.*, 2018; Dahliwal *et al.*, 2019).

Together the three isotopes ratios, and especially $\delta^{13}C$ and $\delta^{34}S$, show that marine exploitation ($\delta^{13}C$>-20‰) occurred early on during the Medieval period. Figure 6.51 summarises the isotope data for *P. platessa* and *P. flesus* for the three main time periods, Early, High and Late Medieval. The overlapping time periods have been removed for clarity. During the Early Medieval period, most of the fish caught seem to have originated from close-coastal and estuarine or freshwater-influenced marine habitats (5‰<$\delta^{34}S$<15‰) and a large amount was brought to inland sites for consumption. During the High Medieval period there is a decrease of samples originating from a estuarine/coastal environment and relatively more southern North Sea marine samples ($\delta^{34}S$>10‰). During the Late Medieval period, only few estuarine samples were detected. The shift towards more open sea fisheries is mostly apparent in *P. platessa*.

Freshwater flatfish exploitation ($\delta^{13}C$<-20‰ and $\delta^{34}S$<10‰) seems to have been more abundant during the Early Medieval period, but continued on well into the Late Medieval period, showing that local, freshwater fisheries did not end with the start of the marine fish event horizon.

6.4.4.3 Size

A note regarding the bone growth of fish: as fish bones, especially vertebrae, grow by adding a new layer of bone around the younger layer, growth rings can be observed. As fish grow, their ecology, habitat preferences and diet might change (e.g., moving into higher trophic levels and to more marine environments; see also Chapter 1 of this thesis and introduction above). Currently, it is not well understood how the isotope values between these growth layers differ and to which extent young layers undergo remodelling, incorporating more recent isotope signatures of the fish's life. To avoid any biases regarding growth layers and as the fish bones were often of a small size, whole bones were preferably used for analysis. This of course could create a bias with the young layers influencing and averaging the signature obtained for the whole bone, while the old layers would provide the most relevant information regarding fish exploitation.

Size is an important variable that impacts the isotope values of flatfish as was seen in raincloud plots, ANOVA and the GLM models. In particular, $\delta^{13}C$ and $\delta^{34}S$ seem to be related to the size of the fish. When looking at different size classes, the absence of samples of both *P. platessa* and *P. flesus* with lower $\delta^{13}C$ values is noticeable in the larger size classes. As these fish grow larger, they tend to move out to more marine environments, with fewer individuals occupying more estuarine and freshwater habitats, resulting in an average increase of $\delta^{13}C$. The freshwater samples of *P. flesus* all originate from small-sized individuals (10-30 cm SL), which can be expected as this species can often be found in freshwater environments when they are young, while moving towards the estuaries and marine habitats when they get bigger (Russo *et al.*, 2008). Size classes do not show clear differences in $\delta^{34}S$ for either species, although in *P. platessa* only the larger size classes have samples with higher $\delta^{34}S$ values. This matches the trends observed in $\delta^{13}C$, in which only larger *P. platessa* go out to more marine environments, while the smaller specimens of *P. platessa* and all *P. flesus* can be found closer to the coast or in estuaries and freshwater systems (Russo *et al.*, 2008). The trend is less pronounced in $\delta^{34}S$ than in $\delta^{13}C$, as large *P. platessa* still occur in systems where the influence of freshwater more depleted in ^{34}S is strong, while the primary producers could perhaps already cause the elevation in $\delta^{13}C$ in open marine environments. The changes in nitrogen isotope values can be related to the changes in the diet as the fish grow larger and different prey species might become more abundant in the diet as the fish can more easily catch and consume certain prey. Pleuronectidae do not change their diet much when getting larger and generally eat similar prey items throughout their lives, which could explain the lack of large and distinct differences between the size classes. A similar slight average decrease in $\delta^{15}N$ related to size of *P. flesus* was noticed by Ervynck *et al.* (2018).

6.4.5 Evaluation of statistical approaches

ANOVA and generalised linear models were applied on this dataset to evaluate the applicability of these approaches, hoping these would be able to provide more insight into the data to allow for better interpretations. ANOVA can be used to detect differences in the means of groups, while a generalised linear model explores the relationship between variables and if successful, can be used to make predictions.

The ANOVA was applied successfully to the archaeological dataset, but several assumptions were not met (e.g., normal distribution, homogeneity of variance, and equal sample sizes of groups), resulting in output of the analysis which has to be treated with caution.

Unfortunately, generalised linear models did not work well on this dataset for any of the isotopes. Although several of the variables turned out to be good predictors of the data, none seems to explain the majority of the variation observed. This would indicate that other factors are at play that explain the isotopic variation, which are not related to time, location or size of the fish. An alternative explanation for the lack of good-fitting models could be the complexity of the data, as some groups showed non-normal distributions and heterogeneity of variance, and as there was correlation between the variables.

Contrary to biological and modern datasets, palaeo-datasets, such as the one from this study, are troubled by the failure to meet many assumptions necessary for statistical tests, which are often met when dealing with experimental set-ups. Furthermore, in palaeo-datasets there is often a limited availability of certain material, e.g. only from certain regions, taxa, time periods etc., reducing the resolution of many analyses that would be required to untangle the environmental changes and changes in human behaviour using a statistical approach. Archaeological sample selection is further prone to many biases and correlation between variables. As sites typically are restricted to certain phases and time periods, a strong correlation between these two variables exists, which is not ideal for statistical analysis. Furthermore, as samples were selected prior to knowing the species, equal group sizes could not be obtained and a strong correlation between sites and species could also occur, as is the case in this dataset. Of course, a high abundance of one species in a site could be archaeologically meaningful, but it complicates statistical analysis. Due to the unknown species identity and the lack of additional material, many of the groups within a variable only have a few samples, making it difficult to build strong models and draw conclusions on trends that appear in the dataset. Although we use sites as a geographical proxy here, these do not reflect the actual catch habitats where the samples were caught. All this might explain why the use of GLMs on this data was not successful.

6.4.6 Impact on our understanding of the marine fish event horizon

Much of the research carried out on medieval fish remains in western Europe during the past two decades has explored their results in the context of the marine fish event horizon (e.g., McGovern *et al.*, 2006; Orton *et al.*, 2014; Orton *et al.*, 2017; Oueslati, 2019), described by Barrett *et al.* (2004a). Other research has discussed the marine fish event horizon from a different point of view, namely the human diet and society approach (e.g., Barrett & Richards, 2004; Müldner & Richards, 2005; Müldner, 2016; Bird *et al.*, 2022). A recent meta-analysis on human bone and dentine remains explains the lack of a general increase in $\delta^{13}C$ for the second part of the Early and High Medieval period by a later start of the marine fish event horizon than proposed by Barrett *et al.* (2004a) and by a smaller contribution of marine fish to the diet than anticipated (Leggett, 2022). The observed increase in $\delta^{15}N$, which could be explained by the increase in the consumption of marine fish such as Gadidae in the hypothesis of the marine fish event horizon, is thought to be related to changes in terrestrial plant exploitation (Leggett, 2022). Based on the data in our study on flatfish isotopes, an alternative hypothesis should be put forward. As marine fish consumption is already going strongly during the Early Medieval period 1, with people even in inland sites consuming (flat)fish with a clear marine signal in $\delta^{13}C$ (this study; Müldner & Richards, 2007; Ervynck *et al.*, 2018), and there is a large proportion of marine fish recovered from the Early Medieval period 2 (figure 2.4), it can be expected that when Gadidae and Clupeidae became relatively more important for the human diet around the North Sea around the 11th century, that there is no clear additional shift in $\delta^{13}C$ visible. The increase of $\delta^{15}N$ in human bone collagen observed by Leggett (2022) can be explained by the growing importance of Gadidae, as it is shown in this study that fish from this family show higher $\delta^{15}N$ values than flatfish (also see Müldner, 2016). This would push the onset of the marine fish event horizon forward, instead of backward, with a sudden increase in Gadidae and Clupeidae exploitation at the start of the High Medieval period (Barrett *et al.*, 2011) or even slightly earlier, as seen in chapter 2 (figure 2.4).

This study provides the first in-depth analysis of one specific fish taxon combining sulfur isotope values with carbon and nitrogen isotope values in western Europe. Although the resolution of this multi-isotope approach is limited, the addition of sulfur isotope analysis provided much more insight than possible with just carbon and nitrogen isotope analysis.

The early marine exploitation of flatfish could have been a stepping stone in the gradual expansion of catch habitats throughout the Medieval period, although little insight into Late Roman/Early Medieval marine fish consumption around the North Sea is available (e.g., Nehlich *et al.*, 2011; Fuller *et al.*, 2012; Ervynck *et al.*, 2018; Jørkov *et al.*, 2010; Dalle *et al.*, 2022). In order to better understand the actual onset of marine fishing, a multi-isotope analysis on Roman and Early Medieval fish remains is required. Only then can the relative importance of marine flatfish consumption during the onset of marine fishing be understood as well. Furthermore, there is a lack of a general insight into freshwater fish exploitation during the High, Late and Post-Medieval periods, despite several case studies having been carried out (e.g., Brinkhuizen, 1979; Van Neer & Ervynck, 1996; Lentacker *et al.*, 1997; Pigière *et al.*, 2002; Müldner & Richards, 2005; Prummel & Heinrich, 2005; Müldner & Richards, 2007; Nehlich *et al.*, 2011; Fuller *et al.*, 2012; Harland *et al.*, 2016; Orton *et al.*, 2017; Ervynck *et al.*, 2018; Dahliwal *et al.*, 2019; Maccarinelli, 2021). This absence of insight can be resolved in the future by analysing more freshwater fish taxa zooarchaeologically and isotopically in combination with human dietary studies in order to determine the relative importance of ongoing local freshwater exploitation. To understand flatfish fisheries better, precise provenancing of the fish would elucidate the exact economic decisions made, how far people went to catch them and if there are changes in catch location, which can be linked to any environmental or societal change. This might be achieved by analysing flatfish remains with aDNA (Hoarau *et al.*, 2004; Hemmer-Hansen *et al.*, 2007, although Hoarau *et al.*, 2002; Nielsen *et al.*, 2004; Ulrich *et al.*, 2017), isotope analysis (e.g., Dufour *et al.*, 2007; Sisma-Ventura *et al.*, 2018; Kato *et al.*, 2020; Kato *et al.*, 2021) or growth ring analysis (e.g., Van Neer *et al.*, 1999; Ulrich *et al.*, 2017) in combination with historical analyses to try to uncover the populations or regions that were exploited in the North Sea and surrounding areas.

6.5 Conclusion

A multi-isotope approach has been performed on a species-specific level, revealing a detailed image of catch habitats of flatfish throughout the Medieval period in the southern North Sea area. The results show an early onset of coastal and potentially open marine exploitation and inland trade of flatfish, occurring from the 7th century CE, and possibly earlier, predating the marine fish event horizon described for Gadidae based on zooarchaeological methods. Throughout the Medieval period, a slight outward movement of flatfish fisheries might have occurred. Freshwater flatfish fisheries of *P. flesus* occurred throughout the whole Medieval period to a small extent, and were seemingly slightly more common during the Early Medieval period. Regional environmental differences and species' ecologies seem to be more important drivers of isotopic ratios of flatfish than time and socio-economic changes in human societies. This study also provides a first in-depth analysis of $\delta^{34}S$ in combination with $\delta^{13}C$ and $\delta^{15}N$ for fish from the North Sea.

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Chapter 7. General discussion

This PhD has significantly contributed to our understanding of flatfish exploitation in the past, expanding current zooarchaeological and palaeoecological research on flatfish on multiple fronts. The main research questions were:

- Which flatfish species were fished throughout the Medieval period and is there a difference in importance of certain species prior and after the marine fish event and between regions (see section 7.1)?
    - Can we distinguish the main commercial and archaeologically recovered flatfish species, and if so, which methodology is the most useful for archaeological remains?
    - Which species of flatfish do we find in archaeological sites dating from the Medieval period around the North Sea and are there changes through time or differences between regions?
- Where were flatfish captured throughout the Medieval period, and is there a difference between prior and after the marine fish event horizon and between regions (see section 7.2)?

This chapter demonstrates how these aims have been met and what has been learned about the exploitation of flatfish through time and about the individual sites analysed.

7.1 Identification methods

The identification possibilities of three techniques have been explored and their success evaluated. These identification methods allow for future research to make species-specific analyses. This will help to better understand the historical exploitation and ecologies of flatfish in the North Sea and surrounding areas, as it has done in this thesis.

Initially Wouters *et al.*'s (2007) comparative osteological analysis of flatfish was expanded by including eight additional species frequently found in the North Sea and eight skeletal elements of flatfish that were not included in previous descriptive research (Chapter 3). This effort resulted in the definition of many new diagnostic features that can be used to resolve the plaice/flounder/dab-complex. Clear differences between other species were also found, and several elements were described for some species for the first time. However, this technique is still limited when attempting to identify the most common flatfish species using particular elements due to a lack of clear morphological differences, even more so when they are fragmented. This is especially the case for vertebrae, but also certain cranial elements such as the preoperculum, ceratohyal, and quadrate. The difficulty of applying comparative osteology on archaeological remains was apparent while analysing the site material during sample selection for molecular techniques. Although the improved osteological guide provided in Chapter 3 will help with identifying flatfish remains to species in future studies, which is also often the first step of biomolecular research, caution is still advised for many elements and alternative techniques to correctly and confidently identify species are still needed.

Geometric morphometrics is a landmark-based shape analysis technique and has been applied in previous studies to identify archaeological remains to certain taxa (e.g., Ponton, 2006; Ibañez *et al.*, 2007; Guillaud *et al.*, 2016; Thieren & Van Neer, 2016) (Chapter 4). Using a large reference dataset of modern, well-identified museum specimens, the shape variation of vertebrae between taxa was described, which showed that flatfish species have quite similar looking vertebrae, as was already noticed by osteologists before. As some differentiation between taxa was still visible, a classification method was developed, which could provide the most probable taxon for a sample by comparing it to the modern reference set. Reclassifying the modern dataset using this method yielded a high success rate for most subsets (often 70% or higher). However, it was noticed that this method has an inadequate success rate to identify archaeological samples, selected from two case study sites available at the time of this study, with fewer than 50% correctly identified to species. This reduction in accuracy is most likely due to fragmentation of the archaeological samples, as landmarks and morphological information are lost. This technique, which uses a combined view approach and has the flexibility to work with specific subsets and landmark configurations, should therefore not be applied on most archaeological flatfish vertebrae to identify species, but it can be easily adopted to identify modern or well-preserved archaeological vertebrae, to test for morphological variation in other taxonomic groups or skeletal elements, and to apply other kinds of shape analyses.

The third identification technique that was used is collagen peptide mass fingerprinting (ZooMS) which is a molecular analysis of the collagen preserved in bones that can be used to identify taxonomic groups (Chapter 5). By analysing modern well-identified museum specimens, eight peptide biomarkers were found that allow the identification of 18 different flatfish species from European waters. This method has a high success rate with >95% of samples from Medieval sites from the North Sea being identified to species, much higher than possible with osteological analysis (up to 15%) (e.g., Ervynck & Van Neer, 1992; Enghoff, 1999; Nicholson, 2009; Reynolds, 2015; Harland *et al.*, 2016; Oueslati, 2019; Chapter 2 and 3 in this thesis). Collagen peptide mass fingerprinting further revealed the presence of unreported flatfish species in archaeological sites from the Medieval period and showed that major exploitation shifts from one species to the other have occurred within sites across Europe. Furthermore, the analysis has indicated that the more limited osteological identifications that were made in the past were mostly correct, confirming the reliability of published osteological data. This technique can also help to avoid identifications made on assumptions (see below in section 7.2.8.1). ZooMS is becoming increasingly important for analysing fish remains from archaeological sites, although the number of published biomarkers for fish species is still limited, and it has vast potential for understanding fish ecologies and exploitation in the past and the present (e.g., Harvey *et al.*, 2018; Dierickx *et al.*, 2022; Harvey *et al.*, 2022). Of the three evaluated and improved identification techniques, collagen peptide mass fingerprinting has the highest success rate, but is unfortunately also the most destructive, although less destructive approaches are available as well (Fiddyment *et al.*, 2015; McGrath *et al.*, 2019; Nahui *et al.*, 2021).

7.2 Analysis of flatfish exploitation by site

The improved identifications carried through osteology (Chapter 3) and collagen peptide mass fingerprinting (Chapter 5) on the selected archaeological samples, alongside the results from the zooarchaeological assemblage analysis (Chapter 2) and the stable isotope analysis (Chapter 6) will be used to provide a detailed discussion for each settlement and site in this section. The findings will also be related to the archaeological site reports, previous analyses, and historical events. This is followed by a general discussion of all sites, providing a regional picture of flatfish exploitation in the North Sea area during medieval times.

7.2.1 England: York

York is a city in the north of England, located inland and connected to the North Sea via the Ouse, a tidal river, and further downstream the Humber. Since Roman occupation in England, the city was an important trading centre, from which many fish remains were uncovered (see Harland *et al.*, 2016).

7.2.1.1 16-22 Coppergate

Coppergate is a site with a large amount of animal bones and a well-studied fish assemblage dating from the Viking Age till the end of the Medieval period in York (Bond & O'Connor, 1999; Harland *et al.*, 2016). There is a high abundance of flatfish throughout the whole Medieval period (7-14th centuries CE) (Harland *et al.*, 2016; also see Chapter 2). The analysis of the Coppergate material has uncovered many interesting changes in flatfish fisheries in terms of species abundances, sizes and catch locations, matching in timing with the marine fish event horizon (Chapters 2, 5 and 6). There seems to have been a slight decrease in the abundance of flatfish and freshwater species in favour of Gadidae during the High Medieval period, corresponding to the marine fish event horizon, while during the Late Medieval period flatfish gained in abundance again (Harland *et al.*, 2016 and noticed in this study, see Chapter 2). No clear sign of processed flatfish on the site was found in this study, although a slight overrepresentation of postcranial bones seems to be present. Flatfish recovered from the site seem to be rather small (<30 cm SL) during the Early Medieval period and become on average larger during the High Medieval period, most likely due to a more marine-oriented exploitation (Chapter 2). A very strong shift in species is observed in this site. *Platichthys flesus* is the dominant species during the Early Medieval period, while after the 11th century CE *P. platessa* is the most abundant flatfish identified using ZooMS. Also *S. maximus* and *L. limanda* were identified from the High and Late Medieval periods (Chapter 5). This shift in species could also be explained by a shift in catch habitats. Isotopically this is difficult to assess further, due to the small number of *P. flesus* that could be analysed. One *P. flesus* from the Late Saxon period originates from a freshwater habitat, while another sample clearly shows a marine signal. One *P. flesus* sample from the High/Late Medieval period also shows a freshwater signal. All *P. platessa* samples clearly originated from marine habitats, although one Late Medieval sample has lower $\delta^{13}C$ values. Sulfur isotope analysis shows that *P. platessa* was exploited mostly from freshwater-influenced marine waters during the Early and High Medieval periods, while during the High and Late Medieval periods, there is a sudden appearance of *P. platessa* from a more open marine environment (Chapter 6). This could potentially indicate either a shift in catch location to a more open, perhaps even more northern marine habitat, linked to the general geographical expansion for other marine fish or trade from a more northern location, which is not unlikely as other fish species were traded to York at that time (Barrett *et al.*, 2004a,b; Barrett *et al.*, 2011). The timing of these shifts (during the 10-11th centuries CE) in exploited species and catch locations also corresponds to the timing of the marine fish event horizon at the start of the High Medieval period (mid-tenth and mid-eleventh centuries CE; Barrett *et al.*, 2004a; Harland *et al.*, 2016).

7.2.1.2 Blue Bridge Lane

The fish remains from Blue Bridge Lane, a trading hub south of the walled city since the Anglo-Saxon (Early Medieval) period, are dominated by Clupeidae, with some flatfish mostly having been recovered from Early and Late Medieval periods (Harland *et al.*, 2016). Although this site is a presumed trading settlement with a landing site for fisheries (Spall & Toop, 2005; Harland *et al.*, 2016), a slight overrepresentation of flatfish postcranial bones is noticed (see Chapter 2 for details). A very slight increase in the average size of flatfish is noticed throughout the Medieval period. ZooMS identified mostly *P. platessa* from this site. *Platichthys flesus* was identified only from the Early Medieval period 1 (Mid Saxon period) and one *L. limanda* was identified from the Late Medieval period, which is the first record of this species for this site (Chapter 5). The shift in species from a large abundance of *P. flesus* to mostly *P. platessa* between the Early and Late Medieval periods could be related to a general shift from freshwater to marine water exploitation. Isotopically this would be a viable hypothesis as well, with two of the three *P. flesus* from the Early Medieval period coming from a freshwater habitat, while all *P. platessa* have a (southern North Sea) marine signal based on $\delta^{13}C$ and $\delta^{34}S$ isotope values (Chapter 6).

7.2.1.3 York as a settlement

In general, the sites in York seem to show typical changes in fisheries activities related and contemporary to the gradual expansion towards more marine habitat exploitation as part of the marine fish event horizon. This thesis provides a first in-depth analysis of flatfish in York in terms of species identifications and stable isotope analysis. Species identifications of flatfish have been limited in previous studies and although plaice, flounder, turbot, halibut and sole were identified in sites from York, most remains could not be identified to species (only ca. 15%; Harland *et al.*, 2016). A relatively high number of *P. platessa* was identified from the 12th century CE onwards in Coppergate and Blue Bridge Lane (Harland *et al.*, 2016). With collagen peptide mass fingerprinting, the species could be identified, revealing a clear change in the exploited species through time. In none of the other analysed settlements is the transition from a dominance of *P. flesus* to *P. platessa* during the Medieval period so clearly visible. Isotopically this rather northern settlement also showed interesting changes and potentially even evidence for a northern exploitation or long-distance trade of flatfish during the High and Late Medieval period, as observed in the sulfur isotope analysis, which was not found in any of the other southern North Sea settlements.

Flatfish exploited from a marine environment, such as estuarine and coastal areas, already appear from the 7th century in York, more specifically the trading hub Blue Bridge Lane, indicating that long-distance trade and economic opportunities across the North Sea could have triggered the onset of marine fish exploitation. The increase in marine fish exploitation at the end of the Early Medieval period could be largely attributed to the arrival and cultural influence of Scandinavians, who inhabited the settlement since the mid/late 9th century (Hall, 1994). This culture has been known to rely more on marine fish consumption, as evidenced by fish remains and human diet analyses from Scandinavia during the Early Medieval period (e.g., Barrett & Richards, 2004; Barrett *et al.*, 2004a,b; Naumann *et al.*, 2014; Barrett, 2016) compared to Anglo-Saxon inhabitants of York during the Early Medieval period (Reynolds, 2015; Harland, *et al.*, 2016). While trade between York and the continent had been ongoing since the Roman and Early Medieval times, the trading network was further expanded during the Viking Age, including Viking-controlled Dublin in Ireland and beyond the North Sea area

(Hall, 1994). This was used to not only trade goods (Hall, 1994), but also fish (Barrett *et al.*, 2011) across large distances. Furthermore, the growing population, making York the second largest settlement in England (Hall, 1994), the mix of cultures after the Norman conquest of England, and the increase in people practising Christianity (as suggested by Barrett *et al.*, 2004a,b), as well as potentially a decrease in freshwater quality as evidenced by invertebrate species presence (O'Connor, 1999), might have further spurred people in York to exploit marine habitats, especially since around the 10-11th centuries CE.

7.2.2 England: London

London is situated around the Thames, a tidal river which flows into the Thames estuary, and has been occupied for over two millennia, serving as an important political and economic settlement. Four sites from medieval London were analysed, providing a thorough insight into the fish exploitation through time at this settlement. These are discussed in chronological order.

7.2.2.3 SGA89 (2-26 Shorts Gardens and 19-41 Earlham Street)

This Anglo-Saxon site from London, situated west of the Thames, is characterised by the presence of industrial and domestic buildings (Cowie *et al.*, 2012). An overabundance of vertebrae was seen in the zooarchaeological analysis (Chapter 2), showing that there might have been an import of processed fish to the site from a landing or processing site somewhere else. Both *P. platessa* and *P. flesus* have been recovered from this site as identified with collagen peptide mass fingerprinting (Chapter 5). All *P. platessa* show an estuarine or marine signal, while the few *P. flesus* samples seem to have come from various habitats based on their $\delta^{13}C$ and $\delta^{34}S$ values. Two samples show a marine signal, one an estuarine signal, and one sample a clear freshwater signal. For $\delta^{15}N$ all *P. flesus* samples, which are also rather small of medium sized (three 10-30 cm SL, one 30-40 cm SL), show an elevated value compared to many sites in York or on the continent. This is not observed for *P. platessa*. The isotopes seem to indicate that some flatfish were caught in the Thames estuary and even occasionally closer to the site in the Thames river, but possibly also in the open area of the southern North Sea.

7.2.2.4 SOT89 (26-27 Southampton Street)

This second Anglo-Saxon site from London, situated west of the Thames, is also characterised by an overabundance of vertebrae, which was observed in the zooarchaeological analysis (Chapter 2), showing that there might have been an import of processed fish to the site from a landing or processing site somewhere else. Both *P. platessa* and *P. flesus* have been identified from this site using collagen peptide mass fingerprinting (Chapter 5). All *P. platessa* show a marine, including southern North Sea signal, while the few *P. flesus* samples seem to have come from both freshwater and estuarine habitats based on their $\delta^{13}C$ and $\delta^{34}S$ values. Like the site above, this site shows a similar trend in carbon, nitrogen and sulfur isotope values, however, occasionally *P. flesus* individuals from freshwater habitats were exploited as well in this site.

7.2.2.2 GSJ06 (54-66 Gresham street)

This site, north of the Thames, is thought to have been situated close to a small tributary of the Thames (Pennington & Wroe-Brown, 2008). During the 10-12th centuries (Early/High

Medieval period) flatfish constituted only a minority of the fish remains, with Clupeidae and Gadidae being more abundant (Chapter 2). In this study, postcranial bones of flatfish were found to be overrepresented in the site, which could indicate the import of processed flatfish. Most flatfish are also rather small (<30 cm SL), with only a minority of medium size (30-40 cm SL). About equal amounts of *P. platessa* and *P. flesus* were identified using ZooMS from this site (Chapter 5). Both *P. platessa* and *P. flesus* mostly originated from estuarine/freshwater influenced marine habitat, while one *P. flesus* shows a freshwater signal, as seen in both $\delta^{13}C$ and $\delta^{34}S$ isotope values. Like the first London site described above, this site shows a similar trend in the isotope data, although there is a larger range for $\delta^{15}N$ in this site compared to the other three London sites.

7.2.2.1 CAO96 (Gateway House)

This site is located north of the Thames and one of its medieval structures is thought to have been a church (Bowsher, 1996; Bowsher, 1998; Elsden, 1999). There is a high abundance of Gadidae during the Early and High Medieval period, while flatfish, and to a lesser extent Clupeidae, become more abundant during the Late Medieval period (Chapter 2 this thesis). Only a slight deviation from a normal skeletal element distribution was noticed, meaning that flatfish were brought to the site as processed fish to some extent (Chapter 2). These flatfish were also rather of medium or small size (<40 cm SL). All flatfish identified from the site were *P. platessa* showing a clear marine signal for carbon. The sulfur isotopes from this species indicate a clear freshwater influenced/southern North Sea catch location. It is possible that with this having been a church area during the Medieval period, that the food consumption pattern is slightly different in this site, than it is in the other analysed London sites.

7.2.2.5 London as a settlement

London is a large settlement at the Thames estuary and the easy connection to the North Sea has resulted in an early use of this sea for trade and also for marine fish exploitation. The analysed flatfish recovered during the Early Medieval period seem to indicate that flatfish fishing occurred nearby the sites located on the Thames, as seen in GSJ06, SGA89 and SOT89 for *P. flesus*, in the Thames estuary and potentially beyond the Thames estuary, as seen in GSJ06, SGA89 for both species, and in the North Sea, as seen in site GSJ06 and SGA89 for *P. flesus* and all four sites for *P. platessa*. The early onset of importing (processed) coastal and marine flatfish to London (7th century CE) seems to pre-date the intensification of marine fishing as evidenced by the increase of Gadidae in London (around 1000 CE; Barrett *et al.*, 2004a,b; Orton *et al.*, 2014).

During the Medieval period processed fish seems to have been transported to the sites, although barely any clear cutmarks were observed on flatfish. A slight relative decrease in postcranial bones is noticed across the four sites, but interpretations need to be made cautiously due to the lack of sieving for the Anglo-Saxon sites, which could mean small cranial remains have not been recovered well, creating a bias in the element representation (also see Chapter 2, section 2.2.2.2). The intensification of marine fishing around 1000 CE is also characterised by a large proportion of *P. platessa* identified from the sites, which could have been caught and landed in nearby coastal areas and brought to London, as whole dried or processed fish. There could have been dedicated landing and processing sites nearer to the coast or in London from where goods could have been brought to markets and households in London (also see Reynolds, 2015).

London also has a characteristically higher nitrogen isotope values for *P. flesus* compared to those from sites on the continent and from York (12-14‰ vs. 9-13‰), which could be related to the local environment or potentially anthropogenic influences, but it is unsure what the exact cause for it is (see Chapter 6, section 6.4.4).

Similar to the early onset of marine fishing in York, which could have been related to long-distance trade, the easy access to the North Sea via the Thames most likely provided opportunities for early marine fish exploitation in London as well. London has been an important and centrally located trading hub in the North Sea area, with evidence for trade with the continent since the Early Medieval period (e.g., Loveluck and Tys, 2006). The growing population and urbanisation during the High Medieval period, which made London the largest settlement on this side of the North Sea, could have further contributed to the changes observed in flatfish fisheries in London indicating a more marine-focused flatfish exploitation at the start of the High Medieval period, which was necessary and possible due to increased demand of the growing population in the city and changes in diet relating to Christian Lent (also see Barrett *et al.*, 2004a,b).

7.2.3 England: Canterbury, Tradescent Lane

Tradescent Lane is a near-coastal site in England and part of St. Augustine's Abbey, which dates from the High and Late Medieval periods (from 12th century onwards). Although flatfish constitute a large part of the fish assemblage during the High Medieval period, their abundance decreases in favour of Gadidae and Clupeidae during the Late Medieval period (see Chapter 2 for details). No evidence was found in this study for processing fish, meaning the fish could have been brought whole to the site. The shift towards other typical marine species and the increase in average size (but sample size small for Late Medieval period, n=9) could indicate a shift towards more open sea exploited flatfish that were landed near Canterbury and brought as whole fish to the site for consumption by the inhabitants of the abbey. Several species of flatfish were identified from this site using collagen peptide mass fingerprinting (see Chapter 5), of which *P. platessa* was the most abundant one. Also *S. solea* was recovered, which is a typically marine living species in the southern part of the North Sea and associated with more wealthy diets and abbeys. A high amount of *S. solea* was also recovered from the Ename Abbey in Belgium from the Late Medieval and Post-Medieval periods (Van Neer & Ervynck, 1996). The diets of monks, and especially abbots are known to reflect a wealthier diet, which could include fresh *S. solea* and *Scophthalmus* sp. (e.g., Ervynck & Van Neer, 1992; Van Neer & Ervynck, 1996; Nicholson, 2015). Their recovery in Tradescent Lane is thus not unexpected. Isotopically this site is also quite remarkable. The average $\delta^{13}C$ value of *P. flesus* is very high compared to the findings from other sites for this species (-11.99‰ vs. -15.27‰ excluding freshwater samples), especially more inland sites, such as those from York, London, Gent and the Netherlands. For *P. platessa* no clear difference was observed between this site and the others. Both species come exclusively from marine habitats, with sulfur isotope values indicating that they might have been fished in an open marine habitat in the southern North Sea, and not in estuaries or freshwater habitats, as is often the case for *P. flesus*. For *P. flesus* elevated $\delta^{15}N$ values (12-15‰) were observed compared to the other sites, similar to the samples from London, which could be related to environmental or anthropogenic factors (see Chapter 6, section 6.4.4). Contrary to the shift in sizes and relative increase of other marine taxa, the isotope data did not reveal a further expansion from freshwater-influenced marine habitats to more open marine habitats.

Potentially, stable isotope analysis cannot provide the same resolution for a change in habitat, especially between specific marine habitats, or fishing practices as certain zooarchaeological evidence can. The change in observed species and sizes could also be related to culinary and economic preferences of the inhabitants and not be caused by a shift in catch location. With the species composition of this site showing potential specific culinary choices, this latter possibility might be a preferred hypothesis. The findings obtained in this thesis further confirm the strong and consistent dependence of marine environments for fisheries of this higher social status and near-coastal site during the High and Late Medieval period, as noted previously by Nicholson (2015).

7.2.4. France: Saint-George-sur-L'Aa, Barreau Saint-George-Desserte ferroviaire

The site of Barreau Saint-George is a briefly occupied site on the French coast during the High Medieval period at the end of the 10th - beginning of the 11th centuries CE. It is characterised by a large abundance of flatfish (Oueslati, 2019). The element distribution indicates that the generally small flatfish were brought to the site whole, which is also confirmed by the presence of suspected gut content from flatfish on the site (Oueslati, 2019) and the proximity of the site to the coastal area where they were being captured. Flatfish might have been consumed on site, while the other species, such as the large Gadidae, were processed for trade (Oueslati, 2019). A large number of *P. flesus* has been identified using osteology (Oueslati, 2019) and ZooMS (Chapter 5 in this thesis). Isotopically, both *P. flesus* and *P. platessa* show a rather marine exploitation, although the samples for *P. flesus* have lower values for both δ^{13}C and δ^{34}S than the conspecific samples from Canterbury. The reason for this might be that the small (two thirds of the assemblage are <20 cm SL) *P. flesus* in Barreau Saint-George were more fished from nearby estuaries or closer to freshwater influenced waters in northern France, while the generally larger *P. platessa* and the fish from Canterbury might have been fished in more open marine habitats further away from the coasts.

7.2.5 Belgium: Koksijde, Hof ter Hille

The occupation type in Hof ter Hille, a coastal site in Belgium, changed during the 11th century CE and went from local farm houses to a more economically oriented agricultural property (Lehouck *et al.*, 2014). Marine fish are the most abundant taxa recovered from the site, although some freshwater species, such as pike were also found (Van der Meer *et al.*, 2018; also see Chapter 2). Isotopically, these pike seem to originate from freshwater habitats, such as the nearby Yser river, rather than brackish environments (see Chapter 6). During the High Medieval period the relative abundance of postcranial bones and the average size of flatfish increased (from mostly 20-30 to mostly 30-40 cm SL), which could indicate an increased import of processed fish to the site, related to the change in occupation during the 11th century CE (Chapter 2). Using ZooMS a high abundance of *P. platessa* is identified, while *P. flesus* and *S. maximus* were of minor importance (Chapter 5). All isotopically analysed samples seem to originate from an estuarine or close-coastal habitat/southern North Sea, with no clear changes through time, as seen in the carbon and sulfur isotope data (Chapter 6). This site, being coastal and occupied throughout the Medieval period by wealthy people, relied mostly on marine fish for their diet, which confirms the ichthyoarchaeological findings by Van der Meer *et al.* (2018).

7.2.6 Belgium: Gent, Zwarte Laag

Gent is a city situated around the Scheldt in Belgium. The site Zwarte Laag had exceptionally well dated refuse layers dating from the Early to High Medieval periods (Ervynck *et al.*, 2004). A clear transition towards more marine species, such as flatfish, Gadidae and Clupeidae, throughout the Medieval period is noticed in this site (Ervynck *et al.*, 2004; also see Chapter 2). Only a slight increase in the number of postcranial flatfish bones was apparent during the second phase of the site, meaning there was no large import of processed flatfish (Chapter 2), which matches descriptions from historical sources, such as the *Visboeck* (Coenen, 1577). All size classes are also represented in this site, with relatively fewer samples from the smallest size classes (5-30 cm SL) during the second phase of the site. These findings follow the general trends of larger marine fish increasing in abundance through time. ZooMS revealed that both *P. platessa* and *P. flesus* were present at the site during the 10th and 11th century and identified a large number of *P. flesus* occuring in the 12th century of the site, which is contrary to the general pattern observed within flatfish in the sites represented here. The presence of both *S. maximus* and *S. rhombus* during the 12th century could indicate clear marine exploitation, which is also shown by the large amount of Gadidae and Clupeidae on the site from that time, or could be linked to trade with other regions. Isotopically, most *P. platessa* and *P. flesus* seem to originate from freshwater influenced marine environments, such as the southern North Sea, although some samples have somewhat lower $\delta^{13}C$ and $\delta^{34}S$ values. This shows that marine exploitation was happening in this site from early on and might have gained more importance during the second phase, but estuarine environments remained relevant for fisheries for people in this city, which might be expected given the location of the city and the tidal influence of the river running through it. It is known from historical sources (Ervynck *et al.*, 2004; Van Neer & Ervynck, 2007) that by the end of the Late Medieval period Flemish fishers ventured to more northern waters for herring fisheries. The relatively high $\delta^{34}S$ values (14-15‰) for some *P. platessa* and the presence of *Scophthalmus* sp. in this site during the 12th century could perhaps also be linked to an earlier northward move of Flemish fisheries, but more research is needed before any conclusions can be made.

7.2.7 Netherlands: Vlaardingen, Gat in de Markt

The site of Gat in de Markt is located on an old terp next to the old church of Vlaardingen (Buitenhuis *et al.*, 2006). The High and Late Medieval periods show a high abundance of both Gadidae and Pleuronectidae and only a minor presence of freshwater taxa compared to the Early Medieval phase in the site, which would indicate a significant exploitation of marine environments after the marine fish event horizon. Flatfish seem to have become slightly more abundant compared to Gadidae during the Late Medieval period (Chapter 2). There seems to be an average reduction in the size of flatfish from the High Medieval to Late Medieval period. The zooarchaeological evidence further suggests a change from processing large marine fish on the site (30-60 cm SL, but the sample size is small) during the High Medieval period to the import of mostly small (5-30 cm SL) whole fish at the start of the Late Medieval period (Chapter 2). ZooMS analysis shows that all samples analysed from the Early and High Medieval period were *P. platessa*, while *P. flesus* was only identified from the Late Medieval period alongside *P. platessa*, which is not what one would expect based on the general trend observed across the whole North Sea region. However, as the sample sizes are rather small, especially for the Early Medieval period (n=6), it cannot be excluded that *P. flesus* was being fished (Chapter 5). The isotopic data for this site suggests that from the Early Medieval period onward, *P.*

platessa was exploited from the open southern North Sea area, while later both *P. platessa* and *P. flesus* might have been fished from more estuarine habitats and freshwater influenced marine habitats, as seen in the carbon and sulfur isotope data (Chapter 6).

During the end of the High Medieval and start of the Late Medieval period, during the 12-13th centuries, the settlement developed further as a city and became politically more independent. It is possible that the High Medieval fish processing site moved away from the excavation site during this time, and the change in fish remains during the Late Medieval period reflects consumption waste, rather than a producing site, although due to the small sample size for the Early and High Medieval material, this cannot be confirmed further. The hydrology of this region started to change drastically during the Late Medieval period, with people expanding the land and constructing dams in the area, while floods would still occasionally occur (Van Loon & de Ridder, 2006). This could have resulted in a change in the environment with novel canals and nearby (tidal) rivers forming (Roorda Van Eysinga, 1988; Van Loon & de Ridder, 2006), favouring the exploitation of estuarine *P. flesus* and *P. platessa* more than during the Early and High Medieval period when marine fishing was more common in this site. The economic and culinary preferences of people simply could also explain this shift. Furthermore, from the 11th century CE (High Medieval) onwards toll needed to be paid for anyone sailing on the Meuse river for trade purposes (Roorda Van Eysinga, 1988), which could have resulted in less intense marine fish exploitation and inland trade in this area and a shift to more local exploitation of fish; although this contradicts the apparent increase in Gadidae during the High Medieval period as seen zooarchaeologically.

7.2.8 Netherlands: Leiderdorp

7.2.8.1 Plantage

At Plantage during the Early Medieval period, a clear increase in the NISP of Cyprinidae, Percidae and Pleuronectiformes was observed by both Beerenhout (2016) and this thesis (Chapter 2). Within flatfish a clear transition from *P. flesus* to a mixture of both *P. flesus* and *P. platessa* is observed with collagen peptide mass fingerprinting between the 7-8th and 9th centuries CE (Chapter 5) on a selection of samples. This species transition matches the general trend observed in the North Sea area, but clearly predates the marine fish event horizon and even similar shifts in other sites. The cause of this earlier shift could be socio-economic, but it could also have been triggered by ecological changes with the trench river of the site being cut off from the main tidal river (Dijkstra *et al.*, 2016), resulting in a bigger need to import fish, which could have been brought from areas nearby or from the coastal area.

The site is also characterised by a large abundance of postcranial bones from flatfish, indicating an import of processed fish to the site, which could have originated from the Kastanjelaan site. Most fish are small (<30 cm SL) (see Chapter 2 for details).

Isotopically all analysed samples showed marine and estuarine signals based on $\delta^{13}C$ (Chapter 6).

These results indicate that the site might have relied mostly on processed flatfish, caught in (near-)coastal environments, such as the tidal influenced river system. None of the analysed samples (n=18) matched the quality criteria for sulfur as there was a strong suggestion of contamination by exogenous sulfur from the burial environment, so the catch habitat could not be further determined for this site.

A comment should be made on the species identification method applied in the original site report (Beerenhout, 2016), in which they used the estimated size to infer species and habitat of some samples. Although the criteria seem to match our own species and habitat identifications in most cases, they do however misidentify and mislabel some samples. For example, one of the larger specimens analysed using collagen peptide mass fingerprinting turned out to be a marine *P. flesus*. If this alternative identification method was applied, this sample would have been labelled as a marine *P. platessa*. About half of the very small specimens (<30cm SL) were identified using ZooMS and isotope analysis as marine *P. platessa*, which using the reported method would have been labelled as freshwater *P. flesus*. Caution is therefore advised when relying too heavily on assumed ecologies of the species for species identifications, as flatfish seem to be less strict in their habitat selection than one might assume at first, and incorrect identifications could lead to misleading interpretations. This case again confirms the importance of applying collagen peptide mass fingerprinting as an identification technique.

7.2.8.2 Netherlands: Kastanjelaan

This Early Medieval site is located in Leiderdorp, only a few hundred meters away from the Plantage site. The site report (Kerklaan, 2014) states that the overabundance of fish vertebrae could indicate the import of processed fish. Though this is a generally accepted theory, when Anguillidae form the majority of the assemblage, caution should be taken to not generalise this to other species. My own zooarchaeological analysis of the site seems to indicate an overabundance of cranial bones for flatfish, which would indicate a processing site (Chapter 2). Nearby sites, such as Plantage, are then suspected to be the consumer sites. The flatfish are also on average very small (majority <20 cm SL and most <30 cm SL), matching the size estimations for Plantage (Chapter 2).

Only a handful of samples from this site could be analysed using biomolecular techniques due to the small sized bones. Four samples were analysed with ZooMS, of which two were *P. flesus* and two were *P. platessa*. The latter species was successfully analysed using stable isotope analysis for carbon and nitrogen only. These results indicate a clear marine exploitation, although the two analysed *P. platessa* also happen to be two of the three slightly larger-sized specimens found in the site. As the sample size is so small, no further conclusions should be made.

7.2.8.3 Leiderdorp as a settlement

The two sites from Leiderdorp show zooarchaeological evidence for an economic connection, with one site resembling a landing and processing site for fish while the other resembles a consumer site, at least for flatfish remains. The zooarchaeological and isotopic evidence seems to show that the onset of marine fishing in this site again pre-dates the marine fish event horizon in the 10-11th century by one to three centuries. Although the settlement is located inland with a tidal river running through it and some samples were most likely exploited locally, a large amount of the flatfish samples seems to originate from the coastal area and were then imported to and processed in the settlement. As no sample could be analysed for sulfur, barely any distinction was made between different kinds of marine habitats, so it is possible that flatfish exploitation could still have been restricted to only estuarine habitats near this settlement.

7.2.9 Regional picture from the southern North Sea

Analysing all samples from the thirteen sites using the various methods (i.e. osteology/zooarchaeology, ZooMS, and stable isotope analysis) has revealed interesting patterns in relation to flatfish fisheries.

Throughout the Medieval period, there seems to have been a slight relative increase in the abundance of flatfish, especially larger specimens, compared to some other common fish families (e.g. Anguillidae, Cyprinidae, Esocidae). Slight differences in isotopic values, species abundances and processing practices between regions and sites, reflecting the local environments or occupation types, were also observed. Furthermore, trends relating to the size classes and ecologies of fish species were also noted.

The sites in London and Leiderdorp, both inland settlements with easy access to the North Sea by large rivers and estuaries, show evidence of imported marine flatfish during the Early Medieval period from the 7th century CE onwards, about three centuries before the marine fish event, as detected zooarchaeologically and by stable isotope analysis (also see Barrett, 2016). With most of the marine flatfish from these sites being larger than 20cm SL (and about half even bigger than 30 cm SL), the chance of them being stomach content from Anguillidae or other animals is very small, making it very likely these fish were brought to the site for consumption, and not by accident as was proposed by Barrett (2016). The large shifts observed in York on the other hand are contemporaneous to the marine fish event, but a few marine flatfish have been recorded from the Early Medieval period as well. The three coastal sites - Tradescent Lane in Canterbury, Barreau Saint-George in Saint-George-sur-L'Aa, and Hof ter Hille in Koksijde - date from after the general marine fish event horizon or are only briefly occupied. These sites relied on marine fish throughout the whole duration of occupation and showed minimal changes in exploited fish. Vlaardingen and Gent also show an early onset of marine fishing dating from around the marine fish event horizon (no earlier samples are available), but both sites keep a large dependence on local coastal, estuarine and freshwater exploited flatfish throughout the Medieval period. In general, it seems that marine flatfish were indeed exploited and traded inland prior to the marine fish event horizon in all areas around the southern North Sea. Furthermore, the observed general switch from *P. flesus* to *P. platessa* was well underway when the marine fish event horizon, which is characterised by a relative increase in Gadidae and Clupeidae and relative decrease in obligate freshwater species, had only just begun. This could mean that flatfish were a stepping stone taxon, as they are ecologically very diverse, yet remain easy to exploit from the coast or at sea near the coast. They could have paved the way to more intense marine exploitation, such as that of Gadidae and Clupeidae, by making the change from riverine and coastal exploitation to open marine fishing a gradual transition (also see Chapter 1, section 1.3.8). Flatfish can be easily caught using nets (e.g., seine nets) either standing on the shore or from a boat, occasionally using hook and line, and even by flounder trampling. These methods were readily available during the Early Medieval period (e.g., Van Neer & Ervynck, 2007).

Further expansion of the catch habitat towards more open marine environments is observed in a few sites. The most remarkable shift is seen in York, where a large amount of open marine *P. platessa* appear during the High and Late Medieval period, while estuarine/coastal samples appear less abundant. As mentioned earlier, this could indicate a more open/northern marine-oriented exploitation, although it remains uncertain how far from the Yorkshire coast these samples would have been caught. Also in London and Gent a slight marine expansion of flatfish fisheries from the Early to the High Medieval period is observed. The coastal sites Canterbury and Koksijde, however, do not show a major change in fisheries through time, as the exploitation remained rather locally marine, similarly for Vlaardingen. It is perhaps unsurprising that a shift towards more open marine environments is only detected in larger cities, such as York, London and Gent, at the start of the High Medieval period, while the smaller cities and coastal areas seemingly relied on more close-coastal focused flatfish fishing throughout the Medieval period. These larger cities, having a larger population and perhaps more of an interest in long-distance trade, could have had a larger need and more opportunities to import marine fish from more specialised fishermen, who were since the start of the High Medieval period focusing more on open marine exploitation of Gadidae and Clupeidae as well (also see Barrett *et al.*, 2004a,b; Van Neer & Ervynck, 2007). Although there is an increased focus on marine fish, the exploitation of estuarine and freshwater flatfish remains active in sites across the southern North Sea during the High and Late Medieval period to a minor extent.

The low observed abundance of other species of flatfish can be attributed to the low occurrence rate in the southern North Sea of several Pleuronectidae and Scophthalmidae species, such as *G. cynoglossus, H. platessoides, S. maximus, S. rhombus,* and *H. hippoglossus*. Furthermore, *P. platessa* and *P. flesus*, both very common in the southern North Sea, can perhaps be more easily and often caught compared to for example *L. limanda* and *M. kitt*. Species such as *S. solea* could have been sold to elite occupation sites (e.g., Ervynck & Van Neer, 1992; Van Neer & Ervynck, 1996; Nicholson, 2015), which were not generally included in this study, except for the one monastic site in Canterbury, Tradescent Lane, in which several *S. solea* were identified. *Scophthalmus* sp. were observed in sites after the Early Medieval period, coinciding with marine focused exploitation. Smaller species of Pleuronectidae, Scophthalmidae and Soleidae not mentioned above, are of lesser interest for fisheries due to their small sizes, which also makes it less likely to recover them from archaeological assemblages, as their bones are only a few millimetres in size, making it difficult to recover and identify them in archaeological analyses.

In conclusion, flatfish were exploited from marine habitats in the southern North Sea basin by at least the 7th century CE, three centuries before the marine fish event horizon and imported to inland sites, but some flatfish fisheries slightly expanded the catch habitats to more open marine southern North Sea environments when the marine fish event horizon occurred, all while local freshwater, estuarine and coastal flatfish fisheries continued. This shift to more marine exploitation of flatfish is also seen in a slight general increase in the size of flatfish and a change in most abundant species. Flatfish fisheries mostly remained local, relatively near-coastal or open southern North Sea fisheries during the High and Late Medieval periods, as they are in modern times (e.g., Gibson *et al.*, 2015). This contrasts with the continuous geographical expansion that occurred during the High and Late Medieval period and thereafter for Gadidae and Clupeidae fisheries, taxa that can also be found further out at sea (e.g., Orton *et al.*, 2014; Holm *et al.*, 2021).

7.3. Reflection of the study

This thesis provides many new scientific results which help to elucidate the historical exploitation of flatfish as well as describe and apply novel approaches to identify remains.
With flatfish remains being difficult to identify to species, especially the distinction between the osteologically similar species plaice, flounder and dab (e.g., Wouters *et al.*, 2007), previous research on historical flatfish exploitation has been rather limited. Furthermore, stable isotope analysis is required to differentiate between flatfish caught in different habitats. These issues have hindered the understanding of how flatfish fitted into the story of economic changes during the marine fish event horizon (e.g, Barrett *et al.*, 2004a,b). The zooarchaeological record had shown previously that flatfish were an important part of the human diet in medieval times, even during the Early Medieval period (e.g., Van Neer & Ervynck, 2007; Reynolds, 2015; Van Neer & Ervynck, 2016; Oueslati, 2019), but it was not possible to infer to what extent this represented marine exploitation.
This study has now resolved these issues and provided a first large-scale insight into the historical exploitation of flatfish. The species identification methods can be easily applied to provide species-specific analysis. The multi-isotope approach can indeed be used to uncover the ecology of flatfish living in the past, which can be used as a proxy for the catch habitat. This multidisciplinary research has proven that flatfish were being caught in different environments and that there were clear changes in flatfish fisheries throughout the Medieval period, some predating and others related to the marine fish event horizon.

Although this study provided a more detailed insight into medieval flatfish fisheries using various techniques, a critical reflection can pinpoint issues with the analysis, the shortcomings and limitations of the methods used, and summarise what still needs to be further investigated.

Using stable isotope analysis, it was hoped to detect the precise catch habitat of flatfish, which proved more difficult than anticipated. While carbon isotope analysis allows for a clear distinction between freshwater and marine environments, it does not provide a clear distinction between estuarine or near-coastal habitats and open marine habitats. For this reason, sulfur stable isotope analysis was applied. The data, however, showed again a restricted distinction between different habitats since estuarine and marine samples, as estimated by carbon isotope ratios, showed the same ranges for sulfur isotope ratios. As the southern North Sea is shallow and so heavily influenced by freshwater outflux, this could be one of the main reasons that there is little difference between these habitats. Unfortunately, this limited the understanding of changes in fisheries throughout the Medieval period by preventing distinction between (near-)coastal and open sea environments; these were grouped into the southern North Sea marine category. Sulfur isotope analysis did provide some additional information that would not have been detected by relying only on carbon and nitrogen isotope analysis. No major changes of flatfish isotope values were observed in relation to time for $\delta^{13}C$ or $\delta^{15}N$, but a slight trend in $\delta^{34}S$ is observed between the Early and Late Medieval periods, which could be linked to a more marine-oriented fishing practice across the southern North Sea. However, since flatfish fisheries remained a local endeavour, which was described by historical sources (e.g., Coenen, 1577), seen in modern day fisheries (e.g., Gibson *et al.*, 2015) and seen in the data here, sulfur isotope analysis might not be able to provide the resolution required to detect the subtler shifts in catch habitats in the southern North Sea region. Until there is a method to make a better distinction between the different habitats, using either stable isotope analysis or another technique, a more detailed insight into the changes in flatfish fisheries through time cannot be obtained.

Sulfur isotope analysis has not been applied in large quantities in previous archaeological fish studies (e.g., Nehlich *et al.*, 2011; Sayle *et al.*, 2013; Drucker *et al.*, 2016; Drucker *et al.*, 2018; although Nehlich *et al.*, 2013). With the accessibility to this kind of analysis increasing (e.g., Sayle *et al.*, 2019), it is expected that there will be an increase in the amount of such studies. In this study, it was found that using sulfur isotope analysis in tandem with carbon and nitrogen isotope analysis was very successful. By first analysing samples for carbon and nitrogen isotope and then selecting samples that matched quality criteria for carbon and nitrogen isotope analysis and that were of interest (e.g., looked estuarine based on carbon isotope ratio), a high success rate for sulfur isotope analysis was obtained with over 70% of samples meeting quality standards. This selection based on the first isotope analysis allowed for a reduction of cost.

The data from sulfur isotope analysis is, however, less straightforward to interpret compared to that of carbon and nitrogen isotope analysis. The sulfur isotope ratio is more influenced by the local bedrock environment, and not solely by the ecosystem (Privat *et al.*, 2007; Nehlich, 2015; Bataille *et al.*, 2021). This causes a clear differentiation between regions, as was seen in the results of this study, especially for the freshwater samples. This dependency on the local environment also results in the need to interpret sulfur data in a relative manner, and not based on absolute values. By comparing the data from this study to data published in similar studies (e.g., Nehlich *et al.*, 2013) and to isoscape maps (e.g., Bataille *et al.*, 2021), the data could be interpreted. It is therefore recommended to try to find good comparative material or to analyse samples with known origins as a means to relate the sulfur isotope data.

Comparative osteology and geometric morphometrics have their limitations as identification methods for archaeological flatfish, mostly due to a lack of morphological differentiation between taxa and to fragmentation. The limitations are discussed in more detail in the corresponding chapters. Although ZooMS also has its own limitations, as discussed in Chapter 5, it provided a breakthrough in analysing flatfish remains. As both ZooMS and stable isotope analysis rely on the same collagen extraction of the sample, they can easily be combined, reducing time and costs to perform the analysis. Unfortunately, using this combined approach, ZooMS cannot identify the species prior to stable isotope analysis, making it difficult to select and analyse specific species before starting the destructive analysis. This results in issues regarding analysis (see Chapter 6, section 6.4.5) and a potential need for more analyses to find enough samples of the species of interest, increasing the cost, time and number of samples needed for destructive analysis. As all flatfish species were of interest for this study, this was not a major issue, although the lack of samples of certain species (such as the less often recovered flatfish and to some extent flounder) occasionally made it difficult to make further interpretations. For this reason, osteology and, in case of well-preserved vertebrae, geometric morphometrics remain of critical value to identify and select samples as well as possible in order to reduce the amount of material required for destructive analysis and to be able to perform taxon-focused analyses.

Conclusion

This thesis has analysed archaeological flatfish at a level of detail never previously achieved. With new identification techniques more in-depth studies can be performed on these bizarre-looking fish, which will provide many more insights into the changes of fisheries throughout time. Of the three techniques (morphological, ZooMS and GMM), ZooMS is by far the most successful, providing reliable and objective species identifications (see research question 1). Using this technique, eighteen different species can be identified using eight peptide biomarkers, including all the main commercial species and those recovered from archaeological sites. Furthermore, this technique can be of use for other research as well, such as modern ecological studies and even food authentication. Osteology remains a vital part of archaeology, however, as the basis for zooarchaeological recording and to help with sample selection for further analysis. A thorough comparison of 34 skeletal elements and eleven species showed that several cranial elements are easy to use to distinguish species, while the others are limited in distinguishing species or difficult or impossible to use for identification purposes. Geometric morphometrics turned out to be poor at identifying archaeological flatfish vertebrae, but the technique shows promise for other applications.
These identification techniques, especially ZooMS, have proven to be invaluable to identify archaeological remains to species. A clear shift was detected across the whole southern North Sea area using selected samples from archaeological sites of interest, matching in time with the marine fish event horizon. This could indicate that people were fishing out more at sea as plaice is more commonly caught than flounder in open marine environments. Some individual sites showed different changes throughout the Medieval period, reflecting the local historic events and ecological circumstances.

The isotope dataset produced here is significant for being the first large-scale application of multi-isotope analysis on flatfish. For the first time stable isotope ratios could be confidently analysed for each flatfish species individually thanks to the newly improved identification techniques, especially ZooMS. This allowed the creation of species-specific timelines across the region (see research question 2). The generated dataset provided useful and novel information on changes in flatfish exploitation during a dynamic time for human society and the environment. Compared to the marine fish event horizon for cod and herring, trading and consuming marine flatfish in inland sites occurred much earlier than anticipated during the 7-8th centuries CE, especially in the sites known to be actively trading across the North Sea at that time (e.g., London and York). In the High Medieval period, a shift towards more open marine environments and fewer estuarine environments has been observed, especially for plaice, coinciding with a clear shift in flatfish species in some sites towards more plaice, as expected during the marine fish event horizon. The larger settlements especially seem to have focused more strongly on flatfish caught in open marine environments during the High Medieval period possibly because the demand for food was higher and opportunities for trade were more abundant in these settlements compared to the smaller inland and coastal settlements. The flatfish fishery as a whole, however, remained a rather local endeavour throughout the whole Medieval period in the North Sea.

The produced dataset can be of use for future studies as well, by combining it with results from analyses on other taxa, in other regions, or during other chronological periods. This study not only helped to clarify the history of flatfish fisheries and the species ecologies, which are relevant to modern day fisheries stock assessments, but also helped to shed light on human history and consumption behaviour through time in the face of socio-economic and climatic changes.

Some questions regarding flatfish fisheries in the Medieval period still remain unanswered. As the applied isotopic analysis did not resolve the precise catch habitat, inferring an exact catch location has also not been possible. This could tell us not only which precise population of flatfish was being targeted but also how the fishing industry was organised and might have changed through time or differed between regions. Two kinds of analyses can contribute to evaluating the catch location. Although it is unclear if there are genetically distinct populations of flatfish in the North Sea (see Hoarau *et al.,* 2002; Nielsen *et al.,* 2004; Ulrich *et al.,* 2017), some studies have found population structure within flatfish species in the North Sea area (see Hoarau *et al.,* 2004; Hemmer-Hansen *et al.,* 2007), which can help to trace the geographical origin of a fish. Carbon and nitrogen isotopes have been used in previous studies to infer specific catch location (e.g., Kato *et al.,* 2020; Kato *et al.,* 2021), but also strontium and oxygen isotopes could be of use to determine the geographic origin of flatfish in the North Sea area, although for the latter isotope analysis there are potential issues with finding material as the teeth of flatfish are not often recovered archaeologically. With these techniques it might be possible to determine how far from the coast and settlements fish were caught and to infer if and where they were being landed and processed prior to transport to a larger settlement. This could potentially also help to reveal if there has been any trade between regions in the North Sea for flatfish, as the isotope analysis revealed the presence of some potentially traded samples from more northern regions in Gent and York.

aDNA analysis can provide further information on anthropogenic influences on the flatfish populations caused by exploitation. By comparing modern-day stock genomes with those of archaeological flatfish the success of management of the modern-day flatfish populations can be assessed (e.g., Oosting *et al.,* 2019; Andrews *et al.,* 2021). Furthermore, as flatfish can be found in environments that can be heavily affected by industries and human settlements, their abundance and health might have been impacted through time, which can be detected with pollution analyses. This can either be done by looking at the zooarchaeological abundances of species sensitive or tolerant to pollution to detect environmental changes (e.g., Van Neer *et al.,* 2009), or by detecting the presence of heavy metals, such as mercury, zinc and lead, in fish remains (e.g., Wang *et al.,* 2019; Alvarez-Fernandez *et al.,* 2020; Biton-Porsmoguer *et al.,* 2021).

Little is known concerning the fish exploitation from the earliest part of the Medieval period, immediately after the disintegration of the Roman Empire in western Europe, due to a small number of sites and fish remains recovered around the North Sea area (e.g., Van Neer & Ervynck, 2007; Reynolds, 2015). As coastal exploitation of flatfish appears to already have been happening during the 7-8th century, the true origins of marine fish consumption might be found during the period between the 4-7th centuries, or even earlier during the Roman period. Some studies already discuss some evidence of inland trading from well before the High Medieval period (e.g., Van Neer & Ervynck, 2007; Reynolds, 2015). A similar multi-technique approach, as performed in this study, on fish material from these earlier periods could help to pinpoint the exact moment in time when people started consuming and trading marine fish around the North Sea and why this might have happened.

Exactly the reason for switching to large-scale marine fish consumption is still unclear. For the increase in Gadidae and Clupeidae at the start of the High Medieval period several explanations have been put forward as factors that might have influenced the economic and culinary choices people made (see Barrett *et al.,* 2004a,b; Barrett, 2016). However, these widespread changes, such as the increased influence of Christianity, urbanisation, growing populations, the Scandinavian diaspora, the expansion of trade routes, climate change, freshwater body pollution, etc., cannot be used to explain the early onset of marine fishing as uncovered here. Other factors must have been at play that resulted in the inland trade of marine fish. Further archaeological, environmental and historical document analyses could be able to uncover the reason for importing and eating marine flatfish, once the timing of the onset is determined.

The question also remains unanswered if flatfish were the only species to be traded inland, or if other coastal species were brought inland as well during the Early Medieval period? There is some evidence in the zooarchaeological record that Clupeidae were regularly consumed inland on both sides of the North Sea during that time (Barrett *et al.,* 2004a,b; Van Neer & Ervynck, 2007; Reynolds, 2015). One Clupeid sample from the Early Medieval period in York was found to show a marine signal (Müldner & Richards, 2007). Although Clupeidae are mostly living in marine environments, some species can be found in estuaries, brackish water and freshwater habitats as well.

Historical sources from the 16th century state that flatfish captured in Belgium and the Netherlands were being dried and brought to cities even further inland in Germany (Coenen, 1577). It is unclear at the moment if during the Early Medieval period marine flatfish were already being brought so far inland, because sites located so far inland and less accessible via rivers were not included in this study. Furthermore, rural areas were also not included in this analysis due to issues of access to rural sites with substantial numbers of fish. Future research could focus on analysing these geographically more distant settlements and rural settlements as well to see when long-distance trade over land and a general marine fish consumption commenced during the Medieval period.

Similar studies to this one on the medieval North Sea would also be valuable in other regions and time periods as well. The northern North Sea as well as the Baltic Sea remain understudied, and previous research has shown that marine fish consumption was happening in this area during the Early Medieval period (e.g., Barrett *et al.,* 2004a,b; Barrett & Richards, 2004). Other species of flatfish can be found in the northern North Sea besides those typical for the southern part. Were these more favoured, or are plaice and flounder the dominant species in the northern part as well? Did the shift towards marine fish consumption and trade occur at the same time as in the southern North Sea, or did it occur earlier?

The Mediterranean Sea could also be of interest to analyse historic flatfish exploitation. Flatfish are recovered from zooarchaeological reports in this area, but not in the same quantities as in the North Sea and not of all taxa. Many different species occur in this area, especially Soleidae, but this family seems to be underrepresented in the zooarchaeological material (e.g., Mylona, 2003; Van Neer *et al.,* 2004; Morales-Muñiz & Roselló-Izquierdo, 2008; Robsinson & Rowan, 2015; Çakirlar *et al.,* 2016; Zohar & Artzy, 2019; and many others). In order to investigate the flatfish exploitation in the Mediterranean, additional ZooMS markers might need to be developed to identify all the Mediterranean species, prior to a general zooarchaeological review of this area.

After the Medieval period, fisheries became even larger-scale endeavours with Gadidae fisheries expanding to the West-Atlantic (e.g., Orton *et al.,* 2014; Holm *et al.,* 2021). In this region, other species of flatfish occur as well. Were these ever dried or salted and brought back to Europe for consumption? As historical sources did not uncover any large-scale evidence for this, ZooMS, with the development of new markers for the West-Atlantic species, might be able to resolve this question.

Even with the number of studies focusing on archaeological fish remains and historical fish exploitation increasing each year, there are still many questions left unanswered regarding the whole phenomenon of fishing, ranging from which species were caught where and how, to how humans used the fish and why, and which impacts humans might have had on fish populations. Future research, applying newly developed or improved scientific methodologies, will be able to answer many, but perhaps not all, of these questions.

- *So long and thanks for all the fish* -

Douglas Adams

Appendix A – Chapter 2. Archaeological assemblages

Table A1. NISP of each of the selected families of fish species per time period and site.

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
Coppergate	**2**	**10**	**61**		**85**	**8**	**116**	**7**		**6**	**295**	
Anguillidae			2		2		2	1			7	2.37
Clupeidae		1	2				3				6	2.03
Cyprinidae		4	8		4		2				18	6.10
Esocidae		1	17		10	2	4				34	11.53
Gadidae			9		30	4	23			2	68	23.05
Pleuronectidae	2	4	23		35	2	77	4			147	49.83
Scophthalmidae					1		5			1	7	2.37
Soleidae										2	2	0.68
flatfish					3			2		1	6	2.03
Blue Bridge Lane		**11**				**30**	**187**	**401**		**516**	**1145**	
Anguillidae							44	23		206	273	23.84
Clupeidae							102	288		302	692	60.44
Cyprinidae							2	16		4	22	1.92
Esocidae		1				4	3				8	0.70
Gadidae						0	29	69		2	100	8.73
Pleuronectidae		9				24	4	4		2	43	3.76
Scophthalmidae						2	1				3	0.26
Soleidae												
flatfish		1					2	1			4	0.35

Table A1 continued

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
CAO96	**65**			**10**	**99**		**26**		**6**		**206**	
Anguillidae	3				1		5				9	4.37
Clupeidae	4			1	8		6		1		20	9.71
Cyprinidae												
Esocidae					2						2	0.97
Gadidae	41			5	81		4				131	63.59
Pleuronectidae	13			4	7		11		5		40	19.42
Scophthalmidae												
Soleidae												
flatfish	4										4	1.94
GSJ06				**410**							**410**	
Anguillidae				29							29	7.07
Clupeidae				145							145	35.37
Cyprinidae				16							16	3.90
Esocidae				4							4	0.98
Gadidae				134							134	32.68
Pleuronectidae				74							74	18.05
Scophthalmidae				1							1	0.24
Soleidae				2							2	0.49
flatfish				5							5	1.22

Table A1 continued

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
SGA89		**116**									**116**	
Anguillidae		12									12	10.34
Clupeidae		1									1	0.86
Cyprinidae		12									12	10.34
Esocidae												
Gadidae		3									3	2.59
Pleuronectidae		87									87	75.00
Scophthalmidae												
Soleidae												
flatfish		1									1	0.86
SOT89		**42**									**42**	
Anguillidae		7									7	16.67
Clupeidae		5									5	11.90
Cyprinidae		5									5	11.90
Esocidae												
Gadidae		1									1	2.38
Pleuronectidae		24									24	57.14
Scophthalmidae												
Soleidae												
flatfish												

Table A1 continued

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
Tradescent Lane					**1018**		**67**				**1085**	
Anguillidae					77		5				82	7.56
Clupeidae					321		28				349	32.17
Cyprinidae					13		2				15	1.38
Esocidae												0.00
Gadidae					237		23				260	23.96
Pleuronectidae					323		9				332	30.60
Scophthalmidae					2						2	0.18
Soleidae					23						23	2.12
flatfish					22						22	2.03
Barreau Saint-George					**861**						**861**	
Anguillidae												
Clupeidae												
Cyprinidae					1						1	0.12
Esocidae												
Gadidae					34						34	3.95
Pleuronectidae					800						800	92.92
Scophthalmidae					2						2	0.23
Soleidae												
flatfish					24						24	2.79

Table A1 continued

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
Hof ter Hille			**24**	**231**	**15**					**185**	**455**	
Anguillidae			1	14						5	20	4.40
Clupeidae				4						6	10	2.20
Cyprinidae				1						1	2	0.44
Esocidae				5						1	6	1.32
Gadidae			3	18	2					16	39	8.57
Pleuronectidae			17	172	13					138	340	74.73
Scophthalmidae				5							5	1.10
Soleidae				2							2	0.44
flatfish			3	10						18	31	6.81
Zwarte Laag			**313**		**962**					**15**	**1290**	
Anguillidae			92		186						278	21.55
Clupeidae			110		217						327	25.35
Cyprinidae			52		101						153	11.86
Esocidae			5		4						9	0.70
Gadidae			5		163					7	175	13.57
Pleuronectidae			49		241					6	296	22.95
Scophthalmidae					5					1	6	0.47
Soleidae					1						1	0.08
flatfish					44					1	45	3.49

Table A1 continued

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
Gat In De Markt			**4**		**44**		**553**			**23**	**624**	
Anguillidae			1				11				12	1.92
Clupeidae							3				3	0.48
Cyprinidae					4		7			1	12	1.92
Esocidae							9				9	1.44
Gadidae					28		203			17	248	39.74
Pleuronectidae			1		11		302			5	319	51.12
Scophthalmidae							2				2	0.32
Soleidae							1				1	0.16
flatfish			2		1		15				18	2.88
Plantage		**985**	**2**							**1**	**988**	
Anguillidae		86									86	8.70
Clupeidae		2									2	0.20
Cyprinidae		387	1							1	389	39.37
Esocidae		39									39	3.95
Gadidae		25									25	2.53
Pleuronectidae		436	1								437	44.23
Scophthalmidae												
Soleidae		2									2	0.20
flatfish		8									8	0.81

Table A1 continued

Site/Taxon	Roman	Early Medieval 1	Early Medieval 2	Early/High Medieval	High Medieval	High/Late Medieval	Late Medieval	Late/Post Medieval	Post-Medieval	unknown	Total	Percent (%)
Kastanjelaan		**227**									**227**	
Anguillidae		112									112	49.34
Clupeidae		5									5	2.20
Cyprinidae		60									60	26.43
Esocidae												
Gadidae		1									1	0.44
Pleuronectidae		49									49	21.59
Scophthalmidae												
Soleidae												
flatfish												
Grand Total	**67**	**1391**	**404**	**651**	**3084**	**38**	**951**	**408**	**6**	**746**	**7746**	

Table A2. Element group per site and chronological period.

Period	**Border**	**Cranial**	**Other**	**Postcranial**	**Total**
Coppergate					
Roman		1		1	**2**
Early Medieval 1				4	**4**
Early Medieval 2	1	6		16	**23**
High Medieval	7	12		20	**39**
High/Late Medieval				2	**2**
Late Medieval	5	22		55	**82**
Late/Post Medieval	1	2		3	**6**
unknown		1		3	**4**
Blue Bridge Lane					
Early Medieval 1				10	**10**
High/Late Medieval	3	5		18	**26**
Late Medieval		2		5	**7**
Late/Post Medieval		1		4	**5**
unknown		1		1	**2**
CAO96					
Roman	1			16	**17**
Early/High Medieval	2			2	**4**
High Medieval		3		4	**7**
Late Medieval	1	3		7	**11**
Postmedieval	1	2		2	**5**
GSJ06					
Early/High Medieval	1	10		71	**82**
SGA89					
Early Medieval 1		3		85	**88**
SOT89					
Early Medieval 1	1	2		21	**24**
Tradescent Lane					
High Medieval	40	111		219	**370**
Late Medieval		3		6	**9**
Barreau Saint-George					
High Medieval	164	181	9	472	**826**

Table A2 continued

Period	Border	Cranial	Other	Postcranial	Total
Hof ter Hille					
Early Medieval 2	17	38		107	**162**
Early/High Medieval	3	8		36	**47**
High Medieval	1	1		11	**13**
unknown	26	27	1	102	**156**
Zwarte Laag					
Early Medieval 2	11	16		22	**49**
High Medieval	29	74	47	141	**291**
unknown		3		5	**8**
Gat in de Markt					
Early Medieval 2		2		1	**3**
High Medieval	1	6		5	**12**
Late Medieval	21	124	4	171	**320**
unknown				5	**5**
Plantage					
Early Medieval 1	18	59		369	**446**
Early Medieval 2				1	**1**
Kastanjelaan					
Early Medieval 1	7	29		13	**49**
Total	**362**	**758**	**61**	**2036**	**3217**

Table A3. Size classes per site and chronological period.

Period	**5-20 cm SL**	**20-30 cm SL**	**20-40 cm SL**	**30-40 cm SL**	**40-60 cm SL**	**unknown**	**Total**
Coppergate							
Roman	2						**2**
Early Medieval 1	3	1					**4**
Early Medieval 2	19	1			3		**23**
High Medieval	5	12		10	11	1	**39**
High/Late Medieval	1			1			**2**
Late Medieval	18	13		18	17	16	**82**
Late/Post Medieval	1	3				2	**6**
unknown		1			1	2	**4**
Blue Bridge Lane							
Early Medieval 1	6	2		1	1		**10**
High/Late Medieval	3	11		7	5		**26**
Late Medieval	3	1	2	1			**7**
Late/Post Medieval		3		1		1	**5**
unknown	1		1				**2**
CAO96							
Roman	5	12					**17**
Early/High Medieval	1	3					**4**
High Medieval	1	2		4			**7**
Late Medieval		2		9			**11**
Postmedieval	2	2	1				**5**
GSJ06							
Early/High Medieval	16	49	1	15		1	**82**
SGA89							
Early Medieval 1	2	42		7	2	35	**88**
SOT89							
Early Medieval 1	1	6			1	16	**24**
Tradescent Lane							
High Medieval	117	148	36	48	10	11	**370**
Late Medieval	3		1	2	3		**9**
Barreau Saint-George							
High Medieval	614	92	14	24	16	66	**826**

Table A3 continued

Period	5-20 cm SL	20-30 cm SL	20-40 cm SL	30-40 cm SL	40-60 cm SL	unknown	Total
Hof ter Hille							
Early Medieval 2	38	73	5	30	11	5	**162**
Early/High Medieval	11	15		17	1	3	**47**
High Medieval	1	2		8	2		**13**
unknown	44	57	8	38	4	5	**156**
Zwarte Laag							
Early Medieval 2	13	15		10	10	1	**49**
High Medieval	43	44		79	68	57	**291**
unknown				5	2	1	**8**
Gat in de Markt							
Early Medieval 2					2	1	**3**
High Medieval				3	9		**12**
Late Medieval	101	125	15	51	10	18	**320**
unknown		4		1			**5**
Plantage							
Early Medieval 1	225	143	18	47	9	4	**446**
Early Medieval 2		1					**1**
unknown							
Kastanjelaan							
Early Medieval 1	26	20		3			**49**
Total	**1326**	**905**	**102**	**440**	**198**	**246**	**3217**

Table A4. Size classes per element group and site.

Element group	5-20 cm SL	20-30 cm SL	20-40 cm SL	30-40 cm SL	40-60 cm SL	unknown	Total
Coppergate							
border	3	3		7	1		**14**
cranial	16	8		6	12	2	**44**
postcranial	30	20		16	19	19	**104**
Blue Bridge Lane							
border	2			1			**3**
cranial		2	3	3	1		**9**
other							
postcranial	11	15		6	5	1	**38**
CAO96							
border		4		1			**5**
cranial		3	1	4			**8**
other							
postcranial	9	14		8			**31**
GSJ06							
border				1			**1**
cranial	1	4		4		1	**10**
other							
postcranial	15	45	1	10			**71**
SGA89							
border							
cranial				3			**3**
other							
postcranial	2	42		4	2	35	**85**
SOT89							
border		1					**1**
cranial		1				1	**2**
postcranial	1	4			1	15	**21**
Tradescent Lane							
border	15	13	3	3	3	3	**40**
cranial	27	51	10	11	8	7	**114**
other							**9**
postcranial	78	84	24	36	2	1	**225**

Table A4 continued

Element group	5-20 cm SL	20-30 cm SL	20-40 cm SL	30-40 cm SL	40-60 cm SL	unknown	Total
Barreau Saint-George							
border	132	17		4	2	9	**164**
cranial	118	24		10	3	26	**181**
other	2					7	**9**
postcranial	362	51	14	10	11	24	**472**
Hof ter Hille							
border	11	16	2	13	4	1	**47**
cranial	9	20	9	21	8	7	**74**
other						1	**1**
postcranial	74	111	2	59	6	4	**256**
Zwarte Laag							
border	6	9		10	14	1	**40**
cranial	11	16		35	26	5	**93**
other						47	**47**
postcranial	39	34		49	40	6	**168**
Gat in de Markt							
border	6	6		7	3		**22**
cranial	16	61	11	25	6	13	**132**
other						4	**4**
postcranial	79	62	4	23	12	2	**182**
Plantage							
border	5	7	1	4	1		**18**
cranial	14	25	7	8	1	4	**59**
other							
postcranial	206	112	10	35	7		**370**
Kastanjelaan							
border	4	2		1			**7**
cranial	16	11		2			**29**
other							
postcranial	6	7					**13**
Total	**1326**	**905**	**102**	**440**	**198**	**246**	**3217**

Table A5. Size classes per element group and chronological period.

Element group	5-20 cm SL	20-30 cm SL	20-40 cm SL	30-40 cm SL	40-60 cm SL	unknown	Total
Roman							
border		1					**1**
cranial	1						**1**
postcranial	6	11					**17**
Early Medieval 1							
border	9	10	1	5	1		**26**
cranial	30	37	7	13	1	5	**93**
other							
postcranial	224	167	10	40	11	50	**502**
Early Medieval 2							
border	10	8	1	6	4		**29**
cranial	12	13	3	16	15	3	**62**
other							
postcranial	48	69	1	18	7	4	**147**
Early/High Medieval							
border		2		3		1	**6**
cranial	3	7		5		3	**18**
other							
postcranial	25	58	1	24	1		**109**
High Medieval							
border	150	35	3	21	20	13	**242**
cranial	156	91	10	59	35	37	**388**
other	2					54	**56**
postcranial	473	174	37	96	61	31	**872**
High/Late Medieval							
border	2			1			**3**
cranial		2		2	1		**5**
postcranial	2	9		5	4		**20**
Late Medieval							
border	7	7		10	3		**27**
cranial	23	66	13	28	10	14	**154**
other						4	**4**
postcranial	95	68	5	43	17	16	**244**

Table A5 continued

Element group	5-20 cm SL	20-30 cm SL	20-40 cm SL	30-40 cm SL	40-60 cm SL	unknown	Total
Late/Post Medieval							
border		1					**1**
cranial		2		1			**3**
other							
postcranial	1	3				3	**7**
Postmedieval							
border		1					**1**
cranial		1	1				**2**
postcranial	2						**2**
Unknown							
border	6	13	1	6			**26**
cranial	3	7	7	8	3	4	**32**
other						1	**1**
postcranial	36	42	1	30	4	3	**116**
Total	**1326**	**905**	**102**	**440**	**198**	**246**	**3217**

Appendix B – Chapter 3. Comparative osteology study of North Sea flatfishes

Part B1: Sample list and expanded figures

Table B1. Overview of the specimens used in this study. (HL: head length of the fish, measured from the tip of the upper lip to the posterior margin of the operculum)

Species	**SL (cm)**	**TL (cm)**	**Collection**	**Collection number**	**Illustration**	**Remarks**
Pleuronectidae						
Glyptocephalus cynoglossus	22	27	YZL	942		
Glyptocephalus cynoglossus	25	30	RBINS	91 017 P55		
Glyptocephalus cynoglossus	25	37	YZL	902		
Glyptocephalus cynoglossus	32	36	RBINS	91 017 P56	hyomandibula, posttemporal	
Glyptocephalus cynoglossus	34.7	41.6	RBINS	DCB359	all other	
Glyptocephalus cynoglossus	41	49	YZL	901		
Glyptocephalus cynoglossus	25?	?	YZL	1954		
Hippoglossoides platessoides	10	12	YZL	1380		
Hippoglossoides platessoides	12	14	YZL	1379		
Hippoglossoides platessoides	12	15.5	YZL	1051		
Hippoglossoides platessoides	14.6	17.8	RBINS	DCB847		
Hippoglossoides platessoides	18	21	YZL	943		
Hippoglossoides platessoides	18	21.5	YZL	1052		
Hippoglossoides platessoides	18	22	YZL	914		
Hippoglossoides platessoides	20	23	YZL	913		
Hippoglossoides platessoides	20	23.5	YZL	1093		
Hippoglossoides platessoides	20	24.6	RBINS	DCB849		
Hippoglossoides platessoides	20	25	YZL	912		
Hippoglossoides platessoides	21.6	26	RBINS	DCB850		
Hippoglossoides platessoides	27.1	31.6	RBINS	DCB851	basioccipital, hyomandibula, posttemporal	
Hippoglossoides platessoides	30.6	36.9	RBINS	DCB767		
Hippoglossoides platessoides	32	38.5	RBINS	91 017 P142	all other	
Hippoglossus hippoglossus	35	41	YZL	1376		
Hippoglossus hippoglossus	35.2	41.4	RBINS	DCB844	all other	
Hippoglossus hippoglossus	38	42.5	YZL	895		
Hippoglossus hippoglossus	40	44.5	YZL	893		
Hippoglossus hippoglossus	42	46.5	YZL	894		
Hippoglossus hippoglossus	47	52	YZL	1614		
Hippoglossus hippoglossus	48.4	55.5	RBINS	91 017 P02	basioccipital	
Hippoglossus hippoglossus	50	56	RBINS	91 017 P78		
Hippoglossus hippoglossus	50	59.2	RBINS	DCB845		
Hippoglossus hippoglossus	60.7	?	RBINS	A4 022 P05		
Hippoglossus hippoglossus	68	80	RBINS	A4 001 P111		
Hippoglossus hippoglossus	240	270	RBINS	23423		
Table B1 continued						
Hippoglossus hippoglossus	?	?	YZL	1304		20 cm HL
Hippoglossus hippoglossus	?	?	YZL	YZL1970		
Limanda limanda	11	13	YZL	1138		
Limanda limanda	12	17	YZL	907		
Limanda limanda	13	20	YZL	909		
Limanda limanda	16.2	19.5	RBINS	A2 028 P41		

Limanda limanda	18	21.6	RBINS	A2 028 P65		
Limanda limanda	20	23	YZL	910		
Limanda limanda	24	27	YZL	911		
Limanda limanda	26	29.6	RBINS	A4 001 P60		
Limanda limanda	27.3	32	RBINS	A4 002 P61		
Limanda limanda	30	?	RBINS	23876		
Limanda limanda	31.5	?	RBINS	A4 022 P02	all	
Limanda limanda	?	22	YZL	852		
Limanda limanda	?	22	YZL	853		
Microstomus kitt	15	18	RBINS	91 017 P80		
Microstomus kitt	20	23	YZL	1096		
Microstomus kitt	20	23.5	YZL	1044		
Microstomus kitt	21.8	26.3	RBINS	A4 001 P91		
Microstomus kitt	22	26	YZL	1097		
Microstomus kitt	23.5	29	RBINS	A4 001 P88		
Microstomus kitt	26.6	32.1	RBINS	A3 001 P62		
Microstomus kitt	28	32	YZL	876		
Microstomus kitt	29	34.8	RBINS	23881		
Microstomus kitt	29.1	?	RBINS	23880	all other	
Microstomus kitt	30	34	YZL	1178		
Microstomus kitt	31.2	37.6	RBINS	DCB383	os anale, atlas, first caudal vertebra, cleithrum, posttemporal	
Microstomus kitt	31.3	37	RBINS	23882	articular	
Microstomus kitt	32	37	YZL	930		
Microstomus kitt	36.55	36.55	YZL	YZL1963		
Platichthys flesus	16	18.5	YZL	1140		left-eyed
Platichthys flesus	20.6	24.7	RBINS	A2 038 P22		right-eyed
Platichthys flesus	26	31	YZL	1151		right-eyed
Platichthys flesus	28.5	34.3	RBINS	A4 001 P125		left-eyed
Platichthys flesus	29	?	RBINS	23801		right-eyed
Platichthys flesus	29.6	?	RBINS	23802	all other	right-eyed

Table B1 continued

Species	**SL (cm)**	**TL (cm)**	**Collection**	**Collection number**	**Illustration**	**Remarks**
Platichthys flesus	30	36	YZL	1152		left-eyed
Platichthys flesus	30.2	?	RBINS	23803	all	left-eyed
Platichthys flesus	32.0	39.0	RBINS	91 017 P48	maxilla, hyomandibula, vomer, basioccipital, preoperculum, metapterygium, parasphenoid, upper hypohyal, first caudal vertebra	left-eyed
Platichthys flesus	32.9	39.3	RBINS	A4 001 P36	maxilla, hyomandibula, vomer, basioccipital, preoperculum, metapterygium, upper hypohyal, first caudal vertebra	right-eyed
Platichthys flesus	33.7	39.4	RBINS	A4 001 P127		left-eyed
Platichthys flesus	35.5	41.7	RBINS	A4 001 P69		left-eyed
Platichthys flesus	?	?	YZL	YZL1973		left-eyed
Platichthys flesus	?	?	YZL	YZL1974		right-eyed
Pleuronectes platessa	15	18	YZL	944		
Pleuronectes platessa	15	18	YZL	948		
Pleuronectes platessa	18.5	22.5	RBINS	91 017 P79		
Pleuronectes platessa	21	24	YZL	950/110		

Pleuronectes platessa	21	26	YZL	947		
Pleuronectes platessa	22	26	YZL	953		
Pleuronectes platessa	29	35	RBINS	96 087 P10		
Pleuronectes platessa	30	?	RBINS	96 087 P05	all	
Pleuronectes platessa	35	43	RBINS	97 003 P336		
Pleuronectes platessa	36.8	36.8	YZL	YZL1966		
Pleuronectes platessa	37	37	YZL	YZL1967		
Pleuronectes platessa	37.4	37.4	YZL	YZL1968		
Pleuronectes platessa	41.8	51	RBINS	A2 057 P27		
Pleuronectes platessa	44	53.5	YZL	1544		
Pleuronectes platessa	49	?	RBINS	97 003 P266		
Pleuronectes platessa	56	65	RBINS	97 003 P81		
Pleuronectes platessa	?	?	YZL	1711		
Scophthalmidae						
Lepidorhombus whiffiagonis	25	28.5	YZL	998		
Lepidorhombus whiffiagonis	25.8	31.2	RBINS	91 017 P14		
Lepidorhombus whiffiagonis	26	31	RBINS	91 017 P26		
Lepidorhombus whiffiagonis	28.5	32.2	RBINS	A4 001 P94		
Lepidorhombus whiffiagonis	29	35	YZL	1404		
Lepidorhombus whiffiagonis	30.1	36.3	RBINS	DCB517	all	
Lepidorhombus whiffiagonis	32	38	RBINS	91 017 P59		
Lepidorhombus whiffiagonis	35	40	YZL	1133		

Table B1 continued

Species	**SL (cm)**	**TL (cm)**	**Collection**	**Collection number**	**Illustration**	**Remarks**
Scophthalmus maximus	18.2	22.9	RBINS	A2 019 P47		
Scophthalmus maximus	25	30.5	RBINS	91 017 P98		
Scophthalmus maximus	27	33	YZL	892		
Scophthalmus maximus	29.2	34.4	RBINS	23600		
Scophthalmus maximus	30	36	YZL	900		
Scophthalmus maximus	32	32	YZL	YZL1964		
Scophthalmus maximus	32.9	39.5	RBINS	A2 023 P02	all	
Scophthalmus maximus	35	41	YZL	1203		
Scophthalmus maximus	36	36	YZL	YZL1962		
Scophthalmus maximus	37.2	45	RBINS	A2 052 P12		
Scophthalmus maximus	41	41	YZL	YZL1965		
Scophthalmus maximus	41	50	YZL	1238		
Scophthalmus maximus	45	53	YZL	1236		
Scophthalmus maximus	47.3	57.8	RBINS	A2 057 P48		
Scophthalmus maximus	48.5	48.5	YZL	YZL1969		
Scophthalmus rhombus	14.5	17.5	RBINS	91 017 P99		
Scophthalmus rhombus	21	23.5	YZL	1145		
Scophthalmus rhombus	24	27	YZL	1205		
Scophthalmus rhombus	26	31	YZL	1153		
Scophthalmus rhombus	27	?	RBINS	24823		
Scophthalmus rhombus	29	?	RBINS	24813	first caudal vertebra, cleithrum	
Scophthalmus rhombus	30	35	RBINS	A3 004 P16	all other	
Scophthalmus rhombus	37.7	45.1	RBINS	23664		

Scophthalmus rhombus	38	44	YZL	1172		
Scophthalmus rhombus	38.14	38.14	YZL	YZL1961		
Scophthalmus rhombus	45	55	RBINS	23771		
Scophthalmus rhombus	47.22	47.22	YZL	YZL1960		
Scophthalmus rhombus	50	?	RBINS	A2 023 P01		
Scophthalmus rhombus	54.5	63	RBINS	24902		
Soleidae						
Solea solea	9.5	10.7	RBINS	A2 041 P13		
Solea solea	12.2	14.6	RBINS	24539		
Solea solea	15	17	RBINS	88 023 P413		
Solea solea	18	20	YZL	1094		
Solea solea	18	24	YZL	903		
Solea solea	18.8	20.4	RBINS	A2 019 P48		

Table B1 continued

Species	**SL (cm)**	**TL (cm)**	**Collection**	**Collection number**	**Illustration**	**Remarks**
Solea solea	22	23.5	YZL	1092		
Solea solea	22.5	25.7	RBINS	91 017 P11		
Solea solea	25.8	?	RBINS	A2 036 P28		
Solea solea	27.39	27.39	YZL	YZL1972		
Solea solea	28.9	28.9	YZL	YZL1971		
Solea solea	29	31.5	RBINS	91 017 P114	all	
Solea solea	29	34.5	RBINS	91 017 P90		
Solea solea	33	36	YZL	1202		
Solea solea	34	38.5	RBINS	91 017 P33		
Solea solea	37	42	YZL	1286		
Solea solea	40.4	45.4	RBINS	A4 001 P133		
Solea solea	56	64	RBINS	24857		

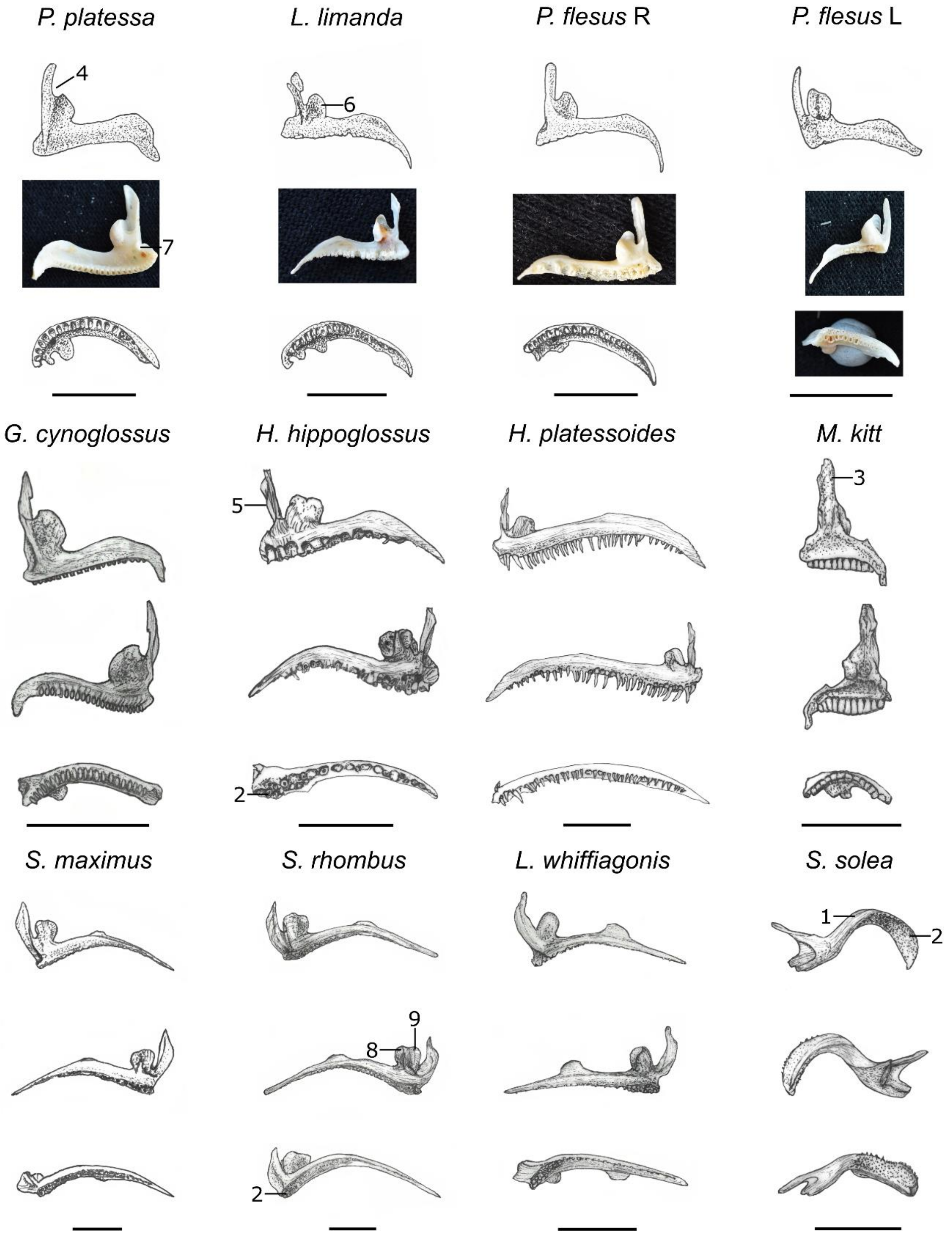


Figure B1. Lateral (top), medial (middle), and ventral (bottom) view of the left premaxilla of all twelve species. The black bar under each species represents 1 cm.

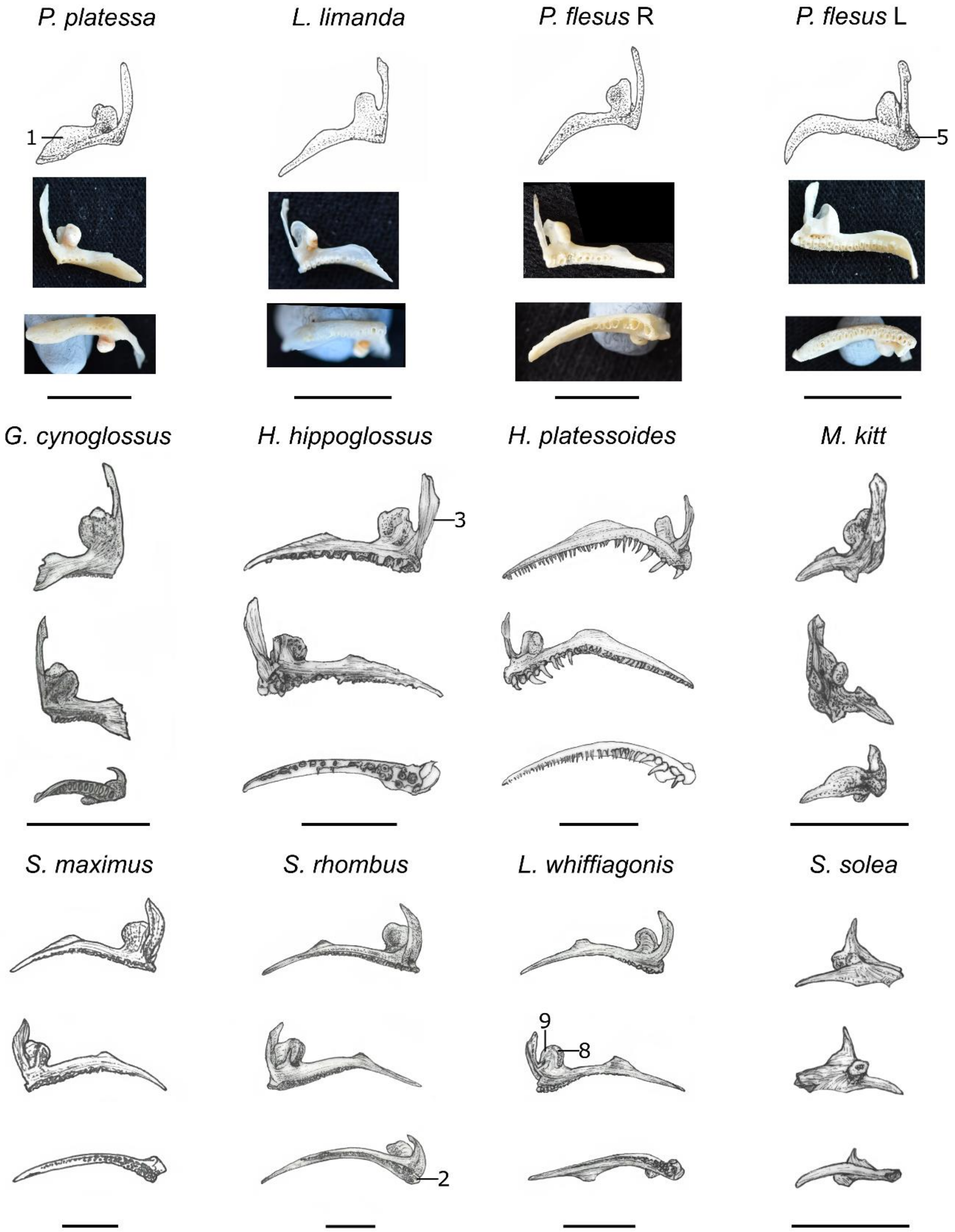


Figure B2. Lateral (top), medial (middle), and ventral (bottom) view of the right premaxilla of all twelve species. The black bar under each species represents 1 cm.

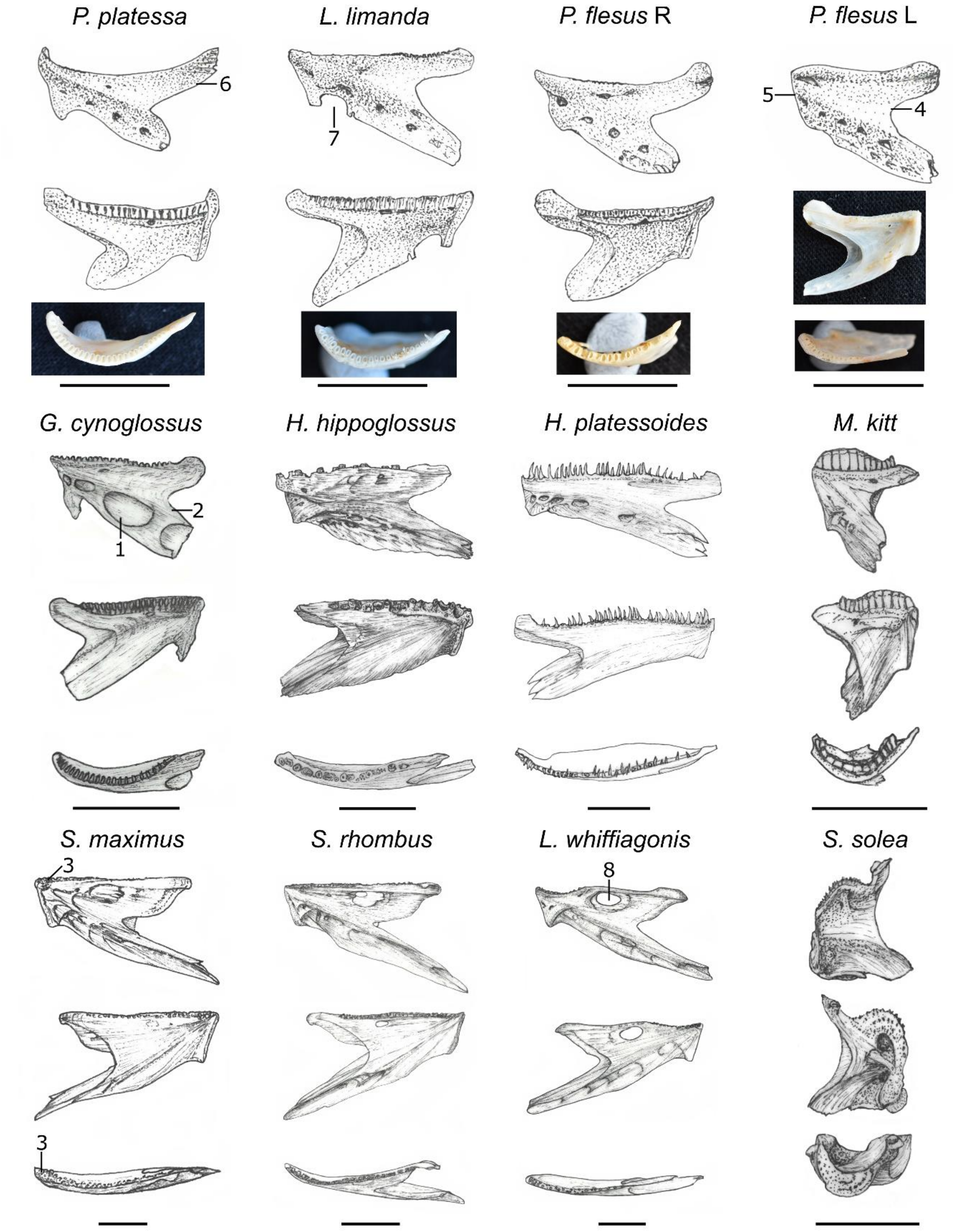


Figure B3. Lateral (top), medial (middle), and dorsal (bottom) view of the left dentary of all twelve species. The black bar under each species represents 1 cm.

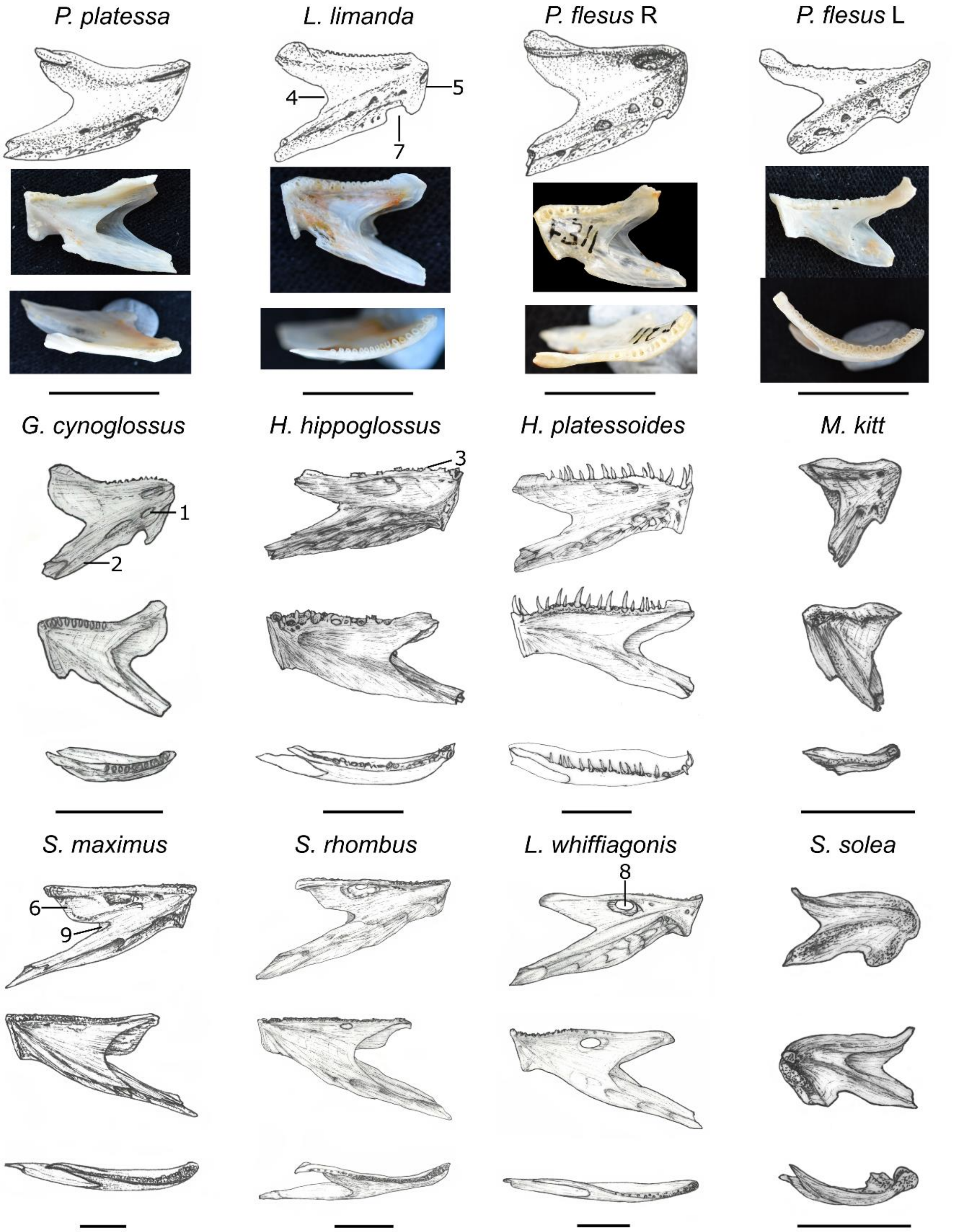


Figure B4. Lateral (top), medial (middle), and dorsal (bottom) view of the right dentary of all twelve species. The black bar under each species represents 1 cm.

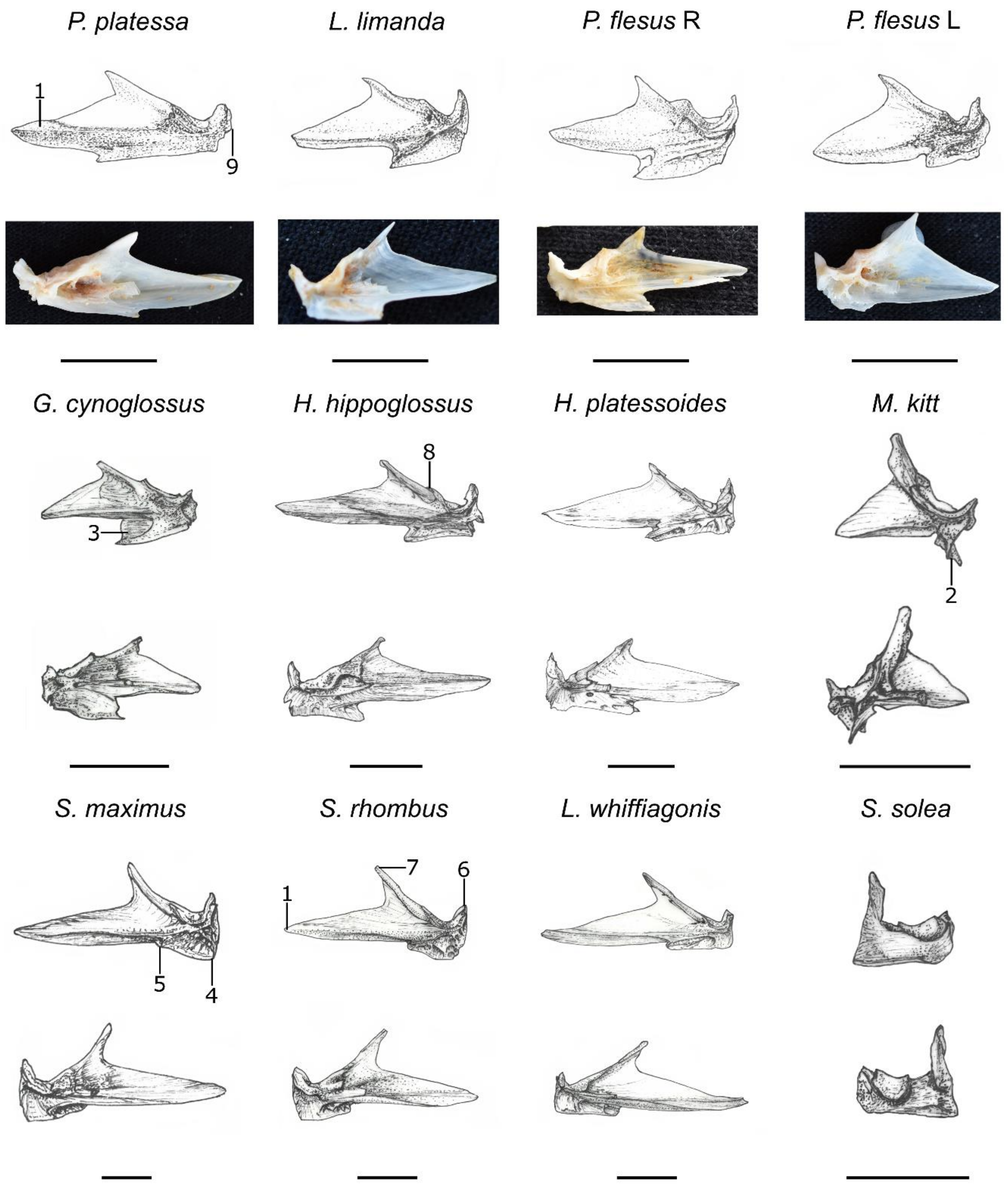


Figure B5. Lateral (top) and medial (bottom) view of the left articular of all twelve species. The black bar under each species represents 1 cm.

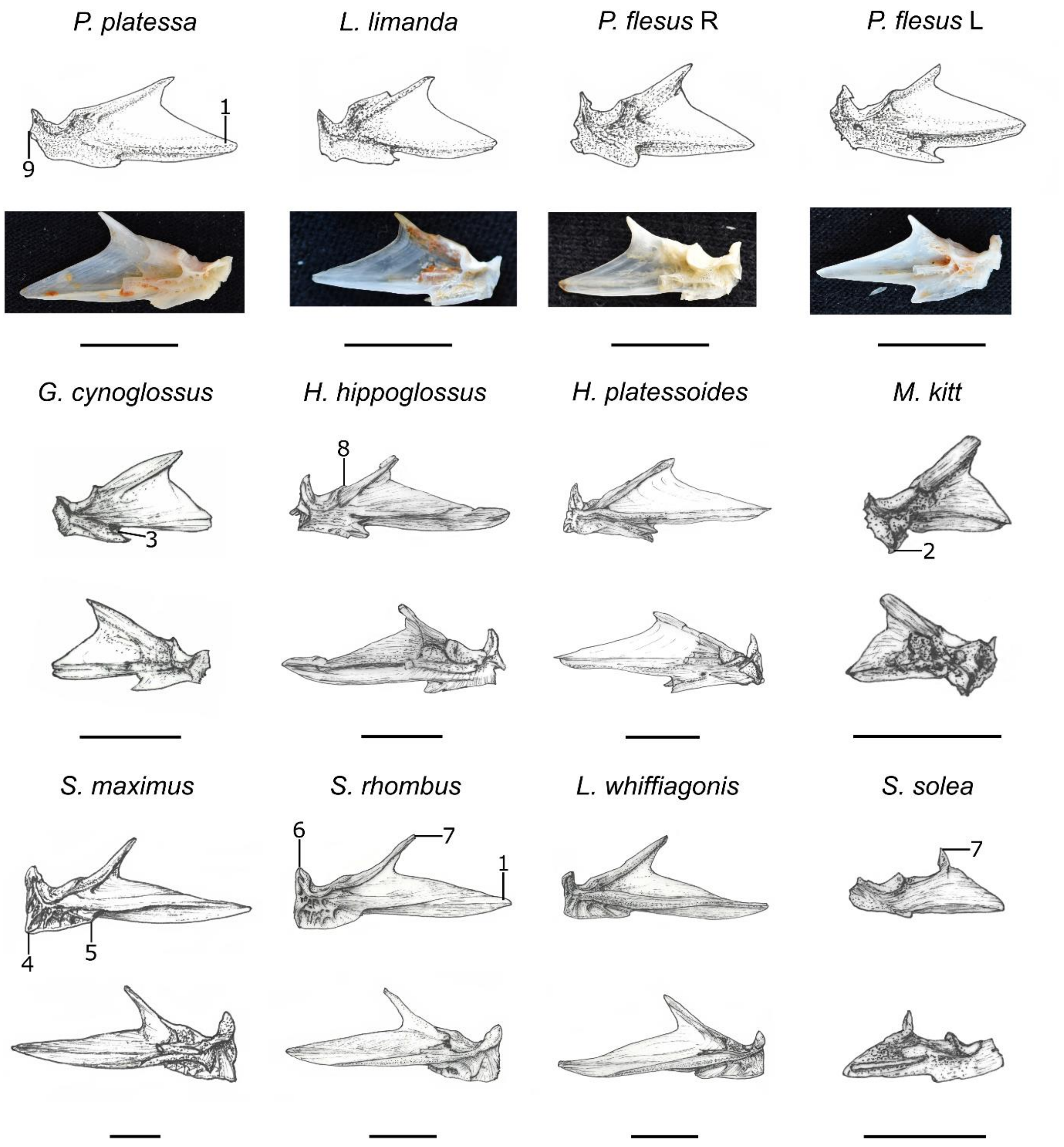
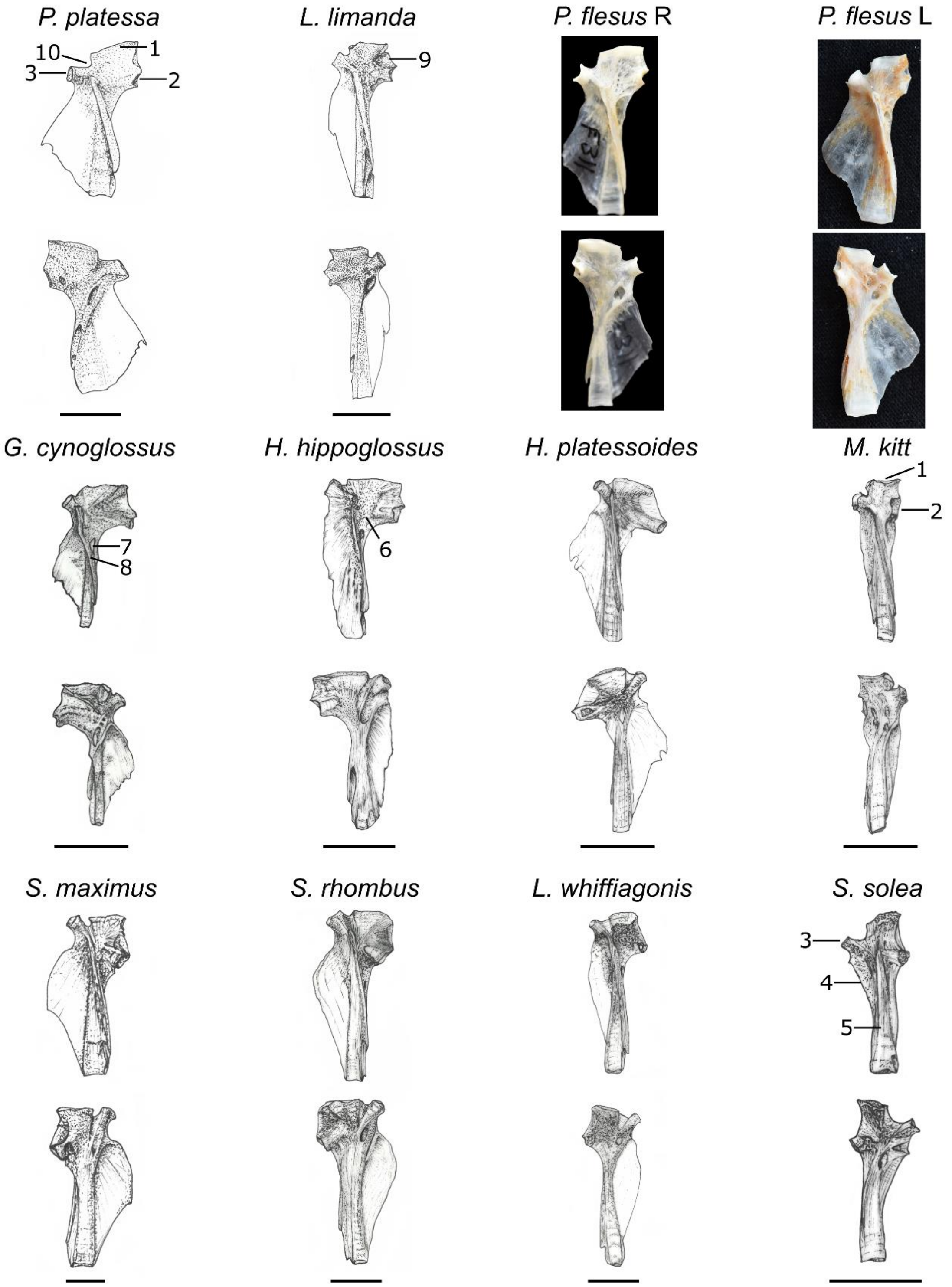


Figure B6. Lateral (top) and medial (bottom) view of the right articular of all twelve species. The black bar under each species represents 1 cm.


P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure B7. Lateral (top) and medial (bottom) view of the left hyomandibula of all twelve species. The black bar under each species represents 1 cm.

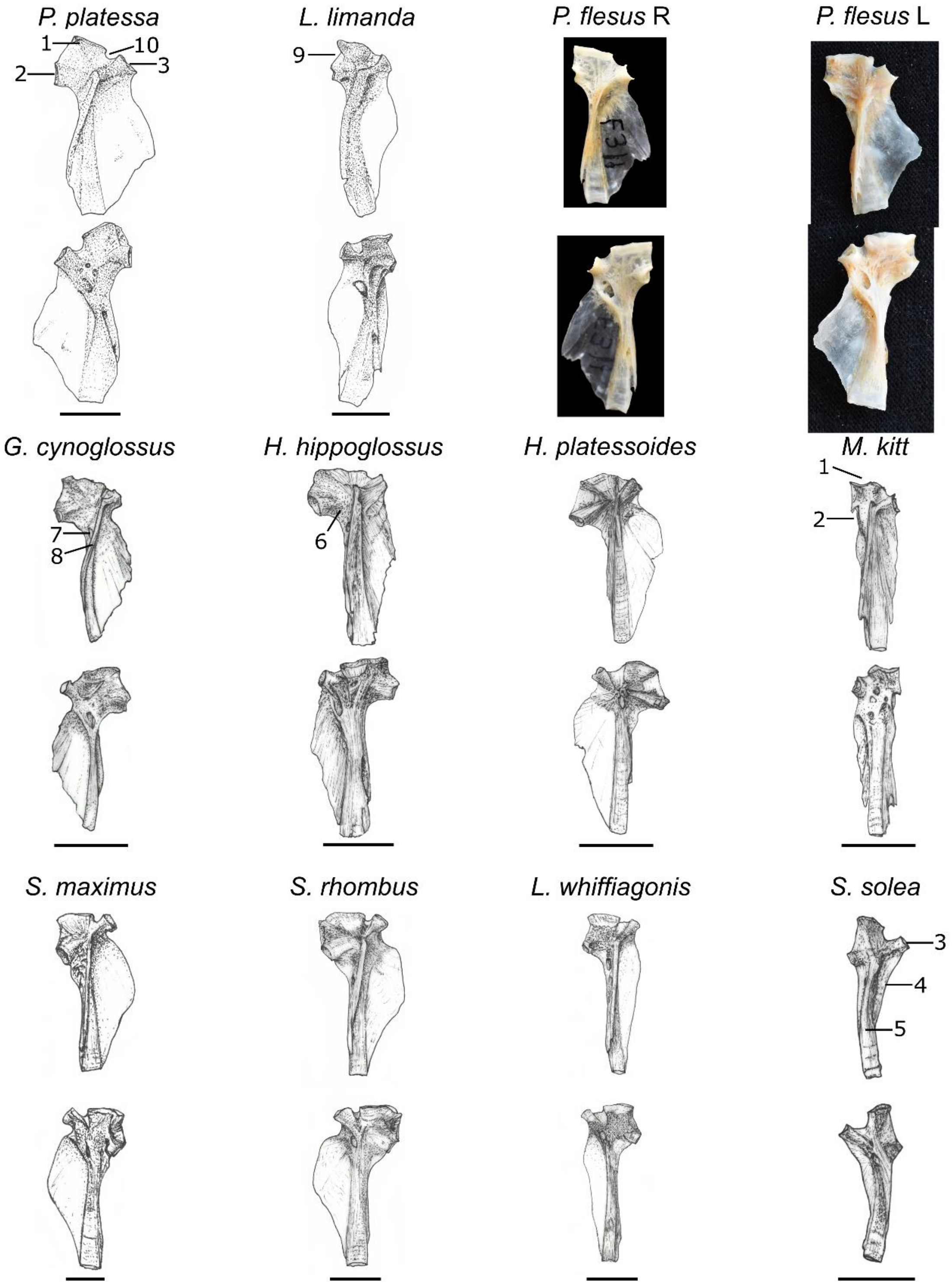


Figure B8. Lateral (top) and medial (bottom) view of the right hyomandibula of all twelve species. The black bar under each species represents 1 cm.

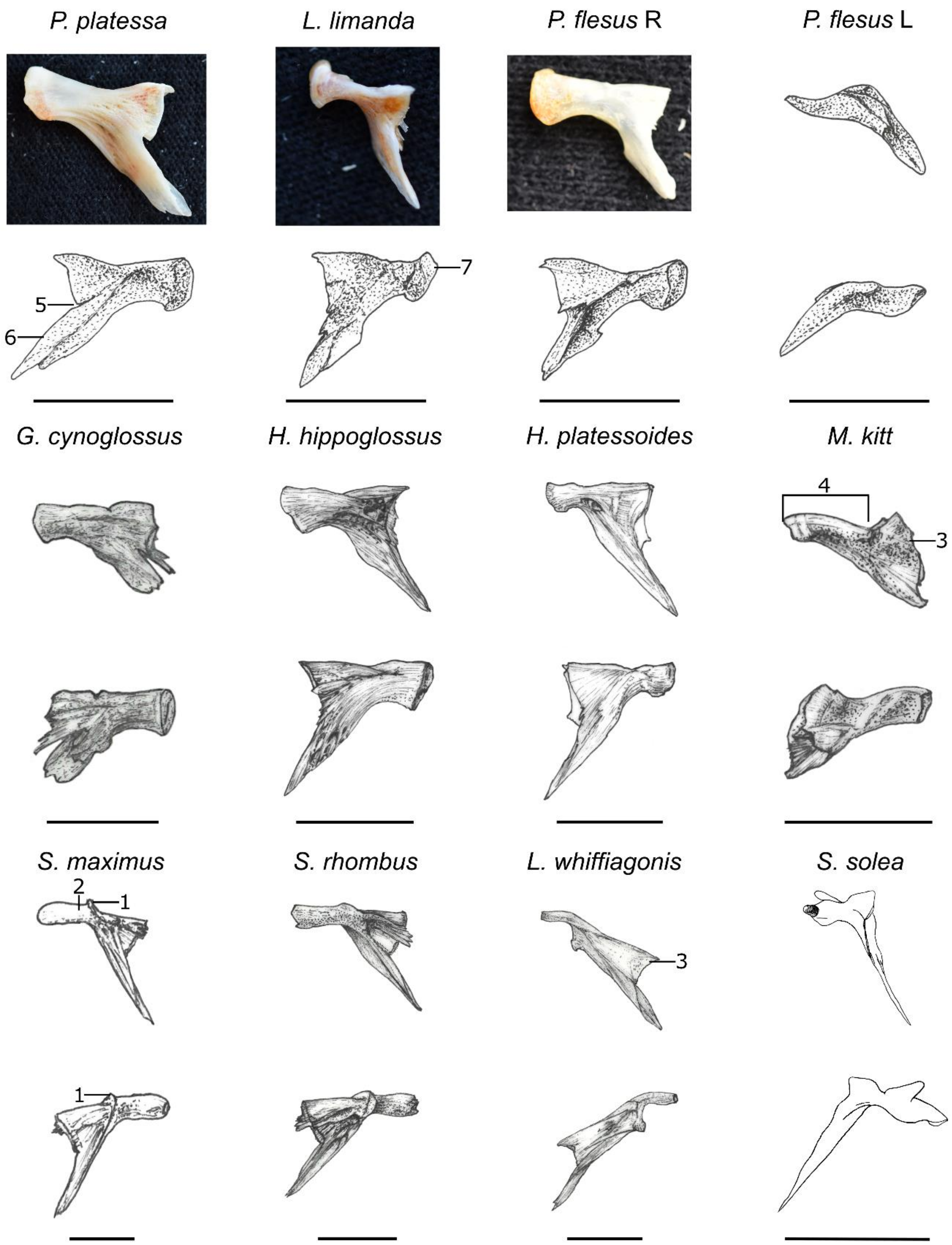


Figure B9. Lateral (top) and medial (bottom) view of the left palatine of all twelve species. The black bar under each species represents 1 cm.

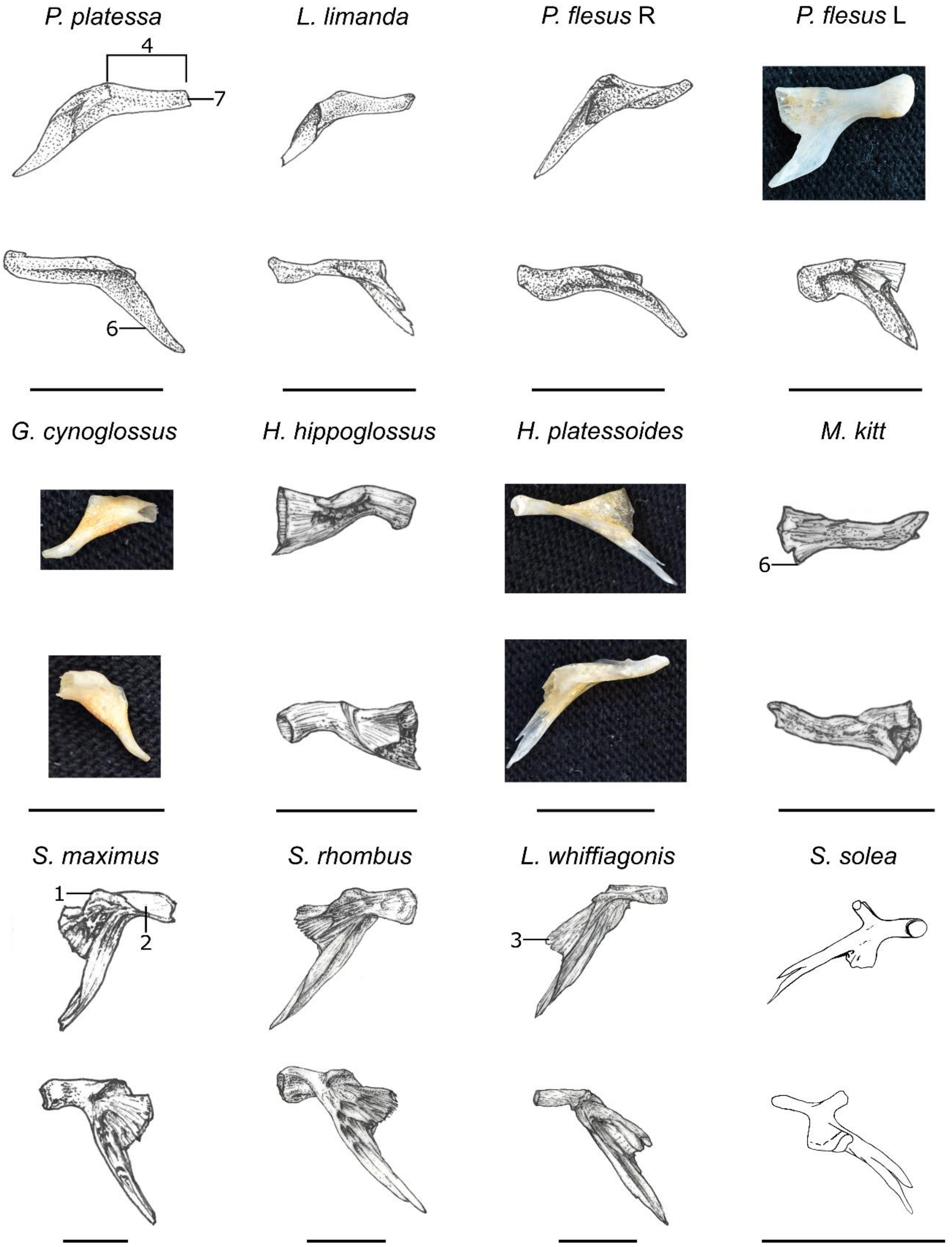


Figure B10. Lateral (top) and medial (bottom) view of the right palatine of all twelve species. The black bar under each species represents 1 cm.

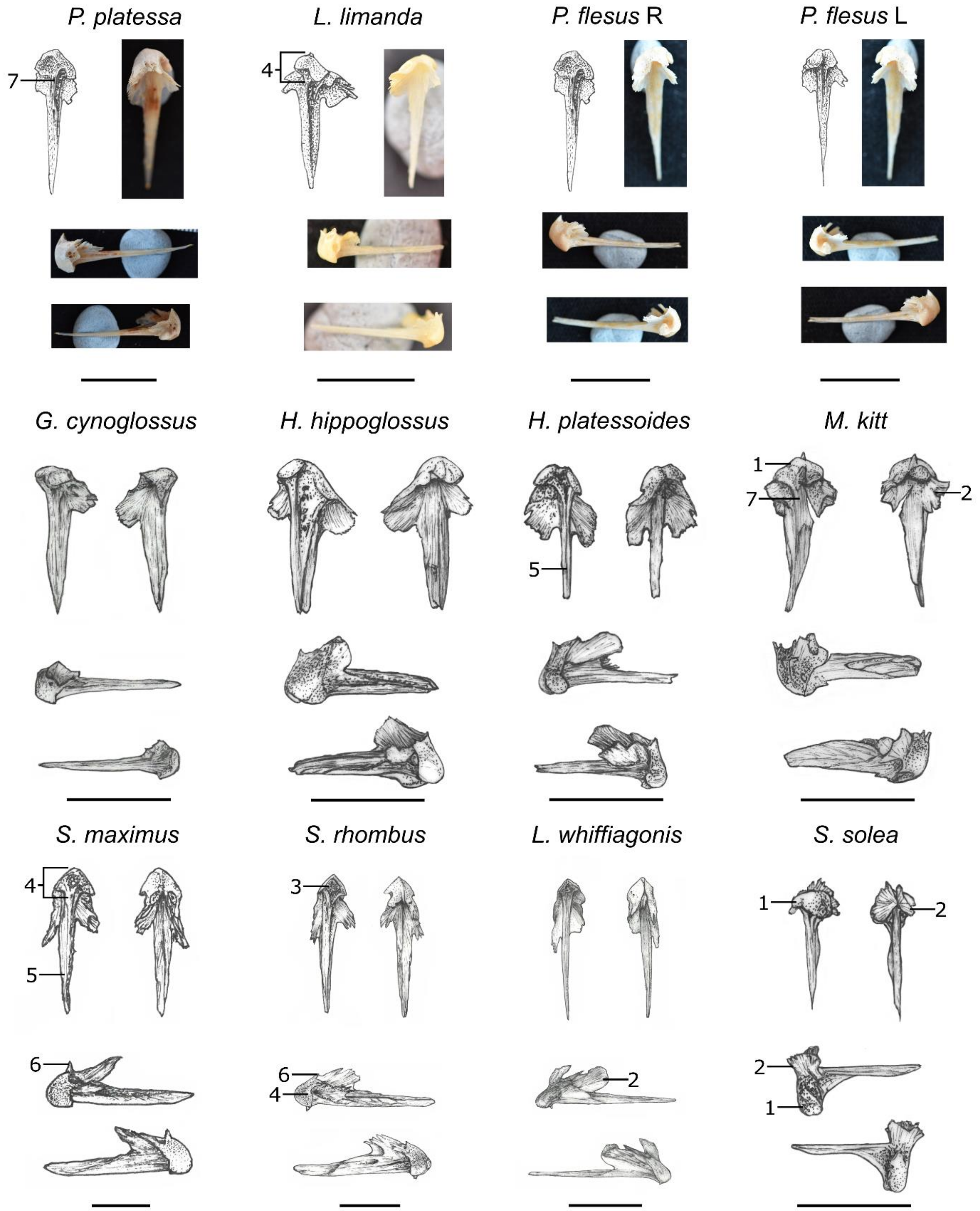


Figure B11. Ventral (top left), dorsal (top right), sinistral lateral (middle), and dextral lateral (bottom) view of the vomer of all twelve species. The black bar under each species represents 1 cm.

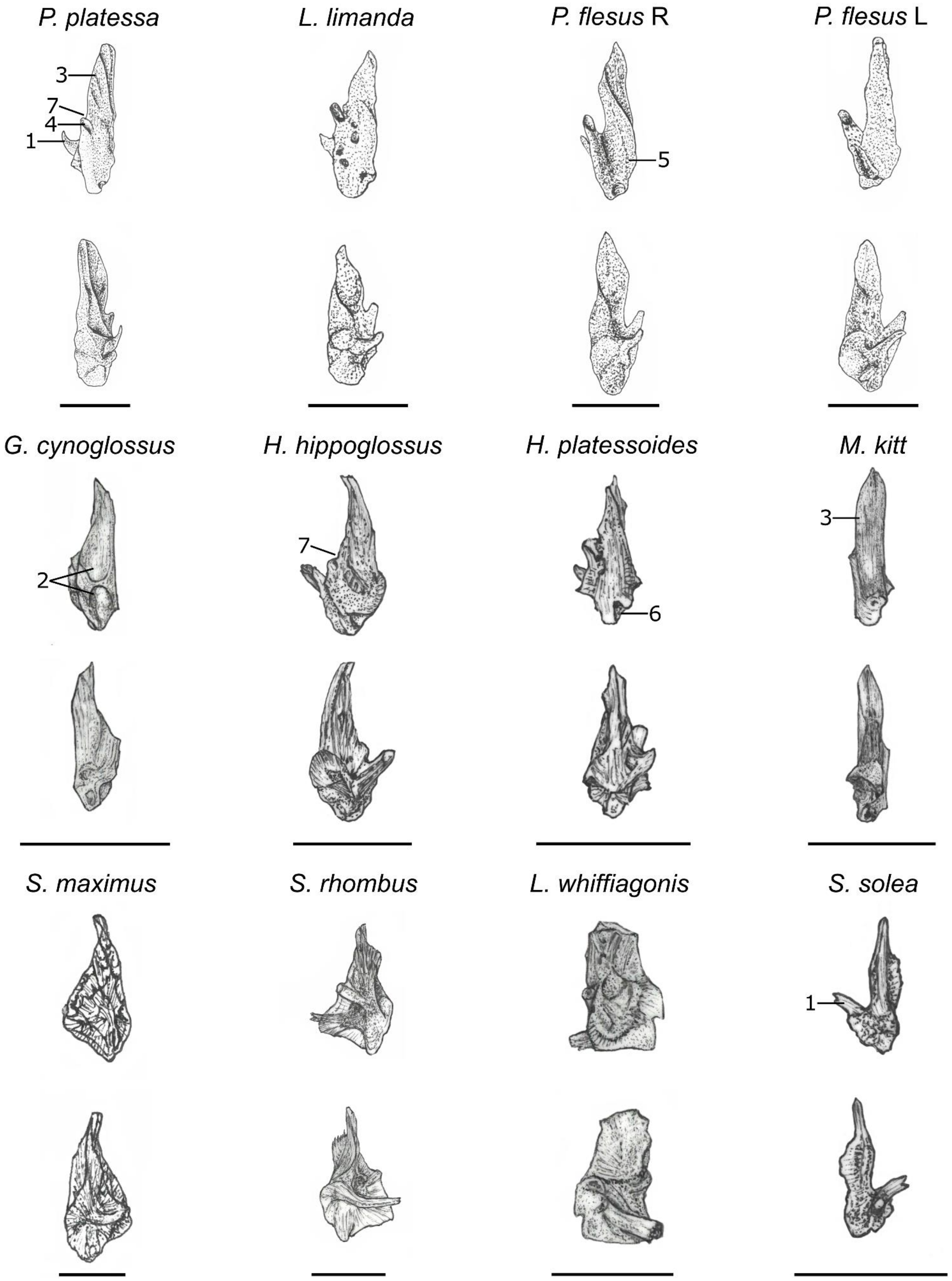
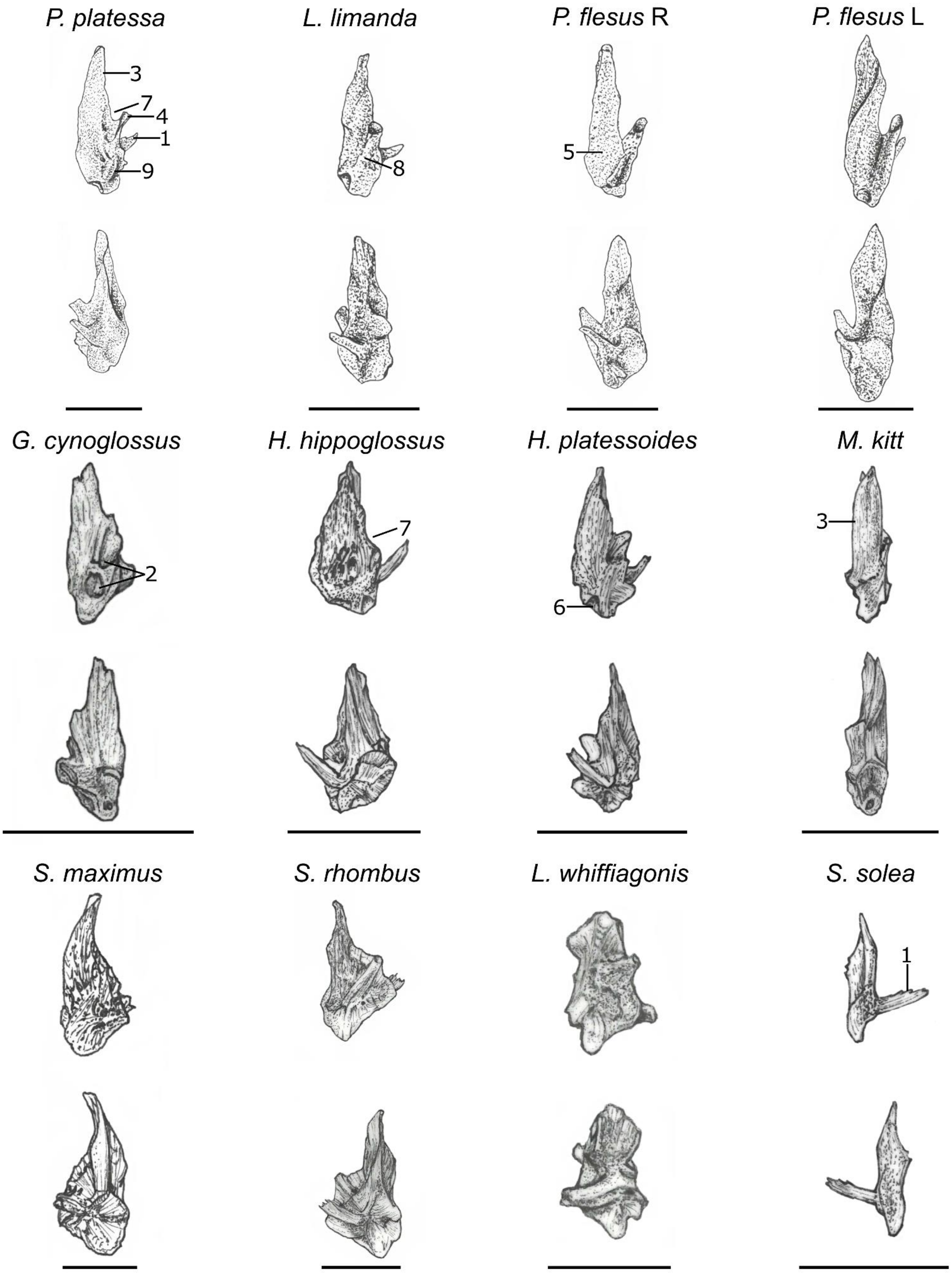


Figure B12. Lateral (top) and medial (bottom) view of the left posttemporal of all twelve species. The black bar under each species represents 1 cm.


P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure B13. Lateral (top) and medial (bottom) view of the right posttemporal of all twelve species. The black bar under each species represents 1 cm.

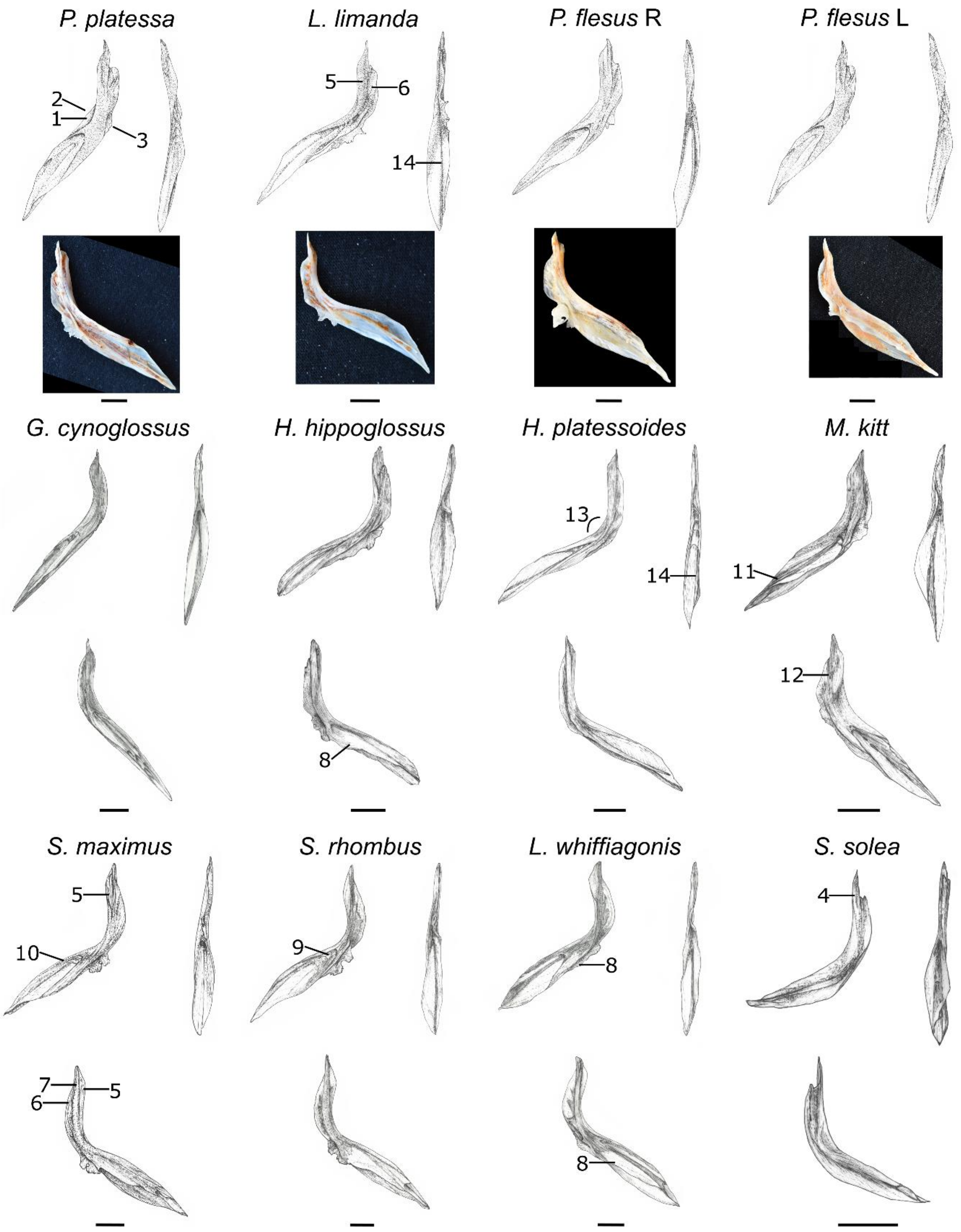


Figure B14. Lateral (left), medial (bottom) and ventral (right) view of the left cleithrum of all twelve species. The black bar under each species represents 1 cm.

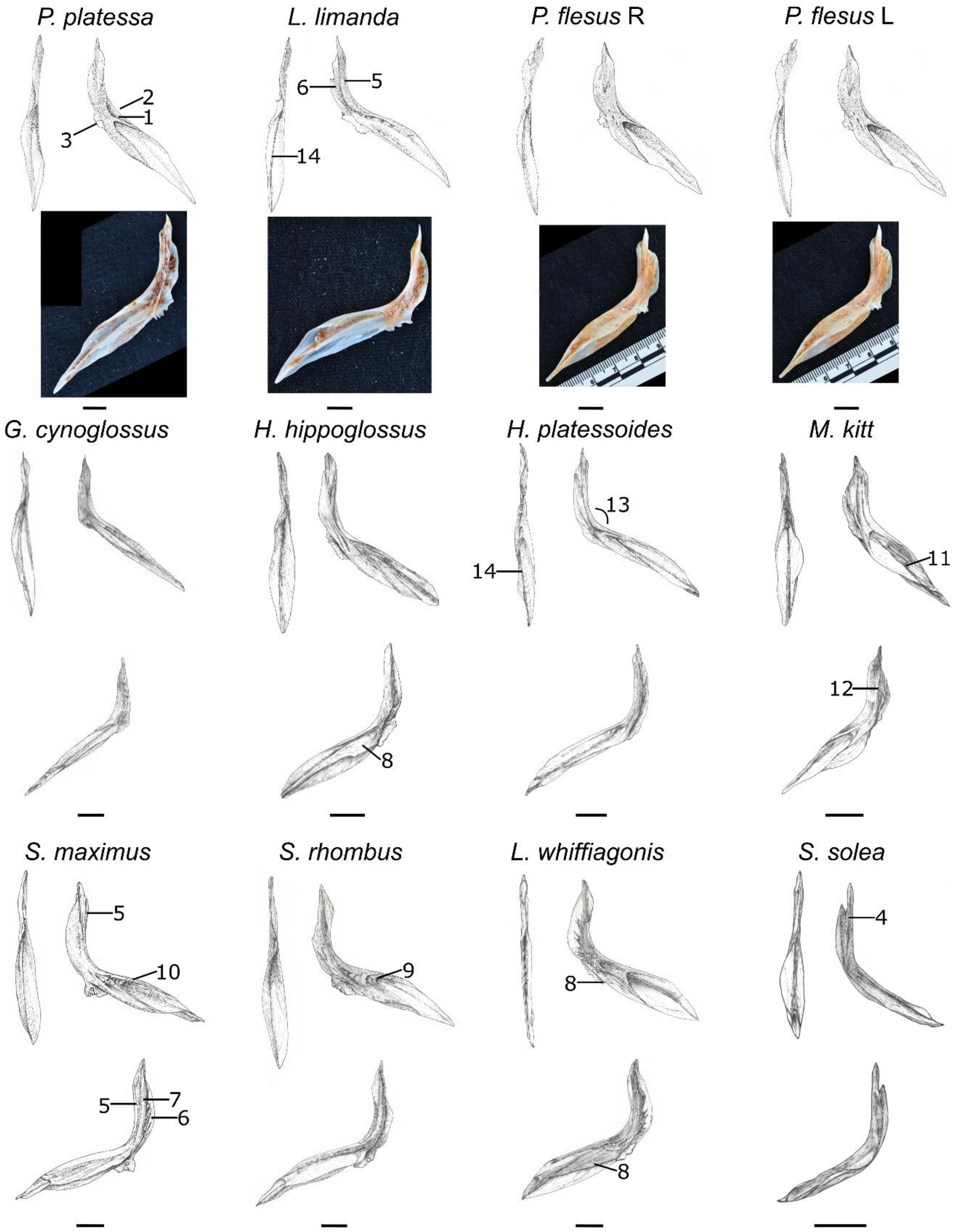


Figure B15. Lateral (left), medial (bottom) and ventral (right) view of the right cleithrum of all twelve species. The black bar under each species represents 1 cm.

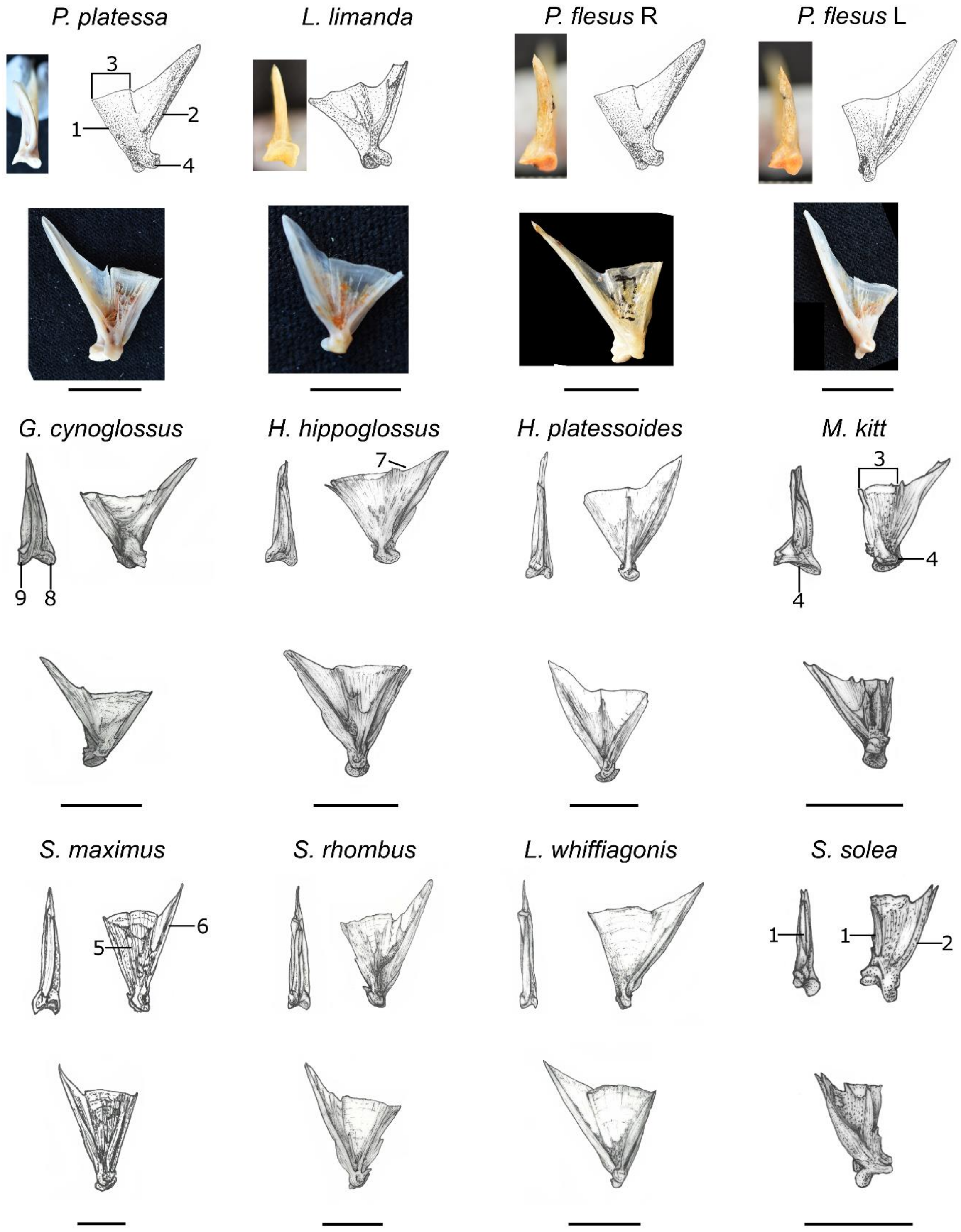
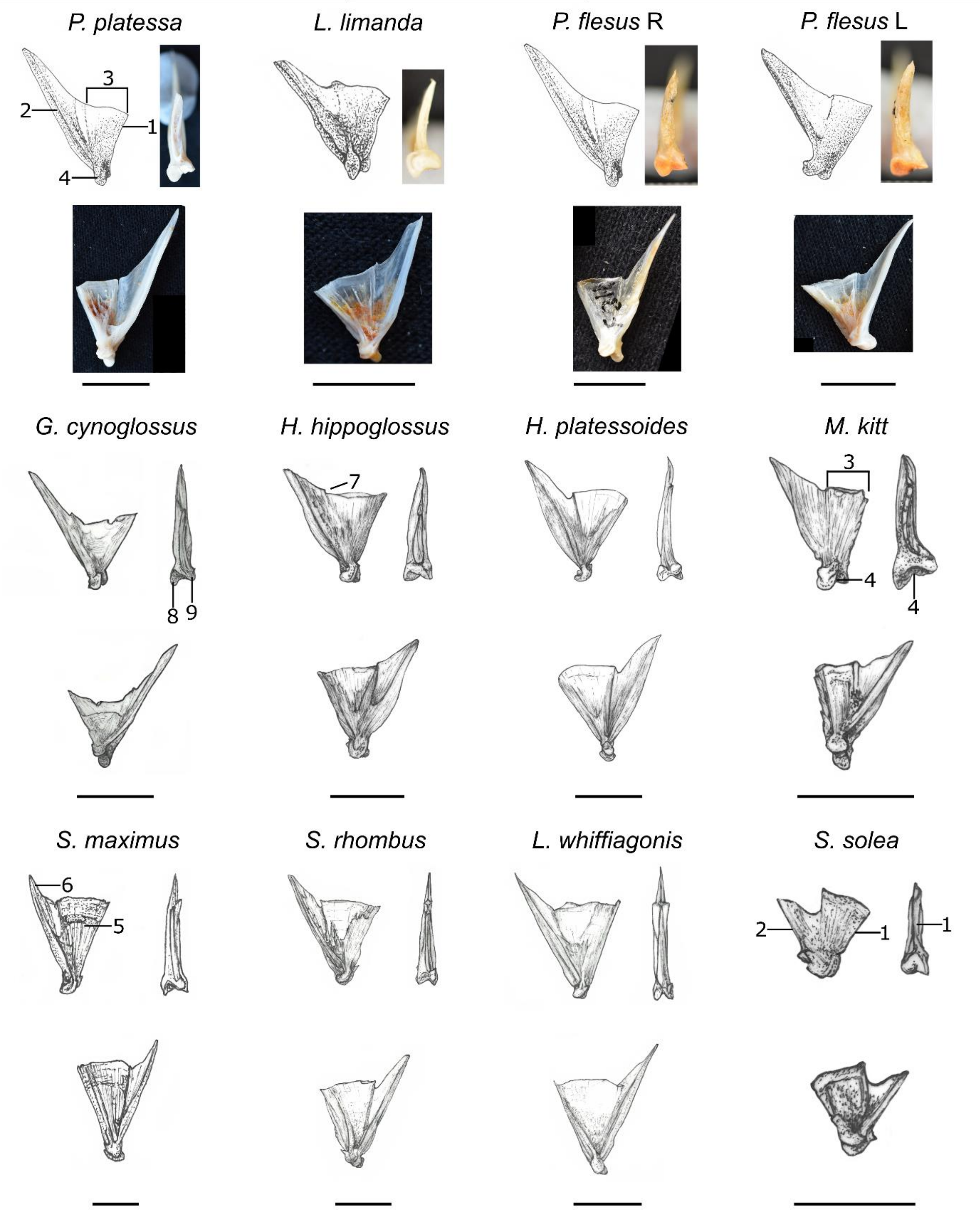


Figure B16. Lateral (right), medial (bottom) and anterior (left) view of the left quadrate of all twelve species. The black bar under each species represents 1 cm.



P. platessa *L. limanda* *P. flesus* R *P. flesus* L

G. cynoglossus *H. hippoglossus* *H. platessoides* *M. kitt*

S. maximus *S. rhombus* *L. whiffiagonis* *S. solea*

Figure B17. Lateral (left), medial (bottom) and anterior (right) view of the right quadrate of all twelve species. The black bar under each species represents 1 cm.

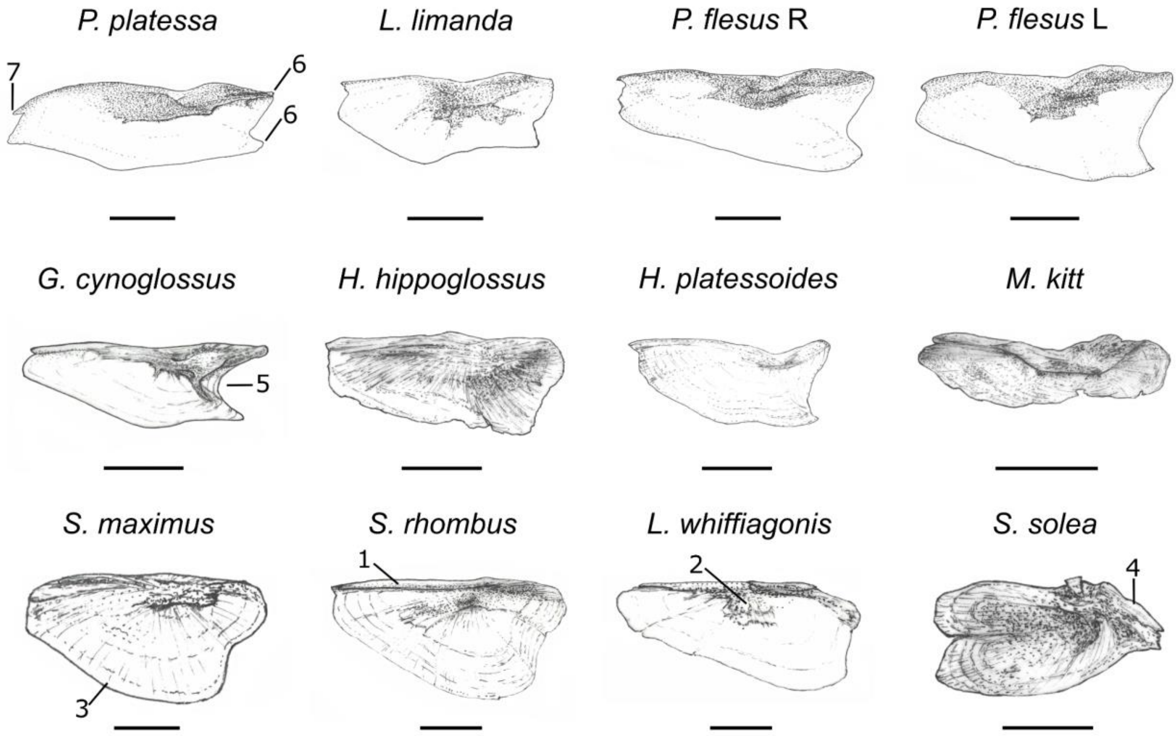


Figure B18. Medial view of the right interoperculum of all twelve species. The black bar under each species represents 1 cm.

Part B2: Tables with diagnostic features

Table B2. Diagnostic features of the left premaxilla.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
corpus length	**short**	short or rather long	**long**	long or short	**long**	long	very long	**very short**	very long	very long	very long	long
lateral corpus curvature	strong	slight or strong	slight or strong	strong	strong	strong	slight	strong	slight	slight	slight	**strong**
ventral corpus curvature	strong at tip	strong at tip	slight at posterior part	strong	strong at tip	strong	clear at tip	clear at tip	strong	strong	strong	**strong**
relative length processus anterior to corpus	corpus 1.5-2x length of processus	corpus 1.5-2x length of processus	corpus 2-3x length of processus	corpus 1.5-2x length of processus	corpus slightly longer	corpus 2-3x length of processus	corpus 3-4x length of processus	**same length or corpus bit shorter than processus**	corpus 2-3x length of processus	corpus 2-4x length of processus	corpus 2-4x length of processus	corpus 2-4x length of processus
processus anterior curvature	straight or subtly posteriorly	straight or slightly posteriorly	straight	straight	straight, tip sometimes slightly posteriorly	straight	straight or slightly posteriorly	straight	**posteriorly**	**posteriorly**	**posteriorly**	anteriorly
processus anterior length	rather long	rather long	rather long	rather short	long	rather short	short	very long	rather long	rather long	rather long	short
processus anterior curvature around axis	none or slight	slight	slight	barely	none	barely	barely	none	none or slight	none or slight	none or slight	none
processus anterior tip shape	rounded	rounded	rounded	pointed	rounded or pointed	pointed	pointed, lateral part higher	pointed, lateral part higher	pointed	pointed	rounded or pointed	rounded or pointed
processus anterior tip orientation	flat laterally	flat laterally	flat laterally	flat anteriorly	flat anteriorly	flat anteriorly	flat anteriorly	rounded	flat anteriorly	flat anteriorly	flat anteriorly	rounded or barely flat laterally
processus anterior pit at base	present	present	present	none	present	present	present	none	barely	barely	barely	none; ridge and foramen present
medial processus at base processus anterior	present	present	present	possible	none	none	none	none	none	none	none	none
additional bumps on processus anterior	none	small to large bulb at tip anteriorly possible	none	none	sometimes small spina oriented ventrally from tip	none	ridge along length anteriorly and posteriorly possible	slight ridge or bump medially near tip; ridge of symphysis at base	subtle groove sometimes	subtle groove sometimes	none	none
number of teeth	17-27 teeth	14-23 teeth	17-30 teeth	13-14 teeth	19-23 teeth	25-75	39-54 teeth	(8)10-14 teeth	82-120 teeth	51-135 teeth	53-121 teeth	min. 80 teeth
tooth rows	1 row	1 row	1 row, 2 rows possible in large specimen	1 row	1 row	1 row, sometimes 2 anteriorly	1 row	1 row	**3-4 multiple rows anteriorly,1-2 rows posteriorly**	**3-5 multiple rows anteriorly,1-2 rows posteriorly**	**3 multiple rows anteriorly,1 rows posteriorly**	**>5 rows in mid; less rows anterior and posterior**
tooth alveoli implantation	tidy	tidy or bit chaotic	tidy or semi chaotic	tidy	tidy	**irregular, gaps between teeth**	rather tidy, sometimes irregular gaps	tidy	chaotic	chaotic	chaotic	chaotic/tidy
tooth alveoli shape	oval	round or slight oval	round or slight oval	round or slight oval	oval	round	round or slight oval; anterior few larger	round	small round	small round	small round	very small round
tooth area	till curvature of corpus	till curvature of corpus or almost tip	till curvature of corpus	**almost till tip/crista end**	till curvature of corpus	almost till tip	till the curvature of corpus	till curvature of corpus	almost till tip	almost till tip	(almost) till tip	**whole length**
processus articularis length	short	short	short	rather long	short	rather long	short	short	long	long	rather long	very short
processus articularis height	rather high	rather high	rather high	rather high	high	rather low	low	high	high	rather high	rather low	low
relative height of bulb and crista on processus articularis	crista higher	crista bit higher	crista bit higher	crista higher	crista higher	crista bit higher	crista higher	no crista	crista bit higher	crista barely higher	same height	**none**
processus articularis bulb implantation	base attached	**base not attached**	base attached	base attached	base attached	base attached	base attached	**base not attached**	base attached	base attached	base attached	none
relative length processus articularis to anterior	about half	about half	half	larger than half	half	about half	half or less	half	about half	half or larger	slightly higher than half	much smaller

Table B2 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative witdth of indentation between processus articularis and	slender	slender or broad	slender	slender	slender	broad	broad	**none**	broad	slender	broad	**none**
depth indentation between processus articularis and anterior	**usually shallow**	shallow or rather deep	**deep**	very deep	**shallow or deep**	deep	deep	**none**	deep	deep	rather deep	**none**
relative depth indentation between processus articularis and anterior	less than half articularis	half or less articularis	half articularis or almost till base	till base	less than half articularis	till base	till (almost) base	**none**	half articularis or almost till base	half articularis or almost till base	half articularis	**none**
pars caudalis width	broad	slender	slender	slender	slender	slender	slender	rather slender	slender	slender	slender	broad
pars caudalis length	long	rather short	long	rather short	short	long	very long	very short	very long	very long	very long	very long
pars caudalis shape	rounded or pointed	pointed	pointed	rounded or pointed	rounded or pointed	pointed	pointed	pointed or angular	rounded or pointed	rounded or pointed	rounded or pointed	pointed
crista on corpus clarity	not delineated	slightly	not delineated	**clearly**	not delineated	not delineated	not delineated	not delineated	**clearly**	**clearly**	**clearly**	none
crista on corpus length	rather long	rather long	very long or short	rather short	rather long	very short	very long	very short	very long	rather short	rather long	none
crista on corpus height	rather high	rather low	very low	rather high	low	low	very low	very low	high	high	high	none
crista on corpus shape	round	round or angular	round	round	round	round or angular	round or rather straight	pointed, angular or round	rather straight	rather straight	rather straight	none
symphysis protrusion	first 2-3 teeth	first 2-3 teeth	first 2-3 teeth	**not protruding**	first 1-2 teeth	protruding strongly	first 2-3 teeth	strongly protruding, with 1-2 teeth	barely protruding	slight protruding	slight protruding	much protruding
symphysis length	short	short	short	short	short	**short**	long	short	short	short	short	long, 2 tips
symphysis height	low	low	high or low	very low	low	**high**	rather low	very high	low	low	rather low	low
symphysis width	slender	slender	slender	slender	very slender	**broad**	slender	rather slender or broad	slender	slender	slender	slender or broad
symphysis pit	at base	at base	at base	none	at base	at base	at base	none	at base	at base	at base	none
lateral foramen	none	sometimes base of processus articularis	sometimes symphysis	none	none	sometimes base of processus articularis	none	none	sometimes symphysis	none	none	none
medial foramen	below processus articularis	none	below processus articularis	none	none	none	none	none	below processus articularis	none	none	symphysis

Table B3. Diagnostic features of the right premaxilla.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
corpus length	**short**	short or rather long	**long**	**long**	rather short	long	long	**very short**	very long	very long	very long	rather short
lateral corpus curvature	slight	slight	slight or strong	slight	slight	strong	strong	none	slight	slight	slight	slight

Table B3 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ventral corpus curvature	slight at tip	strong	strong	slight	strong at tip	strong	strong	strong	strong	strong	strong	strong
relative length processus anterior to corpus	similar or corpus slightly longer	similar or corpus 1.5-2x length of processus	corpus 2-3x length of processus	corpus 1.5-2x length of processus	**similar or processus slightly longer**	corpus 2-3x length of processus	corpus 2-4x length of processus	**similar or processus slightly longer**	corpus 2-3x length of processus	corpus 2-4x length of processus	corpus 2-4x length of processus	corpus 2x length of processus
processus anterior curvature	straight or subtly posteriorly	straight or slightly posteriorly	straight or slightly posteriorly	straight	straight or slightly posteriorly	straight or slightly posteriorly	straight or slightly posteriorly	straight or slightly posteriorly	posteriorly	posteriorly	posteriorly	straight
processus anterior length	rather long	rather long	rather short	rather short	long	rather short	short	very long	rather long	rather long	rather long	short
processus anterior curvature around axis	none or slight	none or barely	none or barely	slight	none	slight	none	none	none or slight	none or slight	none or slight	none
processus anterior tip shape	pointed	pointed	pointed	pointed	rounded or pointed	pointed	pointed, lateral part higher	rounded	pointed	pointed	rounded or pointed	pointed
processus anterior tip orientation	flat anteriorly	flat anteriorly	flat anteriorly	flat laterally	flat anteriorly	flat anteriorly	flat anteriorly	rounded	flat anteriorly	flat anteriorly	flat anteriorly	rounded or barely flat laterally
processus anterior pit at base	none	none or barely	none	present	barely	present	present	none	barely	barely	barely	none
medial processus at base processus anterior	possible	possible	none or barely	present	none	none	none	none	none	none	none	none
additional bumps on processus anterior	lateral bump halfway anterior sometimes	small to large bulb at tip anteriorly possible; slight bump lateral halfway processus possible	none	none	sometimes small spina oriented ventrally from tip	none	none	slight ridge or bump medially near tip; ridge of symphysis at base	subtle groove sometimes	subtle groove sometimes	none	slight bump anterior base possible
number of teeth	**3-6 teeth**	6-13 teeth	9-13 teeth	18-21 teeth	10-14 teeth	28-60 teeth; 92 in 23423	**35-58 teeth**	none	60-115 teeth	40-107 teeth	50-100	none
tooth rows	1 row	1 row	1 row, 2 rows possible in large specimen	1 row	1 row	1 row, sometimes 2 anteriorly	1 row	**none**	**3-4 multiple rows anteriorly,1-2 rows posteriorly**	**3-5 multiple rows anteriorly,1-2 rows posteriorly**	**2-3 multiple rows anteriorly,1 rows posteriorly**	none
tooth alveoli implantation	tidy	tidy or bit chaotic	tidy	tidy or semi chaotic	tidy	**irregular, gaps between teeth**	rather tidy, sometimes irregular gaps	none	chaotic	chaotic	chaotic	none
tooth alveoli shape	oval	round or slight oval	round or slight oval	round or slight oval	oval	round	round or slight oval; anterior few teeth larger	none	small round	small round	small round	none
tooth area	**till processus articularis or halfway corpus**	till crista, halfway corpus	till crista, halfway corpus	almost till tip/crista end	till crista	almost till tip	almost till tip	none	almost till tip	almost till tip	(almost) till tip	none
processus articularis length	short	short	short	rather short	short	rather long	short	short	long	long	rather long	short
processus articularis height	rather high	rather high	rather high	rather high	high	rather low	rather high	high	high	rather high	rather low	low
relative height of bulb and crista on processus articularis	crista bit higher	crista bit higher	crista bit higher	crista higher	crista higher	crista bit higher	crista higher	crista bit higher	crista bit higher	crista barely higher	same height	**no crista**
processus articularis bulb implantation	base attached	**base not attached**	base attached	base attached	base attached	base attached	base attached	**base not attached**	base attached	base attached	base attached	base attached
relative length processus articularis to anterior	about half	about half	half	half or slightly less	half or slightly more	about half	half or less	half	about half	half or larger	slightly higher than half	much smaller
relative witdth of indentation between processus articularis and	slender	slender or broad	slender	slender	slender or broad	**broad**	slender	**none or slender**	broad	slender	broad	**none**
depth indentation between processus articularis and anterior	deep	shallow or rather deep	deep	rather deep	shallow or deep	deep	**deep**	**none or shallow**	deep	deep	rather deep	**none**

Table B3 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative depth indentation between processus articularis and anterior	till base	half or till almost base	till base	half	less than half articularis	till base	**till (almost) base**	**none or barely**	half articularis or almost till base	half articularis or almost till base	half articularis	**none**
pars caudalis width	broad	slender	slender	slender	slender	slender	very slender	slender	slender	slender	slender	very slender
pars caudalis length	very short	rather short	short	long	short	long	very long	short	very long	very long	very long	long
pars caudalis shape	rounded or pointed	pointed	rounded or pointed	rounded or pointed	rounded or pointed	pointed	pointed	rounded or pointed	rounded or pointed	rounded or pointed	rounded or pointed	pointed
crista on corpus clarity	not delineated	slightly	slightly	slightly	clearly	slightly	slightly	slightly	**clearly**	**clearly**	**clearly**	none
crista on corpus length	short	rather short or long	short	rather long	short or long	rather short	long	very short	very long	rather short	rather long	none
crista on corpus height	rather high	rather low	low	rather low	rather low	low	rather low	very low	high	high	high	none
crista on corpus shape	round	round or angular	round or angular	round	round or angular	round or angular	round or angular	pointed, angular or round	rather straight	rather straight	rather straight	none
symphysis protrusion	not	not or slightly	not	**protruding**	not	protruding	protruding	not	barely protruding	slight protruding	slight protruding	much protruding
symphysis length	very short	very short	very short	long	very short	short	short	very short	short	short	short	long; as long as corpus
symphysis height	very low	very low	very low	low	very low	low	high	low	low	low	rather low	high
symphysis width	slender	slender	slender	slender	slender	broad	slender	broad	slender	slender	slender	broad
symphysis pit	none	none or barely	none or barely	at base	none	at base	at base	none	at base	at base	at base	none
lateral foramen	base processus articularis	sometimes base of processus articularis	sometimes symphysis; sometimes base of processus articularis	none	none	sometimes base of processus articularis	sometimes base of processus articularis	none	sometimes symphysis	none	none	none
medial foramen	below processus articularis	none	below processus articularis	none	none	none	none	sometimes below processus articularis	below processus articularis	none	none	none

Table B4. Diagnostic features of the left maxilla.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
corpus length	short or bit long	**long**	**long**	long	**short or long**	long	**very long**	very short	very long	very long	very long	rather long
corpus thickness	rather thick	thin	thick	thick	thin	thick	thin	thick	thick	thick	thick	thin
corpus shape	round	slightly flat	slightly flat	rather round	**flat ventral and medial**	round	rather flat	rather flat	high, flat	high, flat	high, flat	slightly flat
lateral corpus curvature	strong	strong	strong	strong	strong	strong	slight	slight	strong	strong	straight	strong
ventral corpus curvature	slight	strong	slight	barely	slight	strong	slight	barely	strong	slight	slight	strong

Table B4 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
orientation corpus to caput	straight	straight	straight	**caput bit forward**	straight	caput bit forward	straight	straight	caput bit forward	caput bit forward	caput bit medial	straight
pars caudalis curvature around axis	barely	barely	barely	slightly	tip rather strongly	barely	none	none or barely	barely	none or barely	none	bit downward
dorsal pars caudalis broadening	**strongly**	slightly	slightly or strongly	slightly	slightly	strongly	strongly	strongly	**barely**	**barely**	**barely**	none
ventral pars caudalis broadening	**strongly**	strongly	strongly	strongly	strongly	slightly	slightly	slightly	**slightly, gradual**	**slightly, gradual**	**slightly, gradual**	none
pars caudalis edge shape	straight or slight convex, rarely heart shaped	straight or convex	straight or slight convex, rarely heart shaped	straight or slight convex	straight, convex or slight heartshaped; sometimes ventral lobe bit longer than dorsal	convex	straight or convex	straight or slight heart shaped; dorsal lobe larger	straight, irregular or slight concave; ventral lobe bit larger	straight, irregular or slight convex; ventral lobe longer sometimes	straight or convex; ventral lobe longer sometimes	pointed or convex and slender
caput length	rather short	rather short	rather long	short	**short**	long	short	long	short	short	short	short
caput width	broad	slender	broad	broad	**slender**	broad	slender	very broad	rather slender	rather slender	broad	broad
caput depth	shallow	rather deep or shallow	rather shallow	shallow	shallow	deep	deep	rather shallow	shallow	shallow	shallow	shallow
caput height	high	high or low	rather high	rather high	high	rather high	rather low	rather low	high	high	rather low	low
processus relative length	similar	internus usually bit longer	internus longer	similar	similar	similar	similar	internus slightly more ventral	externus longer	externus longer	**externus much longer**	**internus longer**
relative width dorsal and ventral part of caput	similar	similar	ventral wider	ventral bit wider	similar broadest at middle	ventral wider	similar	ventral wider; very broad in middle	ventral barely wider	ventral barely wider	**ventral much wider**	**ventral broader**
caput overhanging posteriorly	slightly	**not**	**possible**	not	not or barely	not	bit	not	not	**clearly**	not	not
processus internus shape	angular or rounded	rounded or pointed	rounded or pointed	rounded	rounded	rounded or pointed	angular or rounded	angular or rounded	angular or rounded	angular or rounded	angular	pointed
processus internus length	short	short	rather short	rather long	short	rather long	short	rather long	short	short	short	long
processus internus edge	rather straight or slight convex	straight or slight concave	straight or slight concave	straight or concave	straight or concave	straight	straight or concave	straight or concave	concave	concave	strong concave	straight or slight convex
processus internus orientation	bit laterally	bit laterally	bit laterally	strong laterally	straight	barely laterally	barely laterally	bit medially	bit laterally	bit laterally	bit laterally	strong laterally
spina position on processus internus	**not clearly separate**	barely separate	slight separate	barely separate	barely separate	separate	bit separate	separate	separate	separate	separate	separate
spina length on processus internus	short	short	short	short	short	long	**long or short**	very long	very long	**rather short**	very long	short
spina width on processus internus	slender	slender	broad	broad	slender	rather broad	slender or broad	slender	rather broad	rather broad	slender	broad
spina shape on processus internus	pointed	pointed or rounded	rounded	pointed or rounded	rounded or angular	pointed or rounded	rounded	pointed or rounded	pointed or angular	pointed or rounded	pointed or rounded	rounded or angular
spina orientation on processus internus	barely protruding; bit upward	forward	bit upward	forward	forward	forward, bit upward	**bit upward**	**bit lateral and upward**	**bit lateral and upward**	**bit lateral and upward**	**bit lateral and upward**	upward
depth of apparent indentation above processus internus	deep	shallow	shallow	shallow	rather shallow	very shallow	shallow	very shallow	shallow	none or very shallow	none or very shallow	very deep
width of apparent indentation above processus internus	wide	slender	wide	wide	slender	wide	slender	wide	slender	slender	slender	very wide
shape of apparent indentation above processus internus	round or angular	round or angular	round	round	angular	round or angular	round or angular	round	round or angular	round or angular	round or angular	round

Table B4 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
transition from caput to processus externus	concave or straight or subtle convex	straight or slight concave	concave	straight or concave	concave or straight or subtle convex	rather straight or concave	straight or slight concave	concave	rather straight or concave	concave or straight or subtle convex	barely or slight concave	straight or slight concave
lateral ridge on processus externus	present	present	present	present	present	present	slight	present	none	none	none	none
crista position	one third	mid-corpus or at one third	one third	one third	mid-corpus	at one third	mid-corpus or at one third	mid-corpus	close to caput	close to caput	close to caput	none
crista length	long	short	long	short	short	long	long	**very long, more than half of corpus**	rather short	short	short	none
crista height	low	low	low	low	high	rather high	low	**very high**	rather low	low	rather high	none
crista shape	pointed	angular or pointed	rounded or pointed	rounded or pointed	angular or pointed	angular or pointed	pointed	rounded or angular	rounded or angular	rounded or angular	rounded or angular	none

Table B5. Diagnostic features of the right maxilla.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
corpus length	**short or bit long**	**long**	**long**	long	short	long	**very long**	very short	very long	very long	very long	rather long
corpus thickness	rather thick	thin	thick	thick	thin	thick	thin	thick	thick	thick	thick	thin
corpus shape	round	slightly flat	slightly flat	rather round	**flat ventral and medial**	round	rather flat	rather flat	high, flat	high, flat	high, flat	slightly flat
lateral corpus curvature	strong	strong	strong	slight	slight	slight	slight	slight	strong	barely	straight	slight
ventral corpus curvature	slight	none or slight	slight	slight	none	slight	slight	slight	strong	slight	slight	barely
orientation corpus to caput	caput bit forward	caput bit forward	caput bit forward or straight	straight	straight or slight medial	straight	straight	straight	caput bit forward	caput bit forward	**caput bit medial**	**90 degrees curved around axis**
pars caudalis curvature around axis	**slightly**	**barely**	**barely or strongly**	slightly or strongly	strongly	barely	barely	**strongly**	barely	none or barely	none	slight
dorsal pars caudalis broadening	**strongly**	slightly or strongly	slightly or strongly	slightly	slightly	strongly	strongly	barely	**barely**	**barely**	**barely**	none
ventral pars caudalis broadening	**strongly**	strongly	strongly	strongly	strongly	slightly	slightly	barely	**slightly, gradual**	**slightly, gradual**	**slightly, gradual**	none
pars caudalis edge shape	straight or slight convex, rarely heart shaped	straight or convex	straight or slight convex, rarely heart shaped	straight or slight convex	straight, convex or slight heartshaped; sometimes ventral lobe bit longer than dorsal	convex	straight or convex	straight or slight convex; ventral lobe bit larger	straight, irregular or slight concave; ventral lobe bit larger	straight, irregular or slight convex; ventral lobe longer sometimes	straight or convex; ventral lobe longer sometimes	pointed or convex and slender
caput length	short	rather short	short	short or rather long	short	long	short	long	short	short	short	short
caput width	broad	rather broad	broad	broad	**broad**	broad	**slender**	very broad	rather slender	rather slender	broad	broad
caput depth	shallow	rather deep or shallow	rather shallow	deep or shallow	rather deep	**deep**	rather deep	deep	shallow	shallow	shallow	shallow
caput height	rather high	rather low	rather high	rather high	**high**	rather high	**rather low**	rather low	high	high	rather low	low

Table B5 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus relative length	similar	similar	similar	similar or internus slightly longer	**externus slightly more ventral**	similar	similar	**externus slightly more ventral**	externus longer	externus longer	internus longer	**externus longer**
relative width dorsal and ventral part of caput	ventral bit wider	similar	ventral wider	similar	ventral wider	ventral wider	ventral bit wider	ventral wider	ventral barely wider	ventral barely wider	ventral wider	ventral broader
caput overhanging posteriorly	not	not	**possible**	clearly	not	not	not	not	not	**clearly**	not	not
processus internus shape	angular or rounded	angular or rounded	angular or rounded	rounded	angular or rounded	angular or rounded	angular or rounded	angular or rounded	angular or rounded	angular or rounded	angular	pointed or angular
processus internus length	short	short	rather short	rather long	short	rather long	short	short	short	short	short	very short, barely present
processus internus edge	rather straight or slight concave	straight	straight or slight concave	straight or concave	straight or convex	straight	straight or concave	straight or concave	concave	concave	strong concave	concave
processus internus orientation	bit laterally	bit laterally	bit laterally	strong laterally	straight	barely laterally	barely laterally	straight	bit laterally	bit laterally	bit laterally	strong laterally
spina position on processus internus	**not clearly separate**	barely separate	slight separate	slight separate	slight separate	separate	bit separate	separate	separate	separate	separate	separate
spina length on processus internus	short	short	short	short	short	long	**long or short**	very long	very long	**rather short**	very long	short
spina width on processus internus	slender	slender	broad	broad	slender	rather broad	slender or broad	broad	rather broad	rather broad	slender	broad
spina shape on processus internus	pointed	pointed or rounded	rounded or angular	pointed or rounded	rounded or angular	pointed or rounded	rounded	pointed or rounded	pointed or angular	pointed or rounded	pointed or rounded	rounded or angular
spina orientation on processus internus	bit upward	forward, bit upward	forward, bit upward	forward	forward	forward	bit upward	bit upward	bit lateral and upward	bit lateral and upward	bit lateral and upward	upward
depth of apparent indentation above processus internus	rather shallow	shallow	shallow	shallow	none or rather shallow	shallow	shallow	very shallow	shallow	none or very shallow	none or very shallow	none
width of apparent indentation above processus internus	wide	rather slender	wide	wide	slender	wide	slender	wide	slender	slender	rather broad	none
shape of apparent indentation above processus internus	round or angular	round or angular	round	round or angular	round or angular	round or angular	round or angular	round	round or angular	round or angular	round or angular	angular
transition from caput to processus externus	concave or straight or subtle convex	concave or straight or subtle convex	concave	concave or straight	subtle convex	rather straight or concave	straight or slight concave	concave or straight	rather straight or concave	straight, slight convex, or concave	barely or slight concave	slight concave or straight
lateral ridge on processus externus	present	slight	present	**present**	**none**	present	slight	slight	possible	none	none or barely	none
crista position	close to caput	close to caput	one third	one third	mid-corpus or at one third	mid-corpus or at one third	close to caput	mid-corpus	close to caput	close to caput	close to caput	one third
crista length	short	short	rather long	long	short	short	short	**rather long, almost half of corpus**	rather short	short	short	rather short
crista height	low	low	low	low	low	low	low	**high**	rather low	low	rather high	very low
crista shape	barely protruding	angular or pointed; barely protruding	rounded or pointed; barely protruding	rounded or pointed	angular or pointed; barely protruding	angular or rounded	barely protruding	rounded or angular	rounded or angular	rounded or angular	rounded or angular	pointed; barely protruding

Table B6. Diagnostic features of the left dentary.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general shape	longer than high	bit longer than high	longer than high	bit longer than high	bit longer than high	longer than high	**much longer than high**	**higher than long**	longer than high	longer than high	much longer than high	**higher than long**
number of teeth	17-28 teeth	16-26 teeth	15-28 teeth	12-14 teeth	22-25 teeth	10-19 teeth; 70 in 23423	**30-48 teeth**	7-14 teeth	75-125 teeth	60-145 teeth	50-90 teeth	min. 80 teeth
number of tooth rows	1 row	1 row	1 row, sometimes 2 anteriorly	1 row	1 row	1 row, sometimes 2 anteriorly; 3-5 in 23423	1 row	**1 row**	**3-4 rows anteriorly, 1 row posteriorly**	**3-5 rows anteriorly, 1 row posteriorly**	**2-3 rows anteriorly, 1 row posteriorly**	**4-5 main rows, with each 1-2 subrows**
tooth area	almost whole length, not at tip	almost whole length, not at tip	almost whole length, not at tip	**till split**	till split or almost till tip	almost whole length, not at tip	almost whole length, not at tip	almost till end, till right after split	almost whole length, not at tip	almost whole length, not at tip	almost till end, till right after split	**till split; broad in middle and protruding laterally**
tooth alveoli implantation	**Tidy**	tidy or bit chaotic	tidy or semi chaotic	tidy	tidy	**irregular, gaps between teeth**	rather tidy, sometimes irregular gaps	tidy	chaotic	chaotic	chaotic	chaotic/tidy
tooth alveoli shape	oval	round or slight oval	round or slight oval	round or slight oval	oval	round	round or slight oval	round	small round	small round	small round	very small round
lateral curvature	**strongly**	strongly	clearly	slightly	slightly	slightly	slightly	strongly	slightly or barely	slightly or barely	slightly or barely	**strongly**
relative length processes	superior much longer; inferior very short in large specimens	**superior bit longer or similar**	**superior longer or similar**	inferior bit longer or similar	rather similar with superior sometimes sligthly longer	rather similar or one slightly longer than other	superior bit longer or similar	inferior longer; superior further	**inferior longer**	**inferior longer**	**inferior longer**	superior longer
processus superior symphysis tip orientation	symphysis forward, upward in small specimens	slightly upward and forward	upward and forward	bit downward	forward	forward and upward	bit upward and forward	slightly forward	slightly forward	not forward	not forward	unclear
processus superior dorsal edge	straight	straight, rarely convex	rather straight or slight convex	convex anteriorly, concave middle	rather straight or subtly concave or convex	straight or slight convex	straight or slight convex with concave anterior and posterior parts sometimes	straight or slight concave anterior, posterior usually convex	straight with convex bump above foramen sometimes	straight with convex bump above foramen sometimes	**convex with concave anterior and posterior parts**	straight; strongly laterally
processus superior tip	slight upward	slight upward	upward	slight upward	slight upward	upward	slightly upward	posterior, upward or downward	posterior	posterior	posterior	strongly upward
processus superior tip ridge	present	slight	unclear	slight	none or unclear	unclear	none	none	present	none or slight	none or slight	none
processus superior tip shape	round or flat	rather flat or slight round or angular	round or pointed	round	round	round or flat	round or flat	pointed	round or flat	round or pointed or flat	round or pointed or flat	angular, broad
lateral ridge along processus superior	possible, slight	rarely, subtle	none	slightly	none or subtle	anteriorly large	none or very slight anteriorly	none	none or slight	none or slight	none or slight	strong along parabole; slight vertical mid superior
processus inferior length	short	rather long	rather short	rather long	short	long	long	short	long	long	long	short
processus inferior curvature	straight or slight	straight or slight	straight	straight or subtle	straight	straight	straight	straight; strongly ventrally oriented	rather straight or slight	rather straight or slight	rather straight or slight	straight or slight ventrally
processus inferior width	broad	slender	broad	broad	broad	very broad	rather broad	broad	rather slender	rather slender	rather slender	broad
processus inferior tip shape	rounded or pointed	rounded or pointed	rounded	broad tube, angular	straight with wide foramen	rounded or angular	rounded	pointed	pointed	pointed	pointed	rounded or angular
indentation on ventral side depth	deep	**deep**	**shallow**	shallow	deep, sometimes shallow	very shallow	deep or shallow	shallow	**none or shallow**	**none or shallow**	**none or shallow**	none or very shallow
indentation on ventral side width	wide	**wide**	**rather slender**	very slender	slender	wide or slender	slender	very slender	**none or rather wide**	**none or rather wide**	**none or rather slender**	none or slender
indentation on ventral side shape	rounded	**rounded or angular**	**rounded**	rounded	rounded	rounded	rounded or angular	rounded or angular	**none or rounded**	**none or rounded**	**none or rounded**	none or small slit
margo inferior shape	convex, sometimes bend	usually straight, sometimes bend	slight convex	slight convex	straight or subtly convex	straight or slight convex	straight or slight convex	straight or subtle convex	slight convex	slight convex	slight convex	straight or slightly concave
foramen on processus inferior	5 to 6	5, small, sometimes unclear	4-7	4-7	4 very large	some very shallow and unclear	5 to 6, exponential distance	2 to 4	few anteriorly	few anteriorly	few	1 possible
foramen on processus superior	1 mid	1 mid or anterior possible	1 to 2 mid possible	1 large	1 mid	1 mid, 1 anterior	none	1 at split	**few; large mid, sometimes hole**	**few; large mid, often hole**	**few; large mid hole**	1 mid, 1 posterior

Table B6 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
pit symphysis	none	slight or none; ridge possible in large specimens	none	slight or none	clear	**clear with ridge above**	slight or none	slight or none	slight or none	slight or none	none	slight or none
symphysis height	high	rather low	high	**very high**	very high	very high	low	very high	high	high	high	**very high**
symphysis edge shape	straight or bit concave	straight or bend	straight	straight or slight convex	straight	straight or slight concave	straight or slight concave	straight or slight concave	straight or concave	straight or concave	straight or suble concave	convex
symphysis ventral part protruding	strongly	clearly	clearly	barely	clear	slightly	clear	slightly	not	not	slightly	not
symphysis ventral part shape	round or angular	round or angular	round	angular	round	round	round	angular	angular	angular	round or angular	**broad**
medial view of crista lateralis of processus inferior	present	present	present	present	present	present	present	present	**present**	**present**	**bit**	present
medial view of crista lateralis of processus superior	sometimes bit	sometimes bit	sometimes bit	present	present	bit	present	none	**present**	**present**	**bit**	none
medial view of crista lateralis at split	bit	bit	bit	present	present	present	present	none	**none**	**none**	**sometimes**	none
lateral view of crista lateralis of processus inferior	none	none	none	none	none	none	none	none	**none**	**none**	**none**	none
lateral view of crista lateralis of processus superior	none	none	none	none	none	sometimes bit	none	none	**none**	**none**	**none**	sometimes tip
lateral view of crista lateralis at split	none	none	none	none	none	none	none	bit	**sometimes bit**	**none**	**sometimes bit**	sometimes

Table B7. Diagnostic features of the right dentary.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general shape	longer than high	bit longer than high	bit longer than high	longer than high	bit longer than high	longer than high	longer than high	**higher than long**	longer than high	longer than high	much longer than high	bit longer than high
number of teeth	**4-8 teeth**	11-18 teeth	12-16 teeth	19-23 teeth	10-15 teeth	8-19 teeth 52 in 23423	22-31 teeth	0-2 teeth	66-110 teeth	64-137 teeth	35-83 teeth	**none**
number of tooth rows	1 row	1 row	1 row, sometimes 2 anteriorly	1 row	1 row	1 row, sometimes 2 anteriorly; 3-5 in 23423	1 row	**1 row**	**3-5 rows anteriorly, 1-2 row posteriorly**	**3-6 rows anteriorly, 1-2 row posteriorly**	**2-3 rows anteriorly, 1 row posteriorly**	**none**
tooth area	**only at anterior part**	almost whole length, not at tip, or till split	till split	**almost whole length, not at tip**	almost till split	almost whole length, not at tip, or till split	almost whole length, not at tip	only tip symphysis	almost whole length, not at tip	almost whole length, not at tip	almost till end, till right after split	**none, sharp edge**
tooth alveoli implantation	**Tidy**	tidy or bit chaotic	tidy or semi chaotic	tidy	tidy	**irregular, gaps between teeth**	rather tidy, sometimes irregular gaps	tidy	chaotic	chaotic	chaotic	none
tooth alveoli shape	rather round	round or slight oval	round or slight oval	round or slight oval	oval	round	round or slight oval	round	small round	small round	small round	none
lateral curvature	slightly	slightly	slightly	**clear**	slightly	slightly	slightly	slightly	slightly	slightly	slightly	slightly
relative length processes	inferior bit longer or similar	inferior bit longer or similar	inferior bit longer or similar	**superior longer**	rather similar, inferior sligthly longer	rather similar or one slightly longer than other	inferior bit longer or similar	inferior longer; superior further or same	**inferior longer**	**inferior longer**	**inferior longer**	inferior bit longer or similar
processus superior symphysis tip orientation	symphysis forward, upward in small specimens	slightly upward and forward	upward and forward	bit downward	forward	forward and upward	bit upward and forward	slightly forward	slightly forward	not forward	not forward	unclear

Table B7 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus superior dorsal edge	concave	straight, rarely convex	rather straight or slight concave	straight or slight concave	straight or slight concave	straight or slight convex	convex with concave anterior and posterior parts sometimes	straight or slight concave anterior, posterior usually convex	straight with convex bump above foramen sometimes	straight with convex bump above foramen sometimes	**convex with concave anterior and posterior parts**	slight convex
processus superior tip	slight upward	slight upward	upward	slight upward	upward	upward or posterior	slightly upward	posterior or upward	posterior	posterior	posterior	slightly upward
processus superior tip ridge	large	slight	slight	slight	none or unclear	unclear	none	none	none or slight	none or slight	none or slight	none
processus superior tip shape	round or flat	rather flat or slight round or angular	round or flat	round or flat	round or pointed	round or flat or angular	round or flat	pointed	round or flat	round or pointed or flat	round or pointed or flat	pointed
lateral ridge along processus superior	large	rarely, subtle	slight	none	slight	slight		none	none or slight	none or slight	none or slight	slight
processus inferior length	short	rather short	rather long	rather short	short	rather short	long	short	long	long	long	rather short
processus inferior curvature	straight or slight	straight or slight	straight or slight	straight or subtle	straight or slight	straight or slight	straight or slight	straight; strongly ventrally oriented	rather straight or slight	rather straight or slight	rather straight or slight	straight
processus inferior width	broad	slender	broad	broad	slender	very broad	rather slender or broad	broad	rather slender	rather slender	rather slender	slender
processus inferior tip shape	pointed	pointed or straight	broad tube, angular	rounded or pointed	round or angular	rounded or angular	rounded or angular	pointed	pointed	pointed	pointed	pointed
indentation on ventral side depth	very deep	**deep, sometimes shallow**	**rather shallow**	shallow	deep, sometimes shallow	rather deep	deep or shallow	shallow	**none or shallow**	**none or shallow**	**none or shallow**	deep
indentation on ventral side width	usually slender	**rather slender**	**rather slender or wide**	wide	slender	rather wide	slender	very slender	**none or rather wide**	**none or rather wide**	**none or rather slender**	slender
indentation on ventral side shape	rounded	**rounded or angular**	**rounded or angular**	rounded or angular	rounded or angular	rounded or angular	rounded or angular	rounded or angular	**none or rounded**	**none or rounded**	**none or rounded**	rounded
margo inferior shape	straight or slight convex	straight or slight convex, rarely concave	straight or slight convex	convex	straight or subtly convex	straight or slight convex	straight or slight convex	straight or subtle convex	slight convex	slight convex	slight convex	straight or slightly concave
foramen on processus inferior	2 to 3	5, small, sometimes unclear	4-7	4-7	4, exponential distance	4 to 5 unclear	4 to 6, exponential distance	2 to 4, small	few anteriorly	few anteriorly	few	1 possible
foramen on processus superior	1 mid	1 mid or anterior possible	1 to 2 mid possible	1 large	1-2 mid	1 mid, 1-2 anterior	1 possible	1-2 mid	**few; large mid, sometimes hole**	**few; large mid, often hole**	**few; large mid hole**	1 mid, 1 posterior
pit symphysis	none	slight or none	none	slight	slight or none	slight or none with ridge above	slight	slight or none	slight or none	slight or none	slight or none	none
symphysis height	rather high	rather high	high	**very high**	high	very high	low	very high	high	high	high	high
symphysis edge shape	straight or bit convex	straight	straight or slight convex	straight or slight concave	straight or slight convex	straight or slight convex	straight or slight concave	straight or slight convex	straight or concave	straight or concave	straight or suble concave	straight or convex; **medial bump**
symphysis ventral part protruding	clearly	clearly	clearly	slightly	clear	slightly	clear	slightly	not or barely	not or barely	slightly	clear
symphysis ventral part shape	round or angular	round or angular	round	round or angular	round	round or angular	angular	angular or pointed	angular	angular	round or angular	**broad**
medial view of crista lateralis of processus inferior	present	present	present	present	present	present	present	present	**present**	**present**	**bit**	none
medial view of crista lateralis of processus superior	present	present	present	possible bit	present	bit	present	none	**present**	**present**	**sometimes**	present
medial view of crista lateralis at split	present	present	present	none	present	none	present	none	**none**	**possible**	**none**	present
lateral view of crista lateralis of processus inferior	none	none	none	none	none	none	none	none	**none**	**none**	**none**	none

Table B7 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
lateral view of crista lateralis of processus superior	none	none	none	none	none	sometimes bit	none	none	**none**	**none**	**none**	sometimes tip
lateral view of crista lateralis at split	none	none	none	none	none	none	none	bit	**sometimes bit**	**none**	**sometimes bit**	sometimes

Table B8. Diagnostic features of the left articular.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
facies articularis quadrati orientation	horizontal or diagonal	diagonal	**diagonal**	**posterior rather horizontal, anterior strong diagonal**	diagonal	diagonal	diagonal	diagonal	slight diagonal	slight diagonal	slight diagonal	horizontal
facies articularis ridge medial	large	rather large	rather small or large	rather small	rather small	**small**	**large, especially posterior**	large	posterior large	posterior large	small	anterior large
facies articularis quadrati shape	round	round or kidney	round or kidney; anterior can be broader	round, kidney or heart	round or kidney	oval or round; ridge along middle possible	angular, square or round; ridge along middle	round or tear	square; ridge in middle	kidney or squared	round or square	round
facies articularis quadrati curvature	straight	straight or slight curve	straight or slight curve	curve; bit saddle shaped	straight or slight curve	barely or slight curve; bit saddle shape	straight; saddle shape	straight or slight curve	rather straight; saddle shape	straight or slight curve; slight saddle shape	straight or slight curve; slight saddle shape	curve; saddle shape
facies articularis quadrati relative size to articular	less than third of length	less than third of length	less than third of length	less than third of length	less than third of length	less than third of length	less than third of length	**almost half of length**	less than third of length	less than third of length	much less than third of length	**almost half of length**
lateral posterior spina	present	**absent**	**possible**	usually present	absent	possible	possible	absent	present	present	present	possible
relative length of lateral and medial posterior spina	medial twice as long	NA	**medial twice as long**	medial twice as long	NA	medial slightly larger	medial twice as long	NA	medial spina twice or 1.5x as long	medial slightly longer or twice as long;	medial twice as long	medial slightly longer
relative length of posterior spina to facies anterior edge	lower than or similar as facies	slightly lower than or similar as facies	similar to facies	slightly lower than or similar as facies	barely higher than half of facies	**higher than facies**	**higher than facies**	barely higher than half of facies	**higher than facies**	**slightly higher than or similar as facies**	bit higher than facies	lower than or similar as facies
angulus ventralis height	low	high	**low**	**high**	high	rather low	rather low	high	**low anterior, high posterior**	**low anterior, high posterior**	low	**very low/absent**
angulus ventralis length	long	short	**long**	**short**	short	long	long	short	rather short	rather short	long	very short
angulus ventralis margin shape	straight	straight or slight convex	straight or slight convex	straight or slight concave	slight convex anterior, concave posterior	straight or barely concave	convex anterior, concave posterior	irregular	**rather straight or slight convex**	**rather straight or slight convex**	**straight or slight concave or bumpy**	straight or slight concave
angulus ventralis tip protruding	slightly	clearly	clearly	slightly	clearly	clearly	slightly	**clearly, ventrally**	not	not	barely or not	not
processus coronoides length	short	short or long	rather short or short	long	very short	long	rather long	short	long	long	long	long; as long as corpus
processus coronoides width	rather slender or broad	slender	slender	slender	slender	slender or broad	slender	broad	rather broad	rather slender	slender	slender laterally, broad anteriorly
processus coronoides crista	not in upper half	barely at tip	halfway or none	not at tip	not at tip	not at tip	not at tip	none	sometimes till tip	sometime till tip	sometime till tip	none
processus coronoides ridge	none	none	none	none	none	**clear**	none	none	**clear**	**slight**	**slight**	none
angle between processus coronoides and corpus	45 degrees	45 degrees	60 degrees	45-60 degrees	30-45 degrees?	45 degrees or bit larger	45-50 degrees	70-90 degrees	**around 60 degrees**	**around 45 degrees**	around 45 degrees	**90-100 degrees**
relative position angulus ventralis and processus coronoides	about same level or one slightly more anterior than the other	about same level or coronoides slightly anterior of ventralis	**about same level**	**coronoides much anterior of ventralis**	coronoides anteriorly of ventralis	coronoides anteriorly of ventralis	about same level or coronoides slightly anterior of ventralis	coronoides clearly anterior of ventralis	coronoides much anterior of ventralis	coronoides much anterior of ventralis	coronoides anterior of ventralis	coronoides much anterior of ventralis

Table B8 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general length	long	long, can be short	rather short	rather short	long	long	long	very short	long	long	very long	very short
general height	low	rather high	high	high	rather high	low	low	rahter low	high	high	rather high	rather high
posterior spina orientation	inclined	inclined or straight	slight inclined or straight	slight inclined	straight	straight	slight inclined	slight inclined	rather straight	rather straight	straight	rather straight
posterior margin height	**low**	**high**	**high**	high	rather low	very high	rather low	low	high	high	rather low	low
posterior margin ventral angle	none	**possible**	none	none	none	**possible**	none	none	none	none	none	none
processus anterior height	high	high	high	very high	high	high	low	high	high base, tip low	high base, tip low	low	high
processus anterior length	rather short	rather short	rather long	rather long	short	long	long	short	long	long	very long	**very short/absent**
processus anterior tip shape	rounded	rounded, angular or pointed	rounded or pointed	rounded or pointed	rounded or pointed	pointed	rounded or pointed	pointed	rounded or pointed	rounded or pointed	rounded or pointed	**none**
processus anterior curvature	subtly upward	subtly upward	subtly upward	straight	straight	straight	straight	straight	straight	straight	subtly upward	**none**
processus anterior ventral margin	ventral part bit horizontally	ventral part bit horizontally	ventral part bit horizontally	ventral part barely horizontally	ventral part horizontal	ventral part bit horizontal	ventral part bit horizontal	ventral part barely horizontal	ventral side flat or hollow	ventral side flat or hollow	ventral side bit horizontal or slight hollow	/
channel angulus ventralis	visible	visible, not always clear	visible	visible	**visible, very large, broad, deep, wide**	**visible, not at edge**	**visible, large at edge, flat**	barely visible, small	not visible	not visible	not visible	not visible
channel posterior edge	visible	visible	visible	visible	**visible, very large, broad, deep, wide**	visible, not on corpus	barely visible, small	visible, near tip of spina	visible at base spina	visible at base spina	visible at base spina	not visible

Table B9. Diagnostic features of the right articular.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
facies articularis quadrati orientation	diagonal, sometimes almost vertical	diagonal	**posterior rather horizontal, anterior strong diagonal**	**diagonal**	diagonal, almost vertical anterior part	diagonal	diagonal	strong diagonal	slight diagonal	slight diagonal	slight diagonal	rather horizontal or diagonal
facies articularis ridge medial	large	large	large	rather small	rather small	rather small	large	large	posterior large	posterior large	posterior large	small
facies articularis quadrati shape	round or square; ridge middle possible	angular, square or round	round or heart	round	round, square or kidney	rather round	round or tear	round or square	square; ridge in middle	round, kidney or squared	round or square	round, kidney, square or triangular
facies articularis quadrati curvature	straight; bit saddle shaped	slight curve	straight or slight curve; bit saddle shaped	straight	curve; bit saddle shaped	straight or slight curve; bit saddle shape possible	rather straight, saddle shape	slight curve	rather straight; saddle shape	straight or slight curve; slight saddle shape	straight or slight curve; slight saddle shape	curve; barely saddle shape
facies articularis quadrati relative size to articular	less than third of length	less than third of length	less than third of length	less than third of length	less than third of length	less than third of length	less than third of length	**almost half of length**	less than third of length	less than third of length	much less than third of length	**about third of length**
lateral posterior spina	present	**absent**	**possible**	possible	absent	possible	absent	absent	present	present	present	possible
relative length of lateral and medial posterior spina	medial similar or bit longer	NA	**medial much longer**	medial bit longer	NA	medial longer	NA	NA	medial spina twice or 1.5x as long	medial slightly longer or twice as long;	medial twice as long	unclear
relative length of posterior spina to facies anterior edge	lower than or similar as facies	slightly lower than or similar as facies, rarely higher	higher than or similar to facies	slightly lower, slightly higher than, or similar as facies	barely higher than half of facies	**higher than facies**	**higher than facies**	barely higher than half of facies	**higher than facies**	**slightly higher than or similar as facies**	bit higher than facies	lower than or similar as facies

Table B9 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
angulus ventralis height	low	high	rather low	low	rather low	rather low	rather low	high	**low anterior, high posterior**	**low anterior, high posterior**	low	**very low**
angulus ventralis length	rather short	rather short	short	long	rather short	long	long	very short	rather short	rather short	long	short
angulus ventralis margin shape	straight	straight or slight convex	straight	rather straight	rather straight or concave	straight or slight convex	slight concave	irregular	**rather straight or slight convex**	**rather straight or slight convex**	**straight or slight concave or bumpy**	straight or slight concave
angulus ventralis tip protruding	slightly	slightly	slightly	clearly	clearly	slightly	slightly	**clearly, ventrally**	not	not	barely or not	slightly
processus coronoides length	rather short	short or long	rather short	rather long	rather long	long	long	short	long	long	long	short
processus coronoides width	slender	slender	slender	slender	rather broad	slender or broad	slender	broad	rather broad	rather slender	slender	slender
processus coronoides crista	not at tip	barely at tip	not at tip	not at tip	not at tip	sometimes till tip	till tip	till halfway	sometimes till tip	sometimes till tip	sometimes till tip	none
processus coronoides ridge	none	none	none	none	none	none	none	none	clear	slight	slight	none
angle between processus coronoides and corpus	bit more than 45 degrees	45 degrees	50-60 degrees	45-60 degrees	around 45 degrees	around 45 degrees	45-50 degrees	around 60 degrees	around 60 degrees	around 45 degrees	around 45 degrees	90-100 degrees
relative position angulus ventralis and processus coronoides	**coronoides much anterior of ventralis**	about same level or coronoides anterior of ventralis	**coronoides anterior of ventralis**	**about same level**	coronoides much anteriorly of ventralis	coronoides anteriorly of ventralis	about same level or coronoides anterior of ventralis	coronoides clearly anterior of ventralis	coronoides much anterior of ventralis	coronoides much anterior of ventralis	coronoides anterior of ventralis	coronoides much anterior of ventralis
general length	rather short	short	rather short	rather long	rather short	long	long	very short	long	long	very long	very short
general height	low	rather high	high	high	rather high	low	low	rahter low	high	high	rather high	rather high
posterior spina orientation	inclined or straight	inclined or straight	slight inclined or straight	slight inclined	straight	straight	rather straight	slight inclined	rather straight	rather straight	straight	rather straight
posterior margin height	low	rather high	high	high	rather low	high	rather low	low	high	high	rather low	low
posterior margin ventral angle	none	**possible**	none	none	none	**possible**	none	none	none	none	none	none
processus anterior height	high	high	high	high	high	high	low	high	high base, tip low	high base, tip low	low	high
processus anterior length	short	short	rather long	rather long	short	long	long	short	long	long	very long	short
processus anterior tip shape	rounded	pointed	rounded or pointed	rounded or pointed	rounded or pointed	pointed	rounded or pointed	pointed or rounded	rounded or pointed	rounded or pointed	rounded or pointed	rounded
processus anterior curvature	subtly upward	subtly upward	subtly upward	straight	straight	straight	straight	straight	straight	straight	subtly upward	straight
processus anterior ventral margin	ventral part bit horizontally	ventral part bit horizontally	ventral part barely horizontally	ventral part bit horizontally	ventral part horizontal	ventral part bit horizontal	ventral part bit horizontal	ventral part not horizontal	ventral side flat or hollow	ventral side flat or hollow	ventral side bit horizontal or slight hollow	ventral side bit flat
channel angulus ventralis	visible	visible, not always clear	visible	visible	**visible, very large, broad, deep, wide**	**visible, not at edge**	visible, large	visible, small	not visible	not visible	not visible	visible, very small
channel posterior edge	visible	visible, not always clear	visible	visible	**visible, very large, broad, deep, wide**	visible, small	visible, small	visible, small	visible at base spina	visible at base spina	visible at base spina	visible, very small

Table B10. Diagnostic features of the left hyomandibula.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general height	rather low	rather low	rather low	rather low	rather high	high	rather high	high	rather high	rather high	high	rather low
general width	rather broad	**slender**	rather slender	rather broad	slender inferior, broad caput	slender, broad caput	slender	slender	rather slender	rather slender	slender	slender or rather broad
caput height	low	low	rather high or low	rather high or low	low	rather low	rather low	rather low	rather high	rather high	rather high	high
crista anterior width	wider than caput	slightly wider than caput	wider than caput	wider than caput	wider than caput	slightly wider than caput or same	slightly wider than caput or same	slenderer than caput	**wider than caput**	**slightly wider than caput**	similar to caput	slenderer than caput
crista anterior widening	clear	clear	clear	clear	clear	barely	slight	slight or none	clear	clear	slight or slenderer	none
crista anterior shape	2 parts equal	2 parts equal	2 parts equal	2 parts equal	2 parts equal	1 part or 2 small equal	1 part or 2 small equal	1 part	2 parts, upper smaller	2 parts, upper smaller	1 or 2 equal	1 part
processus inferior width	broad	slender	rather broad	broad	slender	broad	slender	very broad	broad	broad	**slender**	very broad
processus inferior tip	broader	broader	broader	broader	slight broader sometimes	slightly broader	slightly broader	not broader	slightly broader	slightly broader	slightly broader	broader
processus inferior length	rather short	long	long	long	rather long	long	long	long	long	long	long	rather short
processus inferior length thickness	flat	flat	flat	flat	flat	flat	flat	rather round	flat	rather flat	flat	rather round
processus pteroticum dorsal edge	straight or slight convex	straight or slight convex, bumpy	straight or slight convex	rather straight	slight convex	straight or slight convex	straight or convex	**concave**	straight or convex, sometimes slight concave	straight or convex, sometimes slight concave	straight or slight convex	straight
processus pteroticum relative inclination	posterior higher	posterior higher or same	posterior slightly higher	posterior slightly higher	posterior slightly higher	posterior barely higher	anterior higher	same; protruding	posterior slightly higher or same	posterior slightly higher or same	posterior slightly higher	posterior higher
processus pteroticum shape	oval	oval or posterior broader	**oval, sometimes slight constriction in middle**	**oval, sometimes slight constriction in middle**	oval or slight 8	oval	oval	oval	oval, sometimes slender	oval	oval	round or tear shape, posterior broader
processus pteroticum height	long	rather short	rather long	rather short	rather short	long	long	rather short	long	short or long	long	very short
processus opercularum shape	round	round	round	round	round or oval	round	round or oval	round, irregular	round	round	round or oval	round or oval
processus opercularum width	broad	broad	broad	broad	slender	broad	slender	broad	broad	broad	rather broad	very broad
processus opercularum protruding	slightly	not or slight	not or slight	not or slight	slightly	slightly	slightly	not	slightly	not or slightly	slightly	clear
processus opercularum orientation	posterior	posterior or slight ventral	posterior	posterior	posterior	posterior or slight ventral	ventral	posterior	ventral	ventral	slight ventral	ventral
processus opercularum height	short	short	short	short	long	long	**very long**	**very short**	short	short	rather long	rather short
processus sphenoticum width	broad	slender, sometimes broad	broad	broad	slender	very broad	slender or broad	rather broad	broad	broad	slender	slender
processus sphenoticum length	short	short	rather short	rather short	rather short	rather short	long	very short	very long	rather long	rather short	rather long
depth of transition pr. pteroticum to sphenoticum	rather shallow or deep	shallow	shallow or deep	shallow or deep	shallow	shallow	shallow	shallow	shallow or deep	shallow	shallow	shallow or deep
width of transition pr. pteroticum to sphenoticum	rather broad	slender	rather broad or slender	rather broad	broad or slender	slender	slender	rather slender	slender	rather slender	broad or slender	broad
shape of transition pr. pteroticum to sphenoticum	rounded	angular or rounded	angular or rounded	rounded	rounded	angular or rounded	rounded	angular or rounded	rounded	rounded	rounded	angular or rounded

Table B10 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
height of transition pr. pteroticum to sphenoticum	pteroticum higher	pteroticum slightly higher	pteroticum higher	pteroticum higher	pteroticum higher	**sphenoticum higher or similar**	**sphenoticum higher or similar**	pteroticum higher	**sphenoticum higher or similar**	**sphenoticum higher or similar**	pteroticum barely higher or similar	pteroticum slightly higher or similar
shape of transition pr. opercularum - inferior	concave	concave	rather straight or slight concave	concave	concave	concave	concave	none; straight or slight concave	straight or slight concave	straight or slight concave	concave	straight or concave
depth of transition pr. opercularum - inferior	shallow	shallow	**very shallow**	**shallow**	deep	rather deep	deep	very shallow	very shallow	very shallow	shallow	very shallow
length of transition pr. opercularum - inferior	long	long	long	long	long	rather long	long	very short	short	short	long	very short
height of transition pr. opercularum - pteroticum	high, low in small specimens possible	rather low	rather low	rather low	rather high	rather low	rather high	rather low	high	high	high	very high
protruding transition pr. opercularum - pteroticum	not	**slightly protruding**	not	not	slight	opercularum slight sometimes	opercularum slight sometimes	pteroticum slight	pteroticum slight	not	opercularum slight sometimes	slight
ridges on transition pr. opercularum - pteroticum	none	slight	none	none	none	none	slight	none	**medial and slight lateral**	**slight possible**	none	slight
relative length of transition pr opercularum - pteroticum to pr pteroticum	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	**longer**
length of transition pr. sphenoticum - crista anterior	short	short	short	very short	very long	short	rather short	short	**short**	**long**	short	rather short
shape of transition pr. sphenoticum - crista anterior	round	round or bit angular	round	round or angular	round	round or angular	round or straight	round	**round**	**round**	round or angular	round or straight
depth of transition pr. sphenoticum - crista anterior	deep	rather deep	rather deep	shallow	very deep	shallow	shallow	shallow	**deep**	**deep**	shallow	shallow
orientation pr. sphenoticum - opercularum	not parallel	not parallel	not parallel	not parallel	not parallel	rather parallel	**not parallel**	almost parallel	rather parallel	rather parallel	not parallel	rather parallel

Table B11. Diagnostic features of the right hyomandibula.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general height	rather low	rather low	rather low	rather low	rather high	high	rather high	high	rather high	rather high	high	rather high
general width	rather broad	slender	rather slender	rather broad	slender inferior, broad caput	slender, broad caput	slender	slender	rather slender	rather slender	slender	slender or rather broad
caput height	low	low	rather high or low	rather high or low	low	rather low	rather low	rather low	rather high	rather high	rather high	high
crista anterior width	wider than caput	wider than caput	wider than caput	wider than caput	wider than caput	slightly wider than caput or same	slightly wider than caput or same	slenderer than caput	**wider than caput**	**slightly wider than caput**	similar to caput	slenderer than caput
crista anterior widening	clear	clear	clear	clear	clear	barely	slight	slight or none	clear	clear	slight or slenderer	none
crista anterior shape	2 parts equal	2 parts equal	2 parts equal	2 parts equal	2 parts equal	1 part or 2 small equal	1 part or 2 small equal	1 part	2 parts, upper smaller or equal	2 parts, upper smaller or equal	1 or 2 equal	1 part
processus inferior width	broad	slender	rather broad	broad	slender	broad	slender	rather broad	broad	broad	slender	broad

Table B11 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus inferior tip	broader	broader	broader	broader	slight broader sometimes	slightly broader	slightly broader	not broader	slightly broader	slightly broader	slightly broader	broader
processus inferior length	rather short	long	long	long	rather long	long	long	long	long	long	long	rather short
processus inferior length thickness	flat	flat	flat	flat	flat	flat	flat	rather round	flat	rather flat	flat	rather round or bit flat
processus pteroticum dorsal edge	straight	straight or slight convex, bumpy	straight or slight convex	straight or slight convex	slight convex	straight or slight convex	straight or convex	**concave**	straight or convex, sometimes slight concave	straight or convex, sometimes slight concave	straight or slight convex	straight
processus pteroticum relative inclination	posterior slightly higher	posterior higher or same	posterior slightly higher	posterior slightly higher	posterior slightly higher	posterior barely higher	anterior higher	same; protruding	posterior slightly higher or same	posterior slightly higher or same	posterior slightly higher	posterior higher
processus pteroticum shape	oval	oval or posterior broader	**oval, sometimes slight constriction in middle**	**oval, sometimes slight constriction in middle**	oval, sometimes slight constriction in middle	oval	oval	oval	oval, sometimes slender	oval	oval	round or tear shape, posterior broader
processus pteroticum height	long	rather short	rather long	rather short	rather short	long	long	rather short	long	short or long	long	very short
processus opercularum shape	round	round	round	round	round or oval	round	round or oval	round, irregular	round	round	round or oval	round or oval
processus opercularum width	broad	broad	broad	broad	slender	broad	slender	broad	broad	broad	rather broad	very broad
processus opercularum protruding	slightly	not or slight	not or slight	not or slight	slightly	slightly	slightly	not	slightly	not or slightly	slightly	clear
processus opercularum orientation	posterior	posterior or slight ventral	posterior	posterior	posterior	posterior or slight ventral	posterior or ventral	posterior	ventral	ventral	slight ventral	ventral
processus opercularum height	short	short	short	short	long	long	**very long**	**very short**	short	short	rather long	rather short
processus sphenoticum width	broad	slender, sometimes broad	broad	broad	slender	very broad	slender or broad	rather broad	broad	broad	slender	slender
processus sphenoticum length	short	short	rather short	rather short	rather short	rather short	long	very short	very long	rather long	rather short	rather long
depth of transition pr. pteroticum to sphenoticum	rather shallow or deep	shallow	shallow or deep	shallow or deep	shallow	shallow	shallow	shallow	shallow or deep	shallow	shallow	shallow or deep
width of transition pr. pteroticum to sphenoticum	rather broad	slender	rather broad or slender	rather broad	broad or slender	slender	rather broad or slender	rather slender	slender	rather slender	broad or slender	broad
shape of transition pr. pteroticum to sphenoticum	angular or rounded	angular or rounded	angular or rounded	rounded	rounded	angular or rounded	rounded	angular or rounded	rounded	rounded	angular or rounded	angular or rounded
height of transition pr. pteroticum to sphenoticum	pteroticum higher	pteroticum slightly higher	pteroticum higher	pteroticum higher	pteroticum higher	**sphenoticum higher or similar**	**sphenoticum higher or similar**	pteroticum higher	**sphenoticum higher or similar**	**sphenoticum higher or similar**	pteroticum barely higher or similar	pteroticum slightly higher or similar
Transition pr. opercularum - inferior shape	concave	concave	rather straight or slight concave	concave	concave	concave	concave	none; straight or slight concave	straight or slight concave	straight or slight concave	concave	straight or concave
depth of transition pr. opercularum - inferior	shallow	shallow	**shallow**	**very shallow**	deep	rather deep	deep	very shallow	very shallow	very shallow	shallow	very shallow
length of transition pr. opercularum - inferior	long	long	long	long	long	rather long	long	very short	short	short	long	very short
height of transition pr. opercularum - pteroticum	high, low in small specimens possible	rather low	rather low	rather low	rather high	rather low	rather high	rather low	high	high	high	very high
protruding transition pr. opercularum - pteroticum	not	**slightly protruding**	not	sometimes	slight	opercularum slight sometimes	opercularum slight sometimes	pteroticum slight	pteroticum slight	not	opercularum slight sometimes	slight

Table B11 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ridges on transition pr. opercularum - pteroticum	none	slight	none	none	none	none	slight	none	**medial and slight lateral**	**slight possible**	none	slight
relative length of transition pr opercularum - pteroticum to pr pteroticum	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	shorter	**longer**
length of transition pr. sphenoticum - crista anterior	short	short	very short	short	very long	short	rather short	short	**short**	**long**	short	rather short
shape of transition pr. sphenoticum - crista anterior	round	round or bit angular	round	round or angular	round	straight	round or straight	round	**round**	**round**	round or angular	round or straight
depth of transition pr. sphenoticum - crista anterior	deep	rather deep	rather deep	shallow	very deep	shallow	shallow	shallow	**deep**	**deep**	shallow	shallow
orientation pr. sphenoticum - opercularum	not parallel	not parallel	not parallel	not parallel	not parallel	rather parallel	**not parallel**	almost parallel	rather parallel	rather parallel	not parallel	rather parallel

Table B12. Diagnostic features of the left palatine.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
collum width	broad	broad	**broad**	**slender**	rather slender	broad	slender	slender	rather broad	rather broad	slender	slender
collum length	short	short	**long**	long	short	short	short	rather long	short	short	rather long	short
caput width	broad	broad	broad	rather broad or slender	broad	broad	broad	slender	rather broad	broad	slender	slender
caput edge shape	convex or straight	convex	convex	convex or straight	convex	convex	convex	**straight**	straight or slight convex	straight or slight convex	rather straight	rather straight
caput relative width to collum	broader	broader	broader	slightly broader	broader	broader	**much broader**	slightly broader	slightly broader	slightly broader	not or barely broader	slightly broader
caput shape	laterally flat	laterally flat	laterally flat	laterally flat or round	laterally flat	laterally flat	laterally flat	laterally slightly flat	laterally flat	laterally flat	laterally slightly	**round**
caput curvature axis	slight medial	slight medial	rather straight or slight medial	rather straight or slight medial	slight medial	medial	slight medial	medial	straight	straight	straight	straight
caput curvature	straight	straight or subtle medial	straight	straight	slight medial	straight	straight	straight	slight medial	slight medial	none or barely medial	**straight**
processus inferior length	long or short	long	short	long	**short**	very long	long	**very short**	long	long	very long	very long
relative length of processus inferior to corpus	processus twice as long	processus longer	processus slightly longer	processus slightly longer or similar	processus slightly longer	processus more than twice as long	processus more than twice as long	**processus slightly shorter**	processus twice as long	processus twice as long	processus more than twice as long	processus more than twice as long
processus inferior width	rather broad	broad	rather slender	slender	broad or slender	rather slender or broad	slender	broad	slender	slender	slender	broad
processus inferior tip shape	pointed	pointed	angular or pointed	pointed	pointed or irregular	pointed	pointed	rounded or pointed	rather pointed	pointed	pointed	pointed
processus inferior curvature	rather straight or subtle curve backward	rather straight or subtle curve backward	straight or bend backward	straight	straight	straight or slight bend backward	subtle backward or rather straight	straight	straight or slight backward	straight or slight backward	straight	straight

Table B12 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus inferior thickness	bit flat laterally	bit flat laterally	bit flat laterally	bit flat anteriorly	bit flat laterally	bit flat laterally	barely flat laterally	bit flat laterally	bit flat anteriorly	bit flat anteriorly	bit flat laterally	flat laterally
relative position of processus inferior and pars hypopterygoidea	further or similar	further or similar	bit further or similar	further	bit further or similar	**much further**	further	bit further or similar	further or similar	similar	bit further	further
angle between processus inferior and collum	120 degrees	110-120 degrees	100-110 degrees	100-130 degrees	110-120 degrees	120-140 degrees	110 degrees	120-150 degrees	90-120 degrees; tip more	110-130 degrees	**130-150 degrees**	**90 degrees**
number of pars hypopterygoidea (crista)	1	1	1	**2**	1	1	1	1	1	1	1	1
pars hypopterygoidea (crista) length	short	short	short	short	short	short	short	rather short	long	long	**very long**	very short
pars hypopterygoidea (crista) height	low	low	low	low	**high**	low	low	**high**	rather high	high	**low**	very low
pars hypopterygoidea (crista) edge shape	straight	straight or slight convex	slight convex	slight convex or pointed	straight or slight convex, irregular	straight or slight concave	straight or convex	straight	convex, irregular	convex, irregular	rather straight or slight concave	slightly or strongly convex
pars hypopterygoidea (crista) symmetry	dorsal longer	dorsal longer	dorsal longer	dorsal longer	**similar or ventral longer**	dorsal longer	**ventral slightly longer**	similar	dorsal longer	dorsal longer	dorsal slightly longer	similar or dorsal longer
pars hypopterygoidea (crista) orientation	**upward**	upward or backward	backward	dorsal upward, lateral backward	bit upward or backward	backward	backward	slightly upward	downward	downward	downward	backward
indent between pars hypopterygoidea and processus inferior	**present**	none	sometimes	none	subtle or large	none	none	sometimes, small	barely or none	small	none	none
dorsal margin shape at collum	concave	slight concave	rather straight or slight concave	concave	concave	straight or slight convex	straight	straight or concave	rather straight	rather straight	straight	concave
dorsal margin shape at pars hypopterygoidea	concave	slight concave	rather straight or slight concave	concave	concave	straight or slight convex	straight	concave	concave or straight	concave or straight	straight or slight concave	concave
ventral margin shape at collum	concave	concave	concave	**slight convex**	concave	strong concave	concave	straight or slight concave	straight or concave	straight or concave	straight	concave
ventral margin shape at processus inferior	straight or slight convex	straight or bend	convex or bend	straight	straight or slight convex	straight or convex	straight, bend	straight or slight convex	straight or convex	straight or convex	straight or slight convex; **protruding part crista**	slight convex
dorsal transverse ridge on collum	absent	absent	absent	absent	absent	absent	absent	absent	**present**	**present**	**present**	slight

Table B13. Diagnostic features of the right palatine.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
collum width	broad	slender	**slender**	**broad**	slender	broad	slender	slender	slender	slender	slender	broad
collum length	long	long	long	long	long	short	long	very long	rather long	rather long	very short	short
caput width	broad	rather slender	broad	broad	rather slender	broad	rather slender	slender	slender	slender	slender	slender
caput edge shape	convex	straight or convex	convex	convex	convex or straight	straight	convex or straight	straight or angular/convex	strong convex	convex or straight	rather straight	straight
relative width of caput to collum	slightly broader	broader	broader	broader	slightly broader	**not broader**	broader	**not broader**	slightly broader	slightly broader	barely or slightly broader	**not broader**

Table B13 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
caput shape	**round**	laterally flat	laterally flat	laterally flat	laterally flat	laterally slightly flat	laterally flat or round	rather round	laterally flat	laterally flat	laterally slightly flat	**round**
caput curvature around axis	rather straight	slight medial	rather straight or slight medial	rather straight or slight medial	rather straight or slight medial	medial	slight medial	straight	none	none	none	none
caput curvature	straight	slight medial and slight dorsal	straight or subtle medial	straight	**tip slightly ventral**	medial	slight medial	**tip slightly ventral**	strong medial	strong medial	none	none
processus inferior length	rather short	short	short	short	**very short**	short	long	**very short**	very long	very long	very long	long
relative length of processus inferior to corpus	similar	processus slightly shorter	similar	processus slightly longer	**processus more than twice as short**	**processus shorter**	processus longer	**processus more than twice as short**	processus more than twice as long	processus more than twice as long	processus more than twice as long	processus more than twice as long
processus inferior width	broad	rather slender or broad	slender	rather slender	very broad	slender	slender	rather broad	slender	slender	slender	slender
processus inferior tip shape	pointed, flattened anteriorly	pointed	pointed or rounded	angular or pointed	rounded	pointed	pointed	rounded or pointed	rather pointed	pointed	pointed	pointed
processus inferior curvature	rather straight or tip subtle curve backward	rather straight or subtle curve backward	straight or slightly backward	straight or bend backward	straight	straight or slightly backward	straight	straight	straight or slight backward	straight or slight backward	straight	straight
processus inferior thickness	rather round or tip slightly flattened anteriorly	bit flat anteriorly	bit flat anteriorly	bit flat laterally	as bulb	bit flat laterally	bit flat anteriorly	as bulb	bit flat anteriorly	barely flat	bit flat laterally	bit flat laterally
relative position of processus inferior and pars hypopterygoidea	further	further	further	bit further or similar	**less**	similar	further	**slightly less**	similar or bit further	similar or bit further	bit further	shorter
angle between processus inferior and collum	**130-140 degrees**	110-130 degrees	100-130 degrees	100-110 degrees	90-100 degrees	130-140 degrees	130-140 degrees	110-130 degrees	100-120 degrees	110-130 degrees	100-120 degrees	100-120 degrees
number of pars hypopterygoidea (crista)	2	2	2	**1**	1	2	2	1	1	1	1	0
pars hypopterygoidea (crista) length	short	short	short	short	rather short	rather long or rather short	rather long	rather short	short	short	**long**	barely or absent
pars hypopterygoidea (crista) height	low	low	low	low	rather low, **very broad**	rather high	lateral rather high, medial low	high	low	low	**very low**	barely or absent
pars hypopterygoidea (crista) edge shape	convex	convex	convex	slight convex	straight or convex	slight convex or straight	convex	straight	convex, irregular	convex, irregular	rather straight, irregular	NA
pars hypopterygoidea (crista) symmetry	**similar**	**lateral longer**	**dorsal longer**	dorsal longer	similar	lateral longer	lateral longer	similar or dorsal subtly longer	dorsal longer	dorsal longer	dorsal longer	NA
pars hypopterygoidea (crista) orientation	slight backward and sideways	slight backward and sideways	slight backward and sideways	backward	backward and slightly upward	backward and medial	lateral backward, dorsal medial/upward	backward	**downward**	**downward**	**downward**	NA
indent between pars hypopterygoidea and processus inferior	none	none	none	**sometimes**	none	none	**small**	none	none	none	none	none
dorsal margin shape at collum	concave	slight concave	concave	rather straight or slight concave	straight or slight concave	convex	straight	straight or slight convex	concave	concave	straight	rather straight
dorsal margin shape at pars hypopterygoidea	concave or rather straight, bumpy	slight concave or rather straight	rather straight or slight concave	rather straight or slight concave	straight or slight concave	concave	straight or slight convex	concave	concave or straight	concave	straight or slight concave	rather straight
ventral margin shape at collum	concave	slight convex or straight	slight convex	concave	concave	concave	straight	straight or slight concave	straight or concave	straight or concave	straight	slight convex
ventral margin shape at processus inferior	straight or concave	straight or bend	straight or slight bend	convex or bend	rather straight; very short	straight or convex	straight or slight concave	straight or slight convex	straight or convex	straight or convex	straight or slight convex	straight
dorsal transverse ridge on collum	absent	absent	absent	absent	absent	absent	absent	absent	**present**	**present**	**present**	absent

Table B14. Diagnostic features of the vomer.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
symmetry bulbs	left higher	left higher	left higher	**right higher**	left higher	left higher or same	left higher	left higher	right higher	right higher	similar	left higher
left pars ethmoidalis size	wide, rather long	wide, rather long	wide, short	wide, short	wide, long	wide, short	wide, long	slender or wide; usually short	slender, short	rather slender, short	broad, long	**slender; rather high, short**
right pars ethmoidalis size	short; slender	short; slender	short; broad	short; broad	long, wide	short; wide	long, wide	usually short, slender or wide	long, slender	long, rather broad	long, broad	**slender; rather high**
relative lateral partes ethmoidales size	left wider and longer	left wider and longer	left longer	right longer	similar	left longer	left wider and longer	right longer sometimes	right longer	right longer	right longer; left sometimes wider	left bit longer and wider
orientation of left pars ethmoidalis	diagonal	straight caudal	diagonal	diagonal	rather lateral or slightly more caudal	diagonal; more caudally and dorsally	diagonal	diagonal and more dorsally	slight diagonal or rather caudal	rather diagonal	slightly more diagonal	dorsally; sometimes bit curved laterally
orientation of right pars ethmoidalis	diagonal	slightly lateral	diagonal	straight caudal	rahter lateral	diagonal	slightly laterally curved	**lateral**	strongly straight caudal	strongly straight caudal	strongly straight caudal	dorsally; sometimes bit curved laterally
dorsal center depth between bulbs	shallow	shallow	rather deep	rather shallow or deep	shallow	shallow	shallow	rather shallow	rather deep	rather deep	rather deep	rather shallow
dorsal center hook	subtle small	small or large	none	none	sometimes small	short or long, broad	small; pointed or rounded	sometimes short, slender, rounded	**large; clearly protruding and curved dorsally, pointed or rounded**	**small or none; not protruding, caudally oriented**	**long and broad, dorsally protruding; flat laterally; slight curved caudally**	none
dorsal center shape between bulbs	M-shape with subtle hook	M-shape; broad, sometimes cover bulbs	v-shape; asymmetrical; sometimes small	m- or v-shape	heart-shape, round, v-shape	m-shape; broad	unclear or m-shape	broad	m-shape; slender	m-shape; rather wide	v-shape; rather slender	very small
right bulb lateral structures	edge not clear; **fold ventrally with facies**	edge clear; facies on ventral part possible	edge not clear; **facies ventrally, large and round**	edge not clear; sometimes deep pit	edge rather clear, much anterior positioned	edge very clear	edge very clear; large pit	edge rather clear, short; large pit	edge very clear; angular ventrally	edge clear	clear edge, bit overhanging caudally	edge not clear; sometimes facies
right bulb lateral edge shape	slight concave or straight	slight concave or rather straight	concave	rather straigh or slight convex	slight concave or straight	straight or concave	slight concave	slight concave or rather straight	concave	rather straight	rather straight, ventral part convex, dorsal sometimes slight concave	slight concave or straight
frontal indent width	**broad**	slender	**slender**	slender	slender	broad	rather slender	broad	broad	slender	slender	/
frontal indent depth	**deep**	usually shallow	**shallow**	shallow	shallow	shallow	shallow	very shallow	shallow	shallow	shallow	/
frontal indent shape	**concave, round**	straight, heartshape or concave, round or angular	**heart shaped, round or angular**	concave, round or angular	heart shaped or straight, angular	heart shape or concave, round or angular	concave or straight, round	concave or slight V-shape, round or angular	concave, slight heart shape or slight v-shape, round or slight angular	rather straight, sometimes slight v-shape, angular	rather straight, sometimes slight v-shape or hearth shape, angular or round	straight or convex; sometimes slight indent possible
ventral dentition	absent; few foramen present sometimes	absent; few foramen present sometimes	absent; foramen present sometimes	absent; few foramen present sometimes	absent; few foramen present sometimes	absent; few foramen present sometimes	absent; few foramen present sometimes	absent; **surface can be flat**	**present; few or many large alveoli, often in round**	**present; few or many large alveoli, often in round**	**present, at least one tooth; long teeth; alveoli not clear**	absent
ventral view bulbs relative size	right longer, more caudally positioned	right more anterior and diagonally oriented; left more caudally oriented	right more diagonally, 2 bumps; left more caudally	right broader and diagonal; left slightly more caudal	right more diagonally and anteriorly; left longer, more caudally	right more anteriorly and laterally	left more diagonal, slightly longer	left larger	left bit more caudally	left bit more caudally	right larger, more caudallly; left more diagonally, laterally	bulbs not distinguishable; **very slender; high**
edge right bulb ventral view	well defined	well defined	well defined	not defined	well defined; protruding	well defined	well defined	**not clear**	well defined	well defined	well defined	not clear
edge left bulb ventral view	less defined	well defined	well defined	not defined	well defined; protruding	well defined	well defined	**not clear**	well defined	well defined	well defined	not clear
angle between bulbs in ventral view	less than 90degrees	90degrees; clear; skewed	around 90degrees	less than 90degrees	slightly more than 90degrees	around 90degrees	barely	no clear angle	60-90degrees	60-90degrees	around 90degrees	no clear angle
ridges on frontal/dorsal side	none, sometimes one	none or two slight	none or two	none or two slight	one slight or barely	two barely or none	one large or two small	two or none, usually with base of hook	one or two large	one or two large	one small	none, one or two slight
shape bulbs in dorsal view	ventral part bit wider; rounded	ventral part of bulbs wider	ventral part bit wider; rounded	ventral part bit wider; rounded	right ventral large and round	ventral part bit wider; rounded	ventral part bit wider; rounded	skewed to right ventrally	very wide and angular ventrally	very wide and round ventrally	wider dorsally	slender; high; skewed to left
relative size bulbs in dorsal view	left higher and wider	left broader and longer dorsally and higher and rounder ventrally; right more angular	left wider caudally	right higher and wider	right wider ventrally; left wider dorsally	left wider and longer dorsally	left wider and higher ventrally, longer dorsally	left bit broader	left wider ventrally; right longer dorsally	right longer dorsally	left wider midheigt; right longer caudally	right wider

Table B14 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
left bulb structurs in dorsal view	dorsal facies	caudal facies	caudal facies	none	caudal facies	facies	caudal facies possible	caudal large round facies	caudal facies possible	small facies possible larger specimens	bump possible	none
right bulb structures in dorsal view	none	none	caudal angular bulb	dorsal facies	caudal facies	facies	none	caudal large round facies	caudal facies possible	small facies possible larger specimens	facies possible	bump possible
left bulb lateral shape in dorsal view	rather straight	concave	rather straight	concave	slight concave	straight	slight concave or rather straight	straight or slight convex	strong concave	concave	convex	rather straight
right bulb lateral shape in dorsal view	laterally concave	concave	concave	straight	strong concave	concave	slightly concave	straight or slight convex	rather straight	concave	concave	rather straight
left bulb lateral bump	possible	possible	bump midheight	facies ventrally, large and round	bump or ridge possible midheight	none	none	possible	none	none	bump midheight	facies possible
left bulb lateral edge shape	concave; clear	straight or concave; clear	rather straight or convex; clear	concave; not clear	straight or slight concave; slightly clear	straight or slight concave; very clear	concave; clear; sometimes protrude ventrally	straight or concave; not clear	concave; very clear; angular ventrally	rather straight or slight concave; clear	rather straight; clear; overhanging	straight or slight convex; not clear
apophysis posterior	low; slender	low; slender; slight pit possible	low; slender	low; slender	low; slender; pit possible	very low; rather broad; flat	rather low; very slender	**very high;** slender; thick	rather low; broad; slightly hollow	rather low; very slender	low; slender	low; slender; (almost) as broad as caput

Table B15. Diagnostic features of the left posttemporal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general length	long	long	long	long	long	long	rather short	rather long	rather long	rather short	rather short	short
general width	slender	very slender	slender	slender	slender	slender	slender	slender	**very broad**	**very broad**	**very broad**	slender
general curvature	straight	straight or slight curve	straight	straight	rather straight	straight or slight curve	straight	straight or slight curve	slight curve	slight curve	rather straight	straight
general shape	tear	tear	tear	tear	tear	tear	tear	**cone**	tear	tear	**oval**	**L-shape**
general roundness	bit flat	bit flat	bit flat	bit flat	bit flat	bit flat	bit flat	rounded	flat	flat	flat	rounded
processus medialis length	short or long	short or long	short or long	short or long	very short	long	short or long	short	**short**	**long**	long	very long
processus inferior length	short or long; rarely absent	short or long	long	long or short	very short	very short	rather short or long	very short, as bump	**very short, barely distinguishable from corpus, visible as bump or foramen**	**very short, as foramen or bump**	very short	none or as spina
processus inferior protruding	clear	clear	clear	clear	not	slight	clear	slight	**not or barely**	**not or slight**	not or barely	not
lateral side of processus inferior	short or long indentation	short indentation	short indentation	short indentation	**huge hole**	short indentation	**long indentation**	short indentation	short indentation	short indentation	no or short indentation	no indentation
shape of incision between processus inferior and corpus	**v-shape or round**	**none or v-shape or round**	v-shape or round	v-shape or round	none or round	**none or round or angular**	v-shape or rounded	none	none or v-shaped	none or rounded	none or rounded	none
width of incision between processus inferior and corpus	**slender**	**slender**	slender or broad	slender or broad	slender or broad	**slender or broad**	slender	none	slender	slender	slender	none
depth of incision between processus inferior and corpus	**short; as deep as inferior long**	**short; as deep as inferior long**	long; as deep as inferior long	long; as deep as inferior long	very short	**very short**	short; as deep as inferior long	none	short	short	short	none
processus superior shape	flattened antero-posterior	**slightly flattened antero-posterior**	flattened antero-posterior	flattened antero-posterior	flattened antero-posterior	**flattened antero-posterior**	bit flattened antero-posterior	sometimes slightly flattened antero-posterior	flattened laterally	flattened laterally	**flat laterally**	bit flat antero-posteriorly

Table B15 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus superior length	long	long	long	long	long	long	rather long	rather long	rather short	rather short	**short**	long
processus superior width	rather broad; same as caput	slender; less than caput	rather broad; same or bit less than caput	rahter broad; less than caput	slender; less than caput	rather broad; less than caput	very slender; much less than caput	rather broad; bit less than caput	broad base, slender tip; much less than caput	broad base, slender tip; much less than caput	**broad; same as caput**	slender; same or bit less than caput
processus superior curvature around axis	slightly curved axis	**slightly curved axis**	**slightly curved axis**	**not or barely curved axis**	not or slightly curved axis	strongly curved axis	slightly curved axis	barely curved axis	not curved axis	not curved axis	not curved axis	not curved axis
processus superior curvature	straight	straight	straight	straight	sometimes laterally	**slightly anteriorly**	sometimes	sometmes medially	slightly anteriorly	anteriorly	not	slightly laterally
processus superior tip shape	pointed	pointed	pointed	pointed	pointed or rounded	pointed	pointed or rounded	angular, pointed or rounded	pointed	pointed	**round, barely protruding**	pointed
pars articularis supracleithralis thickness	flat	bit flat	flat	flat	flat edge, center bulbuous	flat	flat	thick	flat	flat	flat	flat
canalis lineae lateralis	clear; sometimes thicker	clear; not thicker	clear; sometimes thicker	clear; sometimes thicker	**clear; very huge holes, almost whole side with only small ridge in between**	slightly; very small holes	clear; very deep hole processus inferior	slightly; very small holes	**not clear**	**not clear**	**not clear**	slightly; small holes
lateral surface	pits possible	pits possible	pits possible	pits possible	pits possible	pits possible	pits possible	smooth	pits possible	pits possible	usually smooth	smooth
lateral side structures	sometimes ridges anteriorly	none	none	none	none	slight ridge at anterior side possible	none	none	none	none	none	**pointed crista at processus superior**
tubercules	none	none	**often, multiple along channel**	**often, multiple along channel**	none	none	none	none; slight bump at ventral tube possible	none	none	none	none

Table B16. Diagnostic features of the right posttemporal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general length	long	long	long	long	rather short	long	rather short	rather long	rather long	rather short	rather short	short
general width	slender	very slender	slender	slender	broad	slender	slender	slender	**very broad**	**very broad**	**very broad**	slender
general curvature	straight	straight or slight curve	straight	straight	straight or slight curve	straight or slight curve	straight	straight or slight curve	slight curve	slight curve	rather straight	straight
general shape	tear	tear	tear	tear	tear	tear	tear	**cone**	tear	tear	**oval**	**L-shape**
general roundness	bit flat	bit flat	bit flat	bit flat	bit flat	bit flat	bit flat	rounded	flat	flat	flat	rounded
processus medialis length	short or long	short or long	short or long	short or long	very short	long	short or long	short	**short**	**long**	long	very long
processus inferior length	short or long; rarely absent	short or long	long	long or short	very short	very short	rather short or long	very short, as bump	**very short, barely distinguishable from corpus, visible as bump or foramen**	**very short, as foramen or bump**	very short	none or as spina
processus inferior protruding	clear	clear	clear	clear	not	slight	clear	slight	**not or barely**	**not or slight**	not or barely	not
lateral side of processus inferior	short or long indentation	short indentation	short indentation	short indentation	**huge hole**	short indentation	**long indentation**	short indentation	short indentation	short indentation	no or short indentation	no indentation

Table B16 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
shape of incision between processus inferior and corpus	**v-shape or round**	**none or v-shape or round**	v-shape or round	v-shape or round	none or round	**none or round or angular**	v-shape or rounded	none	none or v-shaped	none or rounded	none or rounded	none
width of incision between processus inferior and corpus	**slender**	**slender**	slender or broad	slender or broad	slender or broad	**slender or broad**	slender	none	slender	slender	slender	none
depth of incision between processus inferior and corpus	**short; as deep as inferior long**	**short; as deep as inferior long**	long; as deep as inferior long	long; as deep as inferior long	very short	**very short**	short; as deep as inferior long	none	short	short	short	none
processus superior shape	flattened antero-posterior	**slightly flattened antero-posterior**	flattened antero-posterior	flattened antero-posterior	flattened antero-posterior	**tip flattened antero-posterior**	bit flattened antero-posterior	sometimes slightly flattened antero-posterior	flattened laterally	flattened laterally	**flat laterally**	bit flat antero-posteriorly
processus superior length	long	long	long	long	long	long	rather long	rather long	rather short	rather short	**short**	long
processus superior width	rather broad; same as caput	slender; less than caput	rather broad; bit less than caput	rahter broad; less than caput	slender; less than caput	rather broad; less than caput	very slender; much less than caput	rather broad; bit less than caput	broad base, slender tip; much less than caput	broad base, slender tip; much less than caput	**broad; same as caput**	slender; same or bit less than caput
processus superior curvature around axis	slightly curved axis	**slightly curved axis**	**not or barely curved axis**	**slightly curved axis**	slightly curved axis	not or barely curved axis	slightly curved axis	barely curved axis	not curved axis	not curved axis	not curved axis	not curved axis
processus superior curvature	straight	straight	straight	straight	straight	**slightly anteriorly**	sometimes	sometmes medially	slightly anteriorly	anteriorly	straight	slightly laterally
processus superior tip shape	pointed	pointed	pointed	pointed	pointed	pointed	pointed or rounded	angular, pointed or rounded	pointed	pointed	round, barely protruding	pointed
pars articularis supracleithralis thickness	flat	bit flat	flat	flat	flat	flat	flat	thick	flat	flat	flat	flat
canalis lineae lateralis	clear; sometimes thicker	clear; rarely thicker	clear; sometimes thicker	clear; sometimes thicker	**clear; very large holes, small ridge in between**	slightly; very small holes	clear; very deep hole processus inferior	slightly; very small holes	**not clear**	**not clear**	**not clear**	slightly; small holes
lateral surface	pits possible	pits possible	pits possible	pits possible	pits possible	pits possible	pits possible	smooth	pits possible	pits possible	usually smooth	smooth
lateral side structures	**large bump ventral of or on channel;** sometimes ridges anteriorly	none	none	none	none	slight ridge at anterior side possible	none	none	none	none	none	**pointed crista at processus superior**
tubercules	none; **one broad bump often**	sometime slightly	**often, multiple along channel**	**often, multiple along channel**	none	none	none	none; slight bump at ventral tube possible	none	none	none	none

Table B17. Diagnostic features of the urohyal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
incisura collis shape	broad, round V-shape	short or broad U- or round V-shape; almost parallel angulus and processus	round V-shape usually; U-shape in large specimens (min 40cm) possible	round V-shape usually; U-shape in large specimens (min 40cm) possible	round V-shape	broad, round V-shape	round V-shape	**short**, broad U-shape; **rather parallel angulus and processus**	**long**, slender U-shape; **rather parallel angulus and processus**	**long**, very slender U-shape; **rather parallel angulus and processus**	broad, rounded V-shape	L-shape
relative position between angulus inferior and processus hypohyalis	angulus inferior longer or similar	**angulus inferior longer**	angulus inferior longer or similar	angulus inferior shorter or similar than processus hypohyalis	angulus inferior bit shorter or similar	angulus inferior shorter	angulus inferior shorter	angulus inferior bit longer than processus hypohyalis or rather similar	angulus inferior longer	usually angulus inferior slightly shorter or similar	angulus inferior much shorter	angulus inferior much shorter
caput length	long	short or rather long	short or long	short or long	very long	short or long	short	short	short	short	long	short
caput shape	angular	round or bit more pointed	angular/rounded	rounded	very pointed or rounded pointed	angular/rounded	angular	rounded or angular	**angular**	**round or angular**	**caput almost half of length**; angular/pointed	rounded/angular

Table B17 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
angulus inferior curvature	**straight or slight posterior curve near tip**	curved	**straight or curved ventrally**	**straight or curved ventrally**	**straight or slight posterior curve near tip**	rather straight or slightly curved	**straight or curved ventrally**	curved	curved strongly	curved or rather straight	straight	straight or slightly curved
processus hypohyalis length	short	short	short	short	long	long	long	short	long	long	short	long
processus hypohyalis curvature	straight	straight	straight or slightly curved	straight or slightly curved	straight	curved or rather straight	straight	straight or s-curved	straight or slightly curve	straight or slightly curve	slight curve	straight
processus hypohyalis tip width	same width	bit broader	bit broader or rather same	bit broader	bit broader	same width	broader; 2 points sometimes	broader	broader	broader	broader	broader
processus hypohyalis relative length	**only as long or slightly longer than crista angulus inferior**	**only as long or slightly longer than crista angulus inferior**	**only as long or slightly longer than crista angulus inferior**	**only as long or slightly longer than crista angulus inferior**	**twice as long as the width of the crista angulus inferior**	**twice as long as the width of the crista angulus inferior**	**twice as long as the width of the crista angulus inferior**	twice as long as the width of the crista angulus inferior	much longer (>3) than crista angulus inferior	much longer (>3) than crista angulus inferior	shorter than crista angulus inferior	much longer (>3) than crista angulus inferior
broadest point	caput or ventral part of lamina	caput or ventral part of lamina	caput or ventral part of lamina	caput or ventral part of lamina	caput	caput or mid part lamina	mid or ventral part of lamina	caput or ventral part of lamina	caput or ventral part of lamina	dorsal or ventral part lamina	caput	caput
relative position between angulus inferior and processus hypohyalis	processus hypohyalis further or similar	angulus inferior further or rather similar	processus hypohyalis further	processus hypohyalis further	processus hypohyalis slightly further or similar	angulus inferior till halfway of processus hypohyalis	angulus inferior till halfway of processus hypohyalis	angulus inferior further or similar	processus hypohyalis bit further or similar	processus hypohyalis slightly furter or similar	angulus inferior till halfway of processus hypohyalis	processus inferior much further
general thickness	thin	thin	thin	thin or thick	thick	thick	thin	thick	thick	thick	thin	rather thin
angulus inferior orientation	diagonal; tip sometimes curved horizontally	diagonal; tip horizontal	ventral or diagonal	ventral or diagonal	rather horizontal	rather diagonal	diagonal; tip sometimes curved anteriorly or posteriorly	horizontal; tip sometimes upward	horizontal; tip sometimes upward	horizontal; tip sometimes upward	diagonal	ventral or diagonal
dorsal margin shape	straight; concave near tip	convex; straight or concave possible near tip	rather straight; sometimes concave at tip	rather straight; concave at tip	rather straight; straight or concave at tip	convex or straight	straight; concave near tip possible	convex or concave	straight or slight concave; concave near tip	straight or slight concave, rarely convex; concave near tip	concave	rather straight

Table B18. Diagnostic features of the first precaudal vertebra.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
length corpus	normal	normal	normal	normal	normal or rather short; **sometimes shorter at ventral side**	normal or rather short; sometimes shorter at ventral side	normal or rather short; sometimes shorter at ventral side	very short or short	**very short**	normal	short; shorter at ventral side	very short
distance between condyli	at least half length	half or third length	at least half length	at least half length	less than half length or almost no distance	almost no distance	almost no touching	almost no distance	**almost no distance or no distance**	**almost no distance or no distance**	half length or almost no distance	**no distance**
condyli protruding dorsally	no	no	no	no	sometimes bit	bit	clearly	no	**clearly**	**clearly**	no	**strongly**
inclination condyli	diagonal	diagonal	diagonal	diagonal	slight diagonal	slight diagonal	slight diagonal	**strongly diagonal**	**strongly diagonal**	**strongly diagonal**	diagonal	**strongly diagonal**
condyli protruding laterally	clearly; at level chorda	clearly; at level chorda	clearly; at level chorda	clearly; at level chorda	strongly; at level chorda	strongly; at level chorda	clearly; at level chorda	slightly; at level chorda	barely; below level chorda	clearly or barely; at level chorda	slightly; at level chorda	barely or slightly; at level chorda
dorsal part between condyli	curved	curved	curved	curved	curved	curved	curved	**horizontally straight/flat**	curved	curved	sometimes slightly flattened	curved
shape condyli	oval or slight bean shaped	oval or kidney	oval, kidney, tear	oval, kidney, tear	oval	**8-shape with lateral lobes broader than medial lobes**, kidney or tear-shaped; lateral part can be almost as broad as corpus	oval, 8-shape or bean-shaped; **edge protruding**	oval or slight kidney	irregular shape	bean shaped or oval	bean-shaped or round oval	**elongated oval;** dorsal part can be pointed

Table B18 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
indent condyli	concave or rather straight	rather straight	straight	straight	concave or rather straight	rather straight	slight concave	slight concave	rather straight	slight concave	rather straight	slight concave
depth condyli	shallow	shallow	shallow	shallow	shallow	rather deep	deep	shallow	sometimes deep	deep	shallow	shallow
condyli size	short; broad	rather long; slender	**rather long; rather slender**	**rather long; rather slender**	long; rather broad	very large; long; broad	long; broad	long; slender	very long; slender	short or long	short; rather broad	long; broad
neural arch shape	slender; broader at lower half	slender	rather slender, **broader at lower half**	rather slender, **broader at lower half**	slender; long	rather slender, **very broad at lower half**	slender; long	rather slender, broader at lower half	short; broad, broader at lower half	rather short; broad; broader at lower half sometimes	**rather short; broad**; broader at lower half sometimes	**short, no tip; very slender arch, as wide as center; slightly broader at lower half sometimes**
neural arch curvature	straight	straight	straight	straight	straight	straight	straight	straight, tip bit anteriorly curved	tip anteriorly curved	tip anteriorly curved	**tip anteriorly curved**	**straight or curved**
relative implant neural zygapophyses	**anterior lower than posterior**	**anterior higher than posterior**	anterior higher than or same as posterior	anterior higher than or same as posterior	barely anterior; anterior higher or same	anterior higher than or same as posterior	anterior higher than posterior	anterior lower than or same as posterior	barely anterior; anterior lower	anterior lower	barely anterior; anterior lower or same	barely anterior; anterior lower or same
postzygapohysis neural arch shape	rounded or pointed; rather short	pointed; long; slender	rounded; short	rounded; short	rounded; short	angular or rounded; short	rounded or pointed; short; slender	pointed or rounded; short	angular; large, broad	angular; large, broad	pointed; large, long	round; short; or absent
postzygapohysis neural arch orientation	**posterior**	**ventral**	**posterior**	**posterior**	posterior or lateral	posterior, slight lateral	ventral or slight lateral	slight lateral	lateral	lateral or dorsal	ventral	posterior or ventral
transition between center and lateral edge of condyli	short; straigh	short; straight	rather short; straight or subtle concave	rather short; straight or subtle concave	long; **straight or concave**	long; straight or concave	rather long; **straight or slightly convex;** base can be concave	short; slight concave or straight	no or long or short; straight or bit concave	very short; straight	short; slight concave or straight	very short; straight or slight concave
implant of transition between condyli and center	mid center	mid center	lower half	lower half	lower half	mid center	mid center	mid center or upper half	mid center	mid center or upper half	upper half	mid center
shape center	tear	anterior tear; **posterior hexagonal or rounded**	anterior round or tear; posterior round	anterior round or tear; posterior round	round or tear	diamond or round	almost round; ventrally sometimes slightly wider	tear, rounded or bit blocky; posterior side can be concave	tear	round or tear	round or tear	oval, round or hexagonal; posterior larger than anterior; sometimes corpus bend posteriorly
bumps center	2 posterior possible	2 posterior possible	2 posterior possible	2 posterior possible	2 posterior possible	2 posterior possible	posterior possible	none	none	posterior possible	none	2 posterior possible
lateral surface center	smooth; hole below condyli possible	smooth; hole below condyli possible	smooth	smooth	smooth	smooth	smooth; hole below condyli possible	smooth; hole below condyli possible	smooth	smooth or bumpy	smooth; hole below condyli possible	smooth

Table B19. Diagnostic features of the metapterygium.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general shape	asymmetrical rectangular	round rectangular	rather rectangular	rather rectangular	rather round	trapezoid	rectangular	square	rounded or square	rounded or square	rounded or square	triangular
general length	very long	long	very long	very long	long	rather short	long	short	short	rather long	short	short
relative length	longer than high	**slightly longer than high or rather similar**	longer than high	longer than high	**longer than high**	slightly longer than high	longer than high	**as high as long**	higher than long	longer than high	higher than long	longer than high
relative height	anterior higher than posterior	anterior higher than posterior	anterior higher than posterior	anterior higher than posterior	**anterior not higher than posterior**	**anterior not higher than posterior**	anterior slightly higher than posterior	anterior slightly higher than posterior	anterior not higher than posterior	anterior rather similar as posterior	posterior higher than anterior or similar	posterior much higher than anterior
thickness	thin	**thin**	**lower half can be thicker**	**lower half can be thicker**	**thin**	thin	thin	**thick lower half**	rather thick	thin	thin	thin

Table B19 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus ventralis protruding	anteriorly and dorsally	slightly anteriorly	**anteriorly and dorsally**	**anteriorly and dorsally**	slightly dorsally sometimes, barely anteriorly	barely, slightly dorsally sometimes	slightly dorsally and anteriorly	slightly anteriorly and dorsally	**strongly anteriorly and dorsally**	**strongly anteriorly and dorsally**	slight anteriorly	strongly anteriorly
processus ventralis length	long	short	long	long	short	short	short	short	long	very long	short	very long
processus ventralis width	broad	broad	broad	broad	broad	rather slender	slender	broad	rather broad	rather broad	slender	broad
processus ventralis shape	rounded or pointed	rounded	rounded	rounded	rounded	rounded	rounded or pointed	round	pointed	rounded or pointed	rounded	pointed or rounded
processus ventralis position	dorsally	dorsally	dorsally	dorsally	dorsally	dorsally	dorsally	dorsally	dorsally	dorsally	**midheight**	dorsally
articulation tube height	low	high	low	low	high	very high	low	high	very high	rather high	high	very high
articulation tube length	long	long	short	short	long	rather long	long	rather long	rather long	rather long	short	short
articulation tube proportions	**longer than high**	as high as long	as high as long	as high as long	as high as long	higher than long	**longer than high**	higher than long	higher than long	as high as long	higher than long	higher than long
articulation tube shape	rather straight	rather straight	rather straight	rather straight	straight or concave	straight or slight convex	rather straight	rather straight	convex	rather straight	straight or convex	convex
articulation tube protrusions	none	none	none	none	none	none	ventral slightly protrusion of crista	none	none	ventral and dorsal slight protrusion of crista possible	ventral long protrusion of crista	none
margo dorsalis	slight concave	straight or slight concave, irregular	straight or concave	straight or concave	straight or concave, irregular	short, concave	straight	concave or rather straight, sometimes irregular	straight	straight	straight	straight or bumpy
margo inferior	**straight, can be irregular**	rather straight	rather straight or convex, sometimes bumpy	rather straight or convex, sometimes bumpy	slight convex or concave	rather straight	convex or rather straight	slight concave or straight	bumpy	bumpy	bumpy	strongly concave
posterior edge shape	S-curve	convex	convex, sometimes concave	convex, sometimes concave	convex or concave	straight or slight convex	**irregular,** convex or straight	slight convex, concave or rather straight	S-curve	S-curve	S-curve	strongly concave

Table B20. Diagnostic features of the basioccipital.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ventral view of anterior margin of lateral cristae	long; convex	short or long; straight or convex; sometimes bumps	rather long; convex or straight	rather long; convex or straight	short; broad; convex	short; convex	long; broad; convex	short; slender; straight or convex	**very short; slender; concave**	**short; rather broad; concave**	short; rather broad; concave	short; slender; convex
ventral view of posterior margin of lateral cristae	concave or straight	short; straight or concave; sometimes bumps	long; straight, gradual	long; straight, gradual	rather straight	long; slight concave	long; broad; straight	unclear	**straight; slender**	**straight**	concave or straight	short; slender; convex
number of lateral spina at center	2; right larger	0 to 2; small	0 to 2	0 to 2	2; large; low on center	2; small	very small or absent; rather dorsally	2; large; right larger	2	2	none or 2; small	2
number of dorsal spina at center	low; 1 broad or 2 smaller fused	1 or 2; small	1 or 2	1 or 2	large; broad	1; broad	1 or 2; broad	0 to 2 dorsal; small to large	1	1	1 or 2; small	1
number of ventral spina at center	none	none	none	none	2 unclear	2; large; rather laterally	0 to 2; small	2; small or large	2	2	none	1 or 2

Table B20 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative height of lateral cristae to center	**crista much lower than center; fits between min and max height of corpus**	crista lower than center or similar height; crista starts around mid-center posteriorly and can be above center anteriorly	**crista similar height as center, not protruding dorsally or ventrally**	crista similar height as center, not protruding dorsally or ventrally	crista similar height; not till ventral edge and dorsally protruding	crista low, less high than center; till ventral edge, not till dorsal edge	crista lower than center or similar height; not till dorsal edge, bit protruding ventrally	crista low, less high than center; till ventral edge, not till dorsal edge	crista higher than center; very slender in ventral view; only in anterior part	crista higher than center or similar height; very slender in ventral view; only in anterior part	crista as high as center; ventrally protruding	crista lower than center; protrude bit or barely ventrally
lateral cristae orientation	**laterally oriented; anterior edge diagonal**	laterally oriented	**laterally oriented; anterior edge vertical**	laterally oriented	laterally oriented	laterally oriented	**laterally oriented**	**dorsally oriented**	**dorsally oriented**	**dorsally oriented**	**dorsally oriented**	laterally oriented; dorsally implanted
dorsal protrusion of cristae	no	no	no	no	**yes**	no	no	no	no	no	no	no
ventral protrusion of cristae	no	no or bit	no	no	no	no	**yes**	no or yes	no	no	no	no
facies articularis parasphenoidalis ridges orientation	parallel or widening anteriorly	parallel or slightly widening anteriorly	slightly widening anteriorly	slightly widening anteriorly	slightly widening anteriorly	slightly widening anteriorly; horizontal folded ridges, broadest in middle	strongly widening anteriorly; **ridges can be slightly curved**	parallel, not widening; ridge in pit	usually parallel, sometimes slightly widening anteriorly	usually parallel, sometimes slightly widening anteriorly	rather parallel or subtly widening	slightly wider in middle
facies articularis parasphenoidalis width	slender	rather broad	slender	slender	broad or rather slender	**very broad**	rather broad	rather slender	broad	broad	broad	very slender
facies articularis parasphenoidalis depth	deep	deep	deep	deep	deep	shallow	deep	rather deep	deep	deep	deep	deep
facies articularis parasphenoidalis curvature	straight	straight	straight	straight	slight convex	straight or slight convex	sometimes slight convex	straight or barely convex	slight convex	slight convex	slight convex	straight
facies articularis parasphenoidalis proportion	higher than wide	higher than wide	higher than wide	higher than wide	higher than wide	**wider than deep**	higher than wide	higher than wide	higher than wide	higher than wide	higher than wide	higher than wide
ventral condyli	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent	**present; high, rounded**
general length	short	very short	long	long	short	short	short	short	long	long	short	very short
general height	low	low	low	low	low	low	low	**high**	**high**	**high**	**high**	high
general width	broad	broad	broad	broad	broad	very broad	broad	slender	slender	slender	broad	slender
shape center	tear	tear or slight hexagonal/pentagonal	round or tear shape	round or tear shape	round or slight tear	tear or triangular	round or oval	round/oval or tear	tear	tear or round	round or tear; ventral edge can be rather straight	round
crista anterior edge shape lateral view	slight convex	straight	convex	convex	straight or slight convex	straight or slight convex	straight or slight convex	concave or straight	concave	concave	concave	S-curve or convex
ridge along corpus at posterior part	small	**large**	small	small	**very large**	small	very small	**large**	**none**	**none**	**none or very small**	none

Table B21. Diagnostic features of the left cleithrum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
angle between angulus superior and angulus anterior	around 135-140 degrees	**around 135-140 degrees**	around 135-140 degrees	around 135-140 degrees	around 130-150 degrees	around 130 degrees	**around 120-130 degrees**	around 130-140 degrees	around 120-135 degrees	around 120-135 degrees	around 130-140 degrees	around 130-135 degrees
angulus superior length	short	long	rather short or long	long	long	long	rather long	**short**	very long	long	long	long
angulus superior width	slender	slender	rather broad or slender	rather broad	slender or very slender	usually slender	very slender	broad	slender	slender	rather broad	slender
angulus superior curvature	slightly curved or rather straight	curved	slightly curved	rather straight	slightly curved	straight or curved	curved	rather straight	curved	rather straight or curved	curved	straight
angulus superior posterior crista shape	convex or rather straight	slender, convex or rather straight	**straight or convex**	slender, convex or rather straight	**slender, slight convex**	slender, slight convex	convex or rather straight	convex	slender, convex	convex or rather straight	convex	slight convex or rather straight
angulus superior medial side	rather flat or thick	slightly thick	slightly thick	flat and thick	rather flat or thick	**very thick**	thick, rounded	thick, flat	**thick**	**thick**	**thick**	flat, thin
angulus superior medial rib	no	no	no	no	**slight or no**	**slight**	no	no	**clear**	**clear**	**clear**	no
processus dorsalis width	rather broad	rather broad	broad	rather broad	slender	rather broad	slender, broad anterior sometimes	broad or slender	broad	slender or broad	broad	slender
processus dorsalis length	short	long	short, longer in small specimens	short or long	long	long, shorter in larger specimens	usually short, rather long from posterior edge	short	short or long	usually long	short	anterior long, posterior short
processus dorsalis curvature	subtle anteriorly	straight	straight	straight	straight	sometimes slightly inclined anterior or posterior	straight or slightly inclined posteriorly	straight	straight	straight	straight	straight
processus dorsalis tip shape	broadly pointed	rounded or pointed	pointed	pointed	pointed	broadly pointed	pointed	pointed or rounded	rather rounded	broadly rounded or pointed	pointed or rounded	rounded or pointed
processus dorsalis number of tips	1	1	1	1	1	1	1	1	1	1	1	**2**
relative height cristae on angulus superior	anterior higher	anterior higher	anterior higher	anterior higher	similar height	similar height or anterior slightly higher	anterior higher	anterior higher	anterior higher	anterior higher	similar height	not clear, anterior higher?
angulus anterior length	long	long	long	long	long	very long	long	long	very long	very long	very long	short
angulus anterior curvature	straight; sometimes tip bit ventrally	first half or tip ventrally	straight or bit ventrally	straight or bit ventrally	straight or bit ventrally	straight; sometimes tip bit ventrally	straight; sometimes tip bit ventrally	sometimes tip bit dorsally	rather straight or bit ventrally	rather straight or bit ventrally	rather straight or bit ventrally; sometimes around axis	straight; tip sometimes bit dorsally
angulus anterior tip shape	pointed	pointed	pointed	pointed	pointed	broad rounded or pointed	slender rounded or pointed	**pointed; flat**	broad rounded or pointed	pointed	pointed	pointed; bit flat
lamina dorsalis width	broad	broad or slender	**broad**	broad	**slender**	slender	rather slender	broad	usually broad	rather broad	very broad	slender
lamina dorsalis groove	clear	clear	slight	slight	clear	none or slight	slight	none or subtle	slight	none or subtle	none or subtle	none
lamina dorsalis broadening	none or slight	none or slight	clear	clear	none	none or slight	none or slight	none	none or slight	none or slight	slight	none
lamina dorsalis orientation	more dorsal	more dorsal	more dorsal	**bit flat; more lateral**	more dorsal	more dorsal	more lateral	more dorsal	more lateral	more lateral	more lateral	more dorsal
depth at posterior part of lamina dorsalis indentation	deep	deep	deep	deep	deep	**very shallow**	deep	shallow	**deep**	**shallow**	very shallow	none or barely
dorsal ridge of lamina dorsalis indentation	deep	deep	deep	deep	deep	slight or smooth	deep	deep or none	deep or shallow	shallow	deep or shallow	smooth
lateral ridge of lamina dorsalis indentation	smooth	smooth	smooth	smooth	smooth	smooth	smooth	shallow or smooth	shallow or smooth	smooth	smooth	smooth
lamina medialis height	low	low	**rather low**	low	**high**	low	very low	rather high	low	high	**high**	high near corner
lamina medialis laterally visible	yes	not or barely	**not**	not	**small part**	not or small part	not	yes	not	very small part	**sometimes at corner**	yes

Table B21 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
lamina medialis edge shape	straight or slight concave	rather straight edge	**slight convex or straight**	slight convex or rather straight	**convex**	rather straight	slight convex	convex	rather straight	slight convex or rather straight	rather straight	strong convex
lamina medialis tip implantation	till tip angulus anterior	**not at tip angulus anterior**	**till tip angulus anterior**	till tip angulus anterior	**till tip angulus anterior**	till tip angulus anterior	**not at tip angulus anterior**	not till tip angulus anterior	till tip angulus anterior	till tip angulus anterior	till tip angulus anterior	not till tip angulus anterior
ventral groove of angulus anterior position	slight medial or medial of center	**rather medial or rather central**	**slight medial or medial of center**	rather central, medial at tip	**central**	central, more medial tip	**strongly medial, slightly central near corner**	central	usually central, sometimes slightly medial at corner and tip	central	central, tip more medial	central/lateral
ventral groove of angulus anterior width	rather broad	**rather slender**	**rather slender**	broad	**broad**	broad	**very slender**	broad	broad	rather broad	slender	broad
ventral groove of angulus anterior depth	rather shallow	**rather shallow**	**rather deep**	rather deep	**deep**	rather deep	**shallow**	rather deep or shallow	rather shallow	deep	deep	rather shallow
lateral indentation at corner	**present**	possible	possible	**present**	none; smooth	present	none; smooth or striations; surface sometimes flattened	**none; slight hollow surface**	possible; rather medial side	possible; rather medial side	possible	none; smooth, flat or hollow
lateral indentation at corner width	**very broad pit**	slender pit	slender or broad pit	**broad pit**	none	**slender groove**	none	**none**	none or slender pit/groove	none or slender pit/groove	none or very very slight, slender pit	none
lateral indentation at corner depth	**deep**	shallow or unclear	very shallow	**rather deep or shallow**	none	shallow	none; sometimes flat surface	**none**	shallow	shallow	shallow	none
dorsal bone width at corner	**broader**	**not broader**	**sometimes broader**	**broader, clear or slightly**	**sometimes broader**	not broader	**not broader**	**broader**	not broader	not broader	not broader	not or subtle broader
groove lateral crista (double crista)	present, till (almost) corner	none	present, not till corner usually	present, not till corner usually	possible, slightly, only short part, not till corner	possible; not till corner	none	none	none or wide/irregular groove possible	none	none	none

Table B22. Diagnostic features of the right cleithrum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
angle between angulus superior and angulus anterior	around 135-140 degrees	**around 135-140 degrees**	around 135-140 degrees	around 135-140 degrees	around 130-150 degrees	around 130 degrees	**around 120-130 degrees**	around 130-140 degrees	around 120-135 degrees	around 120-135 degrees	around 130-140 degrees	around 130-135 degrees
angulus superior length	long or short	long	rather short or long	long	long	long	rather long	**short**	very long	long	long	long
angulus superior width	slender	slender	rather broad or slender	rather broad	slender or very slender	usually slender	very slender	broad	slender	slender	rather broad	slender
angulus superior curvature	rather straight	slightly curved	slightly curved	rather straight	slightly curved	straight or curved	curved	rather straight	curved	rather straight or curved	curved	straight
angulus superior posterior crista shape	convex, slender	straight, broad	convex or straight, broad or slender	convex or straight, slender	convex, slender	slight convex or rather straight, broad or slender	convex, broad or slender	convex or straight, rather slender	convex, slender or broad	convex, slender or broad	convex, slender	straight or slight convex, slender
angulus superior medial side	rather flat or thick, rounded	slightly thick, rounded	slightly thick, flat or rounded	thick, flat	rather thin, flat	**thick, rounded**	thick, rounded	thick, flat	**thick, rounded**	**thick, rounded**	**thick, rounded**	flat, thin
angulus superior medial rib	none or slight	none	none	none	none or slight	**slight**	none	none	**clear**	**clear**	**clear**	none
processus dorsalis width	rather slender	rather broad or slender	broad	rather broad	slender	rather broad	slender, broad anterior sometimes	broad or slender	broad	slender or broad	broad	slender
processus dorsalis length	short or long	long, sometimes short	short, longer in small specimens	short or long	long	long, shorter in larger specimens	usually short, rather long from posterior edge	short	short or long	usually long	short	anterior long, posterior short

Table B22 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus dorsalis curvature	subtle anteriorly	straight or slight anteriorly	straight	straight	straight	sometimes slightly posteriorly or anteriorly	straight or bit posteriorly	straight	straight	straight	straight	straight
processus dorsalis tip shape	pointed	rounded or pointed	pointed	pointed	pointed	round or broadly pointed	pointed	pointed or rounded	rather rounded	broadly rounded or pointed	pointed or rounded	rounded or pointed
processus dorsalis number of tips	1	1	1	1	1	1	1	1	1	1	1	**2**
relative height cristae on angulus superior	anterior higher	anterior higher	anterior higher	anterior higher	similar height	similar height or anterior slightly higher	anterior higher	anterior higher	anterior higher	anterior higher	similar height	not clear, anterior higher?
angulus anterior length	long	long	long	long	long	very long	long	long	very long	very long	very long	short
angulus anterior curvature	straight; sometimes tip bit ventrally	first half or tip ventrally	straight or bit ventrally	straight or bit ventrally	straight	straight; sometimes tip bit ventrally	straight; sometimes tip bit ventrally	sometimes tip bit dorsally	rather straight or bit ventrally	rather straight or bit ventrally	rather straight or bit ventrally; sometimes around axis	straight; tip sometimes bit dorsally
angulus anterior tip shape	pointed	pointed	pointed	pointed or round, sometimes bit flat	pointed	broad rounded or pointed	slender rounded or pointed	**pointed; flat**	broad rounded or pointed	pointed	pointed	pointed; bit flat
lamina dorsalis width	broad	broad or slender	**broad**	broad	**slender**	rather slender or broad	rather slender	broad	usually broad	rather broad	very broad	slender
lamina dorsalis groove	slight	slight	slight	slight	clear	none or slight	slight	none or subtle	slight	none or subtle	none or subtle	none
lamina dorsalis broadening	none or slight	none or slight	clear	clear	none or slight	none or slight	none or slight	none	none or slight	none or slight	slight	none
lamina dorsalis orientation	more dorsal	more dorsal	**more lateral, bit flat**	more dorsal	more dorsal	**more lateral, bit flat**	more lateral	more dorsal	more lateral or dorsal	more lateral or dorsal	very lateral; **flat**	more dorsal
depth at posterior part of lamina dorsalis indentation	deep or rather shallow	deep	deep	deep	deep	**very shallow**	deep	shallow	**usually deep**	**usually shallow**	very shallow	none or barely
dorsal ridge of lamina dorsalis indentation	deep	rather deep	deep	deep	deep	slight or smooth	deep	deep or none	deep or shallow	shallow	deep or shallow	smooth
lateral ridge of lamina dorsalis indentation	smooth	smooth	smooth	smooth	smooth	smooth	smooth	shallow or smooth	shallow or smooth	smooth	smooth	smooth
lamina medialis height	low	low	rather low	low	**high**	low	very low	rather high	low	high	**high or low**	high near corner
lamina medialis laterally visible	no	not or barely	not	not	**small part**	not or small part	not	yes	not	very small part	**sometimes at corner**	yes
lamina medialis edge shape	straight or slight concave	rather straight edge	slight convex or straight	slight convex or rather straight	**convex**	rather straight	slight convex	convex	rather straight	slight convex or rather straight	rather straight	strong convex
lamina medialis tip implantation	not till tip angulus anterior	not at tip angulus anterior	not till tip angulus anterior	not till tip angulus anterior	(almost) till tip angulus anterior	(almost) till tip angulus anterior	not at tip angulus anterior	not till tip angulus anterior	**till tip angulus anterior**	**till tip angulus anterior**	not till tip angulus anterior	almost or not till tip angulus anterior
ventral groove of angulus anterior position	slight medial or medial of center	**rather medial or rather central**	**slight medial or medial of center**	rather central or medial, medial at tip	**central**	central, more medial tip	**strongly medial, slightly central near corner**	central	usually central, sometimes slightly medial at corner and tip	rather medial	central, tip more medial	central/lateral
ventral groove of angulus anterior width	rather broad	**rather slender**	**rather slender**	broad	**broad or slender**	**broad**	**very slender**	broad	**rather broad**	**rather broad**	**very slender**	broad
ventral groove of angulus anterior depth	rather shallow	**rather shallow**	**rather deep**	rather deep	**deep**	rather deep	**shallow**	rather deep or shallow	rather shallow	deep	deep	rather shallow
lateral indentation at corner	**present**	possible	possible	present	none; smooth	present	none; smooth or striations; surface sometimes flattened	**none; slight hollow surface**	possible; rather medial side	possible; rather medial side	possible	none; smooth, flat or hollow
lateral indentation at corner width	**very broad pit**	slender pit	slender or broad pit	slender	none	**slender groove**	none	**none**	none or slender pit/groove	none or slender pit/groove	none or very very slight, slender pit	none
lateral indentation at corner depth	**deep**	shallow or unclear	very shallow	**rather deep or shallow**	none	shallow	none; sometimes flat surface	**none**	shallow	shallow	shallow	none

Table B22 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
dorsal bone width at corner	**broader**	**not broader**	**sometimes broader**	**broader, clear or slightly**	**sometimes broader**	not broader	**not broader**	**broader**	not broader	not broader	not broader	not or subtle broader
groove lateral crista (double crista)	present, till (almost) corner	none	present, not till corner usually	present, not till corner usually	possible, slightly, only short part, not till corner	possible; not till corner	none	none	none or wide/irregular groove possible	none	none	none

Table B23. Diagnostic features of the os anale.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
angle between angulus anterior-superior	more than 90	more than 90	more than 90	more than 90	more than 90	more than 90	more than 90 or around 90	**around 90**	around 90, sometimes bit more	around 90 or less	around 90	90 or less
left lateral sulcus length	**≥2x length articulation**	very shallow/none	**<2x length articulation**	**<2x length articulation**	**> or < 2x articulation, unclear**	no indent, but ridge till articulation	**1.5x length articulation**	absent	slight ridge along corner; very far from articulation	slight ridge along corner sometimes; very far from articulation	absent	absent
right lateral sulcus length	**>2x length articulation**	**around 2x length articulation**	**<2x length articulation**	**<2x length articulation**	**<2x length articulation**	no indent, but ridge till articulation	**around 2x length articulation**	absent	slight ridge along corner; very far from articulation	slight ridge along corner sometimes; very far from articulation	absent	absent
angulus anterior length	short	short	short	short	long	long	short	short	short	short	long	very long
angulus anterior width	as broad as high	as broad as high; **flat dorsally, with 2 bumps**	as broad as high	as broad as high	higher than broad	**as broad as high**	higher than broad	**flat dorsal/frontal, wider than high**	**higher than wide**	**higher than wide**	**flat laterally; rather similar height - width**	as wide as high
dorsal crista at angulus anterior	absent	absent	absent	absent	absent	absent	absent	absent	**high laterally-flattened, much higher than corpus part**	**laterally-flattened, same height as corpus**	absent	absent
crista width at corner	as broad as corpus or bit more	broad at corner	**very broad at corner**	**very broad at corner**	same as corpus	**slightly slenderer than corpus**	as broad as corpus	very slender	slender	slender	very slender	very slender
posterior ridges implant	till halfway superior	till halfway superior	till halfway superior	till halfway superior	**not at upper half/third superior**	till halfway superior	**till tip or till halfway superior**	till halfway superior	**till superior upper half**	**till superior upper half**	**till superior upper half**	**till lower half**
posterior ridges shape	parallel or subtle widening; close together	parallel or subtle widening; close together	parallel or subtle widening; close together	parallel or subtle widening; close together	sometimes bit wider at corner and bit closer together at lower half superior	parallel or subtle widening; slender	**parallel; close together**	parallel; close together	**long widening along lower half; laterally protruding at upper half**	**very close together lower half; short widening mid**; **laterally protruding at upper half**	**wider laterally**	**parallel; very short, very slender**
posterior part of angulus superior	tube, striations	tube, striations	tube, striations	tube, striations	tube, smooth or slightly rough	tube, striations	tube, smooth or rough	tube, smooth	**cilinder, smooth**	**cilinder, smooth**	**cilinder, smooth**	**tube; smooth**
tip of angulus anterior	short; broad	short; broad	short; broad	short; broad	short; broad	long or short; broad	short; broad	**long; slender;** bit flat laterally	very long; slender; flat laterally	very long; very slender; bit flat laterally	very long; very slender; flat laterally	long; slender; **tube tip**
enlargement at angulus anterior	slightly broader, not higher sometimes	slightly broader, not higher; usually **flat dorsally with 2 bumps laterally**	broader, can be higher sometimes	broader, can be higher sometimes	none or barely in height	barely or none	sometimes slightly enlarged and broader, as bump	none; anterior flat	none	none	none	none
surface striations	enlargement and corner, rarely whole length	enlargement and corner	enlargement and corner, rarely whole length; groove possible at corner	enlargement and corner, rarely whole length; groove possible at corner	corner possible, at tip superior	almost all surface	usually none; very slight at tip of both angulus possible	tip superior possible	bit at corner possible	possible at corner possible, often along tip superior in large specimens	none	none
articulation length	very short	very short	very short	very short	short	short	short	very short	very long	very long	very long	long
articulation tube	absent	absent	absent	absent	absent	absent	absent	absent	present	present	present	present

Table B23 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
articulation width	slenderer than corpus	slenderer than corpus	slenderer than corpus	slenderer than corpus	as wide as corpus	as wide as corpus	as wide as corpus	as wide as corpus	broader than corpus	broader than corpus	slightly broader than corpus	slenderer than or as wide as corpus
angulus superior	rounded; not broader	rounded; not broader	rounded; not broader	rounded; not broader	rounded; not broader	rounded; not broader	rounded; not broader	rounded; not broader	flat anteriorly; broader midheight	flat anteriorly; broader midheight	rounded, not broader	rounded; not broader

Table B24. Diagnostic features of the left quadrate.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative size margo ectopterygoidalis to margo posterior	half or slightly less than half	**half or slightly more than half**	half or slightly less than half	half or slightly less than half	half or slightly more than half	two thirds	half or slightly more than half	half or one thirds	**two thirds**	**two thirds**	**slightly more than half**	two thirds
condyli relative size	**lateral larger**	lateral slightly larger	**lateral larger**	**lateral slightly longer or similar**	**usually lateral larger, wider, longer**	similar	lateral longer, medial sometimes wider	lateral larger, broader, bit longer sometimes	equal or lateral slightly wider and longer	equal or lateral slightly wider and longer	equal or one slighlty longer;	similar or medial slightly wider and longer
condyli relative position	**lateral more posteriorly protruding**	lateral more posteriorly protruding	**lateral more posteriorly protruding; medial more ventrally protruding**	**lateral more posteriorly protruding; medial slightly more ventrally protruding or similar**	**lateral more posteriorly and anteriorly protruding**	lateral more posteriorly protruding	lateral more ventrally	lateral slightly more anteriorly protruding	similar	similar	sometimes lateral slightly more laterally and ventrally protruding	lateral more posteriorly protruding; medial more anteriorly protruding
condyli general shape	large	small	large	rather large	rather large; flat	rather large	**strong V-shaped together and ventrally protruding**	**very large and wide**	rather large	rather large	**strong V-shaped together and ventrally protruding**	**strong V-shaped together and ventrally protruding**
lateral condylus anterior edge	**clear**	not clear	**not clear**	not clear	not clear	not clear	clear	rather clear	not clear	not clear	not clear	rather clear
crista at processus preopercularis tip	none or slightly at tip	present	none or slightly at tip	none or slightly at tip	present	none or slightly at tip	none or slightly at tip	none	present	present	present	none or slightly at tip
crista at processus preopercularis transition to tip	gradual	gradual	gradual	gradual	gradual	gradual	gradual, bend or straight	gradual	gradual	gradual	gradual	gradual
margo posterior length	long	rather short	long	long	rather long	rather short	long	rather short	very long	very long	very long	very long
margo posterior width	very slender	slender; sometimes bit wider at midheight	very slender	very slender	very slender	rather broad; sometimes wider at midheight	very slender; sometimes wider at midheight	rather broad	rather slender	rather slender	very slender; sometimes bit broader at base	rather slender
margo posterior curvature around axis	not or barely medially	not or barely medially	not or bit medially	not or bit medially	not	slightly laterally	slightly laterally	not	not	not	not	not
margo posterior curvature	straight	straight	straight or slight medially	straight or slight medially	straight or slight medially	straight	straight	straight or slight medially; sometimes tip bit posteriorly	straight	straight	straight	straight or slight anteriorly
margo dorsalis length	rather short	rather long	short	short	long	long	short	**very short**	rather short	short	rather long	very short
margo dorsalis curvature	straight	straight or slight concave	straight	straight or slight concave	concave or straight, sometimes bend	straight or subtle convex	concave or straight	rather straight or slight convex	straight or convex	straight or convex	rather straight or convex	straight or slight concave
anterior tip margo dorsalis	not protruding	not protruding	not protruding	not protruding	not protruding	**protruding**	not protruding	not protruding	not protruding	not protruding	not protruding	not protruding
margo ectopterygoidalis length	short	short	short	rather long	rather long	long	rather short	very short	long	long	long	very long
margo ectopterygoidalis width	broad	slender	rather broad	slender	rather slender	rather broad	slender	**very broad**	slender	slender	slender	rather broad

Table B24 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
margo ectopterygoidalis curvature	slight medial	slight medial	slight medial	slight medial or rather straight	slight medial	barely medial	slight medial	slight medial	straight	straight or slight medial	straight or barely medial	straight
margo ectopterygoidalis curvature around axis	slight medial	slight medial	slight medial	slight medial	barely medial	slight medial	slight medial	none or barely medial	none	none	none	slight medial
margo ectopterygoidalis surface shape	flat	bit flat	bit flat; lateral higher ridge	bit flat	bit flat; lateral higher ridge	bit flat; lateral higher ridge	bit flat	bit flat; irregular	barely flat; ridge along middle or lateral higher	barely flat; ridge along middle or lateral higher	barely flat; ridge along middle or lateral higher	bit flat
implantation of crista on processus preopercularis	lateral	**lateral usually, sometimes slightly middle**	lateral	lateral	lateral	lateral side or rather middle	lateral side or rather middle	lateral	**middle**	**middle**	**rather middle**	lateral
angle between margo ectopterygoidalis and processus preopercularis	45-60 degrees	**70-80 degrees**	45-60 degrees	45-60 degrees	50-70 degrees	50-70 degrees	45-60 degrees	45-60 degrees	45-60 degrees	45-60 degrees	50-70 degrees	**20-40 degrees**
incisura symplecti presence	possible	possible	possible	possible	possible	**possible; very smooth transition if none**	present	possible	possible	possible	possible	present
incisura symplecti depth	barely or shallow	barely	barely or shallow	barely or shallow	shallow	barely	shallow	very shallow	shallow or deep	shallow	very deep	shallow
incisura symplecti width	slender	slender	slender	slender	slender	slender	broad	slander	slender	slender	slender	broad

Table B25. Diagnostic features of the right quadrate.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative size margo ectopterygoidalis to margo posterior	slightly less than half	half or slightly more than half	half or slightly less than half	half or slightly less than half	half or slightly more than half	two thirds	half or slightly more than half	half or one thirds	**two thirds**	**two thirds**	slightly more than half	**almost as high**
condyli relative size	lateral larger or similar	lateral slightly larger or similar	**lateral larger**	**lateral slightly longer or similar**	**usually lateral larger, wider, longer**	similar	lateral longer, sometimes wider	lateral larger, broader, bit longer sometimes; sometimes medial larger	equal or lateral slightly wider and longer	equal or lateral slightly wider and longer	equal or one slighlty longer;	lateral slightly longer
condyli relative position	**lateral more posteriorly protruding**	lateral more posteriorly and ventral protruding	**lateral more posteriorly protruding; medial more ventrally protruding**	**lateral more posteriorly protruding; medial slightly more ventrally protruding or similar**	**lateral more posteriorly and anteriorly protruding**	lateral more posteriorly protruding	lateral more ventrally	lateral slightly more anteriorly protruding	sometimes lateral more posteriorly protruding	sometimes lateral more posteriorly protruding	sometimes lateral slightly more laterally and ventrally protruding	lateral more posteriorly protruding; medial more anteriorly protruding
condyli general shape	large	small	rather large	large	rather large; flat	rather large	rather large; **clear constriction in middle**	**very large and wide**	rather large	rather large	rather large	**no clear separation**
lateral condylus anterior edge	**clear**	not clear	**not clear**	not clear	not clear	not clear	clear	rather clear	not clear	not clear	not clear	rather clear
crista at processus preopercularis tip	none or slightly at tip	present	none or slightly at tip	none or slightly at tip	present	none or slightly at tip	none or slightly at tip	none	present	present	present	none or slightly at tip
crista at processus preopercularis transition to tip	gradual	gradual	gradual	gradual	gradual	gradual	gradual, bend or straight	gradual	gradual	gradual	gradual	gradual
margo posterior length	long	rather short	long	long	rather long	rather long	long	rather short	very long	very long	very long	very short
margo posterior width	very slender; sometimes bit wider at midheight	slender; sometimes bit wider at midheight	very slender	very slender	very slender	rather slender; sometimes wider at midheight	very slender; sometimes wider at midheight	rather broad	rather slender	rather slender	very slender; sometimes bit broader at base	rather broad

Table B25 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
margo posterior curvature around axis	not or barely medially	not or barely medially	not or bit medially	not or bit medially	not or slightly laterally	slightly laterally	slightly laterally	not	not	not	not	not
margo posterior curvature	straight	straight	straight or slight medially	straight or slight medially	straight or slight medially	straight	straight	straight or slight medially; sometimes tip bit posteriorly	straight	straight or slight medially	straight	straight
margo dorsalis length	rather short	**rather long**	short	short	long	long	short	**very short**	rather short	short	rather long	short
margo dorsalis curvature	straight or slight convex	straight or slight concave	straigth	straight or slight concave	concave or straight, sometimes bend	straight or slight concave	convex or straight	rather straight or slight convex	straight or convex	straight or convex	rather straight or convex	straight or slight convex
anterior tip margo dorsalis	not protruding	not protruding	not protruding	not protruding	not protruding	**protruding**	not protruding	not protruding	not protruding	not protruding	not protruding	not protruding
margo ectopterygoidalis length	short	short	short	**rather long**	**rather long**	long	rather short	**very short**	long	long	long	short
margo ectopterygoidalis width	rather slender	slender	rather slender	**rather broad**	**rather slender**	rather broad	very slender; posterior sometimes bit broader	**very broad**	slender	slender	slender	very slender
margo ectopterygoidalis curvature	slight medial	slight medial	slight medial	slight medial	slight medial	barely medial	medial	slight medial	straight	straight or slight medial	straight or barely medial	straight
margo ectopterygoidalis curvature around axis	slight medial	slight medial	slight medial	slight medial	barely medial	slight medial	slight medial	none or barely medial	none	none	none	none
margo ectopterygoidalis surface shape	bit flat	barely flat	bit flat; lateral higher ridge	bit flat	bit flat; lateral higher ridge	bit flat; lateral higher ridge	barely flat	bit flat; irregular; sometimes ridge along middle	barely flat; ridge along middle or lateral higher	barely flat; ridge along middle or lateral higher	barely flat; ridge along middle or lateral higher	not flat
implantation of crista on processus preopercularis	rather lateral	rather lateral	lateral	lateral	lateral	rather lateral side	rather lateral side	lateral	**middle**	**middle**	**rather middle**	rather lateral
angle between margo ectopterygoidalis and processus preopercularis	40-50 degrees	70-80 degrees	45-60 degrees	40-70 degrees	50-70 degrees	50-70 degrees	50-70 degrees	40-50 degrees	45-60 degrees	45-60 degrees	50-70 degrees	60-80 degrees
incisura symplecti presence	possible	possible	possible	possible	possible	**possible; very smooth transition if none**	present	possible	possible	possible	possible	present
incisura symplecti depth	barely or shallow	barely	barely or shallow	barely or shallow	shallow	barely	shallow	very shallow	shallow or deep	shallow	very deep	deep
incisura symplecti width	slender	slender	slender	slender	slender	slender	broad	slender	slender	slender	slender	broad

Table B26. Diagnostic features of the left ectopterygoid.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative length crura	anterius bit longer than posterius, 1.5x	anterius bit longer than posterius, 1.5x	**anterius bit longer than posterius or rather similar**	anterius bit longer than posterius	**anterius slightly shorter than posterius or similar**	anterius bit longer than posterius, 1.5-2x	**anterius longer than posterius, 1.5-2x**	anterius bit longer than posterius, 1.5x	**anterius slightly longer than posterius or similar**	**anterius slightly longer than posterius or similar**	anterius bit longer than posterius, 1.5x	**anterius slightly longer than posterius or similar**
angulus dorsalis	present	**sometimes absent**	present	usually present	present	present	present	present	present	present	present	**two tips, lateral and medial**
angle between crura	more than 90degrees	bit more than 90degrees	clearly more than 90degrees (more than platessa)	around 90degrees or slightly more	around 90degrees or slightly more	bit more than 90degrees	more than 90degrees (120)	**less than 90degrees**	bit more than 90degrees	clearly more than 90degrees	**much more than 90degrees**	around 90degrees

Table B26 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
crus posterius shape	**broad;** pointed; bit flat	slender; pointed; bit flat	broad; pointed; barely flat	slender; rounded; not flat	broad; pointed or rounded; bit flat	rather slender; pointed or rounded; tip slenderer; bit flat	slender; pointed; laterally flat	**very broad;** broad, round or angular tip; irregular/serrated edge; very thick	slender; rounded or angular tip; not flat	slender; rounded or angular tip; not flat	**very slender;** rounded or pointed; bit flat	very slender; pointed very slender tip; tip flat antero-postero
crus posterius length	short	short	rather long	short	long	short	short	**very short**	long	long	rather long	rather long
crus anterius shape	pointed; **rather broad,** mainly base; flat tip	pointed; rather slender; tip very slender and bit flat	rather broad; flat tip	slender; flat	**very broad**; hollow/ridge medial side	slender; bit curved laterally axis; flat tip	pointed or irregular tip; slender; very flat	rounded or pointed, irregular tip; **very broad**; thick; bit flattened	pointed or angular; slender; tip bit flat	pointed or angular; slender; tip bit flat	pointed or angular; very slender; flat tip	pointed; slender; flat tip; slight bump laterally at base crus anterius possible
crus anterius length	long	long	rather short	rather long	short	long	very long	**short**	long	long	very long	rather short
crus anterius curvature	straight or slight curve	straight or slight curve	straight or slight curve	slight curve	straight	straight	bit or strongly	straight or slight	straight	straight	rather straight	rather straight
crus anterius processus	none	none	none	**slight halfway**	none	none	none	none	none	none	none	none
crus anterius fossa	deep till half ventrally	till almost half, not well defined	till half or almost corner	till half	at tip, broad, irregular, bit lateral as well	ventrally till third or half	at tip, not clear	ventrally shallow and till corner	laterally till half	laterally till half	rather laterally till almost half	none
bone thickness	thick	**thin**	thick	rather thin	thick	thick	rather thin	**very thick**	**rather thick**	**rather thin**	rather thin	rather thin
transition between crura	smooth, round, shallow	smooth, round, shallow	smooth, round, **very shallow**	gradual, round, smooth	smooth, very round, shallow	smooth, round, shallow	smooth, round, shallow	angular, shallow	smooth, round, rather shallow	smooth, round, shallow	smooth, round, shallow	smooth, round, rather shallow

Table B27. Diagnostic features of the right ectopterygoid.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative length crura	**anterius slightly longer than posterius or similar**	anterius bit longer than posterius, 1.5x	**anterius slightly longer than posterius**	anterius slightly longer than posterius	**anterius shorter than posterius**	anterius longer than posterius, 1.5-2x	anterius slightly longer than posterius	**anterius bit shorter than posterius**	anterius slightly longer than posterius	anterius slightly longer than posterius	anterius bit longer than posterius	anteruis much longer than posterior
angulus dorsalis	**present**	sometimes absent	**present**	present	**present, very small**	present	present	**present**	present	present	present	present, very large, one tip
angle between crura	**around 90degrees**	bit more than 90degrees	**around 90degrees or slightly more**	over 90degrees	**around 90degrees or slightly more**	bit more than 90degrees	more than 90degrees	**less than 90degrees**	clearly more than 90degrees	clearly more than 90degrees	clearly more than 90degrees	more than 90degrees
crus posterius shape	**broad; rounded or pointed**	rather slender; pointed or rounded	**broad; broadly pointed**	broad; pointed or rounded	**broad; pointed or rounded**	rather slender; pointed or rounded; tip slenderer	rather broad; pointed or rounded tip; sometimes slight curve axis	**very broad; broad, rounded or angular tip; irregular/serrated edge**	slender; rounded or angular tip	slender; rounded or angular tip	very slender; rounded or pointed	very slender; pointed
crus posterius length	**short**	short	**rather short**	short	**long**	rather long	rather long	**very short**	long	rather long	rather long	very short
crus anterius shape	**pointed; rather slender**	pointed or irregular tip; slender	**pointed; slender; slight curve axis**	pointed or rounded; slender	**slender; sometimes bit curved medially**	slender; bit curved laterally axis	very slender; bit curved laterally axis	**rounded or pointed, irregular tip; very slender; thick**	pointed or angular	pointed or angular	pointed or rounded; slender	pointed; rather slender, halfway slightly broader
crus anterius length	**rather short**	long	**rather long**	rather long	**short**	long	long	**short**	long	long	very long	very long
crus anterius curvature	**straight or slight**	straight	**rather straight or slight**	straight or slight	**straight**	straight or slight curve	strong	**straight or slight**	straight	straight	rather straight	rather straight or slight curve
crus anterius processus	**laterally, broad round**	slight bump/thicker possible	**slender angular possible**	none	**sometimes**	none	none	**none**	none	none	none	none
crus anterius fossa	**shallow, slender and short, at tip or half**	till almost half	**till half or almost corner**	till half	**barely, at tip, irregular or none**	none	till third	**at tip**	till half	till half	till third or almost half	none

Table B27 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
bone thickness	**rather thick; anterius less thick**	thin	**rather thin or thick**	rather thick	**rather thick**	thick	thin	**very thick**	rather thick	rather thin	rather thin	very thin
transition between crura	**smooth, round, shallow**	smooth, round, shallow	**smooth, round, very shallow**	smooth, round, shallow	**smooth, very round, shallow**	smooth, round, shallow	smooth, round, shallow	**smooth, round, shallow**	smooth, round, rather shallow	smooth, round, shallow	smooth, round, shallow	smooth, round, very shallow

Table B28. Diagnostic features of the left preoperculum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative length of angulus	**rather similar or anterior (bit) longer**	superior longer, 1.5-2 times anterior; less difference in small specimens	**rather similar or anterior bit longer**	**anterior bit longer**	about same size or superior bit longer	superior longer, 1.5-2 times anterior	superior longer, 1.5-2 times anterior	superior longer, 1.5 times anterior	superior longer, bit to 1.5 anterior	superior longer, bit to 1.5 anterior	superior bit longer	rather similar or anterior bit longer
processus s.l. anterior	present, clear	present, rarely absent, clear	present, clear	present, clear	possible, clear	possible, barely	present, barely	possible, barely, can be medially	**possible, barely, can be medial**	**possible, barely, can be medial**	**present, rarely absent, clear or barely, can be medial**	possible, barely
angulus anterior tip type	tube	tube	tube	tube	very wide tube	small tube	wide tube	tube, **flat dorso-ventrally**	wide tube	tube	slender tube	no tube, **flattened dorso-ventrally**
angulus anterior tip symmetry	dorsal longer	dorsal longer	dorsal bit longer	dorsal bit longer	dorsal longer	dorsal bit longer	dorsal longer	dorsal longer	dorsal and medial longer	dorsal and medial longer	dorsal longer	NA
angulus anterior tip curvature	straight	straight	straight	straight	straight	straight	straight	**sometimes bit dorsally**	straight	straight	straight	straight
margo interopercularis shape	convex	straight or bit convex, in mid slight concave	straight or slight convex	straight or slight convex	straight, slight concave or slight convex	straight or slight convex	rather straight or slight concave	rather straight	**rather straight or slight convex**	**slight convex, anterior part sometimes concave**	**rather straight**	straight or barely convex, thick
angulus anterior crista width	rather wide	rather slender	rather wide	rather wide	wide	**wide**	rather slender	very slender, bit wider near corner	**rather slender**	**rather slender**	**very slender**	very slender
angulus anterior length	long	short	long	very long	rather short	short	rather long	long	rather long	rather long	very long	long
margo opercularis shape	convex lower, concave upper	convex lower, concave or convex upper	convex or rather straight lower, concave upper	convex lower, concave or slight convex upper	rather straight, convex in middle	convex or straight	convex or rather straight lower, straight or slight concave upper	straight lower, slight convex or concave upper	slight convex or rather straight	slight convex or rather straight	convex	convex
angulus superior crista width	very broad lower, slender upper	broad or slender lower, slender upper	broad lower, slender upper	broad lower, slender upper	broad	slender	very slender	very slender	very slender	very slender	very slender	very slender, thick
angulus superior crista implantation	usually not at tip	usually not at tip	usually not at tip	not at tip	at tip, barely	not at tip	not at tip or barely	not at tip	not at tip	not at tip	not at tip	not at tip
angle between angulus	bit more or more than 90 degrees	bit more than 90 degrees	more than 90 degrees	around 90 degrees	bit more than 90 degrees	bit more than 90 degrees	bit more than 90 degrees	**90 degrees or slightly less**	around or bit more than 90 degrees	more than 90 degrees	more than 90 degrees	bit more than 90 degrees
curvature angulus anterior	possible, slightly dorsally	possible, slightly dorsally	possible, barely dorsally	possible, slightly dorsally	possible, slightly ventrally	none	none	possible, slightly dorsally	possible, slightly dorsally	possible, slightly dorsally	possible, slightly dorsally	possible, slightly dorsally
curvature angulus superior	possible, slightly anteriorly	possible, slightly anteriorly	none	possible, slightly anteriorly	possible, slightly anteriorly	**slightly anteriorly**	possible, slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	none
lateral foramen	small	small	rather small	rather small	**very large, most of side**	small	small or large	very small	small or none	small or none	none	small or none
lateral ridge on corner	usually none or slight close to corner	none	none	none	none	none	no or very slightly close to corner	ridge close to corner	**midcorpus or close to corpus**	**midcorpus or close to corpus**	**midcorpus or close to corpus**	none
general surface	smooth	smooth, superior sometimes bit rougher	bit rough	bit rough	smooth	rough	smooth	rather smooth	**lateral side bit rougher**	**rather smooth**	**smooth**	rather smooth

Table B28 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ridges along angulus	none	none	none	none	none	none	none	none	**possible**	**possible**	**possible**	sometimes very subtle
second medial pit (halfway corpus near corner on angulus anterior)	possible	**none**	present	present	possible	possible, barely	possible	none	none	none	none	none

Table B29. Diagnostic features of the right preoperculum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
relative length of angulus	**rather similar, anterior (bit) longer**	superior longer; less difference in small specimens	**anterior bit longer**	**rather similar or anterior bit longer**	about same size, superior bit longer	superior longer, 1.5 times anterior	superior bit longer	superior longer, 1.5 times anterior	superior longer, bit to 1.5 anterior	superior longer, bit to 1.5 anterior	superior bit longer	superior longer, 1.5 times
processus s.l. anterior	present, clear	present, rarely absent, clear	present, clear	present, clear	possible, clear	possible, barely	present, barely	possible, barely, can be medially	**possible, barely, can be medial**	**possible, barely, can be medial**	**present, rarely absent, clear or barely, can be medial**	possible, barely
angulus anterior tip type	tube	tube	tube	tube	tube	small tube	wide tube	tube, **flat dorso-ventrally**	wide tube	tube	slender tube	small tube, bit **flattened dorso-ventrally**
angulus anterior tip symmetry	dorsal and medial longer	dorsal longer	dorsal bit longer	dorsal bit longer	dorsal longer	dorsal bit longer	dorsal longer	dorsal longer	dorsal and medial longer	dorsal and medial longer	dorsal longer	dorsal bit longer
angulus anterior tip curvature	straight	straight	straight	straight	straight	straight	straight	**sometimes bit dorsally**	straight	straight	straight	straight
margo interopercularis shape	slight convex or rather straight	**straight or bit convex, in mid slight concave**	straight or slight convex	straight or slight convex	straight, slight concave or slight convex	straight or slight convex	**rather straight or slight concave**	rather straight or slight convex	rather straight or slight convex	slight convex, anterior part sometimes concave	**slight concave, convex near corner**	straight; thick
angulus anterior crista width	slender	rather slender	rather wide	rather wide	very slender	**wide**	rather slender	very slender, bit wider near corner	rather broad	rather slender	very slender	very slender
angulus anterior length	long	short	long	very long	long	short	long	long	rather long	rather long	very long	long
margo opercularis shape	convex or rather straight lower, concave upper	convex lower, concave or convex upper	convex or rather straight lower, concave upper	convex lower, concave or slight convex upper	rather straight, convex in middle	convex or straight	convex or rather straight lower, straight or slight concave upper	straight lower, slight convex or concave upper	slight convex or rather straight	slight convex or rather straight	convex	straight lower, concave upper
angulus superior crista width	very broad lower, slender upper	broad or slender lower, slender upper	broad lower, slender upper	broad lower, slender upper	rather slender	slender	very slender	very slender	very slender	very slender	very slender	very slender, thick
angulus superior crista implantation	usually not at tip	usually not at tip	usually not at tip	not at tip	not at tip	not at tip or barely	not at tip or barely	not at tip	not at tip	not at tip	not at tip	not at tip
angle between angulus	bit more or more than 90degrees	**bit more than 90degrees**	bit more or around than 90degrees	bit more around 90degrees	around 90degrees	bit more than 90degrees	**bit more than 90degrees**	**90degrees or slightly smaller**	around or bit more than 90degrees	more than 90degrees	**more than 90degrees, rather 110**	bit more than 90degrees
curvature angulus anterior	possible, slightly dorsally	possible, slightly dorsally	possible, barely dorsally	possible, slightly dorsally	possible, slightly ventrally	none	none	possible, slightly dorsally	possible, slightly dorsally	possible, slightly dorsally	possible, slightly dorsally	possible, slightly dorsally
curvature angulus superior	possible, slightly anteriorly	possible, slightly anteriorly	none	possible, slightly anteriorly	possible, slightly anteriorly	slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	possible, slightly anteriorly	none
lateral foramen	small	small	rather small	rather small	**very large**	small	small or large	very small	small or none	small or none	none	small or none
lateral ridge on corner	usually none or slight close to corner	possible near corner	possible near corner	possible near corner	none or barely	**clear, close to corner**	no or very slightly close to corner	ridge close to corner	**none or very slight near corner**	**none or very slight near corner**	**none or barely**	none
general surface	smooth	smooth, superior sometimes bit rougher	bit rough	bit rough	smooth	rough	smooth	rather smooth	**lateral side bit rougher**	**rather smooth**	**smooth**	rather smooth

Table B29 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ridges along angulus	none	none	none	none	none	none	none	none	**subtle**	**subtle**	**none**	none
second medial pit (halfway corpus near corner on angulus anterior)	possible	**usually none**	present	present	possible	possible, barely	possible	none	none	none	none	none

Table B30. Diagnostic features of the interoperculum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ridge along margo superior medial side	slight ridge or none anterior, bigger at middle and posterior	slight ridge or none anterior, bigger at middle and posterior	**none posterior, sometimes slight anterior**	**none posterior, sometimes slight anterior**	slight ridge or none anterior, bigger at middle and posterior	very slight bump at center; edge not delineated	very slight and slender ridge	ridge center and anterior	barely ridge at anterior part; edge not well delineated	no ridge; edge not well delineated	no ridge; edge well delineated	no ridge
medial edge of margo superior	well delineated	not well delineated	**well delineated**	**well delineated**	not well delineated	not delineated	not well delineated	**well delineated**	not well delineated	not well delineated	well delineated	not delineated
fold of margo superior	no	no	no	no	no	no	no	**medially**	no	no	no	no
margo superior mineralisation	bit thicker, usually whole length	barely or not thicker at center	slightly center, sometimes posterior and anterior	slightly center, sometimes posterior and anterior	thicker center and posterior, bit anterior	bit thicker center and posterior, anterior possible	thicker at center, posterior and bit anterior	bit thicker whole length or center	bit thicker whole length or center	thicker laterally whole length or center	barely thicker whole length or center	**not thicker**
margo superior anterior edge shape	convex, sometimes straight in elongated side	convex or straight	convex or straight	convex or straight	slight convex or straight	straight	convex or straight	slight convex or straight	**rather straight**	**straight**	**straight; bump possible**	slight convex or straight
margo superior center edge shape	concave	concave, shallow or deep	concave	concave	concave	concave; **bump before**	concave	concave; bump before possible	**straight; convex bump; crista possible**	**straight or slight concave; bumpy**	**straight**	concave
margo superior posterior edge shape	convex	convex or straight; sometime bumpy	convex	convex	slight convex or straight	slight convex or straight	convex or straight	convex	bumpy	**straight**	**straight or slight concave**	bumpy
inclination of anterior half	slightly downward	slightly downward	downward	downward	downward	downward	slightly downward	**slightly upward**	**straight or subtle downward**	**straight**	**straight**	**rather straight**
spina anterior width	broad	slender, sometimes broad	broad or slender	broad or slender	slender or bit broad	broad	**slender**	rather slender or bit broader	rather broad	slender	slender or very slender	broad
spina anterior shape	pointed	pointed	rounded, angular or pointed	rounded, angular or pointed	pointed or angular	pointed or rounded	**pointed**	rounded or pointed	rounded or pointed	angular or pointed	pointed	rounded or angular
spina anterior delineation	separate	rather separate	separate	separate	separate or not	not or barely separate	**not or slightly separate**	not or slightly separate	not separate	not or slightly separate	not or barely separate	separate
spina anterior length	short	long, sometimes short	short or long	short or long	short	short	**very short**	short	short	short or absent	short	long
angulus inferior width	**slender**	**broad**	rather broad	rather broad	broad	broad	rather slender	rather broad	broad	broad	rather broad or rather slender	slender
angulus inferior shape	angular, pointed in large specimens	angular or rounded	angular	angular	angular or rounded	angular or rounded	pointed, angular or rounded	rounded or angular	rounded	rounded	rounded or angular	round or angular; can be absent
angulus inferior length	short	rather short	long or rather short	long or rather short	long	short	short	short	short	short	short	short
angulus inferior protruding	**much protruding**	**bit protruding**	much protruding	much protruding	much protruding	not or barely protruding	bit protruding	not or barely protruding	not or bit protruding	not or bit protruding	barely protruding	not or bit protruding; can be absent
angulus superior width	broad	broad	broad	broad	broad, but base not broader than tip	very broad	rather broad	very broad	broad	broad	slender	slender
angulus superior shape	**angular or pointed**	**round or angular**	sharp angular	sharp angular	angular or rounded	rounded	rounded	rounded or bit broadly pointed	rounded	rounded	pointed or angular	round, bumpy

Table B30 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
angulus superior length	long	long	long	long	very long	short	long	short	short	short	short	short
angulus superior protruding	much protruding	much protruding	much protruding	much protruding	much protruding	bit protruding	much protruding	bit or barely protruding	bit protruding	bit protruding	bit protruding	not or bit protruding
angulus superior orientation	bit upward	bit upward	bit or strong upward	bit or strong upward	strong upward; sometimes slight curve	bit or not upward	strong upward	bit upward	backward	backward	backward	sometimes bit dorsal
transition posterior side depth	deep concave	deep or shallow concave	rather shallow concave	rather shallow, concave	**very deep** concave	very shallow concave	rather shallow concave	shallow or rather deep concave	very shallow concave or straight	shallow concave	rather shallow concave	very shallow concave
transition posterior side shape	rounded	angular or sometimes rounded	angular or rounded	angular or rounded	rounded	rounded	rounded	rounded or angular	round	angular or rounded	rounded	angular or rounded
general shape						**more than half bone is mineralized; high anterior side**					**elongated shape**	**wavy structure, no ventral edge**
inclination of posterior half	upward	upward	slight or strong upward	slight or strong upward	strong upward	slight upward	upward	strong upward	slightly downward	straight or slightly downward	straight or slightly downward	upward
spina anterior relative length	same level or shorter than lamina	shorter than lamina or same level	bit further than lamina or same level	bit further than lamina or same level	same level	shorter than lamina or same level	same level or shorter than lamina	shorter than lamina	much shorter than lamina	much shorter than lamina	shorter than lamina	no lamina
relative position angulus superior and inferior	superior further	superior bit further or same	superior further	superior further	superior further or same	superior slightly further	superior slightly further	superior slightly further	superior bit further	superior bit further	superior further	inferior further

Table B31. Diagnostic features of the parasphenoid.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ridge between posterior part and lateral cristae	none	none	none	none	none	none	none	**present**	none	none	none	none
horizontal curve angulus anterior	slight to right	slight to right	strong or slight to right	**strong or slight to left**	strong or bit to right	very slightly to right	strong to right	strong to right	**slightly to left**	**strong to left**	**strong to left,** concave	strong to right
horizontal curve ventral crista	straight	straight	straight	straight	straight	bend	bend	bend	bend	bend	**strong bend**	bend
horizontal curve facies articularis basioccipitalis	barely to left	slight to left	sometimes slight to left	sometimes slight to right	very slight to left	slight to left (or right?)	slight to left	sometimes slight to left	sometimes to right	bit to right	strong to right	straight
vertical curvature at ventral crista	slight dorsal	barely or rather clear dorsal	slight dorsal	slight dorsal	none or slight dorsal	none	slight dorsal	slight dorsal or none	slight dorsal	none	none or barely	**strong ventral**
vertical curvature angulus anterior	slight dorsal	barely or rather clear dorsal	slight dorsal	slight dorsal	**slight ventrally**	none	barely dorsal	none	none	slight dorsal or none	none or barely	sometimes slight ventral
facies articularis length	long	long	long	long	long	**short**	long	short or rather long	**short**	**short**	long	very short
facies articularis width	very slender; base sometimes broader	broader in middle	very slender; base bit broader	very slender; base bit broader	slender	**very broad, broader in middle**	slender	broad or slender	**broad; tip sometimes broader**	**broad**	slender	very slender
facies articularis shape	straight	slight round or angular diamond shape	straight	straight	straight or bit diamond	diamond shape, flat	straight or slight diamond shape	straight; no ridges	**straight or diamond shape**	**straight or diamond shape**	straight or diamond shape	barely present sometimes
facies articularis groove depth	shallow	deep or shallow	rather deep	rather deep	rather shallow, rarely deep	shallow or none	rather shallow, sometimes deep	shallow or deep	shallow	deep or none	rather shallow	none
facies articularis groove shape	slender	slender	slender	slender	rather broad	broad	rather broad	broad	broad	rather broad	broad	none

Table B31 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
second ventral crista	none	none	none	none	none	none	none	none	none	none	none	anterior of midpart, small, short, convex, bit inclined to left
ventral crista height	high	rather low or rather high	low	rather low	high	low	rather low	high	low	low	low	rather low or high
ventral crista length	short	rather short or long	short	short	long	short	rather short or long	very long	short	very short	short	short
lateral cristae relative length	anterior left longer	anterior left longer	anterior left longer	anterior right longer	anterior left longer	anterior left longer	anterior left longer	anterior left longer	anterior right longer	anterior right longer	anterior right longer	anterior left longer

Table B32. Diagnostic features of the ceratohyal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
margo ventralis upper part height	low	low	low	low	low	high	high	rather low	high	high	very high	low
margo ventralis upper part edge shape	straight	straight	straight	straight	straight or slight concave	straight	rather straight	straight	slight S-curve or straight	slight S-curve or straight	straight	rather straight or subtle convex
margo ventralis transition at midheight	concave or angle, bump possible	concave or angle	concave or angle	concave or angle	angle	concave	angle	concave or angle	concave	slight round angle	angle	strong concave
margo ventralis midpart	slight inclined, rather straight or slight concave	inclined, straight	slight inclined, rather straight or slight concave	slight inclined, rather straight or slight concave	straight	inclined, straight	concave or straight	concave	convex	convex	straight or slight concave	convex, round or angular
ventral margo of processus ceratohyalis	concave	straight, can be inclined	convex at base, straight or slight concave	convex at base, straight or slight concave	straight or slight concave	**slight concave or straight**	straight or slight concave, very slender	straight	straight	straight	straight or subtle convex	convex, round or angular, sometimes with bump
ventral crista of processus ceratohyalis	present	present	present	present	present	present	present	present, usually more lateral	**absent**	**absent**	**absent**	present
transition length between margo dorsalis and processus ceratohyalis	short	short	short	short	long	long	long	long	short	very short	very short	short
transition depth between margo dorsalis and processus ceratohyalis	rather deep	deep	rather shallow or deep	rather shallow or deep	shallow	shallow	shallow	shallow	shallow	shallow	shallow	shallow
transition shape between margo dorsalis and processus ceratohyalis	round or irregular concave	round or angular concave	round concave	round concave	round concave	round or irregular slightly concave or rather straight	slight concave	straight or concave, irregular	**rather straight**	**rather straight or slight concave**	rather straight or slight concave	irregular or round concave
transition orientation between margo dorsalis and processus ceratohyalis	diagonal	diagonal	diagonal	diagonal	diagonal	rather horizontal or diagonal	diagonal	diagonal	**horizontal**	**slight diagonal**	**slight diagonal**	slight diagonal
transition processus between margo dorsalis and processus ceratohyalis	small processus	small processus possible	small processus	small processus	multiple processus	small processus possible	none usually	often ventrally long spina	none	none	none	none

Table B32 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
transition distance between margo dorsalis and processus ceratohyalis	1-2 foveola length	1-2 foveola length	1-2 foveola length	1-2 foveola length	2 foveola length	1-2 foveola length	2 foveola length	2-3 times foveola length; unclear	1 foveola length	1 or less foveola length	1 or less foveola length	1-2 times foveola length
procesuss ceratohyalis lateral base	broad	**slender, well delineated**	broad	broad	**slender, well delineated**	broad	broad	**slender, well delineated**	broad	broad	broad, flat	**slender, well delineated**
procesuss ceratohyalis relative length	less than corpus	less than corpus	less than corpus	less than corpus	**more than corpus**	about half	much less than corpus	less than corpus	less than corpus	less than corpus	less than corpus	about half
foramen externum	none	none	none	none	none	short, slender, elongate; sometimes none	none	none	**very slender, elongated; sometimes none**	**slender, elongated; sometimes none**	none	none
processus hypohyalis laterally	flat	flat	flat	flat	flat	flat	flat	flat	flat	flat	flat	**bulbuous**
processus hypohyalis position	not protruding	not protruding	not protruding	not protruding	not protruding	not protruding	slight protruding	not protruding or absent	not protruding	not protruding	slight protruding	not or slightly protruding
processus hypohyalis orientation	diagonally	diagonally	diagonally	diagonally	diagonally	diagonally	diagonally	**posteriorly** or absent	diagonally	diagonally	diagonally	diagonally
processus hypohyalis to margo synchondrosis	continous	sometimes continuous	continous	continous	continous	continous	not continuous	not continuous	not continuous	not continuous	not continuous	not continuous
margo dorsalis height	**rather low**	**rather low**	**rather low**	**rather low**	**rather low**	**high**	**high**	**low**	**high**	**high**	**high**	**rather low**
margo dorsalis width	**broad**	**broad**	**broad**	**broad**	**broad**	**rather slender**	**very slender**	**rather broad**	**rather broad**	**rather broad**	**slender**	**broad**
margo dorsalis edge shape	**convex**	**convex**	**convex**	**convex**	**rather straight or convex**	**straight or slight concave**	**concave**	**convex**	**straight, sometimes concave**	**straight or slightly concave**	**concave lower part, straight or slightly convex upper part**	**convex lower part, straight upper part**
margo synchondrosis shape	rather straight	straight	rather straight	rather straight	straight or slight concave	straight	straight or slight concave	straight or convex, irregular	straight or convex	straight or slight concave	**concave**	slight concave or straight
margo synchondrosis ridges	present	present	present	present	present	present	present	present	present	present	**often absent**	present

Table B33. Diagnostic features of the epihyal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
general shape	trapezoid	trapezoid	trapezoid	trapezoid	trapezoid	long trapezoid	round, comma shape	**P- shape/round rectangular**	triangular	triangular	elongate triangular	**rectangular**
symmetry corpus	asymmetrical	asymmetrical	asymmetrical	asymmetrical	asymmetrical	rather asymmetrical	asymmetrical	rather asymmetrical	almost symmetrical	almost symmetrical	rather asymmetrical	asymmetrical
parallellity of margo anterior and ventralis	anterior and ventral margo parallel	anterior and ventral margo parallel	anterior and ventral margo parallel	anterior and ventral margo parallel	anterior not parallel with ventral margo	anterior and ventral rather parallel	anterior not parallel with ventral	anterior parallel ventral	anterior and ventral parallel	anterior and ventral rather parallel	anterior and ventral rather parallel	anterior and ventral parallel
relative length margos	**anterior twice length ventral**	**anterior twice length ventral**	**anterior twice length ventral**	**anterior twice length ventral**	**anterior 2-3 times length ventral**	**anterior twice as long as ventral**	**anterior 3 times length ventral**	**anterior 1-2 times length ventral**	**anterior and ventral similar length**	**anterior and ventral similar length**	**anterior slightly longer than ventral**	**anterior bit longer than ventral**
apex epihyalis	clear, broad	clear, broad	clear, broad	clear, broad	clear, broad	clear, broad	clear, broad	not clear, broad	clear, **broad**	clear, **broad**	clear, **small**	not clear, broad
margo ventralis shape	straight or slight concav	slight concave	slight convex or concave	slight convex or concave	concave	slight concave	slight concave	convex	slight concave or rather straight	slight concave or rather straight	concave	concave

Table B33 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
margo ventralis shape	**short**	**short**	**short**	**short**	**short**	**long**	**short**	**short**	**long**	**long**	**long**	**long**
margo ventralis orientation	**almost horizontal**	**almost horizontal**	**almost horizontal**	**almost horizontal**	**almost horizontal**	**diagonal**	**diagonal**	**horizontal**	**diagonal**	**diagonal**	**diagonal**	**horizontal**
lateral side	**pit at ventral side**	**pit at ventral side**	**pit at ventral side**	**pit at ventral side**	**pit at ventral side**	**slight pit ventral side**	no pit or indent	indent ventrally with clear ridge	**slight pit ventrally**	slight pit ventrally; ridge below caput possible	slight pit ventrally; slight ridge below caput	clear indent ventrally
medial side	bump below caput anteriorly	bump below caput anteriorly	bump below caput anteriorly	bump below caput anteriorly	bump below caput anteriorly	ridge or bump below caput anteriorly	ridge or bump below caput anteriorly	**convex**	bulb with clear ridge below caput	bulb with clear ridge below caput	bulb with clear ridge below caput	bulb below caput
margo synchondrosis	2 parts	2 parts	2 parts	2 parts	2 parts	2 parts	2 parts	2 parts	1 part, only slight curve	1 part, only slight curve	1 part, only slight curve	2 parts

Table B34. Diagnostic features of the upper hypohyal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
ratio height-length	slightly to clearly longer than high, more so in larger specimens	longer than high or rather similar	longer than high	longer than high	**as long as high or slightly higher than long**	longer than high	much longer than high (2x)	much longer than high	slightly longer than high	**much longer than high (more than maximus)**	much longer than high	as long as high or slightly longer than high
foramen implantation, relative distance from anterior margo	third	third or half	third	third	third or quarter	third or half	third or quarter	half	third or half	third medial; two-thirds lateral	third	half
foramen implantation, height	lower half, close to articularis hypohyalis	lower half	mid height or slightly lower half	mid height or slightly lower half	mid height; second foramen possible	mid height or slightly lower half	mid height	midheight	lower half, can be close to articularis hypohyalis	close to articularis hypohyalis	**midheight**	midheight
foramen size	large	**usually large**	**rather small**	**rather small**	rather small	large	rather small	very small usually	large or small	large medial, unclear lateral	**very small or absent medially; very small laterally**	large
articularis ceratohyalis shape	very wide; round	very wide; round	wide; round or oval	wide; round or oval	wide; round or triangular, wider than high sometimes	very wide; round or oval; not delineated	rather small; round, sometimes irregular, with multiple pits	round, small	wide; round; high	wide; round; rather low	slender; round; low	wide; round; protruding spina at dorsal margo sometimes
articulares connection shape	**slight inclined**	**rounded**	**angular or rounded**	**angular or rounded**	angular	inclined	slight inclined	inclined	**angular**	**inclined**	rounded, slight inclined	rounded, slight inclined
margo posterior lateral view	straight to convex	straight to convex	straight to convex	straight to convex	convex, bend	strong convex	rather straight	straight or convex	rather straight or convex	rather straight	convex or straight	slight convex
margo dorsalis shape	concave in large, sometimes straight in small specimens	concave in large, sometimes straight in small specimens	concave in large, sometimes straight in small specimens	concave in large, sometimes straight in small specimens	straight, sometimes slightly concave; very broad	slight concave or straight	rahter straight or slight concave	straight or slight concave; bump in middle possible	concave or rather straight	rather straight or slight concave	**straight or subtly convex**	concave or rather straight
margo dorsalis inclination	posterior higher and broader	posterior slightly higher and broader	posterior higher and broader	posterior higher and broader	**posterior much higher, inclined**	posterior higher or rather same height	posterior higher, can be convex	posterior same height	posterior slightly higher	posterior subtle higher and wider	posterior same height	posterior same height, bit wider
margo anterior shape	concave or bend	concave or bend	concave or bend	concave or bend	**strong concave**	straight or concave or bend, ventral part rarely convex	straight or slight concave or bend	straight; slightly inclined; **articulation present, wide, rounded**	rather straight or slight bend	rather straight or slight concave or bend; ventral part can be slightly convex sometimes	straight or slight concave or bend	straight or concave
margo anterior ventral part protruding	sometimes protruding	sometimes protruding	protruding	protruding	not protruding	sometimes protruding	protruding	protruding	protruding clearly or barely	sometimes protruding	protruding	**protruding; long; barely in larger specimens (40cm SL)**
articularis hypohyalis shape	oval	**oval or rather round; slender**	**round**	**round**	round, oval, or tear	oval	oval; **very slender**	**at anterior side**	oval; broad	oval; slender	**oval; broad**	oval; slender
articularis hypohyalis length	long	**long**	**short**	**short**	rather long	long	long	**at anterior side**	long	long	**long**	rather short

Table B34 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
opening articularis hypohyalis	further than foramen	till or further than foramen	till foramen	till foramen	much further than foramen	further than foramen	till foramen	**none**	further than foramen	further than foramen	much further than foramen	till foramen
articulares connection	constriction, rarely not continuous	constricted or not continuous	slight constriction	slight constriction	not continuous	slight constriction or continuous	**not continuous**	not continuous	**not continuous, filled**	**not continuous, filled**	constriction	not continuous, filled with bone?
medial side	flat; pit behind caput	flat; sometimes pit behind caput	flat; pit behind caput	flat; pit behind caput	posteriorly slightly hollow	posteriorly slightly hollow	posteriorly slightly hollow	smooth slight convex	pit below caput	pit below caput	slight hollow below caput	convex or flat; subtle ridge above foramen
lateral side	slight pit around foramen	slight pit around foramen	slight pit around foramen	slight pit around foramen	posteriorly slightly hollow	**clear ridge above foramen;** posteriorly slightly hollow	slight ridge above foramen; posteriorly slightly hollow	slight ridge above foramen	slight pit around foramen	slight pit around foramen	slight ridge around foramen	pit around foramen

Table B35. Diagnostic features of the infrapharyngeal V.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
number of teeth (lateral row, medial row, middel rows)	6-14+7-17+ 0-3	8-16+4-17	7-29+8-24+2-12	7-29+8-24+2-12	10-13+ 10-18	11-21 + 17-32	12-14 + 11-22	7-20+5-15	64- 150	66-115	80-120	40-71
tooth implantation	**tidy; very broad alveoli**	rather tidy or bit chaotic	**chaotic**	chaotic	rather tidy or bit chaotic	rather tidy	rather tidy	rather tidy	chaotic	chaotic	chaotic	rather chaotic
tooth rows	2-3 rows	2 rows, 3 possible	1-2 rows; 3-4 possible in middle part	1-2 rows; 3-4 possible in middle part	1-2 rows; sometimes slight 3rd in middle part	2 rows	2 rows	2-3 rows	**3-5 rows**	**5-6 rows**	**2-3 or more rows**	3-4 rows
relative size tubes	toothed broader, higher; similar or shorter	toothles longer	toothed broader, higher; similar or shorter	toothles longer	toothles longer	toothles longer	toothles longer	toothles longer	**toothles longer**	**toothles longer**	**toothles longer**	**similar**
tooth surface width	**wide triangular; not broader than corpus**	slender; not broader than corpus	**slender or wide triangular; not broader than corpus**	**slender or wide triangular; not broader than corpus**	slender; not broader than corpus	slender; not broader than corpus	slender; not broader than corpus	slender; not broader than corpus	slender; **broader than corpus**	slender; **broader than corpus,** clearly protruding laterally	slender; **slightly broader than corpus,** bit curved laterally	slender; **slightly broader than corpus**
general length	long	**rather short**	long	long	long	long	long	short	long	long	long	short
general width	**very broad**	**slender**	**broad**	**broad**	slender	slender	slender	slender	slender	slender	slender	slender
curvature	straight	bend	straight	straight	strongly	slight, sometimes bend	slightly bend or curve	none or slightly	sligthly	sligthly	slightly bend	slightly or strongly
crista ventralis shape	long; high; convex or angular	short; rather high; convex or angular	long; high; convex or angular	long; high; convex or angular	short; very low; convex; can be absent	none	short; very low; convex; can be absent	long; low; very slender; straight	**very low and slender; slight convex or angular**	**very low and slender or absent**	**long; low; convex, clear delineation at toothless tube**	none
crista ventralis position	mid part	mid part	mid part	mid part	midpart or none	none	midpart or none	whole length	mid part	mid part	**anterior half**	none

Table B36. Diagnostic features of the first caudal vertebra.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
neural arch length	long	long	long	long	long	long	long	long	long	long	long	short
neural arch width	slender	slender	slender	slender	very slender	slender	slender	rather slender	broad	broad	slender	slender
neural arch curvature	straight	straight	straight	straight	straight	straight	straight	slight curve anteriorly	rather straight	rather straight	straight	curved anteriorly
flattening neural arch	**slightly anterior-posterior**	barely anterior-posterior or none	**slightly anterior-posterior**	**slightly anterior-posterior**	barely anterior-posterior or none	**slightly anterior-posterior**	barely anterior-posterior or none	**slightly anterior-posterior**	**flat anterior-posterior**	**flat anterior-posterior**	**slightly anterior-posterior**	**laterally**
implant neural arch on center	mid	rather anterior	mid or anterior	mid or anterior	mid	anterior	mid	anterior	very anterior	rather anterior	rather or very anterior	mid
haemal arch length	long	long	long	long	long	long	long	long	long	long	long	short
haemal arch width	broad; wider than center; wider at center	broad; sometimes right wider	broad; wider than center; wider at center	broad; wider than center; wider at center	rather slender; not wider near center	**slender**; not wider near center	rather broad; slightly wider near center; sometimes right wider	rather slender; barely wider near center	rather slender; wider near center	slender; slightly wider near center; sometimes left wider	slender; wider near center; left bit wider	slender; **no crista,** as 2 ventral ridges on corpus
haemal arch depth	deep	deep	rather deep	rather deep	rather deep	rather deep	deep	rather shallow	rather deep	shallow	rather deep	NA
opening haemal arch shape	round	round	large, square or round or oval	large, square or round or oval	large round or oval	oval	small oval	long round	long round	large	oval	NA
anterior spina neural arch shape	long pointed	long, round or angular	short, broad, angular	short, broad, angular	short, angular/rounded	long, broad, rounded	long, angular or rounded	short, broad, round or angular	long, broad, rounded or pointed	long, broad, pointed or angular	long, slender; pointed or angular	long, broad, pointed
anterior spina neural arch orientation	forward	forward	forward	forward	forward or bit upward	forward	forward or downward	forward or upward	forward or upward	forward	forward or upward	forward
posterior spina neural arch shape	short, angular or pointed	short, pointed	short, pointed	short, pointed	short, pointed	long, round	short, angular or pointed	long, slender, rounded or pointed	rather short, rounded, slender	short, pointed or rounded	short, slender, pointed	long, broad pointed or rounded
posterior spina neural arch orientation	diagonally	upward or backward	bit upward	bit upward	diagonally	upward or diagonally	backward	upward	upward or backward	upward or backward	upward or diagonally	backward
relative position neural spina	similar level	similar level	rather similar level	rather similar level	similar level	**posterior higher**	similar level	**posterior higher**	similar level	similar level	similar level	**posterior higher**
center laterally	**1-3 ridges**, sometimes unclear borders; many holes	**1 broad ridge**	**1-2 ridges,** sometimes unclear borders; holes possible	**1-2 ridges,** sometimes unclear borders; holes possible	**smooth or up to 4 unclear ridges**	**rather smooth, no ridges**	**1-2 ridges;** holes present	**2-3 large ridges, sometimes bit fused and appearing smooth;** holes possible; deep between ridges	**rough surface or many ridges, irregular, can be grouped into large ridges (up to 3)**	**rough surface or many ridges, irregular, can be grouped into large ridges (up to 3)**	**2-4 smooth ridges on surface**; holes; very deep between	**1 ridge from lateral anterior spina**
lateral pits	deep pit below and often above	deep pit below and clear pit above	deep below and above	deep below and above	rather deep below, shallow pit above	shallow pit below; **no pit above usually**	deep pit below, pit above deep or rather shallow	deep pit below and above, less clear when ridges fused	small pit below and above	small pit below and above	deep pit below and above	shallow pit below, deep pit above
processus on lateral side	long	long	long	long	long	no clear anterior, short	short	sometimes no clear anterior, long or short	long	short	short or long	rather long
transition between anterior and posterior lateral spina	usually not continuous and long distance in large specimens, continuous and short in small specimens	continuous or not, short distance	usually continuous, long distance, short possible in small specimens	usually continuous, long distance, short possible in small specimens	not continuous, long distance	not continuous, huge distance	not continuous, huge distance	not continuous, huge distance	**no posterior**	**no posterior**	**no posterior**	not continuous, huge distance
anterior lateral processus connected to lateral side	connected to crista at tip	connected to crista at tip op only part or not connected	connected at tip or halfway to crista, less left	connected at tip or halfway to crista	**not connected to crista**	connected to crista	connected at tip to crista, left sometimes less	connected to crista	connected at tip	connected halfway to crista	connected halfway to crista or almost tip	**not connected to crista**
center shape	rather round or hexagonal	round	hexagonal or round; ventral bit broader often	hexagonal or round; ventral bit broader often	round; large chorda opening	round or long oval	round or oval	hexagonal or rounded; ventral can be bit wider	round or square; bit wider than high sometimes; ventral and dorsal indents possible	square or oval or round; posterior ventral indent possible	hexagonal or round	hexagonal or round; bit wider than high sometimes

Part B3: Descriptions of unusable elements

The following elements are unusable to distinguish flatfish species, except for a few cases and family level identification.

Operculum

The operculum is a large, flat and thin bone. On the anterior medial side lies the foveola articularis, an articulation. The processus supra-articularis protrudes laterally from the foveola. Posteriorly of the foveola a low crista posterior can be seen. When viewed medially with the thicker part of the crista opercularis on the bottom, the foveola is on the right side in the left operculum and on the left side in the right operculum.

Identifying species using the operculum is difficult. There are not many structures present that show clear differences between taxa, especially within a family. Usually they overlap in qualitative characteristics.

Supracleithrum

The supracleithrum has a caput on the dorsal side of the corpus that can have the facies articularis posttemporalis on the lateral side. The part below the caput is the collum ossis supracleithralis. The ventral part of the corpus is the pars cleithralis, which fits in the impression supracleithralis on the cleithrum. The left and right elements differ slightly in shape, but the characteristics remain the same. In lateral view, the caput is bent to the left in the left supracleithrum and to the right in the right supracleithrum.

The different families can be identified by the lateral indents and the width of the corpus. Most Pleuronectidae and Scopthalmidae species are difficult to distinguish from each other, although in some cases they might be identified using a reference collection based on the curvature of the corpus, the ridges of the collum, and the presence of processus of the caput.

Basipterygium

The basipterygium articulates with the fin rays of the pelvic fin. It is an elongated bone that can be curved. The corpus is slender and can have a crista anterior. The ventral part of the basipterygium has an articulation. There is a large processus posterior behind the articulation. On the medial side there is a processus medialis. The processus lateralis is not always present in Pleuronectiformes. In medial view, the processus medialis is oriented right in the left basipterygium and left in the right basipterygium.

The basipterygium can only be used to identify the families of flatfish. Within Pleuronectids, only *M. kitt* can be somewhat identified.

Coracoid

The coracoid is part of the pectoral girdle to support the pectoral fin. The dorsal margin or corpus can be a bit thicker and protrudes slightly more on the lateral side. The posterior part of the bone has a wide and thin crista cleithralis. The dorsal side has an articulation scapularis as wide as the bone itself. Left and right sides can differ from each other in length and curvature. In medial view, the caput is on the left in the left coracoid and on the right in the right coracoid.

The coracoid can only be used to identify the families of flatfish. To some extent, *M. kitt* and *H. platessoides* show some diagnostic criteria. The remaining Pleuronectidae do not seem to show diagnostic features that would allow identification.

Basihyal

The basihyal is a slender, straight bone. The anterior side is a large articulation, called the caput. The posterior side is a slender processus posterior. The mid part of the corpus is broader, while the collum of the caput is more slender.

The basihyal can only be used to identify some species. The length and width of the processus inferior and corpus differ between species, but these characteristics are prone to subjective interpretation and the processus inferior can be broken. The basihyal is a very small bone that is unlikely to be recovered.

Lower hypohyal

The lower hypohyal is a triangular bone that articulates with the ceratohyal with the articularis ventralis. Anteriorly it has an apex anterior. Between the articularis ventralis and the apex anterior on the medial side, there can be ridges and small processus present. The lateral side is usually smooth, without processus. In lateral view, the caput is on the left side in the left lower hypohyal and on the right side in the right lower hypohyal.

The lower hypohyal does not allow adequate family or species identification since many of the structures do not show characteristics that are taxon specific. Scophthalmidae can be somewhat differentiated by the horizontal anterior apex and the absence of ridges between the articularis ventralis and the apex anterior, while the apex of Soleidae and Pleuronectidae is inclined and ridges present. *Microstomus kitt* has a slightly different shape from all other species, where the caput protrudes anteriorly from the articularis ventralis.

Pharyngeal 2

The second pharyngeal is a small bone in the back of the mouth ventrally of the neurocranium that has teeth. It is a slender bone that sometimes has a broader base. The dorsal part of the corpus can be broader and hollow. The lateral side on the margo dorsalis has a pit. On the dorsal medial side there is a processus medialis. When viewed ventrally (with the processus medialis on top), the concave margo of the tooth area and the processus medialis are on the left side in the left pharyngeal and on the right side in the right pharyngeal.

The second pharyngeal can only be used to differentiate families of flatfish and usually not lower taxonomic levels. *Scophthalmus* sp. can not be identified confidently. Pleuronectidae are difficult to identify to species, although some slight differences between species might be used cautiously.

Pharyngeal 3

The third pharyngeal is a small bone in the back of the mouth ventrally of the neurocranium that has teeth. It is placed posteriorly of the second pharyngeal and is usually a bit broader. The tooth area is less protruding. The dorsal part of the corpus can be broader and hollow. On the dorsal medial side there is a processus medialis. When viewed ventrally (with the processus medialis on top), the concave margo of the tooth area and the processus medialis are oriented to the left in the left pharyngeal and to the right in the right pharyngeal.

The third pharyngeal allows for easy family identification. The species within Scophthalmidae and Pleuronectidae are difficult to identify and only show differences in certain characteristics sometimes.

Pharyngeal 4

The fourth pharyngeal is a small bone in the back of the mouth ventrally of the neurocranium that has teeth. It is placed posteriorly of the third pharyngeal. It is a rather small and slender bone and often curved. Dorsally it has a processus dorsalis in the middle of the corpus. When viewed ventrally (with the processus dorsalis on top and the concave margo of the tooth area downward), the larger alveoli are on the left side of the pharyngeal in the left pharyngeal and on the right side in the right pharyngeal.

The fourth pharyngeal can only be used to differentiate families of flatfish, but not lower taxonomic levels.

Ultimate vertebra

The last vertebra of the spine carries the caudal fin complex. The anterior part of the center is shaped like a vertebra. The posterior part is ventrally fused with hypurals. The dorsal part of the caudal complex articulates to the center of the ultimate vertebra.

The ultimate vertebra can be used to distinguish Scophthalmidae from the two other families. If the lateral ridges are present, *Lepidorhombus whiffiagonis* can be easy to identify. Within the Pleuronectidae, *Hippoglossus hippoglossus* is the only species that potentially can be identified by its enlarged thick ridges around the center.

Table B37. Diagnostic features of the operculum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
foveola articularis shape	round, oval or triangular	round or oval	round or oval	round or oval	round or oval	**elliptical**	oval; at angle with crista	oval; **medial part shallower**	round or oval	round or oval	round, oval or triangular	**strong oval**
processus supra-articularis shape	square or round	square or round	**rounded, but can have angular ventral side**	**rounded, but can have angular ventral side**	round or square	**round; thick**	round or angular; bumps possible	round or square; bumps	round or angular	round or angular	round or angular	round
processus supra-articularis length	long or short	long or short	short	short	long	short	short	short	short	short	very short or absent	short
foveola - processus orientation	rather dorsally	midheight	rather dorsally	rather dorsally	midheight/rather dorsally	mid	**rather ventrally**	midheight or rather dorsally	dorsal half	dorsal half	dorsal half	midheight
relative length between foveola articularis and processus supra-articularis	as long as foveola or only half as long	half as long as foveola; can be as large as foveola in small specimens	half as long as foveola	half as long as foveola	half or almost as long as foveola	much shorter than foveola	much shorter than foveola	half as long as foveola	**half as long or third of foveola**	**half as long or third of foveola**	**much shorter than foveola**	half as long as foveola
relative height between foveola articularis and processus supra-articularis	processus about as high as foveola or slightly lower	processus less high than foveola, can be as large as foveola in small specimens	processus about as high as foveola, can have additional bumps to make it higher	processus about as high as foveola, can have additional bumps to make it higher	processus as high as foveola usually	processus much lower than foveola	processus lower than foveola	processus as high or slightly higher than foveola	**processus lower than foveola**	**processus lower than foveola**	**processus lower than foveola**	processus as high as foveola
crista posterior relative width	not wider than foveola	not wider than foveola	not wider than foveola	not wider than foveola	not wider than foveola	as wide as foveola	much slenderer than foveola	very short; crista barely visible	wider than foveola	wider than foveola	as wide as foveola	slenderer than foveola

Table B38. Diagnostic features of the supracleithrum.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
pars cleithralis indentation on lateral side	1 or 2; anterior clear; deeper sometimes in left side	**none or 2 very deep with slender ridge midcorpus**	0-2, not clear	0-2, not clear	none or slightly in left side on posterior side	2, posterior one clear and deep, at one side, anterior one slender and less clear	0-1, sometimes not clear	1 on posterior side below collum, **not at tip** corpus	**none**	**none**	**none**	**none**
ridge on collum	large, not protruding much	not well delineated, not much protruding	large, more protruding in left	large, more protruding in right	very unclear sometimes; anterior bump possible	unclear	unclear; bump on anterior side	**very clear, round and high, protruding**	none; slight ridge/bump possible on corpus, not crista	none; very subtle ridge/bump possible on corpus, not crista	none; very subtle ridge/bump possible on corpus, not crista	none; very slight bump possible, very close to caput
general width	broad; small specimen sometimes slender	rather slende	broad	broad	rather slender	rather slender	slender;	broad	slender	slender	broad	slender
relative width between pars cleithralis and caput	caput slightly slenderer	caput much slenderer	caput slightly or much slenderer	caput slightly or much slenderer	caput slenderer or similar	caput slightly slenderer	caput slenderer or similar	caput slightly slenderer	caput slightly slenderer	caput slenderer or similar	caput slightly slenderer	caput barely slenderer
broadest part	**midpart and collum**	**midpart**	**midpart**	**midpart**	**midpart**	**midpart and collum**	**midpart**	**midpart and collum**	**collum**	**midpart and collum**	**midpart**	**midpart, barely difference**
processus on caput	medial anterior side	medial anterior side possible	slight bump medially sometimes	slight bump medially sometimes	bump medially	none	slight bump medially	bump medially	sometimes, on right side, posterior edge	sometimes, on right side, posterior edge	sometimes, on left side, anterior edge	subtle bump medially sometimes
curvature pars cleithralis	anterior midpart convex, posterior collum convex; small specimens sometimes rather straight	collum posterior convex	anterior midpart convex; posterior collum convex	anterior midpart convex; posterior collum convex	rather straight	rather straight, only slight S-curve of collum	rather straight; sometimes slightly curved caput	straight	S-curved anterior convex midpart; posterior collum convex	rather straight or bend between midpart and collum; collum posterior convex	rather straight or slight curve at collum	straight
pars cleithralis length	short	long	short	rather short	long	long	rather long	short	long	long	rather long	rather long
pars cleithralis width	broad	slender	broad	broad	rather broad	slender	slender	broad	slender	slender	rather broad	slender
pars cleithralis tip shape	broadly pointed tip	slight pointed tip	pointed tip	pointed tip	pointed or broadly rounded	pointed or rounded tip	pointed tip	roundly pointed tip	rounded or slightly pointed tip	rounded or slightly pointed tip	pointed or broadly pointed tip	rounded or slightly pointed tip

Table B38 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
medial side	hollow	hollow	hollow	hollow	slight pit	slight hollow	slight pit	sometimes slightly hollow	slight pit	slight pit	flat	very slight hollow

Table B39. Diagnostic features of the basipterygium.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus posterior length	rather long	long	long or rather long	long or rather long; rather slender or broad; pointed	short	long	rather long	short or long	rather short	short	short	**absent**
processus posterior width	slender	slender	rather slender or broad	rather slender or broad	rather broad	rather broad	slender	rather broad	broad	broad or slender	broad or slender	**absent**
processus posterior tip shape	pointed	pointed	pointed	pointed	rounded or pointed	rounded or pointed	pointed or rounded; slight bump at base dorsally possible	rounded; slightly flattened dorsally	pointed or rounded; bit flat dorsally	pointed or rounded; dorsally bit flat	pointed or rounded; dorsally bit flat	**absent**
processus posterior orientation	backward or slightly upward	backward	backwardor slightly upward	backward or slightly upward	slightly upward	slightly upward or backward	backwardor slightly upward	laterally	slightly upward or backward	slightly upward	upward	**absent**
processus posterior curvature	sometimes subtly upward	straight	straight or subtly upward	straight or subtly upward	slight forward or rather straight	straight	straight	**upward**	straight; sometimes laterally	upward	upward	**absent**
processus medialis length	short	short	short	short	long	long	short	**very short**	short	short or long	short	short
processus medialis width	broad	broad or slender	broad or slender	broad or slender	slender	very slender	rather slender	**very broad base; continuous with processus anterior**	very broad	very broad	very broad	**slender**
processus medialis tip shape	pointed or rounded pointed	pointed or angular	pointed	pointed; flat	pointed	pointed	pointed	**rounded or pointed; as ridge**	pointed or irregular	rounded, sometimes pointed	rounded, sometimes pointed	**pointed or bit irregular**
processus medialis orientation	flat; ventral	flat; ventral	flat; ventral or bit backward	flat; ventral or bit backward	flat; ventral	flat; ventral	flat; ventral or subtly backward	**flat; ventral**	**laterally protruding**	**laterally protruding**	**laterally protruding**	**ventral or bit backward**
processus lateralis	absent	absent	absent	absent	absent	absent	absent	absent	**present**	**present**	**present**	absent
crista dorsalis	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent	**short, convex**
crista ventralis width	slender	very slender	rather broad	rather broad	rather broad	broad	slender	slender	**very broad, but short**	**very broad, but short**	**very broad, but short**	**absent**
crista ventralis edge shape	rather straight or slight concave; gradual decrease	concave or rather straight; gradual decrease	straight or slight concave, can be bit wavy; gradual decrease;	straight or slight concave, can be bit wavy; gradual decrease	concave or rather straight, sometimes bit bumpy; gradual decrease	rather straight or slight convex; gradual decrease	short; concave; gradual decrease	short; concave; gradual decrease	**straight vertical decrease**	**straight or convex vertical decrease**	**straight vertical decrease**	**absent**
crista ventralis implant	till halfway (straight) or almost tip (curved)	till bit more than halfway of almost tip, not at tip usually	till end or near tip	till end or near tip	till end or almost till tip	till bit more than half or till end	till halfway corpus	till halfway corpus or till end	**caput**	**caput**	**caput**	**absent**

Table B40. Diagnostic features of the coracoid.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
crista cleithralis implant	till tip or almost tip	not till tip or till halfway	slender till halfway or almost tip	slender till halfway or almost tip	till tip or almost	till halfway	till halfway or (almost) end of tail	till end	till halfway or end	till bit further halfway	till halfway	till halfway
crista cleithralis edge shape	concave or straight, stronger halfway	strong concave or rather straight	rather concave or straight	rather concave or straight	rather straight	strong concave behind articulation or gradual	gradual, or strong straight or concave	straigt or slight concave	concave or straight in first half	rather straight or slight concave gradual	concave	slight concave or straight
articulation scapularis edge shape	slight concave or straight	rather straight or subtle concave	S-curve or rather straight	S-curve or rather straight	slight S-curve, or only dorsal part convex	convex	**slight convex or straight**	concave	straight, convex ventral part	concave, ventral convex	slight concave, ventral convex	straight
ventral part articulation scapularis	longer	slightly longer	longer	longer	longer	slightly longer	**not longer**	sometimes longer	longer	slightly longer	longer	much longer
dorsal crista	absent	absent	absent	absent	absent	absent	absent	absent	**present only at articulation**	**present only at articulation**	**present whole length**	**present whole length**
corpus	rather short	short	long	long	rather long	long	short	rather long	long	rather long	very long	short

Table B41. Diagnostic features of the basihyal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
processus posterior	rather long; very slender	long or short; very slender	long; very slender	long; very slender	short; very slender	short; slender	rather long; slender	short; slender	short; rather broad	short; rather broad	short or long; slender	short; slender
relative width corpus - caput	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	similar or corpus broader	**caput broader than corpus**	caput slightly broader than corpus
caput shape in frontal view	square	square	square	square	square, rarely flat	square	square, **very flat**	square or round	**diamond**	**diamond**	**diamond**	square
indentation collum	long; shallow; round or angular/bend	long; shallow round/smooth	long; shallow; round	long; shallow; round	short; shallow; angular or round; no clear indent, but only transition to wings	long; shallow; round, sometimes bit angular/pointed	short; shallow; v-shaped	very short; shallow; round or irregular	short; shallow or deep; angular or V-shape	long or short; not obvious or only slightly shallow; round or angular	very long; shallow or deep; round	short; shallow; rather round

Table B42. Diagnostic features of the lower hypohyal.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
dorsal side of apex anterior	inclined	inclined	inclined	inclined	inclined	inclined	inclined	angular	**horizontal**	**horizontal**	**horizontal**	inclined
ridge between articularis ventralis and apex anterior	present	present	present	present	present	present	present	**absent**	**absent**	**absent**	**absent**	present
apex anterior shape	not protruding	not protruding	not protruding	not protruding	not protruding	not protruding	not protruding	**protruding**	not protruding	not protruding	not protruding	not protruding

Table B43. Diagnostic features of the pharyngeal II.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
number of teeth	5-10+0-8	5-8+0-4	6-9+0-6	6-8+2-7	7	7-13, of which few small; or 24-32	6-8	4-5	53-91; or 27	53-73; or 34	50 or more	13-27
tooth implantation	tidy; **very broad alveoli**	rather tidy	rather chaotic	rather chaotic	tidy	chaos	rather tidy	tidy	chaos	chaos	chaos	chaos
tooth rows	1-2 rows	1 row, extra few teeth sometimes in 2nd row	1-2 rows	1-2 rows	1 row	1-2 rows; rarely multiple rows	1 row	1 row	**3-5 rows**	**6 rows**	**3-6 rows**	**3-5 rows**
tooth area	whole length; flat or slight convex	whole length; flat	whole length; flat or slight convex	whole length; flat or slight convex	whole length; flat	whole length; convex	whole length; slightly convex	whole length; flat; very short	over half, almost whole length; **flat**	over half, almost whole length; **flat**	almost whole length; **convex**	whole length
dorsal lateral pit shape	triangular, U, or kidney shape	triangular or kidney shape	kidney, v or u-shape; slender	kidney, v or u-shape; slender	U-shaped	triangular or rather round	triangular, rounded or bean	triangular or rather round	round, bean or triangular	bean or triangular shaped	round	not clear, round
distance between dorsal tubes	none	none	none	none	none	none	none	none	**larger than diameter of tube**	**smaller or about diameter of tube**	**much smaller than diameter tube**	none
additional dorsal tube	no extra	no extra	no extra	no extra	no extra	no extra	no extra	no extra	**1 extra**	**1 extra**	**1 extra or no extra**	no extra
processus medialis orientation	same orientation as corpus	strongly dorsally oriented, bit laterally	same orientation as corpus	same orientation as corpus	dorsally oriented	dorsally oriented, bit laterally	same orientation as corpus	dorsally oriented	**same orientation as corpus**	**same orientation as corpus**	**dorsally oriented**	dorsally oriented
processus medialis length	further than corpus	not or slightly further than corpus	not further than corpus	not further than corpus	further than corpus	further than corpus	further than corpus	slightly further than corpus	further than corpus	further than corpus	further than corpus	further than corpus

Table B44. Diagnostic features of the pharyngeal III.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
number of teeth	2-11+2-11	5-8+4-8	7-10+2-7	7-10+2-7	6-7	8-22 of which few small	5-6	3-4	50-90; 37 in P98	(34)53-85	40-50; 22	15-58
tooth rows	1-2 rows	1-2 rows	1-2 rows	1-2 rows	1 row	1-3 rows, 3rd unclear	1 row	1 row	**6 rows; less posteriorly**	**9 rows; less posteriorly**	**4-5 rows**	**min. 3 rows**
tooth implantation	tidy; **very broad alveoli**	tidy	**chaos; alveoli badly delineated**	**chaos; alveoli badly delineated**	tidy	**rather tidy or chaos**	tidy	tidy	chaos	chaos	chaos	chaos
tooth area implantation	first half of surface	first half of surface	more than half surface	more than half surface	half of surface	half of surface	half of surface	only at tip; protruding dorsally	half or 2/3 surface	half of surface	half or bit less of surface	bit more than half or half of surface
tooth area relative width	corpus broader than tooth area	corpus barely or clearly broader than tooth area	corpus broader or same as tooth area	corpus broader or same as tooth area	corpus much broader than tooth area	corpus broader than tooth area	corpus slightly broader than tooth area	corpus much broader than tooth area	**corpus broader than tooth area**	**corpus bit broader than tooth area**	**corpus bit broader than tooth area**	**corpus not broader than tooth area**
dorsal side	slight hollow	slight hollow or straight	slight hollow	slight hollow	slight hollow	slight hollow	hollow	hollow	clear hollow	clear hollow	clear hollow	slight hollow
dorsal pit	broad U-shape	none or small; round, triangular, square, or large slender U	slender, rather oval, U or 8 shape	slender, rather oval, U or 8 shape	U or V-shaped; sometimes triangular; medial side much slenderer	V or U shaped; medial side much slenderer	U or triangular; medial side much slenderer	round; very small	semi-closed or open u shape; large	semi-closed or open u shape; large	broad U-shape	shallow, can be filled; 1 or 2 lobes; round or triangular usually; unclear
processus medialis shape	flat; short; broad	flat; **long**; broad	flat; short; broad	flat; short; broad	flat; rather short; broad	flat or rather round; broad	round; **long**; slender	round; very short; slender	round; rather long; slender	round; rather long; slender	bit flat; very long; broad	rounded tip, bit flat; short
relative width processus medialis to corpus	as broad as corpus	slightly broader or as broad as corpus	subtle broader than or as broad as corpus	subtle broader than or as broad as corpus	as broad as corpus, tip slenderer	slightly slenderer than corpus	slightly broader or as broad as corpus	slenderer than corpus	**slenderer than corpus**	**slenderer than corpus**	**much slenderer than corpus**	**much slenderer than corpus**
processus medialis curvature	straight	**dorsally**	straight	straight	straight	straight	**dorsally**	straight	straight	straight	slightly curved	slightly curved
medial crista of processus medialis dorsally visible	**no**	yes	yes	yes	yes	yes	yes	**no**	yes	yes	yes	yes

Table B44 continued

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
posterior edge protrusion	**large**	none	small or none	small or none	**large**	slightly	slightly or none	large	slightly	slightly or none	slightly	none

Table B45. Diagnostic features of the pharyngeal IV.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
number of teeth	6-8+0-3 teeth	5-9 teeth	8-13+0-4 teeth	8-13+0-4 teeth	7 teeth	5-7+0-1 teeth; 16-17 in 23423 ; 4 in yzl895	5-6 teeth	?	20-27 teeth	25-42 teeth	10-26 teeth	22-30
tooth rows	1 row, rarely 2	1 row	1 row, rarely 2	1 row, rarely 2	1 row	1-2 rows	1 row	?	**6 rows**	**7-8 rows**	**3-6 rows**	3-4 rows
tooth area	curved; half length	highly curved, 90degrees; (almost) whole length	curved; almost whole length	curved; almost whole length	slight curve; whole length	short, half or almost whole length	straight or slight curve; whole length	?	**round, broad; entire caput; chaos**	**round, broad; entire caput; chaos**	**round, small; entire caput; chaos**	**round or triangular, small; entire caput; chaos**
general shape	slender caput, straight or slight convex tooth area	broad caput, straight tooth area	slender caput, straight or slight convex tooth area	slender caput, straight or slight convex tooth area	slender caput, straight tooth area	slender caput, slight convex tooth area	slender caput, straight tooth area	?	**round caput,** rather flat and bit convex tooth area; caput bit shorter	**round caput,** rather flat and bit convex tooth area, caput bit longer	**round caput,** rather flat and bit convex tooth area, caput bit shorter	**round or triangular caput,** rather flat and bit convex tooth area
processus dorsalis	1-2 tips, T-shape	1-2 tips, T- or U-shape	1 tip, T-shape	1 tip, T-shape	2 tips, U-shape	1-2 tips in U-shape; long	1-2 tips,T-shape or slight U-shape perpendicular on caput	?	**2 spina in U shape in same plane caput**	**2 spina in U shape in same plane caput**	**2 spina in U shape in same plane caput**	2 tips in U- or V-shape, one big, one small

Table B46. Diagnostic features of the ultimate vertebra.

Diagnostic feature	Pleuronectidae								Scophthalmidae			Soleidae
	Pleuronectes platessa	*Limanda limanda*	*Platichthys flesus R*	*Platichthys flesus L*	*Glyptocephalus cynoglossus*	*Hippoglossus hippoglossus*	*Hippoglossoides platessoides*	*Microstomus kitt*	*Scophthalmus maximus*	*Scophthalmus rhombus*	*Lepidorhombus whiffiagonis*	*Solea solea*
lateral ridges on center	none	none	none	none	none	none	none	none	none	none	**possible**	none
articulation	slight to barely anterior ridge	slight to barely anterior ridge	slight to barely anterior ridge	slight to barely anterior ridge	slight to barely anterior ridge	slight to barely anterior ridge	slight to barely anterior ridge	slight to barely anterior ridge	**strong anterior ridge**	**strong anterior ridge**	**strong anterior ridge**	slight to barely anterior ridge
anterior edge around center	thin edge of center	thin edge of center	thin edge of center	thin edge of center	thin edge of center	**thickened edge of center**	thin edge of center	thin edge of center	thin edge of center	thin edge of center	thin edge of center	thin edge of center
collum	slightly constricted	strongly constricted	barely constricted	barely constricted	strongly constricted	barely constricted	rather clear constricted	clearly constricted	clearly constricted	slightly constricted	slightly constricted	slightly constricted

Appendix C – Chapter 4. Geometric morphometric analysis of Pleuronectiformes vertebrae: a new tool to identify archaeological fish remains?

Table C1. List of specimens used in this study.

Collection number	Genus	Species	SL (cm)	TL (cm)	Atlas	Cervical	Precaudal	Caudal	Total
Bothidae									
RBINS A2-038-P-17	*Arnoglossus*	*laterna*	12	?	1	3	3	10	17
YZL1184	*Arnoglossus*	*laterna*	13	?	0	3	3	2	8
RBINS A2-038-P-0018	*Arnoglossus*	*laterna*	13.7	16	1	3	5	7	16
Citharidae									
RBINS 24632	*Citharus*	*linguatula*	13.7	?	1	3	4	7	15
RBINS DCB842	*Citharus*	*linguatula*	16.9	20.7	1	3	6	9	19
Pleuronectidae									
YZL942	*Glyptocephalus*	*cynoglossus*	22	?	1	2	4	11	18
YZL902	*Glyptocephalus*	*cynoglossus*	25	37	1	1	5	11	18
RBINS 91-017-P-56	*Glyptocephalus*	*cynoglossus*	32	36	1	1	3	11	16
RBINS DCB359	*Glyptocephalus*	*cynoglossus*	34.7	41.6	1	3	5	11	20
YZL1954	*Glyptocephalus*	*cynoglossus*	?	25?	1	3	4	8	16
YZL943	*Hippoglossoides*	*platessoides*	18	21	1	2	5	9	17
YZL1052	*Hippoglossoides*	*platessoides*	18	21.5	1	3	5	9	18
YZL0912	*Hippoglossoides*	*platessoides*	20	25	1	2	3	5	11
RBINS DCB849	*Hippoglossoides*	*platessoides*	20	24.6	1	3	4	9	17
YZL913	*Hippoglossoides*	*platessoides*	20	23	1	2	5	10	18
RBINS DCB850	*Hippoglossoides*	*platessoides*	21.6	26	1	2	4	7	14
RBINS DCB767	*Hippoglossoides*	*platessoides*	30.6	36.9	1	2	5	9	17
YZL1376	*Hippoglossus*	*hippoglossus*	35	41	1	3	3	7	14
YZL0895	*Hippoglossus*	*hippoglossus*	38	42.5	1	2	4	5	12
YZL894	*Hippoglossus*	*hippoglossus*	42	46.5	0	2	6	12	20
RBINS 91-017-P02	*hippoglossus*	*hippoglossus*	48.4	55.5	1	3	5	8	17
RBINS DCB845	*hippoglossus*	*hippoglossus*	50	59.2	1	3	7	10	21
YZL907	*Limanda*	*limanda*	12	17	1	2	5	8	16
YZL906	*Limanda*	*limanda*	15	?	1	2	3	10	16
RBINS A2 028 P41	*Limanda*	*limanda*	16.2	19.5	1	2	3	8	14
YZL0911	*Limanda*	*limanda*	24	27	0	1	4	6	11
RBINS A4 001 P60	*Limanda*	*limanda*	26	29.6	1	2	4	10	17
RBINS A4 022 P02	*Limanda*	*limanda*	31.5	?	1	3	4	8	16
YZL1044	*Microstomus*	*kitt*	20	23.5	1	3	3	6	13
RBINS A4-001-P-0088	*Microstomus*	*kitt*	23.5	29	1	3	4	10	18
RBINS A3-001-P62	*Microstomus*	*kitt*	26.6	32.1	1	2	8	11	22
RBINS 23881	*Microstomus*	*kitt*	29	34.8	1	3	5	11	20
RBINS 23882	*Microstomus*	*kitt*	31.3	37	1	3	4	10	18
YZL930	*Microstomus*	*kitt*	32	37	1	3	3	10	17
YZL1096	*Microstomus*	*kitt*	?	23	1	2	5	8	16
YZL1140	*Platichthys*	*flesus right*	16	18.5	1	1	5	8	15
RBINS A2 038 P22	*Platichthys*	*flesus right*	20.6	24.7	0	2	3	10	15
YZL1151	*Platichthys*	*flesus right*	26	31	1	2	3	5	11
RBINS 23801	*Platichthys*	*flesus right*	29	?	1	2	4	9	16
RBINS A4-001-P36	*Platichthys*	*flesus right*	32.9	39.3	1	2	6	8	17
YZL1974	*Platichthys*	*flesus right*	NA	NA	1	2	4	9	16
YZL1973	*Platichthys*	*flesus left*	NA	NA	1	2	4	9	16
RBINS A4-001-P-125	*Platichthys*	*flesus left*	28.5	34.3	1	1	4	9	15
RBINS A4 001 P127	*Platichthys*	*flesus left*	33.7	39.4	1	2	3	7	13
RBINS A4 001 P69	*Platichthys*	*flesus left*	35.5	41.7	1	2	4	10	17
YZL945	*Pleuronectes*	*platessa*	16	?	1	2	6	11	20
YZL0950	*Pleuronectes*	*platessa*	21	24	1	1	5	7	14
RBINS 96 087 P10	*Pleuronectes*	*platessa*	29	35	1	2	5	10	18
RBINS 97 003 P336	*Pleuronectes*	*platessa*	35	?	1	2	5	10	18
YZL887	*Pleuronectes*	*platessa*	44	?	1	2	6	9	18
RBINS 97 003 P266	*Pleuronectes*	*platessa*	49	?	1	2	3	11	17
Scophthalmidae									
RBINS DCB773	*Lepidorhombus*	*boscii*	18	21	1	3	4	4	12
YZL0998	*Lepidorhombus*	*whiffiagonis*	25	28.5	1	3	5	8	17
RBINS 91 017 P26	*Lepidorhombus*	*whiffiagonis*	26	31	1	1	6	4	12

Table C1 continued

Collection number	**Genus**	**Species**	**SL (cm)**	**TL (cm)**	**Atlas**	**Cervical**	**Precaudal**	**Caudal**	**Total**
RBINS A4-001-P-94	*Lepidorhombus*	*whiffiagonis*	28.5	32.2	1	3	4	9	17
YZL0900	*Scophthalmus*	*maximus*	30	36	1	1	4	6	12
RBINS A2-023-P-02	*Scophthalmus*	*maximus*	32.9	39.5	1	2	4	10	17
YZL1962	*Scophthalmus*	*maximus*	34.65	36	1	2	4	6	13
RBINS A2 052 P12	*Scophthalmus*	*maximus*	37.2	45	1	2	4	9	16
YZL1153	*Scophthalmus*	*rhombus*	26	31	1	2	3	5	11
RBINS 24823	*Scophthalmus*	*rhombus*	27	?	1	2	5	9	17
RBINS 23664	*Scophthalmus*	*rhombus*	37.7	45.1	1	2	5	9	17
YZL1146	*Zeugopterus*	*punctatus*	?	14?	1	2	4	5	12
RBINS A2-019-P-30	*Zeugopterus*	*regius*	9.5	?	1	2	4	9	16
Soleidae									
RBINS 23080	*Buglossidium*	*luteum*	12.3	14.6	1	2	0	16	19
RBINS 88-19-P-107	*Dicologlossa*	*hexophthalma*	14	16.5	1	0	0	3	4
RBINS A2-057-P-52	*Pegusa*	*lascaris*	23.7	26.5	1	3	1	10	15
RBINS A2-057-P-51	*Pegusa*	*lascaris*	24.2	26.8	1	2	1	12	16
YZL0903	*Solea*	*solea*	18	24	1	3	0	8	12
RBINS A2-019-P-48	*Solea*	*solea*	18.8	20.4	1	2	1	14	18
YZL1972	*Solea*	*solea*	27.39	25.33	1	2	2	11	16
RBINS 91-017-P-33	*Solea*	*solea*	34	38.5	1	0	0	0	1
RBINS A4-001-P-133	*Solea*	*solea*	40.4	45.4	1	2	1	13	17
Total					**69**	**157**	**285**	**625**	**1136**

Part C1. PCA plots of modern dataset

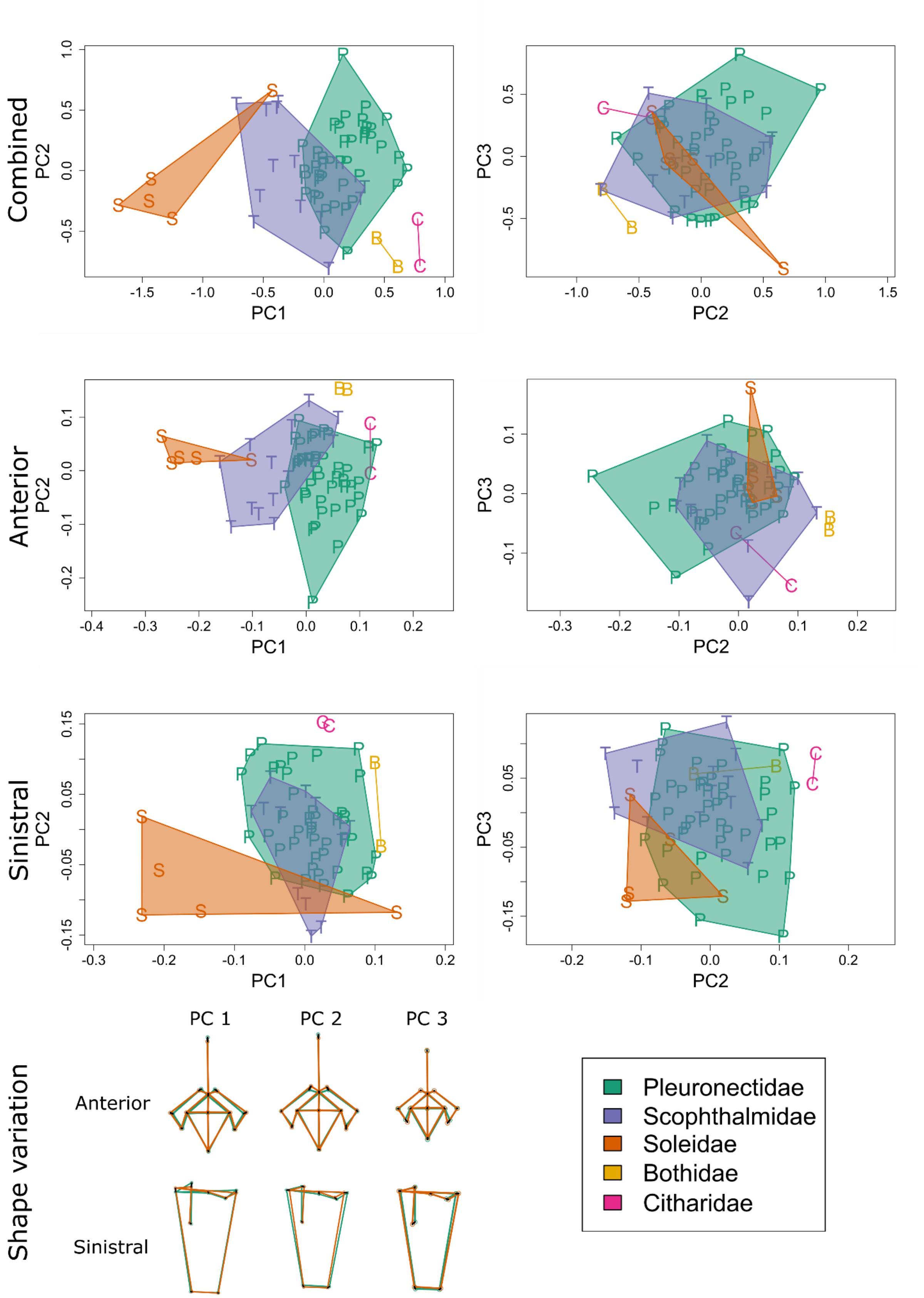


Figure C1. PCA and deformation grids of the atlas vertebra per family for the different views.

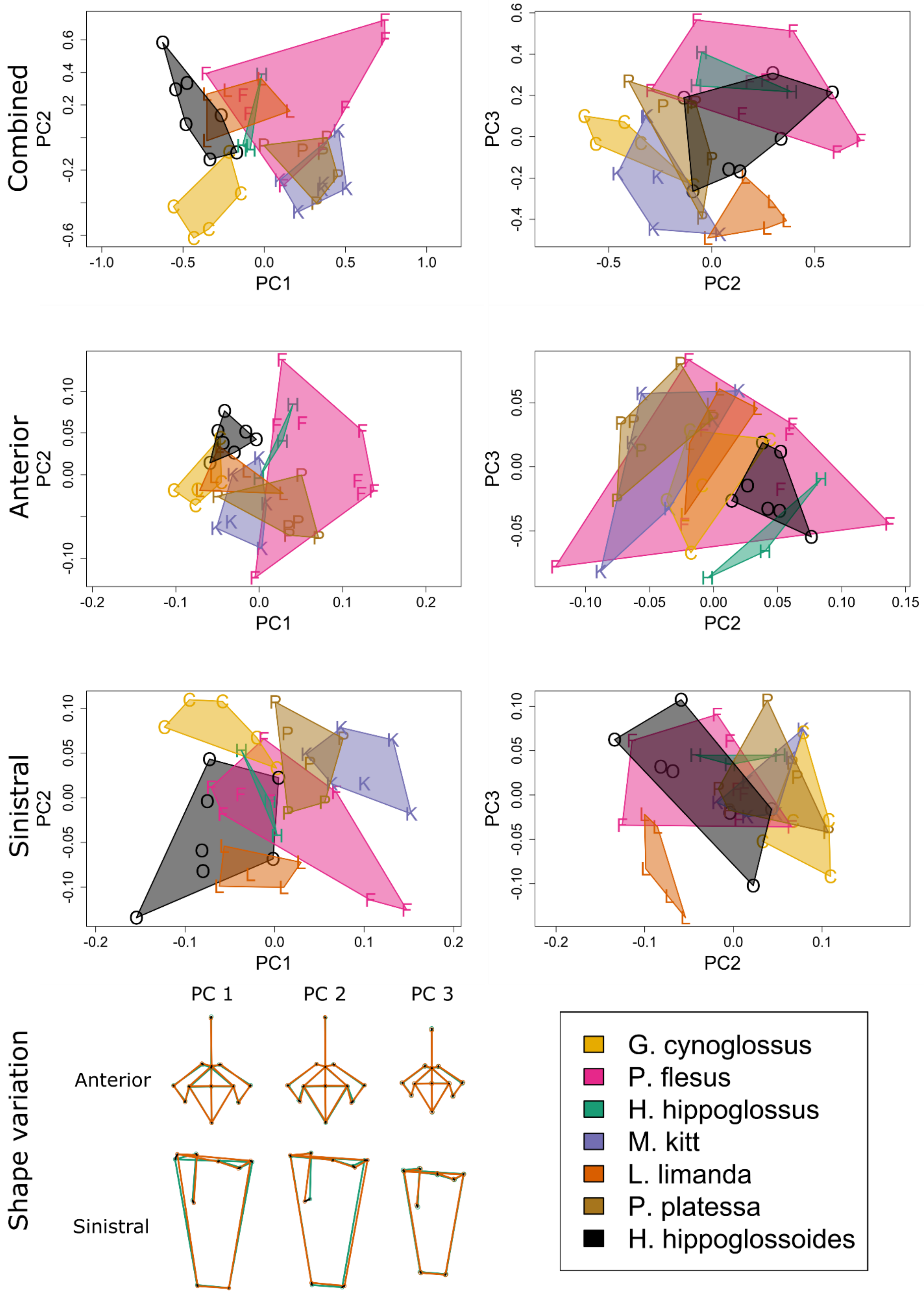


Figure C2. PCA and deformation grids of the atlas vertebra of Pleuronectidae for the different views.

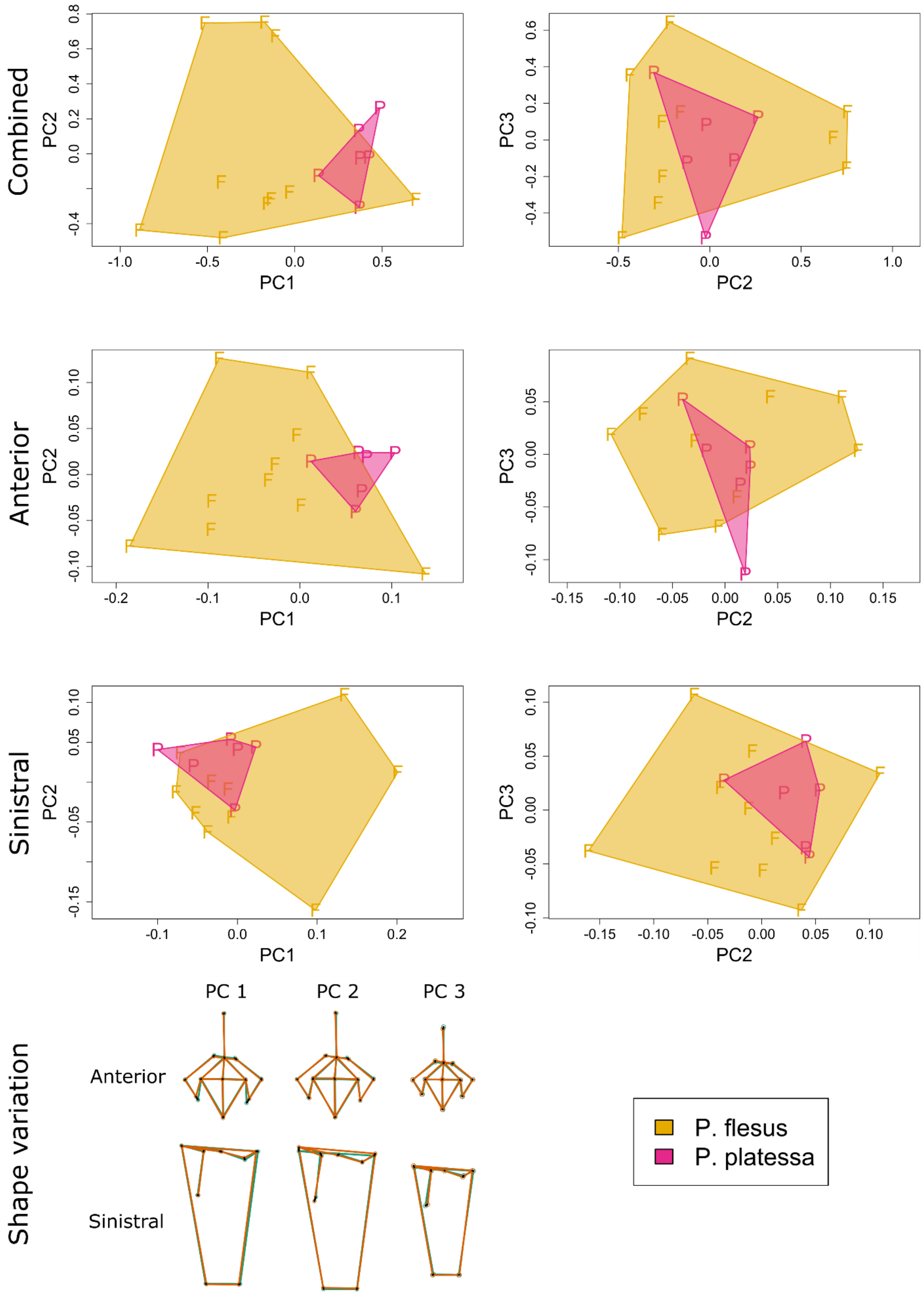


Figure C3. PCA and deformation grids of the atlas vertebra of plaice and flounder for the different views.

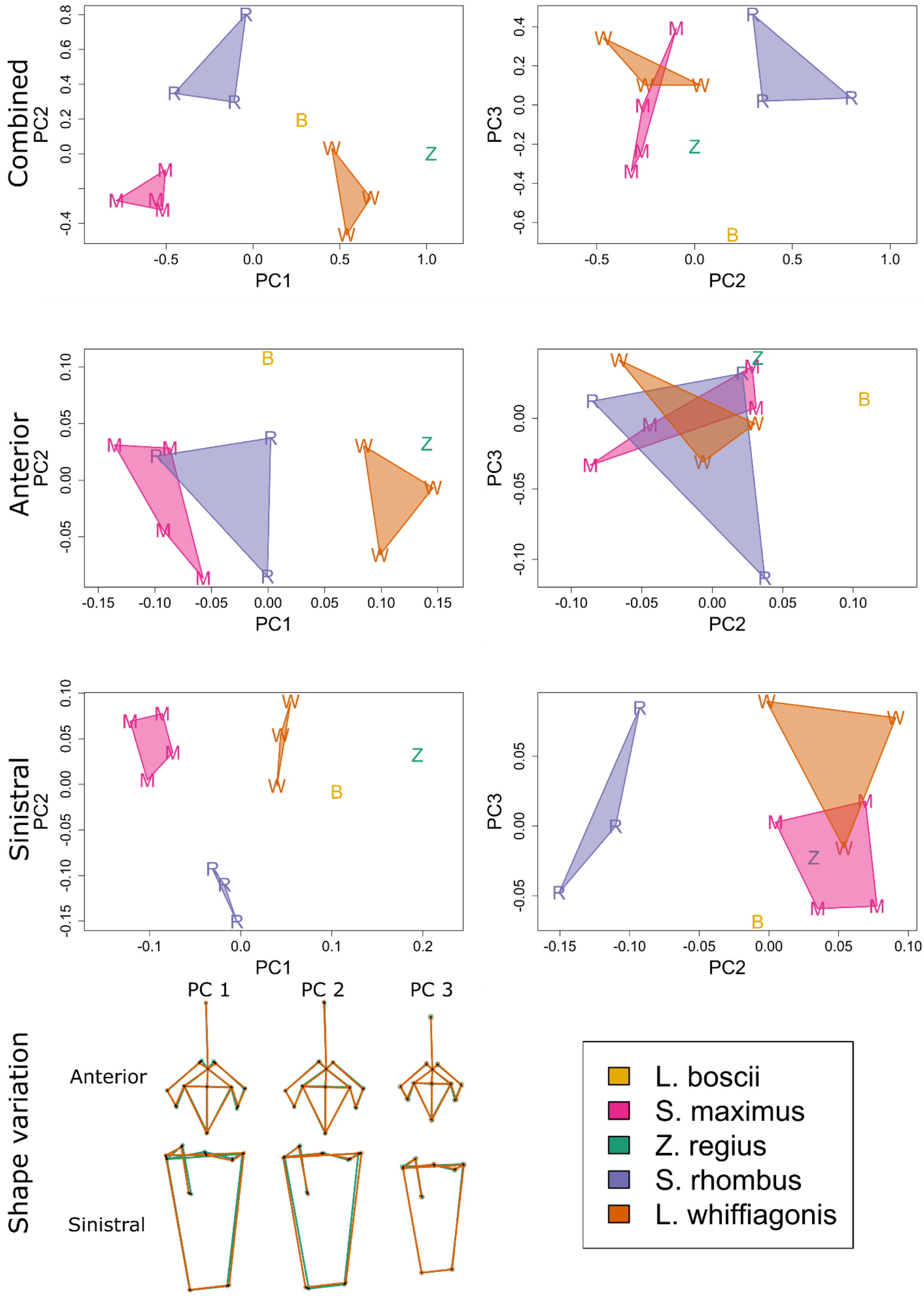


Figure C4. PCA and deformation grids of the atlas vertebra of Scophthalmidae for the different views.

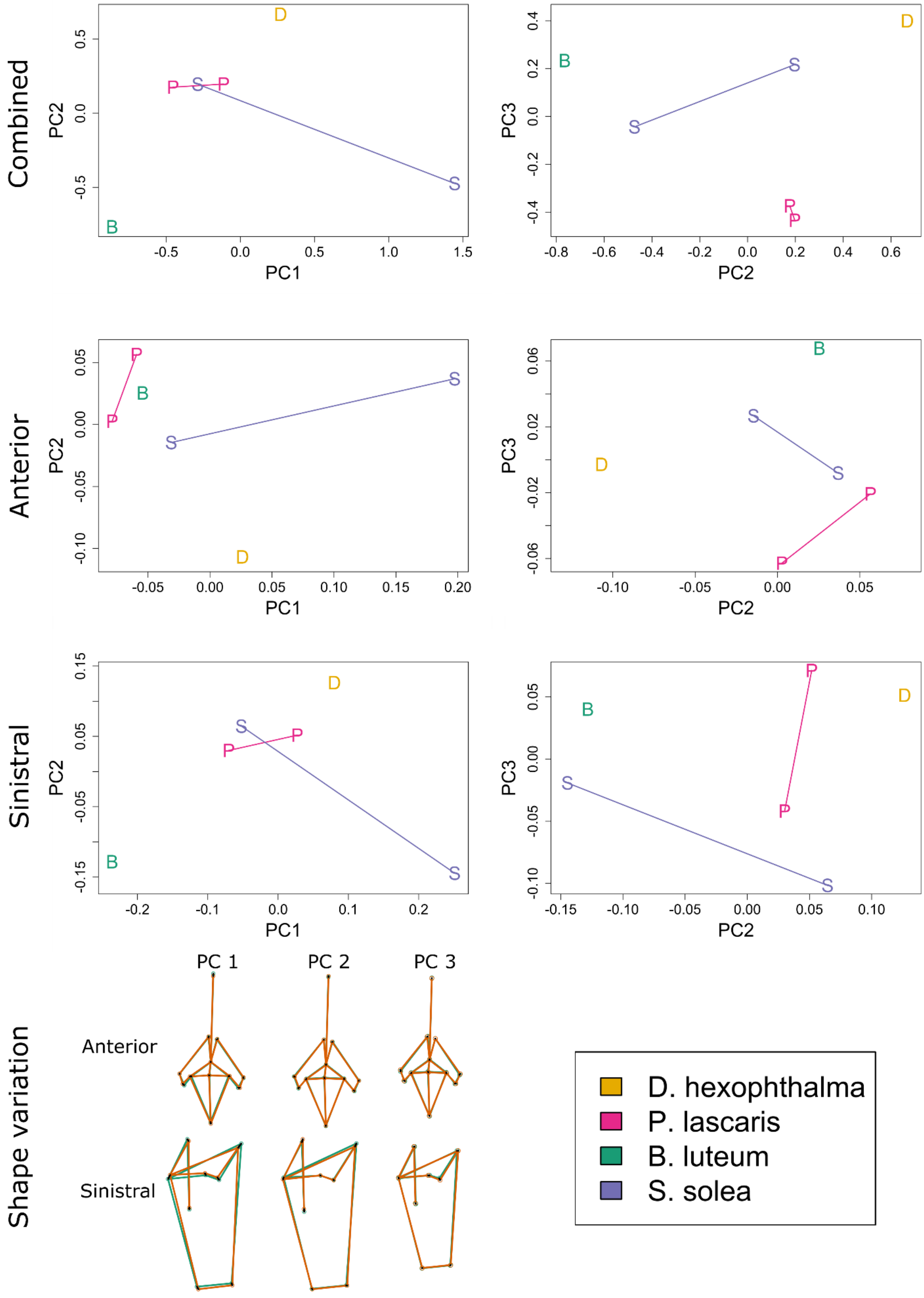


Figure C5. PCA and deformation grids of the atlas vertebra of Soleidae for the different views.

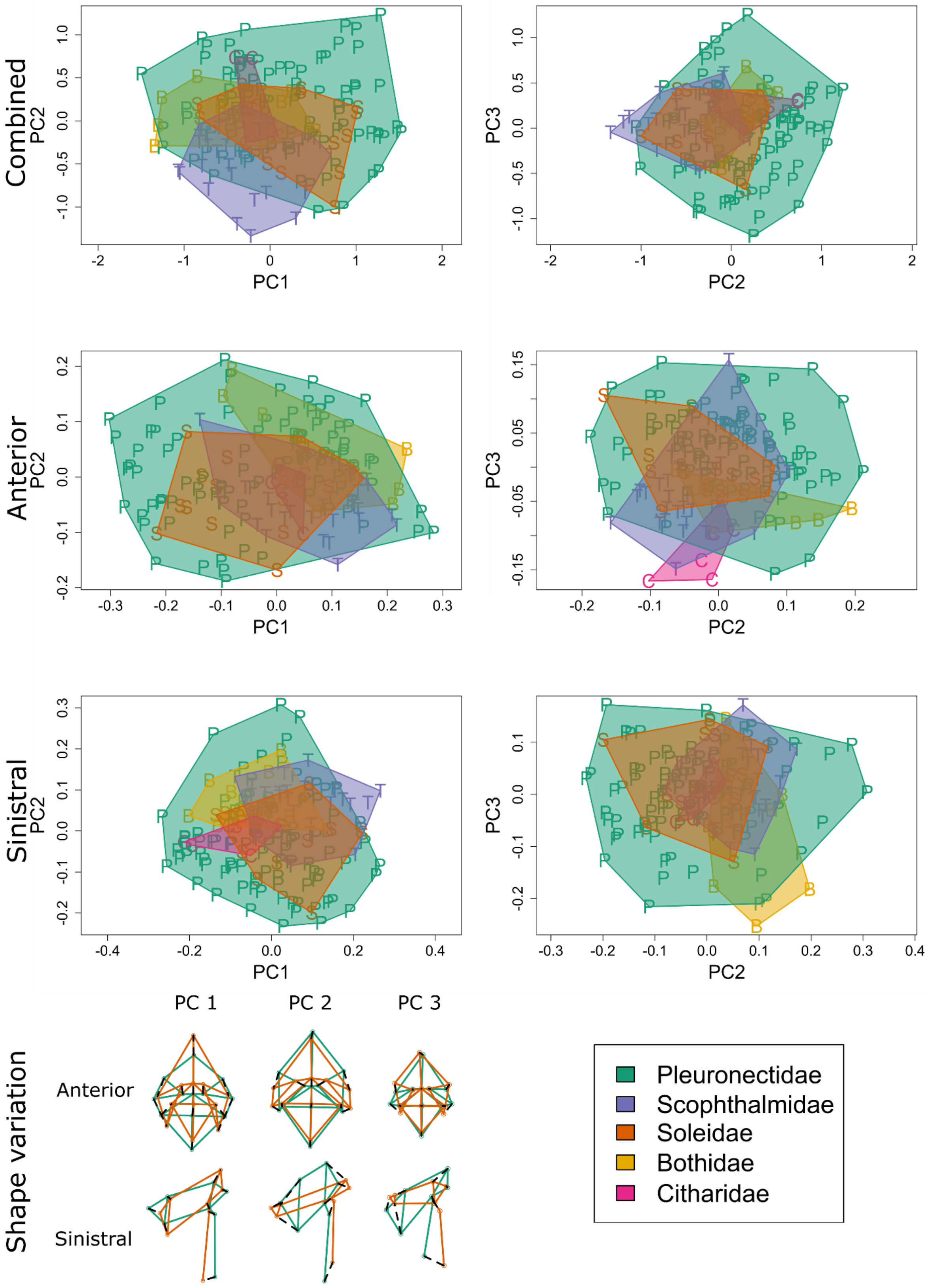


Figure C6. PCA and deformation grids of the cervical vertebra per family for the different views.

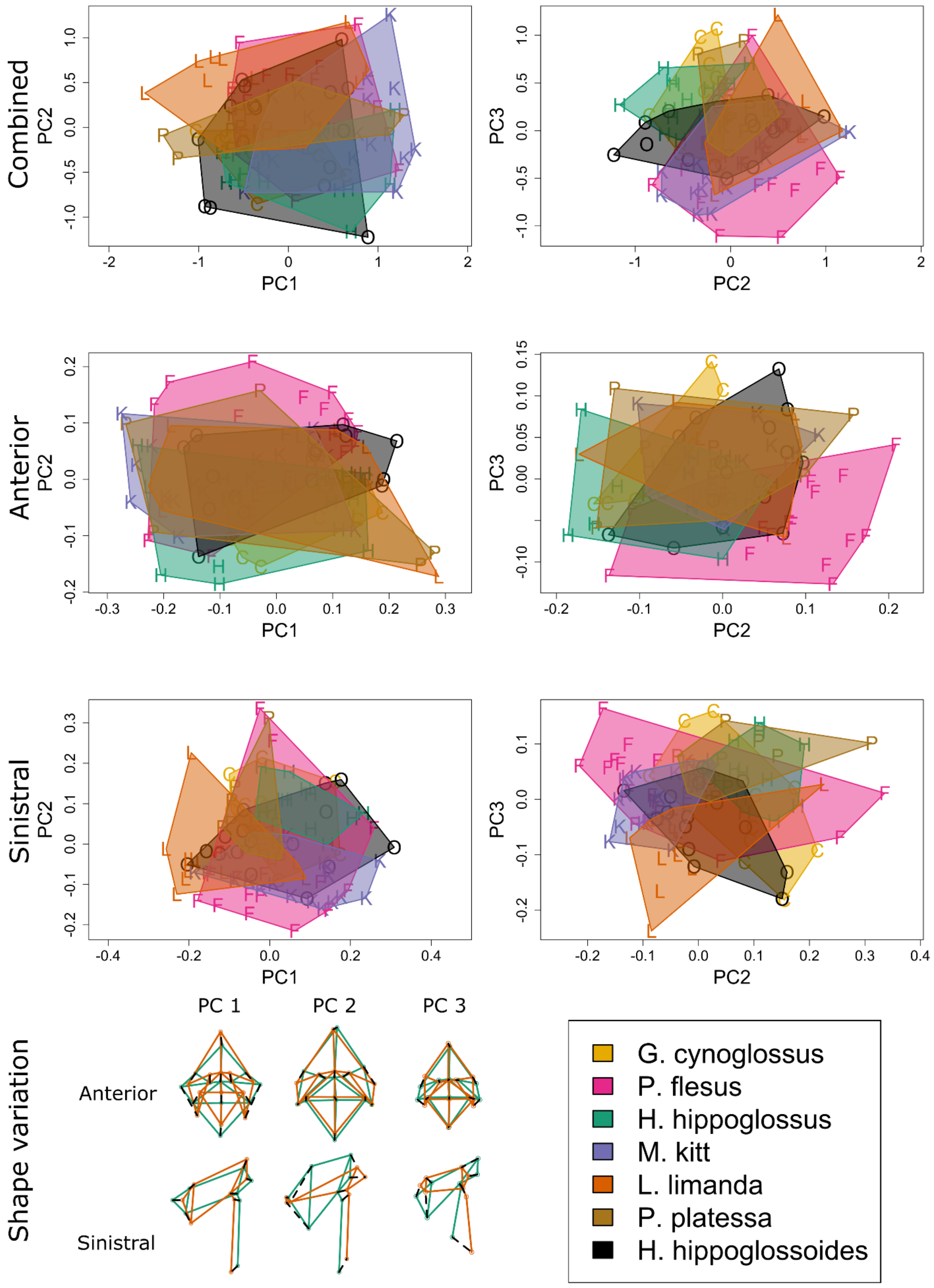


Figure C7. PCA and deformation grids of the cervical vertebra of Pleuronectidae for the different views.

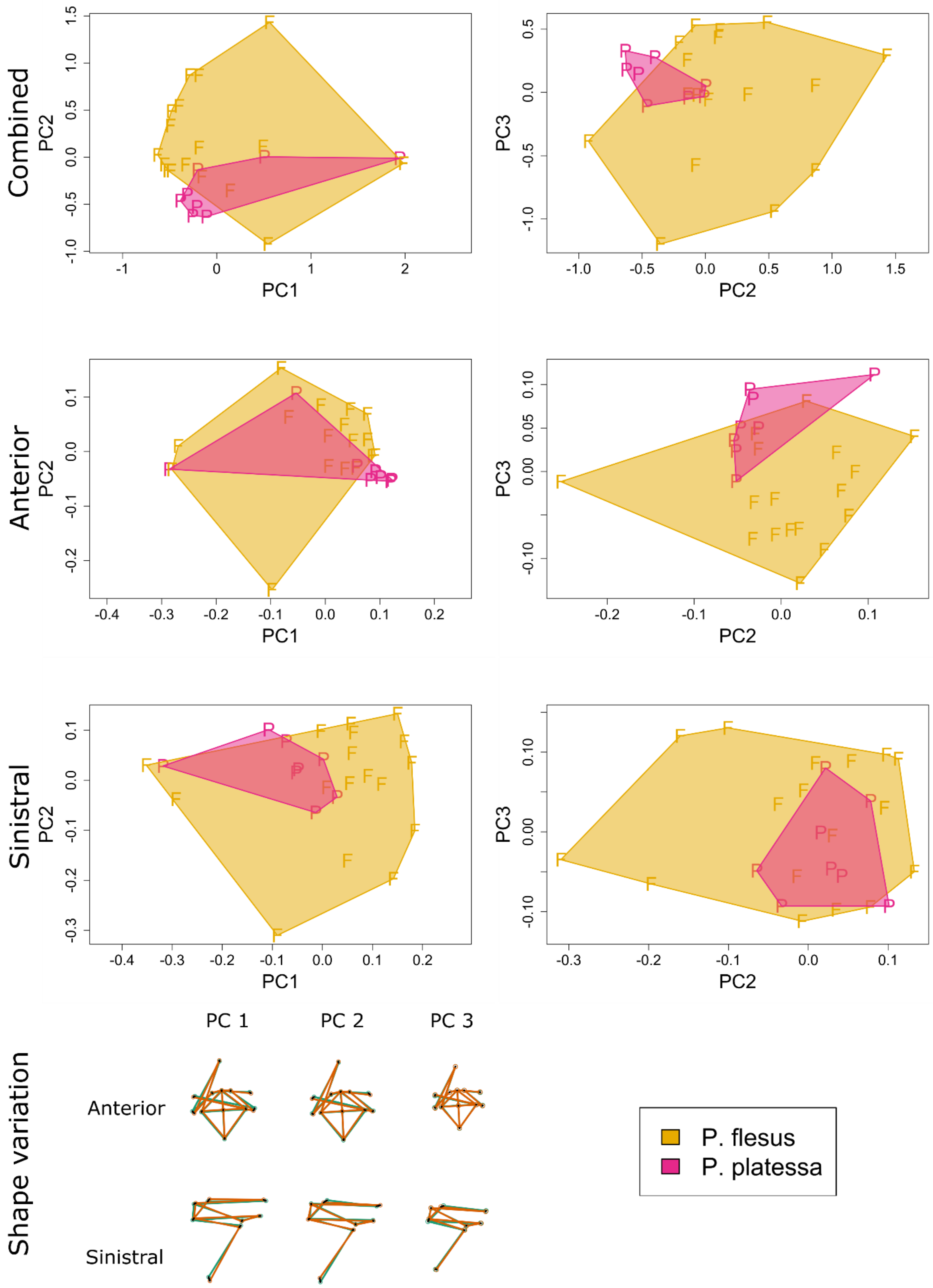


Figure C8. PCA and deformation grids of the cervical vertebra of plaice and flounder for the different views.

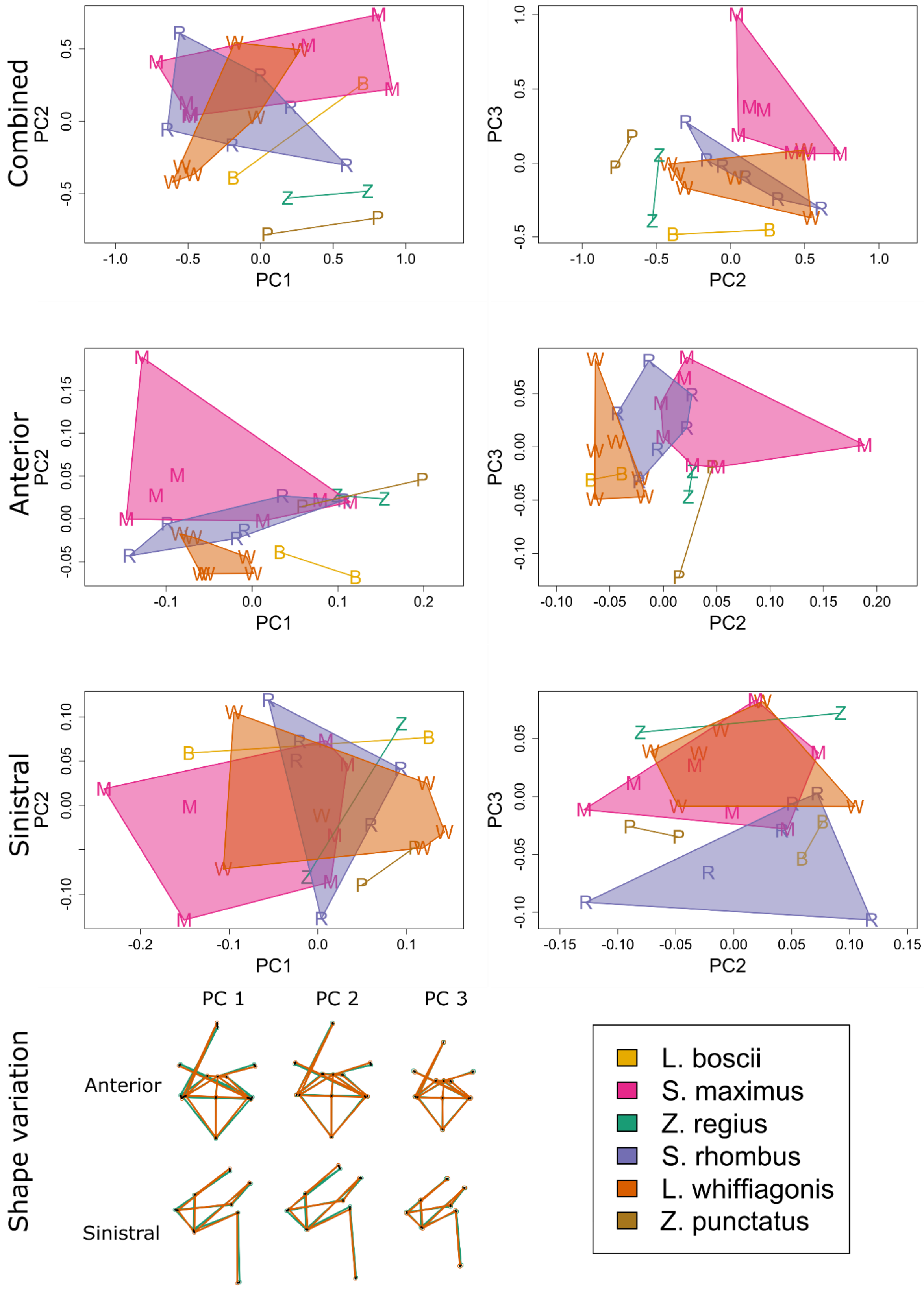


Figure C9. PCA and deformation grids of the cervical vertebra of Scophthalmidae for the different views.

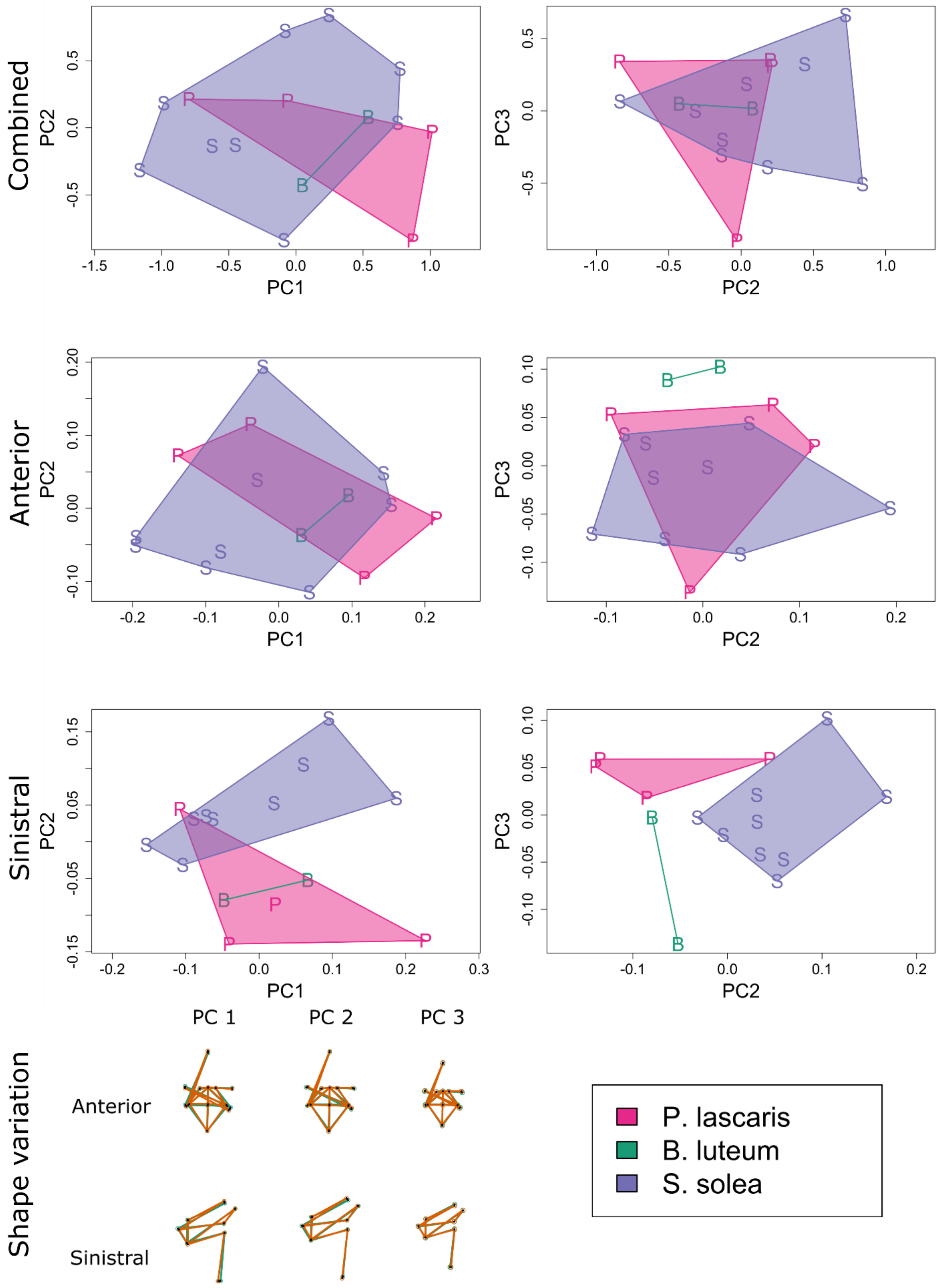


Figure C10. PCA and deformation grids of the cervical vertebra of Soleide for the different views.

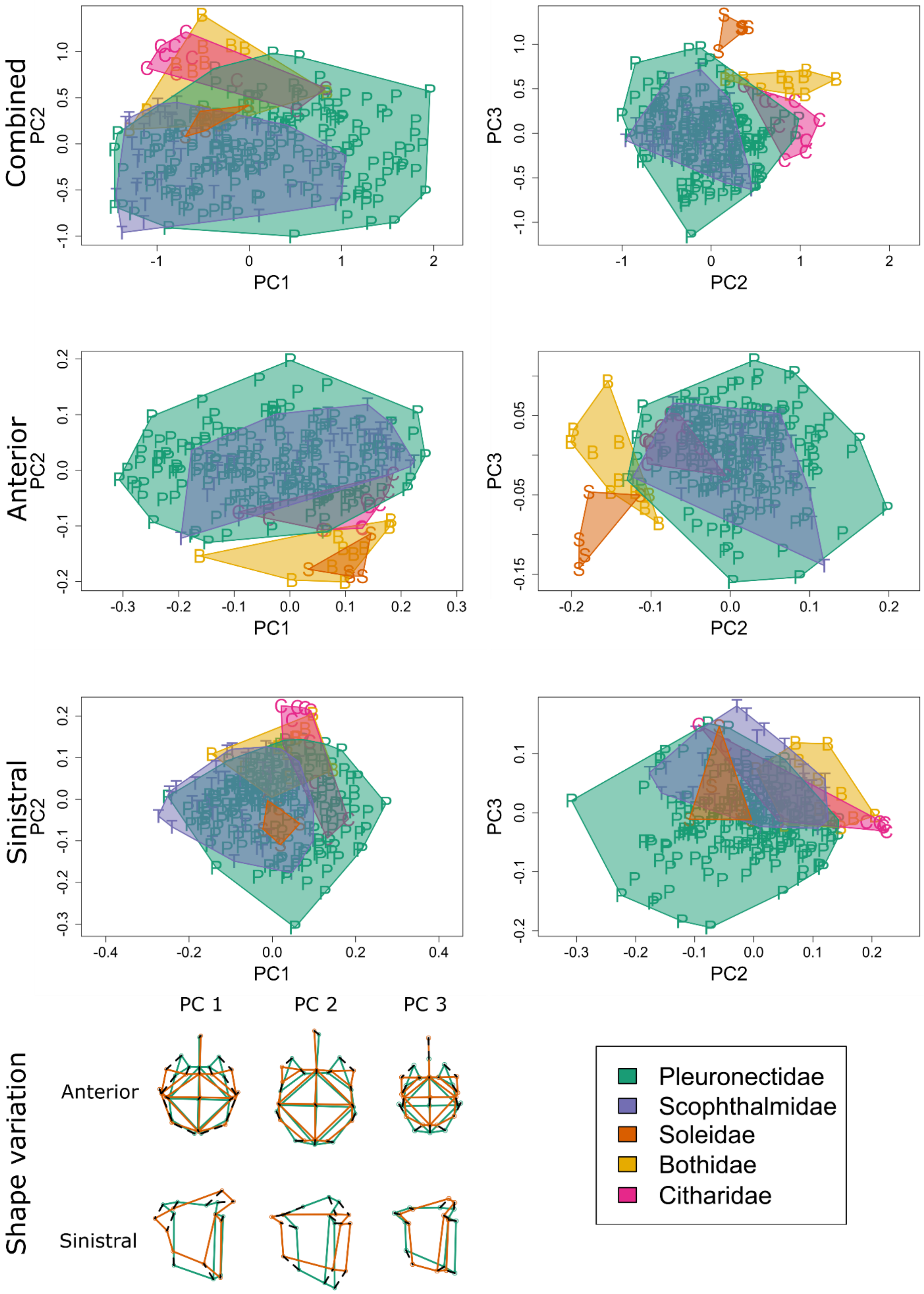


Figure C11. PCA and deformation grids of the precaudal vertebra per family for the different views.

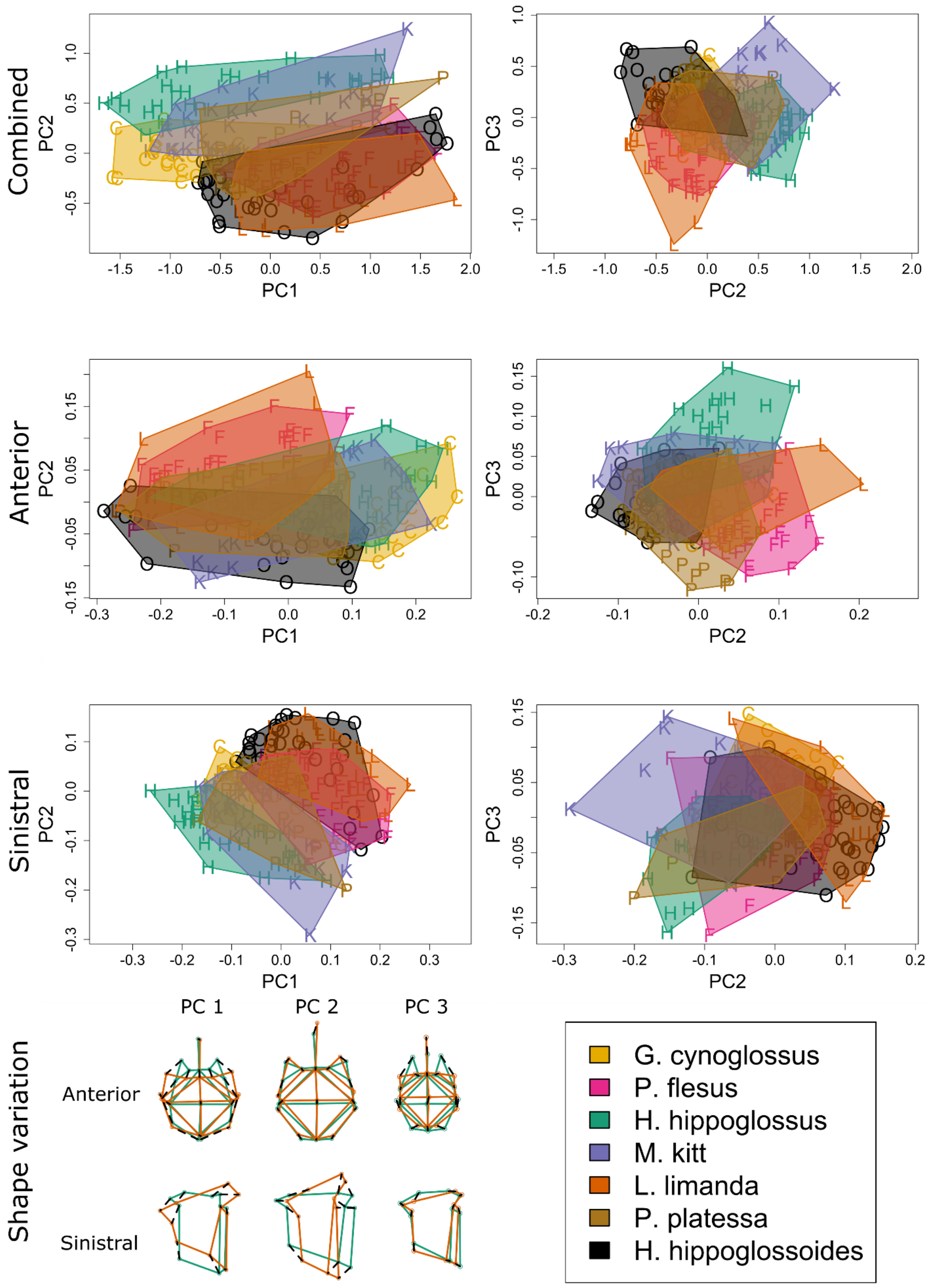


Figure C12. PCA and deformation grids of the precaudal vertebra of Pleuronectidae for the different views.

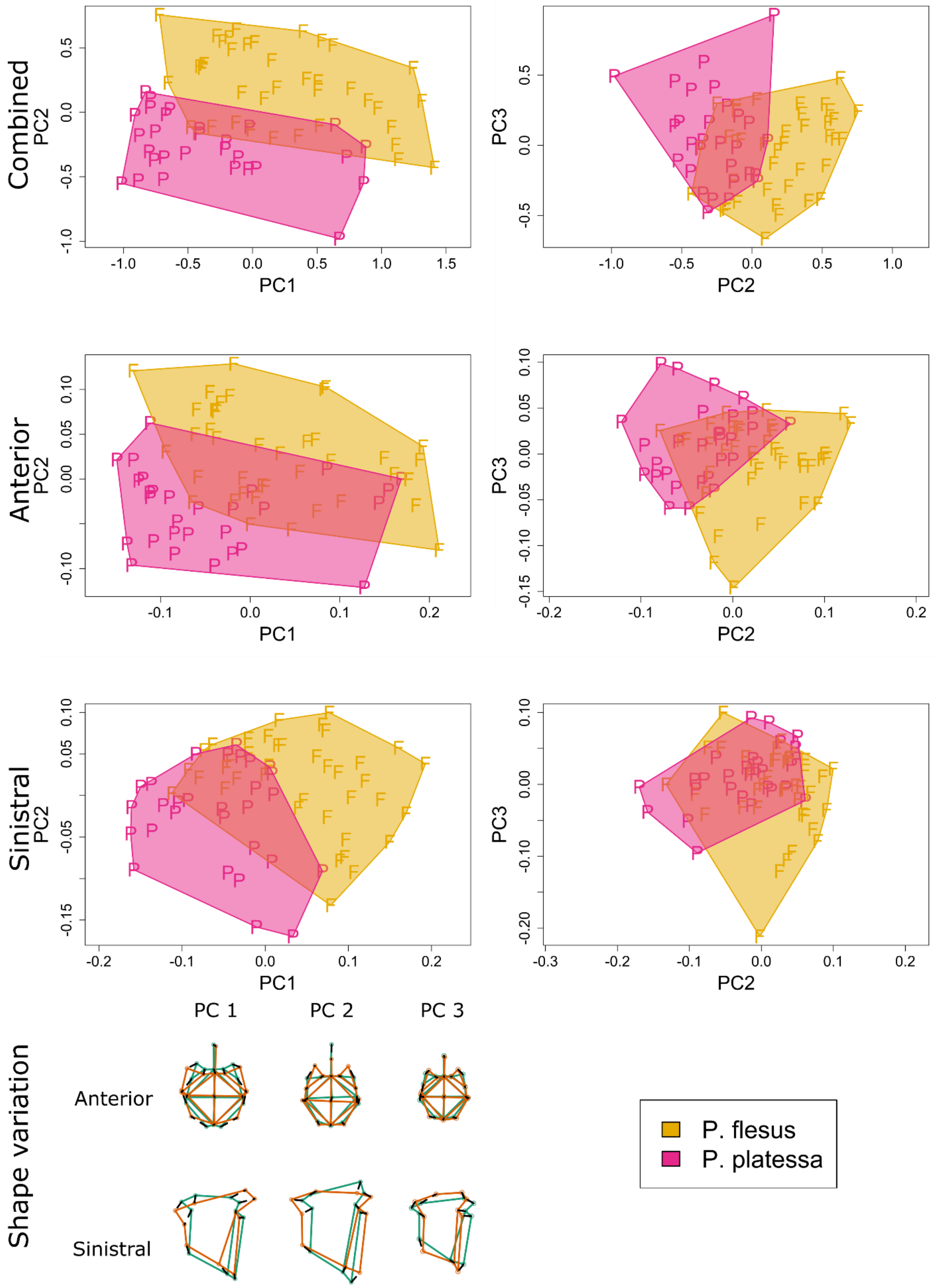


Figure C13. PCA and deformation grids of the precaudal vertebra of plaice and flounder for the different views.

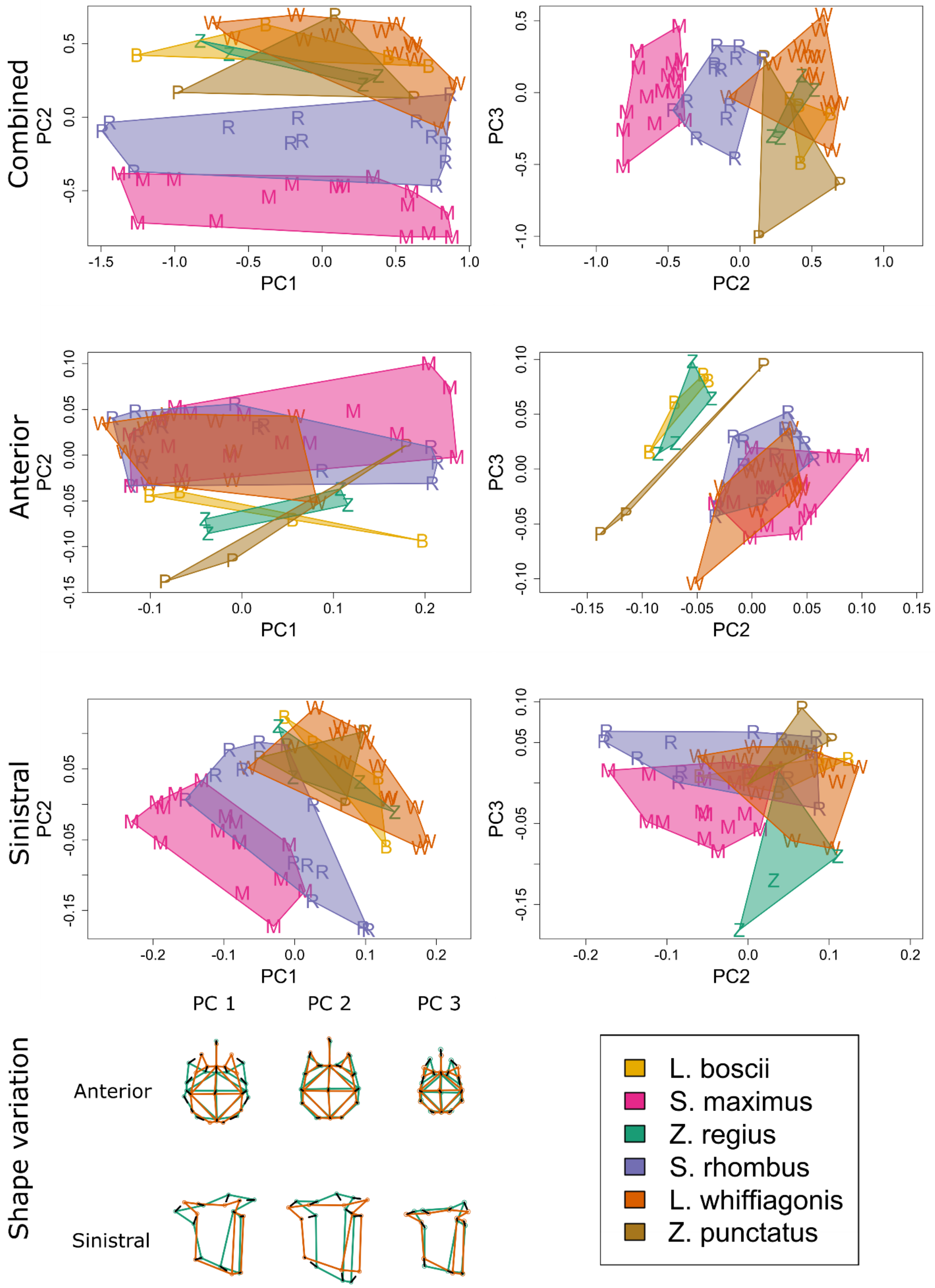


Figure C14. PCA and deformation grids of the precaudal vertebra of Scophthalmidae for the different views.

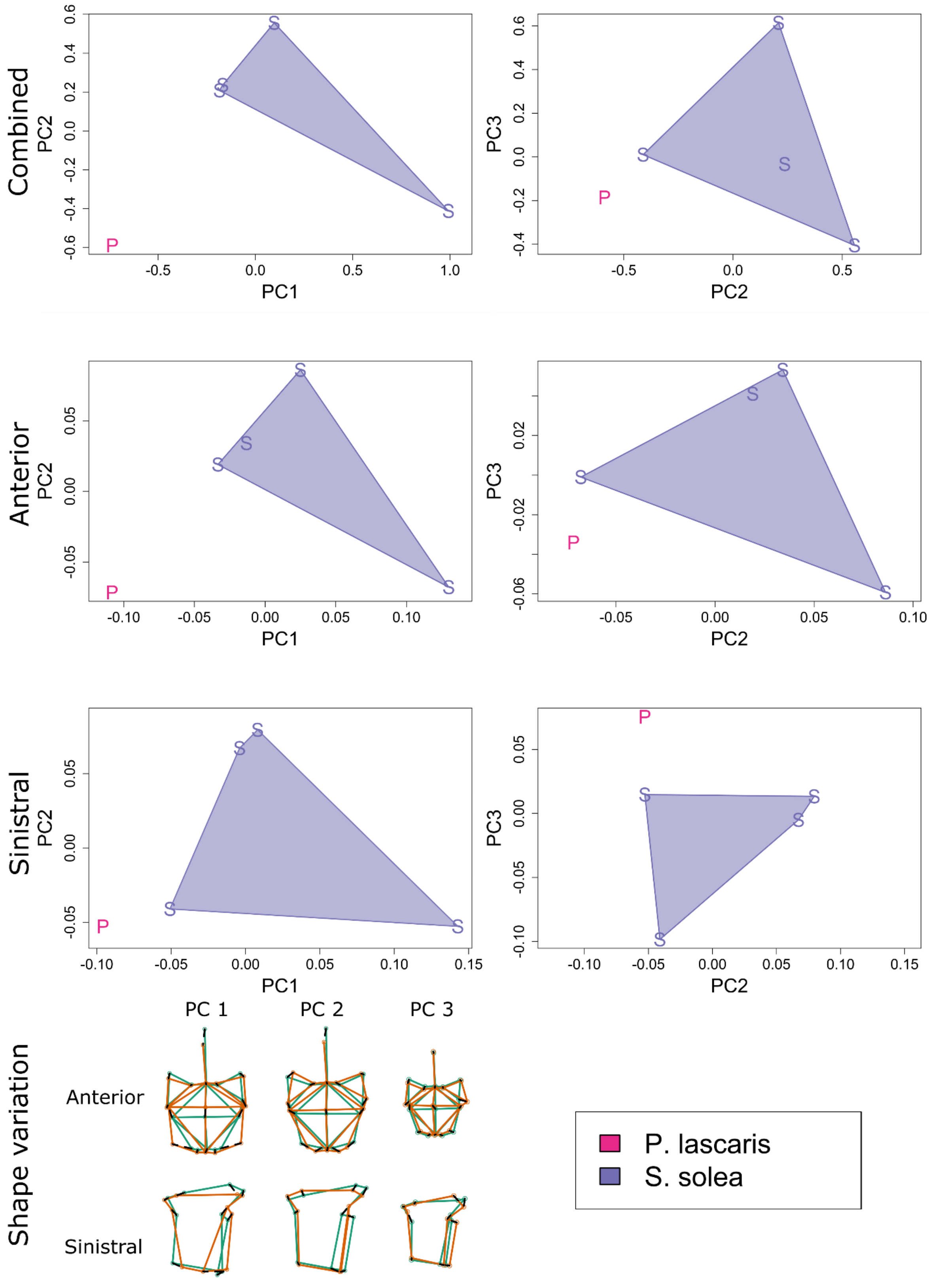


Figure C15. PCA and deformation grids of the precaudal vertebra of Soleidae for the different views.

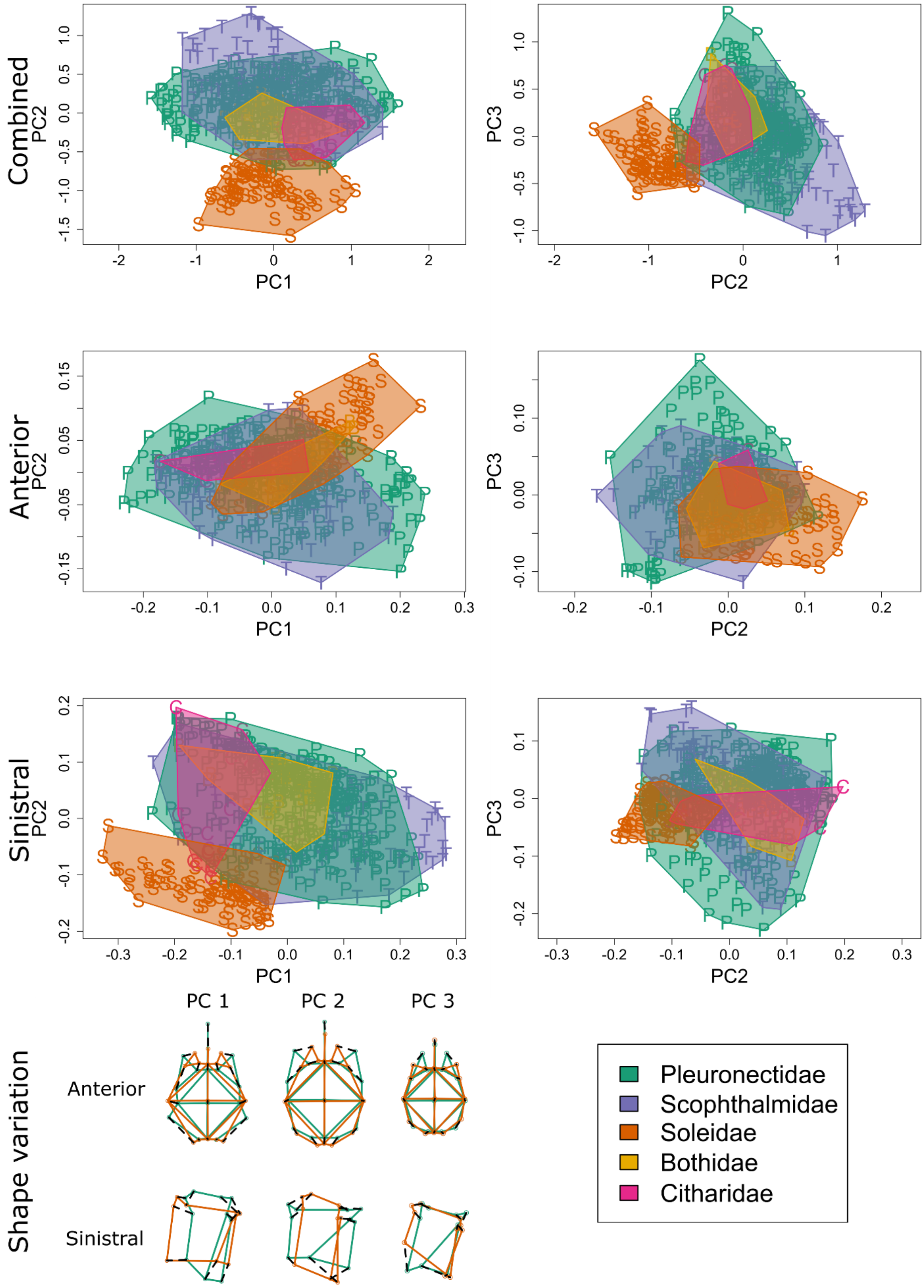


Figure C16. PCA and deformation grids of the caudal vertebra per family for the different views.

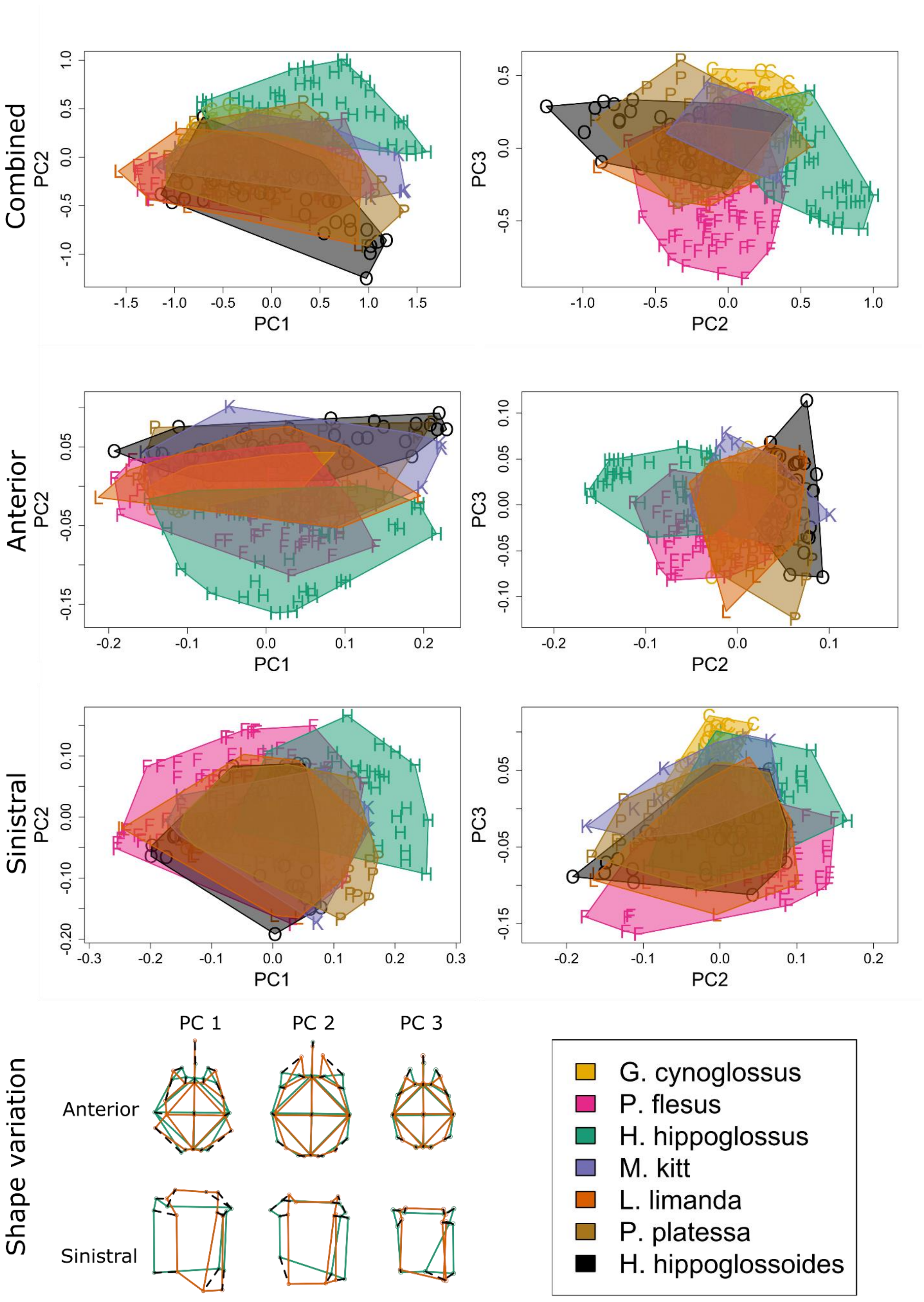


Figure C17. PCA and deformation grids of the caudal vertebra of Pleuronectidae for the different views.

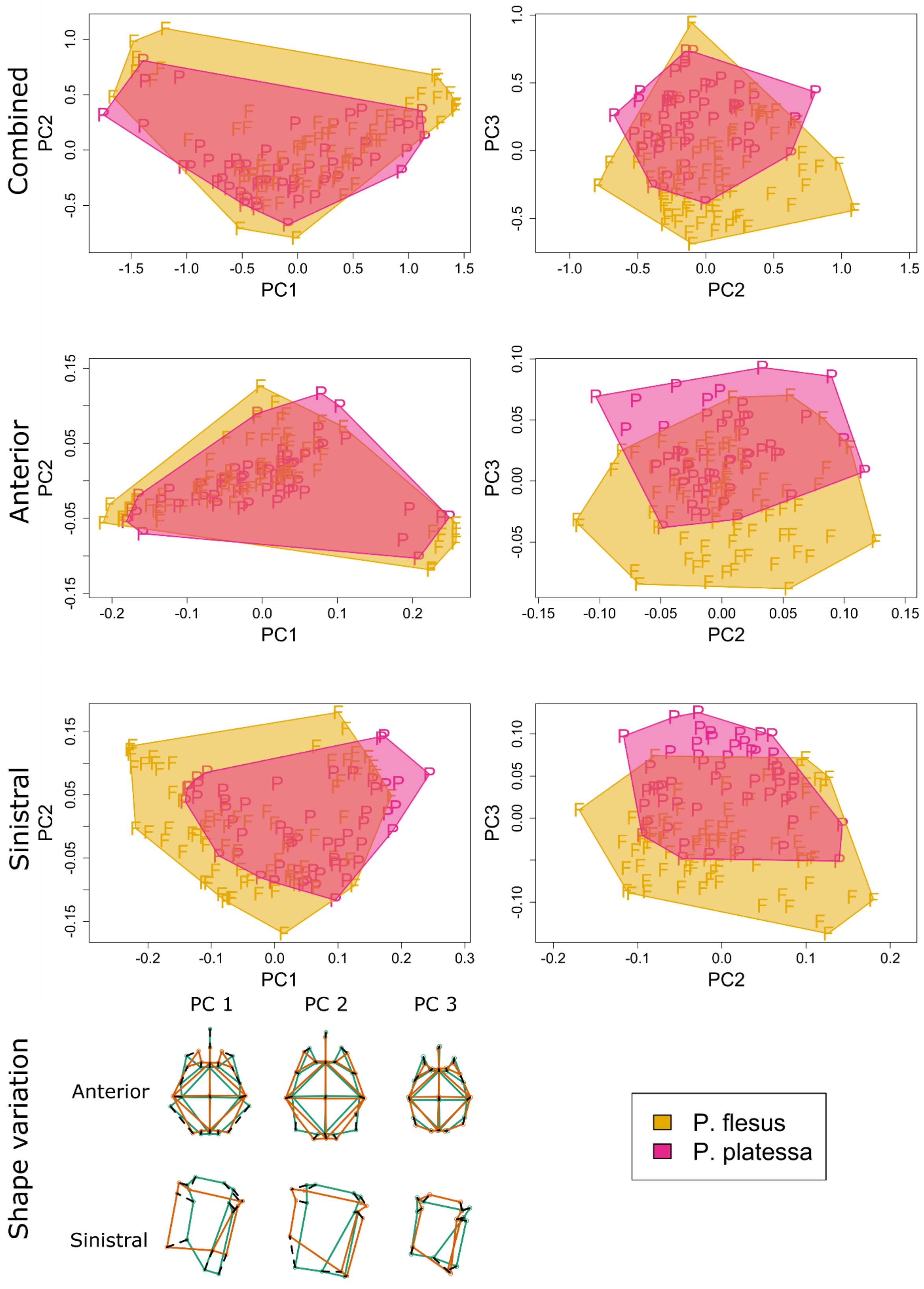


Figure C18. PCA and deformation grids of the caudal vertebra of plaice and flounder for the different views.

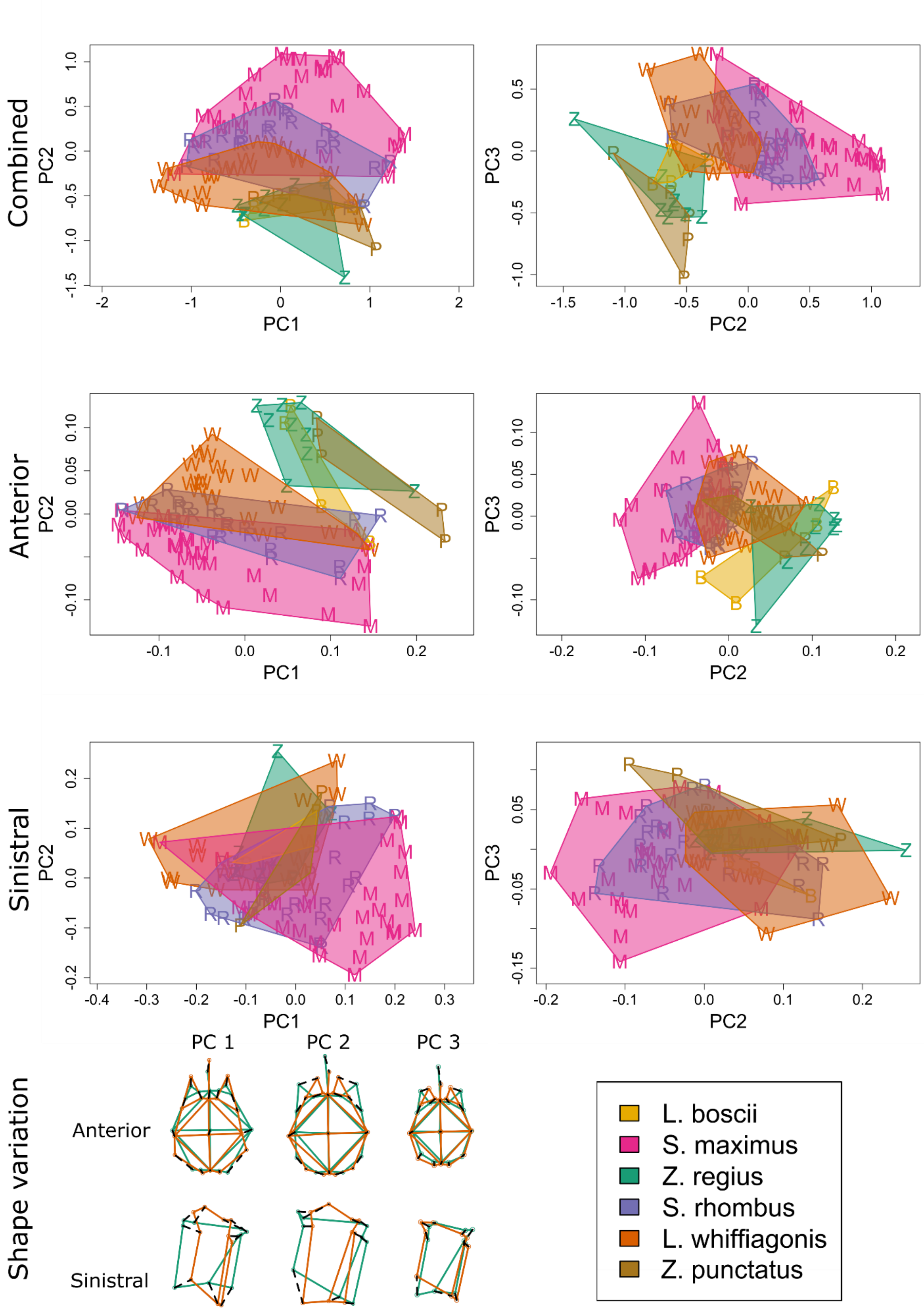


Figure C19. PCA and deformation grids of the caudal vertebra of Scophthalmidae for the different views.

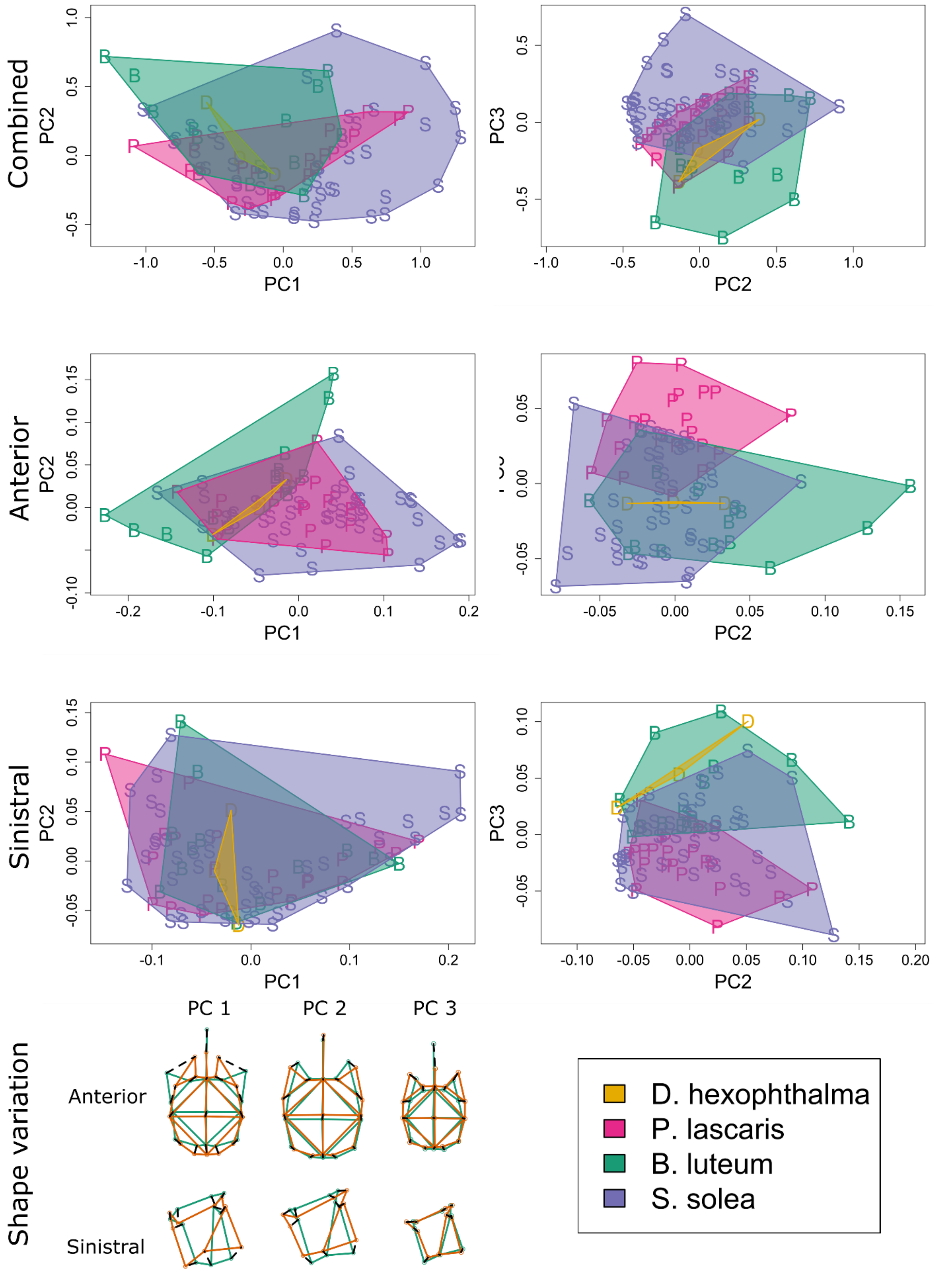


Figure C20. PCA and deformation grids of the caudal vertebra of Soleidae for the different views.

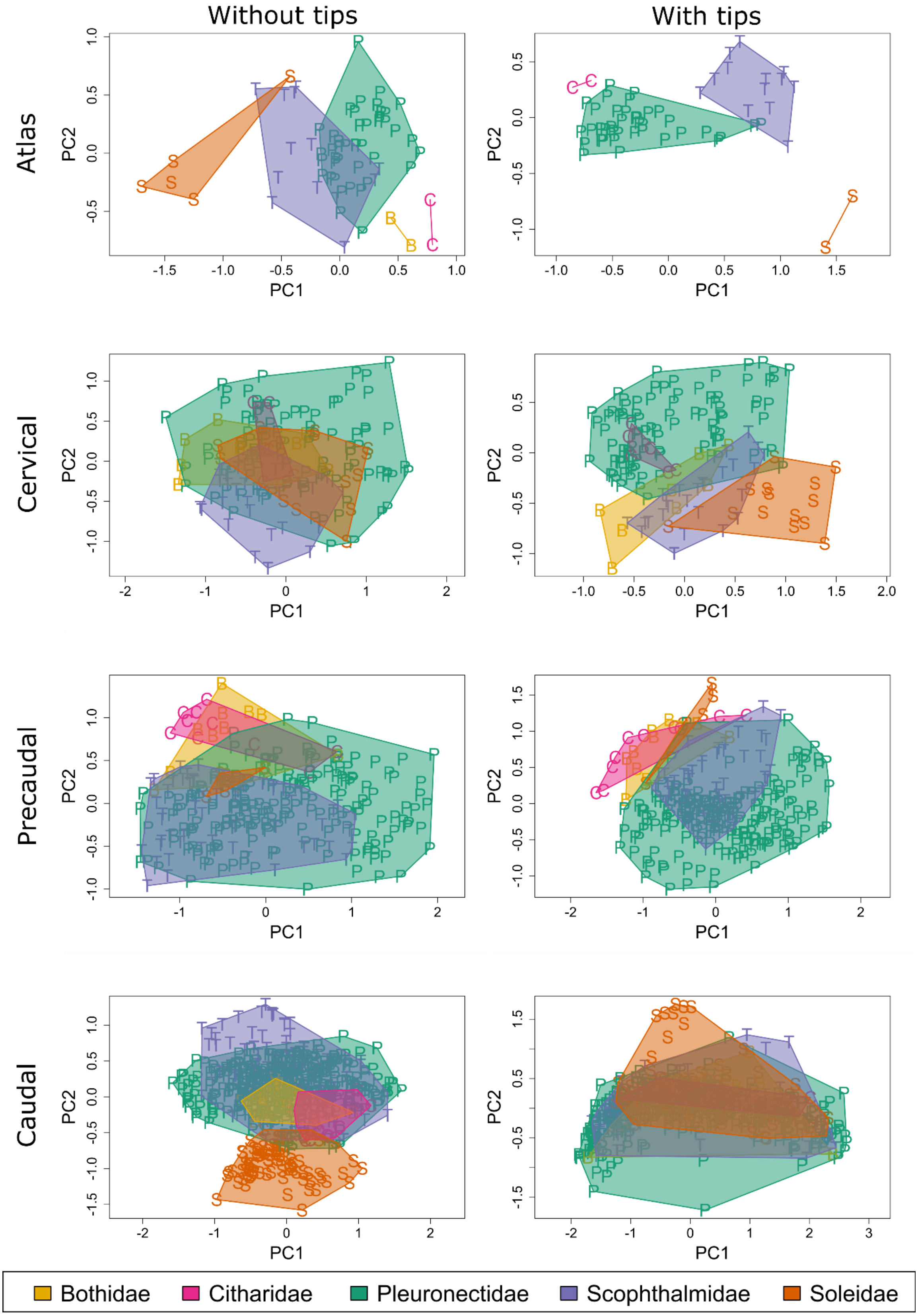


Figure C21. PCA plots for the vertebrae types per family comparing the landmark sets with or without the neural and haemal arch tips.

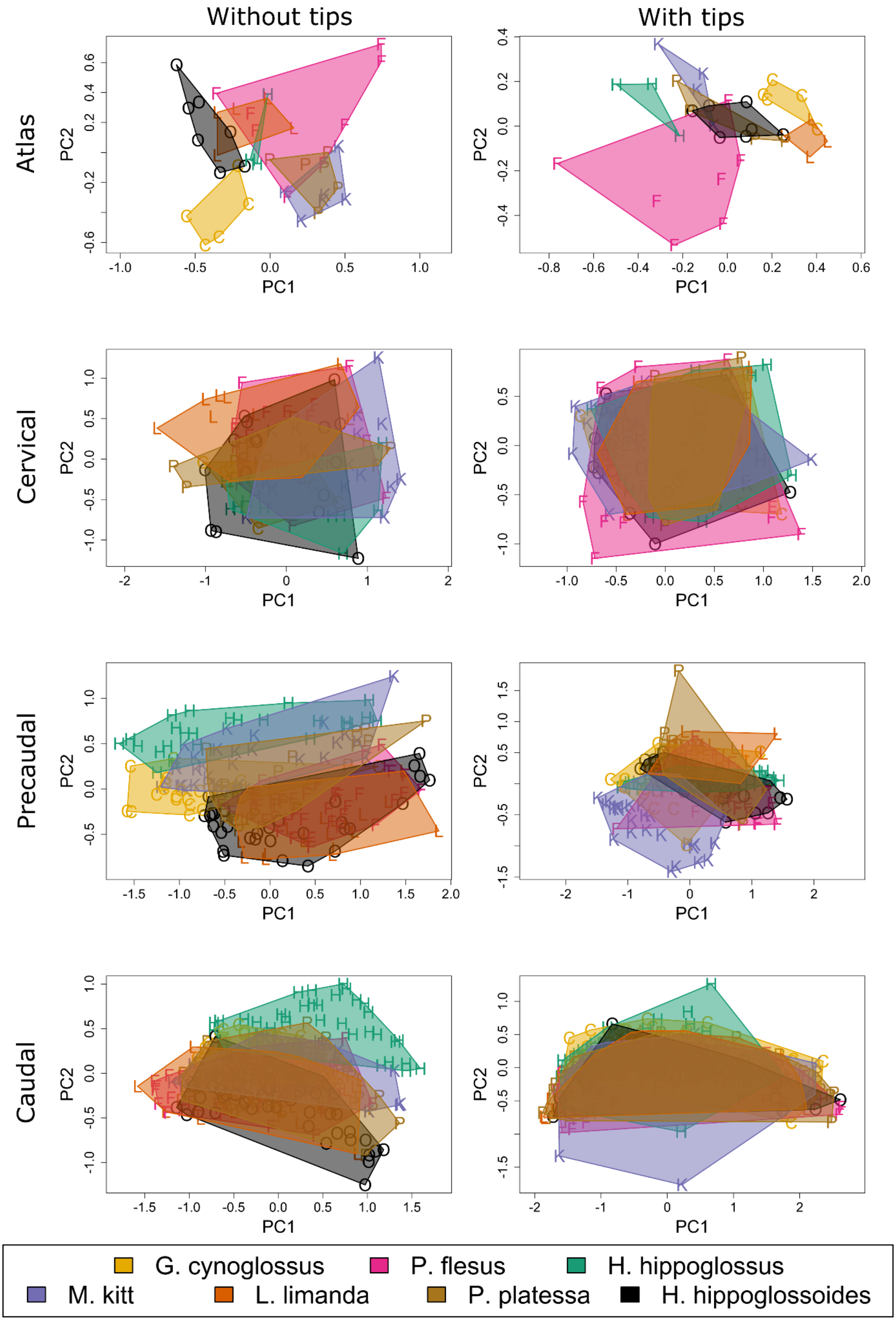


Figure C22. PCA plots for the vertebrae types for Pleuronectidae comparing the landmark sets with or without the neural and haemal arch tips.

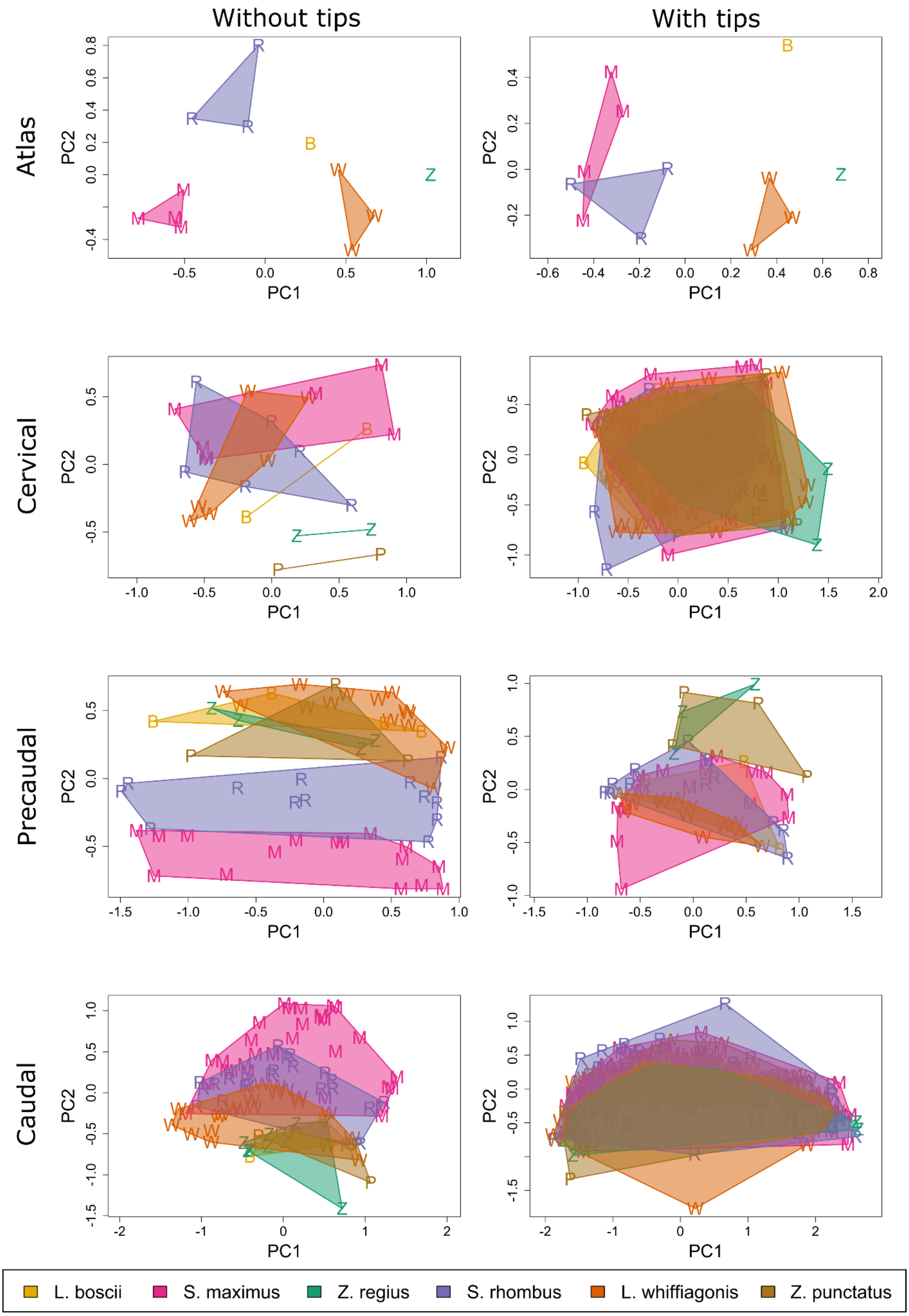


Figure C23. PCA plots for the vertebrae types for Scophthalmidae comparing the landmark sets with or without the neural and haemal arch tips.

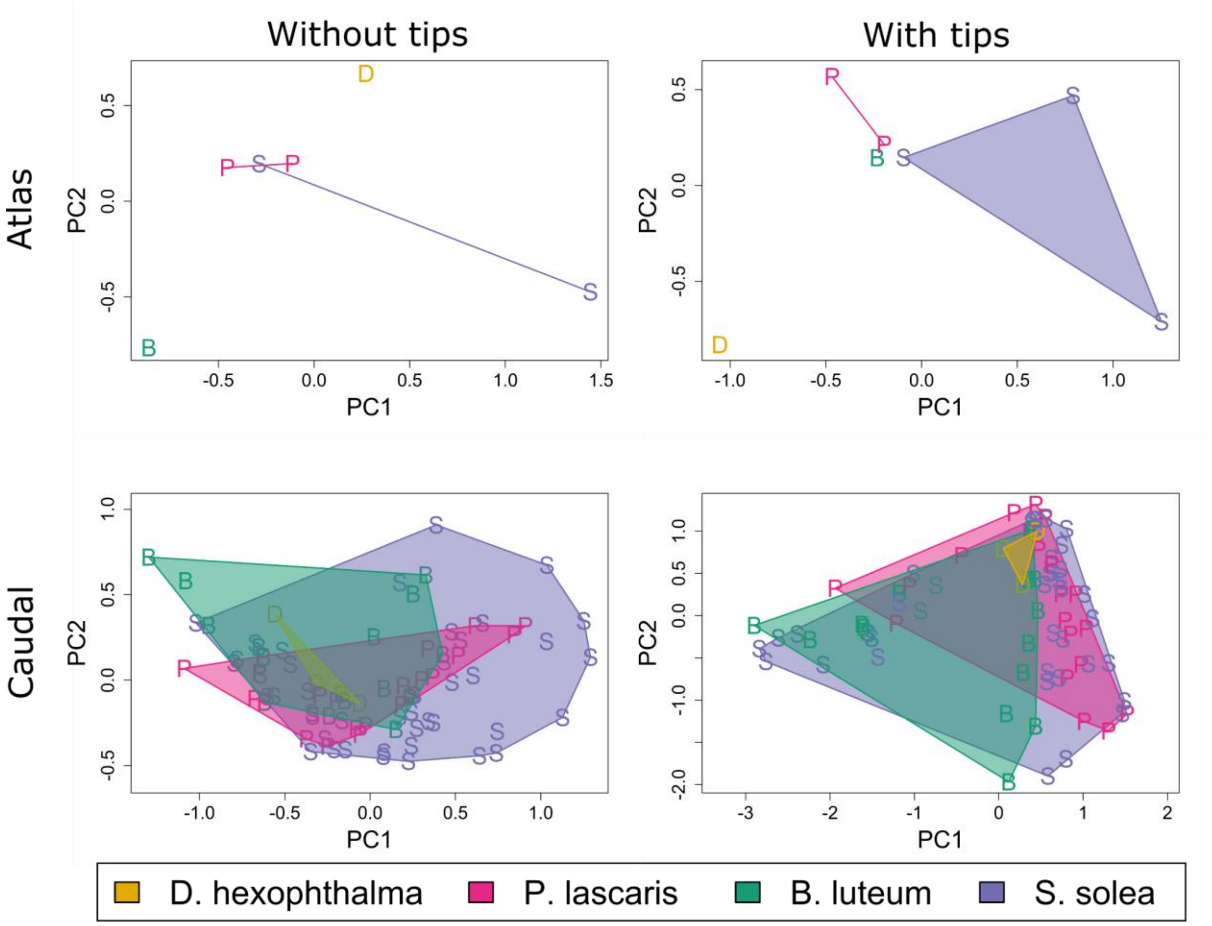


Figure C24. PCA plots for the vertebrae types for Soleidae comparing the landmark sets with or without the neural and haemal arch tips.

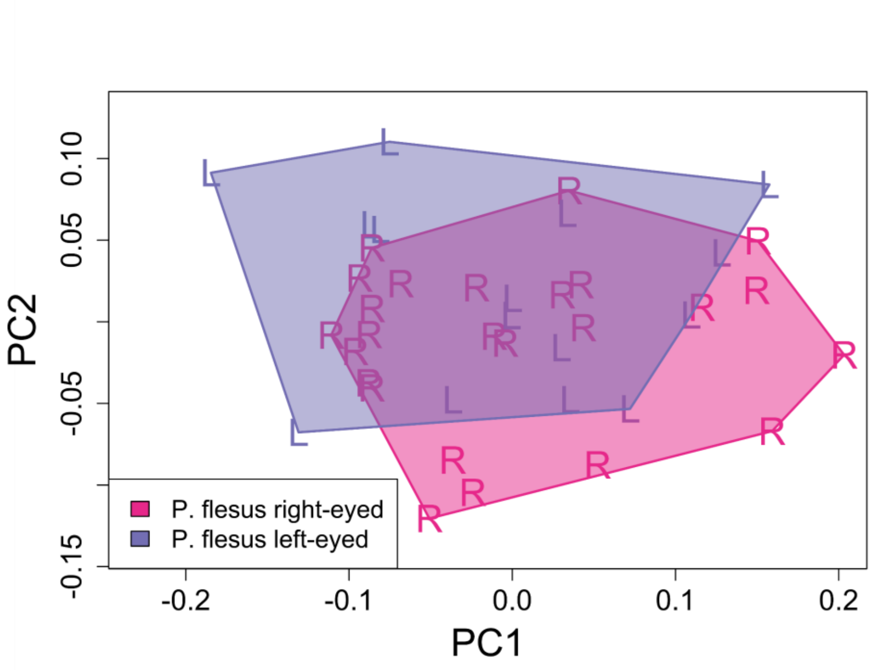


Figure C25. PCA plot of the precaudal vertebra of right-eyed and left-eyed *P. flesus* in anterior view.

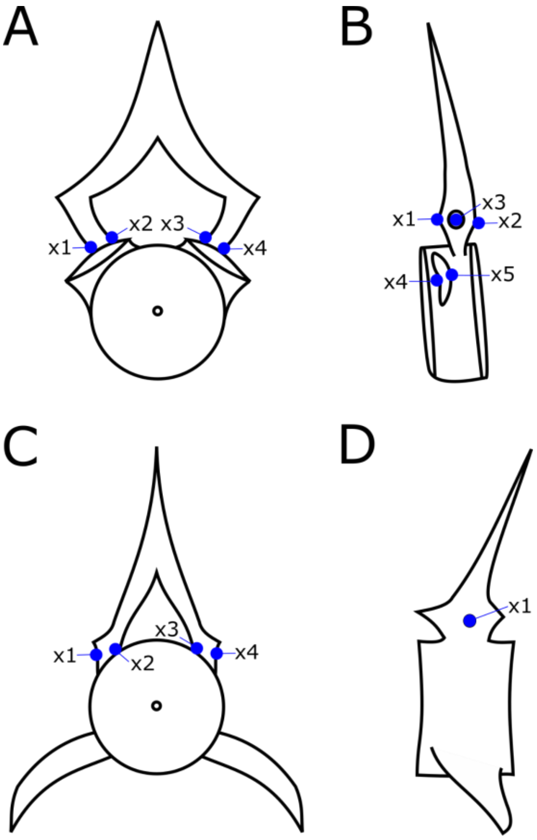


Figure C26. Landmark configurations of unusable landmarks removed from analysis. The description of these landmarks can be found in table C2. A. anterior view of atlas vertebra; B. sinistral view of atlas vertebra; C. anterior view of cervical, precaudal, and caudal vertebrae; D. sinistral view of cervical, precaudal, and caudal vertebrae.

Table C2. Descriptions of unusable landmarks removed from analysis per view and vertebra type.

Nr.	**Anterior atlas**	**Anterior other**	**Sinistral atlas**	**Sinistral other**
x1	Lateral implant of dextral neural processus	Lateral implant of the dextral anterior dorsal spina	Anterior most edge of the neural arch enlargement	Lateral foramen at implant of neural arch
x2	Medial implant of dextral neural processus	Medial implant of the dextral anterior dorsal spina	Posterior most edge of the neural arch enlargement	
x3	Medial implant of sinistral neural processus	Medial implant of the sinistral anterior dorsal spina	Foramen in the neural arch enlargement	
x4	Lateral implant of sinistral neural processus	Lateral implant of the sinistral anterior dorsal spina	Most anterior part of edge condylus or concave part of anterior edge	
x5			Most posterior part of edge condylus or concave part of anterior edge	

Part C2. Archaeological identification results

Table C3. Percentage of correctly identified archaeological samples to *P. platessa* and *P. flesus* using GMM when only these species are considered in the dataset. Other species from both archaeological data and reference data were removed. Species verified by collagen peptide mass fingerprinting. The total number of species is noted between brackets.

Species (ZooMS)	**Species (GMM)**		
	Anterior	**Sinistral**	**Combined**
Atlas vertebra			
P. flesus (n=4)	2 (50.00%)	3 (75.00%)	1 (25.00%)
P. platessa (n=4)	4 (100.00%)	3 (75.00%)	3 (75.00%)
Cervical vertebra			
P. flesus (n=9)	0 (0.00%)	5 (55.55%)	2 (22.22%)
P. platessa (n=2)	0 (0.00%)	1 (50.00%)	1 (50.00%)
Precaudal vertebra			
P. flesus (n=16)	11 (68.75%)	14 (87.5%)	9 (56.25%)
P. platessa (n=11)	10 (90.91%)	6 (54.55%)	3 (27.27%)
Caudal vertebra			
P. flesus (n=29)	18 (62.07%)	17 (58.62%)	18 (62.07%)
P. platessa (n=27)	22 (81.48%)	19 (70.37%)	15 (55.56%)

Table C4. Results of identifying archaeological samples to vertebra type (cervical, precaudal, and caudal.

Sample	Vertebra	ZooMS identification			GMM vertebra type			
			Anterior	Probability	Sinistral	Probability	Combined	Probability
BSG0001	Caudal vertebra	*Platichthys flesus*	Caudal	0.95	Caudal	0.99	Caudal	0.99
BSG0018	Cervical vertebra	*Platichthys flesus*	Cervical	1.00	Cervical	1.00	Cervical	1.00
BSG0020	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.80	Precaudal	0.92	Precaudal	1.00
BSG0021	Caudal vertebra	*Platichthys flesus*	Caudal	0.83	Caudal	0.98	Caudal	0.97
BSG0022	Precaudal vertebra	*Pleuronectes platessa*	Precaudal	0.78	Caudal	0.51	Precaudal	0.51
BSG0023	Precaudal vertebra	*Platichthys flesus*	Caudal	0.67	Caudal	0.89	Precaudal	0.91
BSG0024	Precaudal vertebra	*Platichthys flesus*	Caudal	0.90	Caudal	0.94	Caudal	0.90
BSG0025	Precaudal vertebra	*Platichthys flesus*	Caudal	0.84	NA	NA	NA	NA
BSG0026	Precaudal vertebra	*Platichthys flesus*	Caudal	0.65	Caudal	0.99	Precaudal	0.73
BSG0027	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.95	Precaudal	0.67	Precaudal	0.91
BSG0028	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.82	Caudal	0.68	Precaudal	0.92
BSG0029	First caudal vertebra	*Pleuronectes platessa*	Precaudal	0.39	Caudal	0.63	Caudal	0.55
BSG0030	First caudal vertebra	*Platichthys flesus*	Caudal	0.96	Caudal	1.00	Caudal	0.80
BSG0031	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.82	Caudal	0.97	Caudal	0.99
BSG0032	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.76	Caudal	0.93	Caudal	0.82
BSG0033	Caudal vertebra	*Platichthys flesus*	Caudal	0.98	Caudal	0.99	Caudal	0.50
BSG0034	Caudal vertebra	*Platichthys flesus*	Caudal	0.97	Caudal	0.99	Precaudal	0.67
BSG0035	Caudal vertebra	*Platichthys flesus*	Caudal	0.93	Caudal	0.95	Caudal	1.00
BSG0036	Caudal vertebra	*Platichthys flesus*	Precaudal	0.63	Caudal	0.99	Caudal	0.97
BSG0040	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.80	Caudal	0.61	Caudal	0.57
BSG0041	Caudal vertebra	*Platichthys flesus*	Caudal	0.99	Caudal	1.00	Caudal	1.00
BSG0046	Precaudal vertebra	*Platichthys flesus*	Caudal	0.96	Precaudal	0.51	Precaudal	0.88
BSG0048	First caudal vertebra	*Platichthys flesus*	Caudal	0.84	Caudal	0.98	Caudal	0.99
BSG0049	First caudal vertebra	*Platichthys flesus*	Caudal	0.75	Caudal	0.97	Caudal	0.68
BSG0050	Precaudal vertebra	*Pleuronectes platessa*	Precaudal	0.83	Precaudal	0.77	Cervical	0.87
BSG0051	Precaudal vertebra	*Pleuronectes platessa*	Caudal	0.94	Caudal	1.00	Precaudal	1.00
BSG0052	Caudal vertebra	*Platichthys flesus*	Caudal	0.75	Caudal	0.89	Caudal	0.55
BSG0053	Caudal vertebra	*Platichthys flesus*	Caudal	0.99	Caudal	0.76	Caudal	0.97
BSG0054	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.95	Caudal	0.99	Caudal	0.94
BSG0055	Caudal vertebra	*Platichthys flesus*	Caudal	0.91	Caudal	0.99	Caudal	0.99
BSG0056	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.78	Caudal	1.00	Caudal	0.93
BSG0057	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.78	Caudal	0.51	Caudal	0.54
BSG0058	Caudal vertebra	*Platichthys flesus*	Caudal	0.88	Caudal	1.00	Precaudal	0.88
BSG0059	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.86	Caudal	0.96	Caudal	1.00
BSG0060	Caudal vertebra	*Platichthys flesus*	Caudal	0.95	Caudal	1.00	Caudal	1.00
BSG0061	Cervical vertebra	*Pleuronectes platessa*	Cervical	0.99	Caudal	0.93	Cervical	0.99
BSG0062	Cervical vertebra	*Platichthys flesus*	Cervical	1.00	Cervical	1.00	Cervical	0.99
BSG0063	Cervical vertebra	*Platichthys flesus*	Precaudal	0.69	Cervical	0.99	Cervical	0.97
BSG0064	Cervical vertebra	*Platichthys flesus*	Precaudal	0.65	Caudal	0.59	Caudal	0.85
BSG0065	Cervical vertebra	*Platichthys flesus*	Precaudal	0.90	Caudal	0.68	Cervical	0.79
BSG0066	Cervical vertebra	*Platichthys flesus*	Caudal	0.86	Precaudal	0.60	Caudal	0.52
BSG0067	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.89	Precaudal	0.90	Precaudal	1.00
BSG0068	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.97	Precaudal	0.92	Caudal	1.00
BSG0069	Precaudal vertebra	*Platichthys flesus*	Cervical	0.70	Cervical	0.65	Precaudal	1.00
BSG0070	Precaudal vertebra	*Pleuronectes platessa*	Precaudal	0.82	Caudal	0.99	Caudal	0.88
BSG0071	Precaudal vertebra	*Platichthys flesus*	Caudal	0.77	Caudal	0.64	Caudal	0.86
BSG0083	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.64	Caudal	0.51	Precaudal	0.73
BSG0084	Caudal vertebra	*Platichthys flesus*	Caudal	0.96	Caudal	1.00	Caudal	1.00

Table C4 continued

Sample	**Vertebra**	**ZooMS identification**	**GMM vertebra type**					
			Anterior	**Probability**	**Sinistral**	**Probability**	**Combined**	**Probability**
BSG0085	Precaudal vertebra	*Pleuronectes platessa*	Caudal	0.81	Caudal	0.99	Caudal	0.98
BSG0089	First caudal vertebra	*Platichthys flesus*	Caudal	0.81	Caudal	0.97	Caudal	0.98
BSG0090	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.90	Caudal	0.99	Caudal	0.91
BSG0109	First caudal vertebra	*Platichthys flesus*	Caudal	0.98	Caudal	1.00	Caudal	1.00
BSG0116	First caudal vertebra	*Pleuronectes platessa*	Caudal	0.93	Caudal	0.88	Caudal	0.59
COP0101	Caudal vertebra	*Pleuronectes platessa*	Precaudal	0.95	Precaudal	0.87	Precaudal	1.00
COP0109	Precaudal vertebra	*Pleuronectes platessa*	Precaudal	0.59	NA	NA	NA	NA
COP0113	Precaudal vertebra	*Pleuronectes platessa*	Caudal	0.99	Caudal	0.92	Caudal	0.99
COP0114	Caudal vertebra	*Pleuronectes platessa*	Precaudal	0.99	NA	NA	NA	NA
COP0139	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.61	NA	NA	NA	NA
COP0142	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.94	Caudal	0.88	Caudal	0.99
COP0148	Cervical vertebra	*Pleuronectes platessa*	Cervical	0.95	Cervical	0.61	Precaudal	1.00
COP0161	Caudal vertebra	*Platichthys flesus*	Caudal	0.99	Caudal	1.00	Caudal	1.00
COP0166	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.98	Caudal	0.99	Caudal	0.97
COP0169	Cervical vertebra	*Platichthys flesus*	Precaudal	0.88	Caudal	0.88	Caudal	0.52
COP0170	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.92	Caudal	0.88	Caudal	0.97
COP0171	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.91	Caudal	1.00	Caudal	0.91
COP0174	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.89	Caudal	0.99	Caudal	0.99
COP0175	Caudal vertebra	*Platichthys flesus*	Caudal	0.82	Caudal	0.98	Precaudal	0.75
COP0176	Caudal vertebra	*Platichthys flesus*	Caudal	0.92	Caudal	1.00	Caudal	0.64
COP0177	Caudal vertebra	*Platichthys flesus*	Caudal	0.99	Caudal	1.00	Caudal	0.99
COP0178	Precaudal vertebra	*Limanda limanda*	Precaudal	0.70	Precaudal	0.55	Caudal	0.55
COP0179	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.96	Caudal	0.93	Caudal	0.99
COP0182	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.58	Caudal	0.99	Caudal	0.96
COP0183	Caudal vertebra	*Limanda limanda*	Caudal	0.96	Caudal	0.93	Caudal	0.97
COP0184	Caudal vertebra	*Platichthys flesus*	Caudal	0.95	Caudal	0.98	Caudal	1.00
COP0185	Cervical vertebra	*Platichthys flesus*	Precaudal	0.76	Precaudal	0.51	Precaudal	0.82
COP0187	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.65	Caudal	0.98	Caudal	1.00
COP0188	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.79	Caudal	1.00	Caudal	1.00
COP0189	Precaudal vertebra	*Pleuronectes platessa*	Precaudal	0.63	Caudal	0.80	Precaudal	0.99
COP0190	Caudal vertebra	*Platichthys flesus*	Caudal	0.82	Caudal	1.00	Precaudal	0.78
COP0202	First caudal vertebra	*Platichthys flesus*	Precaudal	0.72	Precaudal	0.58	Caudal	0.98
COP0205	Precaudal vertebra	*Pleuronectes platessa*	Caudal	0.60	Caudal	0.69	Caudal	0.58
COP0208	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.97	Caudal	1.00	Caudal	0.72
COP0216	Caudal vertebra	*Limanda limanda*	Caudal	0.70	Caudal	0.99	Caudal	1.00
COP0217	Precaudal vertebra	*Pleuronectes platessa*	Precaudal	0.94	Precaudal	0.94	Precaudal	1.00
COP0218	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.97	Caudal	0.94	Caudal	0.77
COP0221	Precaudal vertebra	*Platichthys flesus*	Precaudal	0.96	Precaudal	0.90	Precaudal	1.00
COP0222	Precaudal vertebra	*Pleuronectes platessa*	Caudal	0.74	Cervical	0.42	Precaudal	0.77
COP0223	Caudal vertebra	*Platichthys flesus*	Caudal	0.89	Caudal	0.99	Caudal	0.99
COP0237	Caudal vertebra	*Platichthys flesus*	Caudal	0.93	Caudal	1.00	Precaudal	0.66
COP0270	Cervical vertebra	*Platichthys flesus*	Cervical	1.00	Cervical	0.60	Cervical	1.00
COP0279	Caudal vertebra	*Platichthys flesus*	Caudal	0.97	Caudal	1.00	Caudal	0.99
COP0282	First caudal vertebra	*Platichthys flesus*	Precaudal	0.50	Caudal	0.87	Precaudal	0.96
COP0310	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.90	Caudal	0.61	Caudal	0.87
COP0320	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.89	Caudal	0.95	Caudal	0.95
COP0330	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.99	Caudal	1.00	Caudal	1.00
COP0332	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.99	Caudal	0.97	Caudal	0.99
COP0339	Caudal vertebra	*Pleuronectes platessa*	Caudal	0.91	Caudal	0.99	Caudal	0.94

Table C5. Results of identifying archaeological samples to family.

Sample	Vertebra	ZooMS identification	GMM family					
			Anterior	Probability	Sinistral	Probability	Combined	Probability
BSG0001	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.83	Pleuronectidae	0.84	Soleidae	0.78
BSG0014	Atlas	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	0.53
BSG0015	Atlas	*Pleuronectes platessa*	Pleuronectidae	0.90	Pleuronectidae	0.95	Pleuronectidae	1.00
BSG0016	Atlas	*Platichthys flesus*	Citharidae	0.84	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0017	Atlas	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0018	Cervical vertebra	*Platichthys flesus*	Bothidae	0.74	Pleuronectidae	0.89	Pleuronectidae	1.00
BSG0020	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.89	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0021	Caudal vertebra	*Platichthys flesus*	Soleidae	0.70	Pleuronectidae	0.97	Pleuronectidae	1.00
BSG0022	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0023	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.96	Pleuronectidae	1.00	Pleuronectidae	0.97
BSG0024	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0025	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.81	Pleuronectidae	0.91
BSG0026	Precaudal vertebra	*Platichthys flesus*	Bothidae	0.71	Pleuronectidae	1.00	Scophthalmidae	1.00
BSG0027	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.90	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0028	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.97	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0029	First caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.89	Pleuronectidae	0.97	Pleuronectidae	0.99
BSG0030	First caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.74	Pleuronectidae	0.99	Pleuronectidae	0.99
BSG0031	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.97	Scophthalmidae	0.62	Pleuronectidae	1.00
BSG0032	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.44	Pleuronectidae	0.87	Pleuronectidae	0.93
BSG0033	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.90	Pleuronectidae	0.98	Pleuronectidae	0.99
BSG0034	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.87	Pleuronectidae	0.98	Pleuronectidae	0.99
BSG0035	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.68	Pleuronectidae	0.91	Pleuronectidae	1.00
BSG0036	Caudal vertebra	*Platichthys flesus*	Soleidae	0.83	Pleuronectidae	0.99	Pleuronectidae	1.00
BSG0039	Atlas	*Platichthys flesus*	Pleuronectidae	1.00	Bothidae	0.83	Pleuronectidae	0.96
BSG0040	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0041	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.83	Pleuronectidae	0.90	Pleuronectidae	1.00
BSG0043	Atlas	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	0.99	Pleuronectidae	1.00
BSG0046	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.99	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0048	First caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.96	Pleuronectidae	0.98	Pleuronectidae	1.00
BSG0049	First caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.86	Pleuronectidae	0.99	Pleuronectidae	1.00
BSG0050	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0051	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.75	Pleuronectidae	0.86	Pleuronectidae	1.00
BSG0052	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.76	Pleuronectidae	0.97	Pleuronectidae	1.00
BSG0053	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.38	Pleuronectidae	0.96	Pleuronectidae	1.00
BSG0054	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.81	Pleuronectidae	0.98	Pleuronectidae	0.98
BSG0055	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.86	Pleuronectidae	0.97	Pleuronectidae	0.71
BSG0056	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.92	Pleuronectidae	0.95	Pleuronectidae	1.00
BSG0057	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.91	Pleuronectidae	0.83	Pleuronectidae	0.71
BSG0058	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.67	Pleuronectidae	0.91	Pleuronectidae	0.84
BSG0059	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.91	Pleuronectidae	0.88	Pleuronectidae	1.00
BSG0060	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.73	Pleuronectidae	0.84	Pleuronectidae	0.76
BSG0061	Cervical vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Soleidae	0.60	Pleuronectidae	0.97
BSG0062	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Soleidae	0.96	Pleuronectidae	1.00
BSG0063	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.99	Pleuronectidae	1.00
BSG0064	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.90	Pleuronectidae	1.00
BSG0065	Cervical vertebra	*Platichthys flesus*	Soleidae	0.83	Pleuronectidae	1.00	Soleidae	0.99
BSG0066	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	0.98	Pleuronectidae	1.00	Pleuronectidae	0.87
BSG0067	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.51	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0068	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.99	Pleuronectidae	0.82

Table C5 continued

Sample	Vertebra	ZooMS identification	GMM family

Table C5 continued

Sample	**Vertebra**	**ZooMS identification**			**GMM family**			
			Anterior	**Probability**	**Sinistral**	**Probability**	**Combined**	**Probability**
BSG0069	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.99	Pleuronectidae	1.00
BSG0070	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0071	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.98	Pleuronectidae	1.00
BSG0082	Atlas	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.98	Pleuronectidae	0.99
BSG0083	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.99	Citharidae	0.55	Pleuronectidae	1.00
BSG0084	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.83	Pleuronectidae	0.95	Pleuronectidae	0.99
BSG0085	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0088	Atlas	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	0.98	Pleuronectidae	0.92
BSG0089	First caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.70	Pleuronectidae	0.99	Pleuronectidae	0.95
BSG0090	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.92	Pleuronectidae	1.00	Pleuronectidae	1.00
BSG0109	First caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.96	Pleuronectidae	0.96	Pleuronectidae	0.81
BSG0116	First caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.86	Pleuronectidae	0.98	Pleuronectidae	1.00
COP0101	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.75	Pleuronectidae	1.00	Pleuronectidae	0.58
COP0109	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	0.89	Bothidae	1.00
COP0113	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.85	Pleuronectidae	0.77	Pleuronectidae	1.00
COP0114	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.86	Pleuronectidae	0.94	Pleuronectidae	0.63
COP0139	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	0.80	Pleuronectidae	1.00
COP0142	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.96	Pleuronectidae	0.97	Pleuronectidae	1.00
COP0148	Cervical vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	0.82	Bothidae	0.63
COP0161	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.74	Pleuronectidae	0.89	Pleuronectidae	1.00
COP0166	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.87	Pleuronectidae	0.98	Pleuronectidae	0.98
COP0169	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
COP0170	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.99	Pleuronectidae	0.81	Pleuronectidae	0.90
COP0171	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.93	Pleuronectidae	0.98	Pleuronectidae	0.73
COP0174	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.99	Pleuronectidae	0.96	Pleuronectidae	1.00
COP0175	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.59	Pleuronectidae	0.67	Scophthalmidae	0.82
COP0176	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.75	Pleuronectidae	0.65	Pleuronectidae	0.99
COP0177	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.93	Scophthalmidae	0.51	Pleuronectidae	1.00
COP0178	Precaudal vertebra	*Limanda limanda*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
COP0179	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.94	Pleuronectidae	0.77	Pleuronectidae	1.00
COP0182	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.81	Pleuronectidae	0.64	Pleuronectidae	0.98
COP0183	Caudal vertebra	*Limanda limanda*	Pleuronectidae	0.70	Pleuronectidae	0.89	Pleuronectidae	0.99
COP0184	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.90	Pleuronectidae	0.89	Pleuronectidae	0.74
COP0185	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	0.97
COP0187	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	0.99	Pleuronectidae	1.00	Scophthalmidae	1.00
COP0188	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.68	Pleuronectidae	1.00	Pleuronectidae	1.00
COP0189	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	1.00	Pleuronectidae	1.00
COP0190	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.86	Pleuronectidae	0.95	Pleuronectidae	0.99
COP0202	First caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.97	Pleuronectidae	0.95	Pleuronectidae	0.75
COP0205	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.99	Pleuronectidae	0.92	Pleuronectidae	0.85
COP0208	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.76	Pleuronectidae	0.80	Bothidae	0.95
COP0216	Caudal vertebra	*Limanda limanda*	Pleuronectidae	0.94	Pleuronectidae	0.89	Pleuronectidae	1.00
COP0217	Precaudal vertebra	*Pleuronectes platessa*	Pleuronectidae	1.00	Pleuronectidae	0.99	Scophthalmidae	1.00
COP0218	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.80	Pleuronectidae	0.94	Pleuronectidae	0.96
COP0221	Precaudal vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.99	Pleuronectidae	1.00
COP0222	Precaudal vertebra	*Pleuronectes platessa*	Scophthalmidae	0.93	Pleuronectidae	0.80	Pleuronectidae	0.62
COP0223	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.40	Pleuronectidae	0.96	Pleuronectidae	0.95
COP0237	Caudal vertebra	*Platichthys flesus*	Bothidae	0.87	Pleuronectidae	0.99	Pleuronectidae	1.00
COP0270	Cervical vertebra	*Platichthys flesus*	Pleuronectidae	1.00	Pleuronectidae	0.96	Pleuronectidae	1.00
COP0279	Caudal vertebra	*Platichthys flesus*	Pleuronectidae	0.71	Pleuronectidae	0.90	Pleuronectidae	0.98

COP0282	First caudal vertebra	*Platichthys flesus*	Bothidae	0.52	Pleuronectidae	1.00	Pleuronectidae	1.00
COP0310	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.80	Pleuronectidae	0.51	Pleuronectidae	0.87
COP0320	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.95	Pleuronectidae	0.85	Pleuronectidae	0.98
COP0330	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.95	Scophthalmidae	0.56	Pleuronectidae	0.97
COP0332	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.53	Pleuronectidae	0.80	Soleidae	0.66
COP0339	Caudal vertebra	*Pleuronectes platessa*	Pleuronectidae	0.99	Pleuronectidae	0.93	Scophthalmidae	0.84

Table C6. Results of identifying archaeological samples to species. NA indicates that the sample was not correctly identified to family (see table C5).

Sample	Vertebra	ZooMS identification	GMM species					
			Anterior	Probability	Sinistral	Probability	Combined	Probability
BSG0001	Caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.31	*Platichthys flesus*	0.83	*Solea solea*	1.00
BSG0014	Atlas	*Platichthys flesus*	*Pleuronectes platessa*	0.52	*Platichthys flesus*	0.90	*Platichthys flesus*	1.00
BSG0015	Atlas	*Pleuronectes platessa*	*Pleuronectes platessa*	0.70	*Platichthys flesus*	1.00	*Pleuronectes platessa*	0.97
BSG0016	Atlas	*Platichthys flesus*	NA	NA	*Platichthys flesus*	0.98	*Limanda limanda*	1.00
BSG0017	Atlas	*Pleuronectes platessa*	*Limanda limanda*	1.00	*Hippoglossus hippoglossus*	0.66	*Platichthys flesus*	0.99
BSG0018	Cervical vertebra	*Platichthys flesus*	NA	NA	*Glyptocephalus cynoglossus*	0.56	*Hippoglossoides platessoides*	0.86
BSG0020	Precaudal vertebra	*Platichthys flesus*	*Pleuronectes platessa*	0.52	*Limanda limanda*	0.50	*Hippoglossoides platessoides*	0.99
BSG0021	Caudal vertebra	*Platichthys flesus*	*Solea solea*	0.99	*Platichthys flesus*	0.91	*Platichthys flesus*	0.63
BSG0022	Precaudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.35	*Glyptocephalus cynoglossus*	0.63	*Platichthys flesus*	0.88
BSG0023	Precaudal vertebra	*Platichthys flesus*	*Hippoglossus hippoglossus*	0.52	*Platichthys flesus*	0.87	*Platichthys flesus*	1.00
BSG0024	Precaudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.90	*Platichthys flesus*	0.83	*Platichthys flesus*	1.00
BSG0025	Precaudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.35	*Platichthys flesus*	0.39	*Pleuronectes platessa*	0.92
BSG0026	Precaudal vertebra	*Platichthys flesus*	NA	NA	*Hippoglossus hippoglossus*	0.88	*Scophthalmus rhombus*	1.00
BSG0027	Precaudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.84	*Platichthys flesus*	0.65	*Hippoglossoides platessoides*	0.79
BSG0028	Precaudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.91	*Platichthys flesus*	0.82	*Hippoglossoides platessoides*	0.65
BSG0029	First caudal vertebra	*Pleuronectes platessa*	*Hippoglossoides platessoides*	0.53	*Pleuronectes platessa*	0.93	*Pleuronectes platessa*	0.76
BSG0030	First caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	1.00	*Limanda limanda*	0.45	*Pleuronectes platessa*	0.71
BSG0031	Caudal vertebra	*Pleuronectes platessa*	*Hippoglossoides platessoides*	0.47	*Scophthalmus maximus*	0.77	*Hippoglossoides platessoides*	0.49
BSG0032	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.73	*Glyptocephalus cynoglossus*	0.58	*Microstomus kitt*	0.95
BSG0033	Caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.66	*Platichthys flesus*	0.94	*Pleuronectes platessa*	0.55
BSG0034	Caudal vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.63	*Hippoglossoides platessoides*	0.95	*Limanda limanda*	0.56
BSG0035	Caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.82	*Platichthys flesus*	0.98	*Platichthys flesus*	0.93
BSG0036	Caudal vertebra	*Platichthys flesus*	*Solea solea*	0.95	*Platichthys flesus*	0.94	*Platichthys flesus*	0.99
BSG0039	Atlas	*Platichthys flesus*	*Platichthys flesus*	0.57	NA	NA	*Platichthys flesus*	1.00
BSG0040	Precaudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.51	*Platichthys flesus*	0.69	*Platichthys flesus*	0.39
BSG0041	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.56	*Platichthys flesus*	0.57	*Platichthys flesus*	0.88
BSG0043	Atlas	*Pleuronectes platessa*	*Platichthys flesus*	0.56	*Pleuronectes platessa*	0.95	*Platichthys flesus*	1.00
BSG0046	Precaudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.94	*Hippoglossus hippoglossus*	0.52	*Hippoglossoides platessoides*	0.48
BSG0048	First caudal vertebra	*Platichthys flesus*	*Hippoglossus hippoglossus*	0.62	*Limanda limanda*	0.39	*Platichthys flesus*	0.96
BSG0049	First caudal vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.67	*Platichthys flesus*	0.48	*Platichthys flesus*	0.96

Table C6 continued

Sample	Vertebra	ZooMS identification			GMM species			
			Anterior	Probability	Sinistral	Probability	Combined	Probability
BSG0050	Precaudal vertebra	*Pleuronectes platessa*	*Hippoglossoides platessoides*	0.82	*Pleuronectes platessa*	0.86	*Glyptocephalus cynoglossus*	0.89
BSG0051	Precaudal vertebra	*Pleuronectes platessa*	*Glyptocephalus cynoglossus*	0.36	*Glyptocephalus cynoglossus*	0.40	*Platichthys flesus*	0.97
BSG0052	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.27	*Limanda limanda*	0.36	*Limanda limanda*	0.44
BSG0053	Caudal vertebra	*Platichthys flesus*	*Hippoglossoides platessoides*	0.75	*Platichthys flesus*	0.92	*Platichthys flesus*	0.98
BSG0054	Caudal vertebra	*Pleuronectes platessa*	*Glyptocephalus cynoglossus*	0.59	*Microstomus kitt*	0.35	*Platichthys flesus*	0.42
BSG0055	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.68	*Platichthys flesus*	0.78	*Platichthys flesus*	0.54
BSG0056	Caudal vertebra	*Pleuronectes platessa*	*Limanda limanda*	0.48	*Platichthys flesus*	0.85	*Platichthys flesus*	0.47
BSG0057	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.32	*Glyptocephalus cynoglossus*	0.30	*Platichthys flesus*	0.48
BSG0058	Caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.76	*Hippoglossoides platessoides*	0.80	*Limanda limanda*	0.97
BSG0059	Caudal vertebra	*Pleuronectes platessa*	*Limanda limanda*	0.59	*Platichthys flesus*	0.94	*Hippoglossus hippoglossus*	0.85
BSG0060	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.63	*Pleuronectes platessa*	0.32	*Platichthys flesus*	0.39
BSG0061	Cervical vertebra	*Pleuronectes platessa*	*Platichthys flesus*	0.63	*Platichthys flesus*	0.50	*Pleuronectes platessa*	0.83
BSG0062	Cervical vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.89	*Platichthys flesus*	0.61	*Microstomus kitt*	0.93
BSG0063	Cervical vertebra	*Platichthys flesus*	*Limanda limanda*	0.64	*Microstomus kitt*	0.40	*Hippoglossoides platessoides*	0.55
BSG0064	Cervical vertebra	*Platichthys flesus*	*Limanda limanda*	0.49	*Hippoglossoides platessoides*	0.42	*Microstomus kitt*	0.95
BSG0065	Cervical vertebra	*Platichthys flesus*	*Solea solea*	1.00	*Limanda limanda*	0.21	*Platichthys flesus*	1.00
BSG0066	Cervical vertebra	*Platichthys flesus*	*Pleuronectes platessa*	0.39	*Platichthys flesus*	0.75	*Hippoglossus hippoglossus*	0.65
BSG0067	Precaudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.58	*Platichthys flesus*	0.83	*Hippoglossoides platessoides*	1.00
BSG0068	Precaudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.68	*Platichthys flesus*	0.76	*Microstomus kitt*	0.99
BSG0069	Precaudal vertebra	*Platichthys flesus*	*Hippoglossoides platessoides*	1.00	*Hippoglossoides platessoides*	0.72	*Glyptocephalus cynoglossus*	0.62
BSG0070	Precaudal vertebra	*Pleuronectes platessa*	*Hippoglossoides platessoides*	0.50	*Platichthys flesus*	0.70	*Pleuronectes platessa*	0.65
BSG0071	Precaudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.50	*Platichthys flesus*	0.70	*Hippoglossus hippoglossus*	0.78
BSG0082	Atlas	*Platichthys flesus*	*Limanda limanda*	0.68	*Limanda limanda*	0.71	*Hippoglossoides platessoides*	0.99
BSG0083	Precaudal vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.89	NA	NA	*Pleuronectes platessa*	0.97
BSG0084	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.98	*Microstomus kitt*	0.48	*Microstomus kitt*	0.94
BSG0085	Precaudal vertebra	*Pleuronectes platessa*	*Platichthys flesus*	0.79	*Platichthys flesus*	0.62	*Hippoglossus hippoglossus*	0.89
BSG0088	Atlas	*Pleuronectes platessa*	*Microstomus kitt*	0.55	*Pleuronectes platessa*	0.44	*Hippoglossoides platessoides*	0.97
BSG0089	First caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.78	*Limanda limanda*	0.64	*Hippoglossus hippoglossus*	0.91
BSG0090	Caudal vertebra	*Pleuronectes platessa*	*Limanda limanda*	0.54	*Microstomus kitt*	0.60	*Limanda limanda*	0.66
BSG0109	First caudal vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.41	*Pleuronectes platessa*	0.38	*Limanda limanda*	0.35
BSG0116	First caudal vertebra	*Pleuronectes platessa*	*Platichthys flesus*	0.66	*Platichthys flesus*	0.87	*Pleuronectes platessa*	0.46

Table C6 continued

Sample	Vertebra	ZooMS identification	GMM species

Table C6 continued

Sample	Vertebra	ZooMS identification	GMM species Anterior	Probability	Sinistral	Probability	Combined	Probability
COP0101	Caudal vertebra	*Pleuronectes platessa*	*Hippoglossoides platessoides*	0.35	*Pleuronectes platessa*	0.63	*Pleuronectes platessa*	1.00
COP0109	Precaudal vertebra	*Pleuronectes platessa*	*Limanda limanda*	0.91	*Pleuronectes platessa*	0.36	NA	NA
COP0113	Precaudal vertebra	*Pleuronectes platessa*	*Platichthys flesus*	0.37	*Platichthys flesus*	0.90	*Platichthys flesus*	0.98
COP0114	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.81	*Pleuronectes platessa*	0.64	*Pleuronectes platessa*	0.95
COP0139	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.61	*Pleuronectes platessa*	0.38	*Pleuronectes platessa*	0.93
COP0142	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.40	*Limanda limanda*	0.67	*Hippoglossoides platessoides*	0.56
COP0148	Cervical vertebra	*Pleuronectes platessa*	*Hippoglossus hippoglossus*	0.90	*Pleuronectes platessa*	0.26	NA	NA
COP0161	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.88	*Platichthys flesus*	0.35	*Hippoglossus hippoglossus*	0.91
COP0166	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.43	*Limanda limanda*	0.68	*Limanda limanda*	0.99
COP0169	Cervical vertebra	*Platichthys flesus*	*Limanda limanda*	0.61	*Platichthys flesus*	0.97	*Hippoglossoides platessoides*	0.88
COP0170	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.66	*Microstomus kitt*	0.44	*Limanda limanda*	0.68
COP0171	Caudal vertebra	*Pleuronectes platessa*	*Glyptocephalus cynoglossus*	0.38	*Microstomus kitt*	0.49	*Hippoglossoides platessoides*	0.43
COP0174	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.30	*Limanda limanda*	0.63	*Hippoglossoides platessoides*	0.75
COP0175	Caudal vertebra	*Platichthys flesus*	*Hippoglossoides platessoides*	0.60	*Hippoglossoides platessoides*	0.77	*Scophthalmus rhombus*	1.00
COP0176	Caudal vertebra	*Platichthys flesus*	*Hippoglossus hippoglossus*	0.81	*Limanda limanda*	0.56	*Limanda limanda*	0.98
COP0177	Caudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.33	*Scophthalmus rhombus*	0.50	*Pleuronectes platessa*	0.96
COP0178	Precaudal vertebra	*Limanda limanda*	*Limanda limanda*	0.66	*Hippoglossoides platessoides*	0.75	*Limanda limanda*	0.79
COP0179	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.27	*Microstomus kitt*	0.79	*Pleuronectes platessa*	0.32
COP0182	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.44	*Microstomus kitt*	0.74	*Pleuronectes platessa*	0.68
COP0183	Caudal vertebra	*Limanda limanda*	*Limanda limanda*	0.62	*Hippoglossoides platessoides*	0.57	*Limanda limanda*	0.97
COP0184	Caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.59	*Pleuronectes platessa*	0.56	*Platichthys flesus*	0.82
COP0185	Cervical vertebra	*Platichthys flesus*	*Hippoglossoides platessoides*	0.53	*Platichthys flesus*	0.67	*Platichthys flesus*	1.00
COP0187	Precaudal vertebra	*Platichthys flesus*	*Pleuronectes platessa*	0.75	*Hippoglossoides platessoides*	0.78	*Scophthalmus maximus*	1.00
COP0188	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.35	*Limanda limanda*	0.35	*Limanda limanda*	0.51
COP0189	Precaudal vertebra	*Pleuronectes platessa*	*Hippoglossoides platessoides*	0.55	*Pleuronectes platessa*	0.99	*Pleuronectes platessa*	1.00
COP0190	Caudal vertebra	*Platichthys flesus*	*Limanda limanda*	0.66	*Platichthys flesus*	0.96	*Platichthys flesus*	0.89
COP0202	First caudal vertebra	*Platichthys flesus*	*Platichthys flesus*	0.68	*Limanda limanda*	0.30	*Platichthys flesus*	0.91
COP0205	Precaudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.99	*Hippoglossoides platessoides*	0.45	*Pleuronectes platessa*	1.00
COP0208	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.34	*Pleuronectes platessa*	0.67	NA	NA
COP0216	Caudal vertebra	*Limanda limanda*	*Pleuronectes platessa*	0.55	*Hippoglossoides platessoides*	0.60	*Microstomus kitt*	0.62
COP0217	Precaudal vertebra	*Pleuronectes platessa*	*Platichthys flesus*	0.97	*Hippoglossoides platessoides*	0.85	*Scophthalmus rhombus*	1.00

COP0218	Caudal vertebra	*Pleuronectes platessa*	*Microstomus kitt*	0.81	*Pleuronectes platessa*	0.81	*Pleuronectes platessa*	0.99
COP0221	Precaudal vertebra	*Platichthys flesus*	*Microstomus kitt*	0.95	*Hippoglossoides platessoides*	0.49	*Platichthys flesus*	0.77
COP0222	Precaudal vertebra	*Pleuronectes platessa*	*Lepidorhombus whiffiagonis*	0.59	*Glyptocephalus cynoglossus*	0.46	*Pleuronectes platessa*	0.98
COP0223	Caudal vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.53	*Pleuronectes platessa*	0.73	*Microstomus kitt*	0.99
COP0237	Caudal vertebra	*Platichthys flesus*	NA	NA	*Limanda limanda*	0.53	*Limanda limanda*	0.62
COP0270	Cervical vertebra	*Platichthys flesus*	*Hippoglossus hippoglossus*	0.92	*Platichthys flesus*	0.52	*Hippoglossoides platessoides*	0.91
COP0279	Caudal vertebra	*Platichthys flesus*	*Glyptocephalus cynoglossus*	0.41	*Platichthys flesus*	0.86	*Platichthys flesus*	0.70
COP0282	First caudal vertebra	*Platichthys flesus*	NA	NA	*Platichthys flesus*	0.82	*Hippoglossoides platessoides*	0.86
COP0310	Caudal vertebra	*Pleuronectes platessa*	*Platichthys flesus*	0.79	*Microstomus kitt*	0.35	*Glyptocephalus cynoglossus*	0.31
COP0320	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.48	*Pleuronectes platessa*	0.70	*Glyptocephalus cynoglossus*	0.51
COP0330	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.39	*Scophthalmus maximus*	0.56	*Microstomus kitt*	0.88
COP0332	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.47	*Microstomus kitt*	0.83	*Solea solea*	1.00
COP0339	Caudal vertebra	*Pleuronectes platessa*	*Pleuronectes platessa*	0.52	*Microstomus kitt*	0.80	*Scophthalmus maximus*	1.00

Table C7. Results of identifying archaeological *P. flesus* samples to sidedness.

Sample	Vertebra	GMM sidedness Anterior	 Sinistral	 Combined
BSG0001	Caudal vertebra	right	right	left
BSG0018	Cervical vertebra	right	right	right
BSG0020	Precaudal vertebra	left	right	left
BSG0021	Caudal vertebra	right	right	right
BSG0023	Precaudal vertebra	right	left	right
BSG0024	Precaudal vertebra	right	right	right
BSG0025	Precaudal vertebra	right	left	left
BSG0026	Precaudal vertebra	right	left	right
BSG0027	Precaudal vertebra	right	right	right
BSG0028	Precaudal vertebra	right	right	right
BSG0030	First caudal vertebra	left	right	right
BSG0033	Caudal vertebra	right	left	left
BSG0034	Caudal vertebra	right	right	left
BSG0035	Caudal vertebra	left	left	left
BSG0036	Caudal vertebra	left	left	right
BSG0040	Precaudal vertebra	right	left	right
BSG0041	Caudal vertebra	right	right	right
BSG0046	Precaudal vertebra	right	left	left
BSG0048	First caudal vertebra	right	right	right
BSG0049	First caudal vertebra	right	right	right
BSG0052	Caudal vertebra	right	right	right
BSG0053	Caudal vertebra	right	right	left
BSG0055	Caudal vertebra	right	left	left
BSG0058	Caudal vertebra	right	right	left
BSG0060	Caudal vertebra	right	right	right
BSG0062	Cervical vertebra	right	left	right
BSG0063	Cervical vertebra	right	right	right
BSG0064	Cervical vertebra	right	right	right
BSG0065	Cervical vertebra	right	right	right
BSG0066	Cervical vertebra	right	left	left
BSG0067	Precaudal vertebra	right	right	right
BSG0068	Precaudal vertebra	right	right	left
BSG0069	Precaudal vertebra	right	right	right
BSG0071	Precaudal vertebra	right	right	right
BSG0083	Precaudal vertebra	right	right	left
BSG0084	Caudal vertebra	right	right	right
BSG0089	First caudal vertebra	right	right	right
BSG0109	First caudal vertebra	?	?	?
COP0161	Caudal vertebra	right	right	right
COP0169	Cervical vertebra	right	right	left
COP0175	Caudal vertebra	right	right	right
COP0176	Caudal vertebra	right	right	left
COP0177	Caudal vertebra	right	right	left
COP0184	Caudal vertebra	right	right	left
COP0185	Cervical vertebra	right	right	left
COP0187	Precaudal vertebra	right	left	left
COP0190	Caudal vertebra	right	right	right
COP0202	First caudal vertebra	left	right	left
COP0221	Precaudal vertebra	right	left	left

Table C7 continued

Sample	**Vertebra**		**GMM sidedness**	
		Anterior	**Sinistral**	**Combined**
COP0223	Caudal vertebra	right	right	right
COP0237	Caudal vertebra	right	left	right
COP0270	Cervical vertebra	right	left	right
COP0279	Caudal vertebra	left	right	left
COP0282	First caudal vertebra	right	right	right

Table C8. Overview of landmarks present in archaeological samples.

Sample	**Vertebra**	**ZooMS identification**	**Landmarks anterior**	**Landmarks sinistral**
BSG0001	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22	3,4,5,6,8,9,10,11,12
BSG0014	Atlas	*Platichthys flesus*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0015	Atlas	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0016	Atlas	*Platichthys flesus*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0017	Atlas	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0018	Cervical vertebra	*Platichthys flesus*	1,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10
BSG0020	Precaudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0021	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19,20,21,22,23,24,25	3,4,5,6,8,9,10,11,12
BSG0022	Precaudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19	3,4,5,7,8,9,10,11,12
BSG0023	Precaudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,8,9,10,11,12
BSG0024	Precaudal vertebra	*Platichthys flesus*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	2,3,4,5,6,8,9,10,11,12
BSG0025	Precaudal vertebra	*Platichthys flesus*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	2,9,10,11,12
BSG0026	Precaudal vertebra	*Platichthys flesus*	3,4,5,8,11,12,13,14,15,16,17,18,19	2,3,4,5,6,7,8,9,10,11,12
BSG0027	Precaudal vertebra	*Platichthys flesus*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	6,7,8,9,10,11,12
BSG0028	Precaudal vertebra	*Platichthys flesus*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	2,3,4,5,6,7,8,9,10,11,12
BSG0029	First caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0030	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0031	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0032	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0033	Caudal vertebra	*Platichthys flesus*	1,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0034	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0035	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0036	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19,20,21,22,23,24,25	3,4,5,6,7,9,10,11,12
BSG0039	Atlas	*Platichthys flesus*	2,3,4,5,6,7,8,10,11,12	2,3,4,5,7,8,9
BSG0040	Precaudal vertebra	*Platichthys flesus*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	2,3,4,5,6,7,8,9,10,11,12
BSG0041	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0043	Atlas	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0046	Precaudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0048	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0049	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,8,9,10,11,12
BSG0050	Precaudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0051	Precaudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0052	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0053	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0054	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0055	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0056	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0057	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,20,21,22,23,24,25	6,7,8,9,10,11,12
BSG0058	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0059	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0060	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12

Table C8 continued

Sample	Vertebra	ZooMS identification	Landmarks anterior	Landmarks sinistral
BSG0061	Cervical vertebra	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,22	2,3,4,5,6,7,8,9,10,11,12
BSG0062	Cervical vertebra	*Platichthys flesus*	1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10
BSG0063	Cervical vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,13,14,15,17,18,19	3,4,5,6,7,8,9,10
BSG0064	Cervical vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,5,6,7,8,9,10,11,12
BSG0065	Cervical vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,19	6,7,8,9,10,11,12
BSG0066	Cervical vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,5,6,7,8,9,10,11,12
BSG0067	Precaudal vertebra	*Platichthys flesus*	2,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0068	Precaudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0069	Precaudal vertebra	*Platichthys flesus*	1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	1,2,3,4,5,6,7,8,9,10,11,12
BSG0070	Precaudal vertebra	*Pleuronectes platessa*	2,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0071	Precaudal vertebra	*Platichthys flesus*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,19	2,3,5,9,10,11,12
BSG0082	Atlas	*Platichthys flesus*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0083	Precaudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19	3,5,6,7,8,9,10,11,12
BSG0084	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19,20,21,22,23,24,25	3,4,5,9,10,11,12
BSG0085	Precaudal vertebra	*Pleuronectes platessa*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,18,19	2,3,4,5,6,7,8,9,10,11,12
BSG0088	Atlas	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12	2,3,4,5,6,7,8,9
BSG0089	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
BSG0090	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
BSG0109	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19	3,4,6,7,8,9,10,11,12
BSG0116	First caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,15,16,22	9,10,11,12
COP0101	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0109	Precaudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,11,12,13,14,15,16,17,18,19	3,4,6,7,8,9,10,12
COP0113	Precaudal vertebra	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,19	9,10,11,12
COP0114	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,5,6,8,9,10,11,12
COP0139	Caudal vertebra	*Pleuronectes platessa*	1,2,3,4,5,7,8,9,10,11,12,13,14,15,16,17,18,19	9,10,11,12
COP0142	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,5,6,7,8,9,10,11,12
COP0148	Cervical vertebra	*Pleuronectes platessa*	1,2,3,4,5,7,8,9,10,11,12,13,14,15,16,17,18,19	1,2,3,4,5,9,10,11,12
COP0161	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0166	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22	3,4,5,6,7,8,9,10,11,12
COP0169	Cervical vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
COP0170	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,19,20,21,22	3,8,9,10,11,12
COP0171	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0174	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0175	Caudal vertebra	*Platichthys flesus*	4,5,7,8,9,10,11,12,14,15,16,17,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0176	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
COP0177	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0178	Precaudal vertebra	*Limanda limanda*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	2,3,6,7,8,9,10,11,12
COP0179	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,20,21,22,23,24,25	3,7,8,9,10,11,12
COP0182	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,20	3,4,5,8,9,10,11,12
COP0183	Caudal vertebra	*Limanda limanda*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	6,7,8,9,10,11,12
COP0184	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0185	Cervical vertebra	*Platichthys flesus*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	2,3,4,5,6,7,8,9,10,11,12
COP0187	Precaudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
COP0188	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0189	Precaudal vertebra	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,18,19	3,4,5,7,8,9,10,11,12
COP0190	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0202	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,19	3,4,5,9,10,11,12
COP0205	Precaudal vertebra	*Pleuronectes platessa*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	6,8,9,10,11,12
COP0208	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0216	Caudal vertebra	*Limanda limanda*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12

Table C8 continued

Sample	**Vertebra**	**ZooMS identification**	**Landmarks anterior**	**Landmarks sinistral**
COP0217	Precaudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	1,2,3,4,5,6,7,8,9,10,11,12
COP0218	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0221	Precaudal vertebra	*Platichthys flesus*	3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,19	3,4,5,6,8,9,10,11,12
COP0222	Precaudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,22	3,9,10,11,12
COP0223	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,8,9,10,11,12
COP0237	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0270	Cervical vertebra	*Platichthys flesus*	2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,18,19	2,3,4,5,9,10,11,12
COP0279	Caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,18,19,20,21,22,23,24,25	3,4,5,6,7,8,9,10,11,12
COP0282	First caudal vertebra	*Platichthys flesus*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	3,4,5,6,7,8,9,10,11,12
COP0310	Caudal vertebra	*Pleuronectes platessa*	4,5,7,8,9,10,11,12,13,14,15,16,18,19,20,21,23,24,25	8,9,10,11,12
COP0320	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,17,20,21,22,23,24,25	3,4,6,7,8,9,10,11,12
COP0330	Caudal vertebra	*Pleuronectes platessa*	1,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,24,25	1,2,3,4,5,6,7,8,9,10,11,12
COP0332	Caudal vertebra	*Pleuronectes platessa*	4,5,6,7,8,9,10,11,12,13,14,15,16,20,21,23,24,25	3,7,8,9,10,11,12
COP0339	Caudal vertebra	*Pleuronectes platessa*	4,5,6,8,9,10,11,12,14,15,16,19,23,24	3,4,9,10,11,12

Part C3. Rscript for analysis

Modern dataset (description and classification)

```
# Packages needed
library(geomorph)
library(Morpho)
library(caret)
library(MASS)
library(Arothron)
library(stringr)
library(e1071)
library(geometry)

# Data formatting: All TPS files need to follow this built-up of the name of the file; if not certain parts of the code should be
changed to match the names of the files
# "xxxx_yyyy_V_FA_gen_spec.TPS" with x=unique file number; y=sample number; FA=family code; gen= genus code;
spec=species code

# LM numbers:
 # Anterior all
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
  # LM in text: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17    18    19 20 21 22 23 24 25
 # Anterior atlas
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
  # LM in text: 1 2 3 4 5 6 7 8 9 10 11 12         13
 # Sinistral all
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13
  # LM in text: 1 2 3 4 5 6 7 8    9 10 11 12
 # Sinistral atlas
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13 14
  # LM in text: 1     2 3 4 5 6  7  8  9

# Coding:
 # Vertebra type
  # N cervical; P precaudal, C caudal
 # Family
  # PL Pleuronectidae; SC Scophthalmidae; SO Soleidae
 # Genus
  # ple Pleuronectes; pla Platichthys; gly Glyptocephalus; hip Hippoglossus; hpe Hippoglossoides; mic Microstomus; lim
Limanda;
  # sco Scophthalmus; zeu Zeugopterus; lep Lepidorhombus;
  # sol Solea; buglossidium; dic Dicologlossa;
  # cit Citharus; arn Arnoglossus
 # Species
  # plta platessa; fles flesus; cyno cynoglossus; hipp hippoglossus; plte platessoides; kitt kitt; lima limanda
  # maxi maximus; rhom rhombus; regi regius; punc punctatus; bosc boscii; whif whiffiagonis
  # sole solea; lasc lascaris; lute luteum; hexo hexophthalma
  # ling linguatula; late laterna


#######################

# Setting: These are to be changed

vertebra<-"normal"          # Choose vertebra type: normal or atlas
vertebra_subset<-"C"        # Choose vertebra subset: N cervical, P precaudal, C caudal
ID_level<-"family"          # Choose identification level: family, Pleuronectidae, Scophthalmidae, Soleidae, plaiceflounder

#######################


# Set selection
if(vertebra=="normal"){
  landmark_ant_nr<-29
  landmark_sin_nr<-13
  anterior_ref_file<-"Reference_anterior"
  sinistral_ref_file<-"Reference_sinistral"
} else if(vertebra=="atlas"){
```

```
  anterior_ref_file<-"Reference_anterior_atlas"
  sinistral_ref_file<-"Reference_sinistral_atlas"
  landmark_ant_nr<-17
  landmark_sin_nr<-14
}
length_ref_folder<-length(list.files(anterior_ref_file))
anterior_ref_file_cut<-print(paste0(anterior_ref_file,"/"))
sinistral_ref_file_cut<-print(paste0(sinistral_ref_file,"/"))

# Create empty arrays for archaelogical and reference sample
Sin_view_R<-array(NA,dim=c(landmark_sin_nr,2,length_ref_folder))
Ant_view_R<-array(NA,dim=c(landmark_ant_nr,2,length_ref_folder))
dimnames(Ant_view_R)[[3]]<-list.files(anterior_ref_file_cut)
dimnames(Sin_view_R)[[3]]<-list.files(sinistral_ref_file_cut)

# Fill the arrays
for(i in 1:length_ref_folder){
  path_ant_R<-paste(anterior_ref_file_cut,list.files(anterior_ref_file)[i],sep="")
  Ant_view_R[,,i]<-readallTPS(path_ant_R)$LM[[1]]

  path_sin_R<-paste(sinistral_ref_file_cut,list.files(sinistral_ref_file)[i],sep="")
  Sin_view_R[,,i]<-readallTPS(path_sin_R)$LM[[1]]
}

# Rearrange both arrays for reference and archaeological set so they match per sample
sel_ref_match<-match(substr(dimnames(Sin_view_R)[[3]],6,9),substr(dimnames(Ant_view_R)[[3]],6,9))
Ant_view_R<-Ant_view_R[,,sel_ref_match]

# Creating subsets
if(ID_level=="family"){
  subset_taxon<-
which(substr(dimnames(Sin_view_R)[[3]],13,14)=="PL"|substr(dimnames(Sin_view_R)[[3]],13,14)=="SC"|substr(dimnames(Sin
_view_R)[[3]],13,14)=="SO"|substr(dimnames(Sin_view_R)[[3]],13,14)=="CI"|substr(dimnames(Sin_view_R)[[3]],13,14)=="BO")
  Sin_view_temp<-Sin_view_R[,,subset_taxon]
  subset_taxon<-
which(substr(dimnames(Ant_view_R)[[3]],13,14)=="PL"|substr(dimnames(Ant_view_R)[[3]],13,14)=="SC"|substr(dimnames(Ant
_view_R)[[3]],13,14)=="SO"|substr(dimnames(Ant_view_R)[[3]],13,14)=="CI"|substr(dimnames(Ant_view_R)[[3]],13,14)=="BO")
  Ant_view_temp<-Ant_view_R[,,subset_taxon]
} else if(ID_level=="Pleuronectidae"){
  subset_taxon<-which(substr(dimnames(Sin_view_R)[[3]],13,14)=="PL")
  Sin_view_temp<-Sin_view_R[,,subset_taxon]
  subset_taxon<-which(substr(dimnames(Ant_view_R)[[3]],13,14)=="PL")
  Ant_view_temp<-Ant_view_R[,,subset_taxon]
} else if(ID_level=="Scophthalmidae"){
  subset_taxon<-which(substr(dimnames(Sin_view_R)[[3]],13,14)=="SC")
  Sin_view_temp<-Sin_view_R[,,subset_taxon]
  subset_taxon<-which(substr(dimnames(Ant_view_R)[[3]],13,14)=="SC")
  Ant_view_temp<-Ant_view_R[,,subset_taxon]
} else if(ID_level=="Soleidae"){
  subset_taxon<-which(substr(dimnames(Sin_view_R)[[3]],13,14)=="SO")
  Sin_view_temp<-Sin_view_R[,,subset_taxon]
  subset_taxon<-which(substr(dimnames(Ant_view_R)[[3]],13,14)=="SO")
  Ant_view_temp<-Ant_view_R[,,subset_taxon]
} else if(ID_level=="plaiceflounder"){
  subset_taxon<-which(substr(dimnames(Sin_view_R)[[3]],20,23)=="plta"|substr(dimnames(Sin_view_R)[[3]],20,23)=="fles")
  Sin_view_temp<-Sin_view_R[,,subset_taxon]
  subset_taxon<-which(substr(dimnames(Ant_view_R)[[3]],20,23)=="plta"|substr(dimnames(Ant_view_R)[[3]],20,23)=="fles")
  Ant_view_temp<-Ant_view_R[,,subset_taxon]
}

if(vertebra=="normal"){
  if(vertebra_subset=="N"){
    subset_vertebrae<-which(substr(dimnames(Sin_view_temp)[[3]],11,11)=="N")
    Sin_view_temp_temp<-Sin_view_temp[,,subset_vertebrae]
    subset_vertebrae<-which(substr(dimnames(Ant_view_temp)[[3]],11,11)=="N")
    Ant_view_temp_temp<-Ant_view_temp[,,subset_vertebrae]

    sel_ml_Ant<-c(1,2,3,9,10,11,12,18,19,21,22,24:29)
    sel_ml_Sin<-c(1,2,9,12,13)
    Ant_view<-Ant_view_temp_temp[-sel_ml_Ant,,]
```

```
    if(length(which(Ant_view==-1))>0){
      Ant_view[which(Ant_view==-1)]<-NA
      Ant_view_est<-estimate.missing(Ant_view)
    } else if(length(which(Ant_view==-1))==0){
      Ant_view_est<-(Ant_view)
    }
    Sin_view<-Sin_view_temp_temp[-sel_ml_Sin,,]
    if(length(which(Sin_view==-1,arr.ind = TRUE))>0){
      Sin_view[which(Sin_view==-1,arr.ind = TRUE)]<-NA
      Sin_view_est<-estimate.missing(Sin_view)
    } else if(length(which(Sin_view==-1,arr.ind = TRUE))==0){
      Sin_view_est<-(Sin_view)
    }

  } else if(vertebra_subset=="P"){
    subset_vertebrae<-which(substr(dimnames(Sin_view_temp)[[3]],11,11)=="P")
    Sin_view_temp_temp<-Sin_view_temp[,,subset_vertebrae]
    subset_vertebrae<-which(substr(dimnames(Ant_view_temp)[[3]],11,11)=="P")
    Ant_view_temp_temp<-Ant_view_temp[,,subset_vertebrae]

    sel_ml_Ant<-c(1,2,3,18,19,21,22,24:29)
    sel_ml_Sin<-c(1,2,9)
    Ant_view<-Ant_view_temp_temp[-sel_ml_Ant,,]
    if(length(which(Ant_view==-1,arr.ind = TRUE))>0){
      Ant_view[which(Ant_view==-1,arr.ind = TRUE)]<-NA
      Ant_view_est<-estimate.missing(Ant_view)
    } else if(length(which(Ant_view==-1,arr.ind = TRUE))==0){
      Ant_view_est<-(Ant_view)
    }
    Sin_view<-Sin_view_temp_temp[-sel_ml_Sin,,]
    if(length(which(Sin_view==-1,arr.ind = TRUE))>0){
      Sin_view[which(Sin_view==-1,arr.ind = TRUE)]<-NA
      Sin_view_est<-estimate.missing(Sin_view)
    } else if(length(which(Sin_view==-1,arr.ind = TRUE))==0){
      Sin_view_est<-(Sin_view)
    }

  } else if(vertebra_subset=="C"){
    subset_vertebrae<-which(substr(dimnames(Sin_view_temp)[[3]],11,11)=="C")
    Sin_view_temp_temp<-Sin_view_temp[,,subset_vertebrae]
    subset_vertebrae<-which(substr(dimnames(Ant_view_temp)[[3]],11,11)=="C")
    Ant_view_temp_temp<-Ant_view_temp[,,subset_vertebrae]

    sel_ml_Ant<-c(1,2,3,18,19,21,22,24:29)
    sel_ml_Sin<-c(1,2,9)
    Ant_view<-Ant_view_temp_temp[-sel_ml_Ant,,]
    if(length(which(Ant_view==-1,arr.ind = TRUE))>0){
      Ant_view[which(Ant_view==-1,arr.ind = TRUE)]<-NA
      Ant_view_est<-estimate.missing(Ant_view)
    } else if(length(which(Ant_view==-1,arr.ind = TRUE))==0){
      Ant_view_est<-(Ant_view)
    }
    Sin_view<-Sin_view_temp_temp[-sel_ml_Sin,,]
    if(length(which(Sin_view==-1,arr.ind = TRUE))>0){
      Sin_view[which(Sin_view==-1,arr.ind = TRUE)]<-NA
      Sin_view_est<-estimate.missing(Sin_view)
    } else if(length(which(Sin_view==-1,arr.ind = TRUE))==0){
      Sin_view_est<-(Sin_view)
    }

  }
} else if(vertebra=="atlas"){
  subset_vertebrae<-which(substr(dimnames(Sin_view_temp)[[3]],11,11)=="A")
  Sin_view_temp_temp<-Sin_view_temp[,,subset_vertebrae]
  subset_vertebrae<-which(substr(dimnames(Ant_view_temp)[[3]],11,11)=="A")
  Ant_view_temp_temp<-Ant_view_temp[,,subset_vertebrae]

  sel_ml_Ant<-c(1,13,14,15,16)
  sel_ml_Sin<-c(1,2,3,4,13,14)
```

```
  Ant_view<-Ant_view_temp_temp[-sel_ml_Ant,,]
  if(length(which(Ant_view==-1,arr.ind = TRUE))>0){
  Ant_view[which(Ant_view==-1,arr.ind = TRUE)]<-NA
  Ant_view_est<-estimate.missing(Ant_view)
  } else if(length(which(Ant_view==-1,arr.ind = TRUE))==0){
    Ant_view_est<-(Ant_view)
  }
  Sin_view<-Sin_view_temp_temp[-sel_ml_Sin,,]
  if(length(which(Sin_view==-1,arr.ind = TRUE))>0){
  Sin_view[which(Sin_view==-1,arr.ind = TRUE)]<-NA
  Sin_view_est<-estimate.missing(Sin_view)
  } else if(length(which(Sin_view==-1,arr.ind = TRUE))==0){
    Sin_view_est<-(Sin_view)
  }

  }

# Outlier removal
out_Ant<-procSym(Ant_view_est)
out_Sin<-procSym(Sin_view_est)

dists_ant<-apply(out_Ant$rotated,3,function(x) kendalldist(out_Ant$mshape,x))
qq_ant <- quantile(dists_ant, seq(0, 1, length.out = 4), names = FALSE)
r_ant<-qq_ant[3]+((qq_ant[3]-qq_ant[1])*1.5)
dists_sin<-apply(out_Sin$rotated,3,function(x)kendalldist(out_Sin$mshape,x))
qq_sin <- quantile(dists_sin, seq(0, 1, length.out = 4), names = FALSE)
r_sin<-qq_sin[3]+((qq_sin[3]-qq_sin[1])*1.5)

outliers<-unique(c(which(dists_ant>r_ant),which(dists_sin>r_sin)))

if(length(outliers)>0){
Antview_outlier<-Ant_view_est[,,-outliers]
Sinview_outlier<-Sin_view_est[,,-outliers]
} else if(length(outliers)==0){
Antview_outlier<-Ant_view_est
Sinview_outlier<-Sin_view_est
}

#########################################################
### Description of variation – Principal Component Analysis
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# Colouring and shapes
fam<-substr(dimnames(Antview_outlier)[[3]],13,14)
gen<-as.factor(substr(dimnames(Antview_outlier)[[3]],16,18))
spe<-as.factor(substr(dimnames(Antview_outlier)[[3]],20,23))
vert<-as.factor(substr(dimnames(Antview_outlier)[[3]],11,11))

if(ID_level=="family"){
  col<-as.factor(fam)
  levels(col)<-c("#E6AB02","#E7298A","#1B9E77","#7570B3","#D95F02")
  shape<-as.factor(fam)
  levels(shape)<-c("B","C","P","T","S")
} else if(ID_level=="Pleuronectidae"){
  col<-as.factor(spe)
  levels(col)<-c("#E6AB02","#E7298A","#1B9E77","#7570B3","#D95F02","#A6761D","black")
  shape<-as.factor(spe)
  levels(shape)<-c("C","F","H","K","L","P","O")
} else if(ID_level=="Scophthalmidae"){
  col<-as.factor(spe)
  levels(col)<-c("#E6AB02","#E7298A","#1B9E77","#7570B3","#D95F02")
  shape<-as.factor(spe)
  levels(shape)<-c("B","M","Z","R","W")
} else if(ID_level=="Soleidae"){
  col<-as.factor(spe)
  levels(col)<-c("#E6AB02","#E7298A","#1B9E77","#7570B3")
  shape<-as.factor(spe)
  levels(shape)<-c("D","P","B","S")
} else if(ID_level=="plaiceflounder"){
  col<-as.factor(spe)
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  levels(col)<-c("#E6AB02","#E7298A")
  shape<-as.factor(spe)
  levels(shape)<-c("F","P")
}

# Combine arrays of different views into list with both arrays
listviews<-list("sinistral"=array2list(Antview_outlier),"anterior"=array2list(Sinview_outlier))

pca_comb<-twodviews(listviews, scale = TRUE, vector = c(1:2))
pca_ant<-procSym(Antview_outlier)
pca_sin<-procSym(Sinview_outlier)

# Make final plot using combined view, with convex hulls and legend
par(mfrow=c(2,3))

if(ID_level=="family"){
  plot(pca_comb$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5)
  conv1<-chull(pca_comb$PCscores[fam=="BO",c(1,2)])
  conv2<-chull(pca_comb$PCscores[fam=="CI",c(1,2)])
  conv3<-chull(pca_comb$PCscores[fam=="PL",c(1,2)])
  conv4<-chull(pca_comb$PCscores[fam=="SC",c(1,2)])
  conv5<-chull(pca_comb$PCscores[fam=="SO",c(1,2)])
  points(pca_comb$PCscores[fam=="BO",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="CI",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="PL",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="SC",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="SO",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")

#legend("bottomleft",cex=1.3,legend=c("Pleuronectidae","Scophthalmidae","Bothidae","Soleidae","Citharidae"),fill=unique(as.vector(colfam))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5)
  conv1<-chull(pca_ant$PCscores[fam=="BO",c(1,2)])
  conv2<-chull(pca_ant$PCscores[fam=="CI",c(1,2)])
  conv3<-chull(pca_ant$PCscores[fam=="PL",c(1,2)])
  conv4<-chull(pca_ant$PCscores[fam=="SC",c(1,2)])
  conv5<-chull(pca_ant$PCscores[fam=="SO",c(1,2)])
  points(pca_ant$PCscores[fam=="BO",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="CI",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="PL",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="SC",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="SO",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")

#legend("bottomleft",cex=1.3,legend=c("Pleuronectidae","Scophthalmidae","Bothidae","Soleidae","Citharidae"),fill=unique(as.vector(colfam))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5)
  conv1<-chull(pca_sin$PCscores[fam=="BO",c(1,2)])
  conv2<-chull(pca_sin$PCscores[fam=="CI",c(1,2)])
  conv3<-chull(pca_sin$PCscores[fam=="PL",c(1,2)])
  conv4<-chull(pca_sin$PCscores[fam=="SC",c(1,2)])
  conv5<-chull(pca_sin$PCscores[fam=="SO",c(1,2)])
  points(pca_sin$PCscores[fam=="BO",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="CI",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="PL",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="SC",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="SO",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")

#legend("bottomleft",cex=1.3,legend=c("Pleuronectidae","Scophthalmidae","Bothidae","Soleidae","Citharidae"),fill=unique(as.vector(colfam))) #position of label can switch to top/bottom+left/right

  plot(pca_comb$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5)
  conv1<-chull(pca_comb$PCscores[fam=="BO",c(2,3)])
  conv2<-chull(pca_comb$PCscores[fam=="CI",c(2,3)])
  conv3<-chull(pca_comb$PCscores[fam=="PL",c(2,3)])
  conv4<-chull(pca_comb$PCscores[fam=="SC",c(2,3)])
  conv5<-chull(pca_comb$PCscores[fam=="SO",c(2,3)])
  points(pca_comb$PCscores[fam=="BO",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="CI",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="PL",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
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  points(pca_comb$PCscores[fam=="SC",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[fam=="SO",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")

#legend("bottomleft",cex=1.3,legend=c("Pleuronectidae","Scophthalmidae","Bothidae","Soleidae","Citharidae"),fill=unique(as.ve
ctor(colfam))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5)
  conv1<-chull(pca_ant$PCscores[fam=="BO",c(2,3)])
  conv2<-chull(pca_ant$PCscores[fam=="CI",c(2,3)])
  conv3<-chull(pca_ant$PCscores[fam=="PL",c(2,3)])
  conv4<-chull(pca_ant$PCscores[fam=="SC",c(2,3)])
  conv5<-chull(pca_ant$PCscores[fam=="SO",c(2,3)])
  points(pca_ant$PCscores[fam=="BO",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="CI",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="PL",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="SC",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[fam=="SO",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")

#legend("bottomleft",cex=1.3,legend=c("Pleuronectidae","Scophthalmidae","Bothidae","Soleidae","Citharidae"),fill=unique(as.ve
ctor(colfam))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5)
  conv1<-chull(pca_sin$PCscores[fam=="BO",c(2,3)])
  conv2<-chull(pca_sin$PCscores[fam=="CI",c(2,3)])
  conv3<-chull(pca_sin$PCscores[fam=="PL",c(2,3)])
  conv4<-chull(pca_sin$PCscores[fam=="SC",c(2,3)])
  conv5<-chull(pca_sin$PCscores[fam=="SO",c(2,3)])
  points(pca_sin$PCscores[fam=="BO",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="CI",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="PL",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="SC",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[fam=="SO",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")

#legend("bottomleft",cex=1.3,legend=c("Pleuronectidae","Scophthalmidae","Bothidae","Soleidae","Citharidae"),fill=unique(as.ve
ctor(colfam))) #position of label can switch to top/bottom+left/right
} else if(ID_level=="Pleuronectidae"){
  plot(pca_comb$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-2.8,1.2))
  conv1<-chull(pca_comb$PCscores[spe=="cyno",c(1,2)])
  conv2<-chull(pca_comb$PCscores[spe=="fles",c(1,2)])
  conv3<-chull(pca_comb$PCscores[spe=="hipp",c(1,2)])
  conv4<-chull(pca_comb$PCscores[spe=="kitt",c(1,2)])
  conv5<-chull(pca_comb$PCscores[spe=="lima",c(1,2)])
  conv6<-chull(pca_comb$PCscores[spe=="plta",c(1,2)])
  conv7<-chull(pca_comb$PCscores[spe=="plte",c(1,2)])
  points(pca_comb$PCscores[spe=="cyno",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="fles",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="hipp",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="kitt",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="lima",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="plta",c(1,2)][c(conv6,conv6[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="plte",c(1,2)][c(conv7,conv7[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("G. cynoglossus","P. flesus","H. hippoglossus","M. kitt","L. limanda","P. platessa","H.
hippoglossoides"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.35,0.11))
  conv1<-chull(pca_ant$PCscores[spe=="cyno",c(1,2)])
  conv2<-chull(pca_ant$PCscores[spe=="fles",c(1,2)])
  conv3<-chull(pca_ant$PCscores[spe=="hipp",c(1,2)])
  conv4<-chull(pca_ant$PCscores[spe=="kitt",c(1,2)])
  conv5<-chull(pca_ant$PCscores[spe=="lima",c(1,2)])
  conv6<-chull(pca_ant$PCscores[spe=="plta",c(1,2)])
  conv7<-chull(pca_ant$PCscores[spe=="plte",c(1,2)])
  points(pca_ant$PCscores[spe=="cyno",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="fles",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="hipp",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="kitt",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="lima",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="plta",c(1,2)][c(conv6,conv6[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="plte",c(1,2)][c(conv7,conv7[1]),],lwd=2,type="l")
```

```
  #legend("bottomleft",cex=1.3,legend=c("G. cynoglossus","P. flesus","H. hippoglossus","M. kitt","L. limanda","P. platessa","H.
hippoglossoides"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.45,0.2))
  conv1<-chull(pca_sin$PCscores[spe=="cyno",c(1,2)])
  conv2<-chull(pca_sin$PCscores[spe=="fles",c(1,2)])
  conv3<-chull(pca_sin$PCscores[spe=="hipp",c(1,2)])
  conv4<-chull(pca_sin$PCscores[spe=="kitt",c(1,2)])
  conv5<-chull(pca_sin$PCscores[spe=="lima",c(1,2)])
  conv6<-chull(pca_sin$PCscores[spe=="plta",c(1,2)])
  conv7<-chull(pca_sin$PCscores[spe=="plte",c(1,2)])
  points(pca_sin$PCscores[spe=="cyno",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="fles",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="hipp",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="kitt",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="lima",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="plta",c(1,2)][c(conv6,conv6[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="plte",c(1,2)][c(conv7,conv7[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("G. cynoglossus","P. flesus","H. hippoglossus","M. kitt","L. limanda","P. platessa","H.
hippoglossoides"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_comb$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-
2.8,1.2))
  conv1<-chull(pca_comb$PCscores[spe=="cyno",c(2,3)])
  conv2<-chull(pca_comb$PCscores[spe=="fles",c(2,3)])
  conv3<-chull(pca_comb$PCscores[spe=="hipp",c(2,3)])
  conv4<-chull(pca_comb$PCscores[spe=="kitt",c(2,3)])
  conv5<-chull(pca_comb$PCscores[spe=="lima",c(2,3)])
  conv6<-chull(pca_comb$PCscores[spe=="plta",c(2,3)])
  conv7<-chull(pca_comb$PCscores[spe=="plte",c(2,3)])
  points(pca_comb$PCscores[spe=="cyno",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="fles",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="hipp",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="kitt",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="lima",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="plta",c(2,3)][c(conv6,conv6[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="plte",c(2,3)][c(conv7,conv7[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("G. cynoglossus","P. flesus","H. hippoglossus","M. kitt","L. limanda","P. platessa","H.
hippoglossoides"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.35,0.11))
  conv1<-chull(pca_ant$PCscores[spe=="cyno",c(2,3)])
  conv2<-chull(pca_ant$PCscores[spe=="fles",c(2,3)])
  conv3<-chull(pca_ant$PCscores[spe=="hipp",c(2,3)])
  conv4<-chull(pca_ant$PCscores[spe=="kitt",c(2,3)])
  conv5<-chull(pca_ant$PCscores[spe=="lima",c(2,3)])
  conv6<-chull(pca_ant$PCscores[spe=="plta",c(2,3)])
  conv7<-chull(pca_ant$PCscores[spe=="plte",c(2,3)])
  points(pca_ant$PCscores[spe=="cyno",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="fles",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="hipp",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="kitt",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="lima",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="plta",c(2,3)][c(conv6,conv6[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="plte",c(2,3)][c(conv7,conv7[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("G. cynoglossus","P. flesus","H. hippoglossus","M. kitt","L. limanda","P. platessa","H.
hippoglossoides"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.45,0.2))
  conv1<-chull(pca_sin$PCscores[spe=="cyno",c(2,3)])
  conv2<-chull(pca_sin$PCscores[spe=="fles",c(2,3)])
  conv3<-chull(pca_sin$PCscores[spe=="hipp",c(2,3)])
  conv4<-chull(pca_sin$PCscores[spe=="kitt",c(2,3)])
  conv5<-chull(pca_sin$PCscores[spe=="lima",c(2,3)])
  conv6<-chull(pca_sin$PCscores[spe=="plta",c(2,3)])
  conv7<-chull(pca_sin$PCscores[spe=="plte",c(2,3)])
  points(pca_sin$PCscores[spe=="cyno",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="fles",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="hipp",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="kitt",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
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  points(pca_sin$PCscores[spe=="lima",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="plta",c(2,3)][c(conv6,conv6[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="plte",c(2,3)][c(conv7,conv7[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("G. cynoglossus","P. flesus","H. hippoglossus","M. kitt","L. limanda","P. platessa","H.
hippoglossoides"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right
} else if(ID_level=="Scophthalmidae"){
  plot(pca_comb$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-2,1.2))
  conv1<-chull(pca_comb$PCscores[spe=="bosc",c(1,2)])
  conv2<-chull(pca_comb$PCscores[spe=="maxi",c(1,2)])
  conv3<-chull(pca_comb$PCscores[spe=="regi",c(1,2)])
  conv4<-chull(pca_comb$PCscores[spe=="rhom",c(1,2)])
  conv5<-chull(pca_comb$PCscores[spe=="whif",c(1,2)])
  conv6<-chull(pca_comb$PCscores[spe=="punc",c(1,2)])
  points(pca_comb$PCscores[spe=="bosc",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="maxi",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="regi",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="rhom",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="whif",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="punc",c(1,2)][c(conv6,conv6[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("L. boscii","S. maximus","Z. punctatus","Z. regius","S. rhombus","L.
whiffiagonis"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.29,0.12))
  conv1<-chull(pca_ant$PCscores[spe=="bosc",c(1,2)])
  conv2<-chull(pca_ant$PCscores[spe=="maxi",c(1,2)])
  conv3<-chull(pca_ant$PCscores[spe=="regi",c(1,2)])
  conv4<-chull(pca_ant$PCscores[spe=="rhom",c(1,2)])
  conv5<-chull(pca_ant$PCscores[spe=="whif",c(1,2)])
  conv6<-chull(pca_ant$PCscores[spe=="punc",c(1,2)])
  points(pca_ant$PCscores[spe=="bosc",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="maxi",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="regi",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="rhom",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="whif",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="punc",c(1,2)][c(conv6,conv6[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("L. boscii","S. maximus","Z. punctatus","Z. regius","S. rhombus","L.
whiffiagonis"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.41,0.28))
  conv1<-chull(pca_sin$PCscores[spe=="bosc",c(1,2)])
  conv2<-chull(pca_sin$PCscores[spe=="maxi",c(1,2)])
  conv3<-chull(pca_sin$PCscores[spe=="regi",c(1,2)])
  conv4<-chull(pca_sin$PCscores[spe=="rhom",c(1,2)])
  conv5<-chull(pca_sin$PCscores[spe=="whif",c(1,2)])
  conv6<-chull(pca_sin$PCscores[spe=="punc",c(1,2)])
  points(pca_sin$PCscores[spe=="bosc",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="maxi",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="regi",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="rhom",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="whif",c(1,2)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="punc",c(1,2)][c(conv6,conv6[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("L. boscii","S. maximus","Z. punctatus","Z. regius","S. rhombus","L.
whiffiagonis"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_comb$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-2,1.2))
  conv1<-chull(pca_comb$PCscores[spe=="bosc",c(2,3)])
  conv2<-chull(pca_comb$PCscores[spe=="maxi",c(2,3)])
  conv3<-chull(pca_comb$PCscores[spe=="regi",c(2,3)])
  conv4<-chull(pca_comb$PCscores[spe=="rhom",c(2,3)])
  conv5<-chull(pca_comb$PCscores[spe=="whif",c(2,3)])
  conv6<-chull(pca_comb$PCscores[spe=="punc",c(2,3)])
  points(pca_comb$PCscores[spe=="bosc",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="maxi",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="regi",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="rhom",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="whif",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="punc",c(2,3)][c(conv6,conv6[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("L. boscii","S. maximus","Z. punctatus","Z. regius","S. rhombus","L.
whiffiagonis"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right
```

```
  plot(pca_ant$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.29,0.12))
  conv1<-chull(pca_ant$PCscores[spe=="bosc",c(2,3)])
  conv2<-chull(pca_ant$PCscores[spe=="maxi",c(2,3)])
  conv3<-chull(pca_ant$PCscores[spe=="regi",c(2,3)])
  conv4<-chull(pca_ant$PCscores[spe=="rhom",c(2,3)])
  conv5<-chull(pca_ant$PCscores[spe=="whif",c(2,3)])
  conv6<-chull(pca_ant$PCscores[spe=="punc",c(2,3)])
  points(pca_ant$PCscores[spe=="bosc",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="maxi",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="regi",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="rhom",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="whif",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="punc",c(2,3)][c(conv6,conv6[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("L. boscii","S. maximus","Z. punctatus","Z. regius","S. rhombus","L. whiffiagonis"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.41,0.28))
  conv1<-chull(pca_sin$PCscores[spe=="bosc",c(2,3)])
  conv2<-chull(pca_sin$PCscores[spe=="maxi",c(2,3)])
  conv3<-chull(pca_sin$PCscores[spe=="regi",c(2,3)])
  conv4<-chull(pca_sin$PCscores[spe=="rhom",c(2,3)])
  conv5<-chull(pca_sin$PCscores[spe=="whif",c(2,3)])
  conv6<-chull(pca_sin$PCscores[spe=="punc",c(2,3)])
  points(pca_sin$PCscores[spe=="bosc",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="maxi",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="regi",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="rhom",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="whif",c(2,3)][c(conv5,conv5[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="punc",c(2,3)][c(conv6,conv6[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("L. boscii","S. maximus","Z. punctatus","Z. regius","S. rhombus","L. whiffiagonis"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right
} else if(ID_level=="Soleidae"){
  plot(pca_comb$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-1.5,1))
  conv1<-chull(pca_comb$PCscores[spe=="hexo",c(1,2)])
  conv2<-chull(pca_comb$PCscores[spe=="lasc",c(1,2)])
  conv3<-chull(pca_comb$PCscores[spe=="lute",c(1,2)])
  conv4<-chull(pca_comb$PCscores[spe=="sole",c(1,2)])
  points(pca_comb$PCscores[spe=="hexo",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="lasc",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="lute",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="sole",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("D. hexophthalma","P. lascaris","B. luteum","S. solea"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-0.25,0.18))
  conv1<-chull(pca_ant$PCscores[spe=="hexo",c(1,2)])
  conv2<-chull(pca_ant$PCscores[spe=="lasc",c(1,2)])
  conv3<-chull(pca_ant$PCscores[spe=="lute",c(1,2)])
  conv4<-chull(pca_ant$PCscores[spe=="sole",c(1,2)])
  points(pca_ant$PCscores[spe=="hexo",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="lasc",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="lute",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="sole",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("D. hexophthalma","P. lascaris","B. luteum","S. solea"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.25,0.18))
  conv1<-chull(pca_sin$PCscores[spe=="hexo",c(1,2)])
  conv2<-chull(pca_sin$PCscores[spe=="lasc",c(1,2)])
  conv3<-chull(pca_sin$PCscores[spe=="lute",c(1,2)])
  conv4<-chull(pca_sin$PCscores[spe=="sole",c(1,2)])
  points(pca_sin$PCscores[spe=="hexo",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="lasc",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="lute",c(1,2)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="sole",c(1,2)][c(conv4,conv4[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("D. hexophthalma","P. lascaris","B. luteum","S. solea"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right
```

```
  plot(pca_comb$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-1.5,1))
  conv1<-chull(pca_comb$PCscores[spe=="hexo",c(2,3)])
  conv2<-chull(pca_comb$PCscores[spe=="lasc",c(2,3)])
  conv3<-chull(pca_comb$PCscores[spe=="lute",c(2,3)])
  conv4<-chull(pca_comb$PCscores[spe=="sole",c(2,3)])
  points(pca_comb$PCscores[spe=="hexo",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="lasc",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="lute",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="sole",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("D. hexophthalma","P. lascaris","B. luteum","S.
solea"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_ant$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5, xlim=c(-
0.25,0.18))
  conv1<-chull(pca_ant$PCscores[spe=="hexo",c(2,3)])
  conv2<-chull(pca_ant$PCscores[spe=="lasc",c(2,3)])
  conv3<-chull(pca_ant$PCscores[spe=="lute",c(2,3)])
  conv4<-chull(pca_ant$PCscores[spe=="sole",c(2,3)])
  points(pca_ant$PCscores[spe=="hexo",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="lasc",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="lute",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="sole",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("D. hexophthalma","P. lascaris","B. luteum","S.
solea"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right

  plot(pca_sin$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.25,0.18))
  conv1<-chull(pca_sin$PCscores[spe=="hexo",c(2,3)])
  conv2<-chull(pca_sin$PCscores[spe=="lasc",c(2,3)])
  conv3<-chull(pca_sin$PCscores[spe=="lute",c(2,3)])
  conv4<-chull(pca_sin$PCscores[spe=="sole",c(2,3)])
  points(pca_sin$PCscores[spe=="hexo",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="lasc",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="lute",c(2,3)][c(conv3,conv3[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="sole",c(2,3)][c(conv4,conv4[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("D. hexophthalma","P. lascaris","B. luteum","S.
solea"),fill=unique(as.vector(levels(col)))) #position of label can switch to top/bottom+left/right
} else if(ID_level=="plaiceflounder"){
  plot(pca_comb$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-1.3,1))
  conv1<-chull(pca_comb$PCscores[spe=="fles",c(1,2)])
  conv2<-chull(pca_comb$PCscores[spe=="plta",c(1,2)])
  points(pca_comb$PCscores[spe=="fles",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="plta",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("P. flesus","P. platessa"),fill=unique(as.vector(levels(col)))) #position of label can
switch to top/bottom+left/right

  plot(pca_ant$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.2,0.15))
  conv1<-chull(pca_ant$PCscores[spe=="fles",c(1,2)])
  conv2<-chull(pca_ant$PCscores[spe=="plta",c(1,2)])
  points(pca_ant$PCscores[spe=="fles",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="plta",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("P. flesus","P. platessa"),fill=unique(as.vector(levels(col)))) #position of label can
switch to top/bottom+left/right

  plot(pca_sin$PCscores,asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.18,0.12))
  conv1<-chull(pca_sin$PCscores[spe=="fles",c(1,2)])
  conv2<-chull(pca_sin$PCscores[spe=="plta",c(1,2)])
  points(pca_sin$PCscores[spe=="fles",c(1,2)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="plta",c(1,2)][c(conv2,conv2[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("P. flesus","P. platessa"),fill=unique(as.vector(levels(col)))) #position of label can
switch to top/bottom+left/right

  plot(pca_comb$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-1.3,1))
  conv1<-chull(pca_comb$PCscores[spe=="fles",c(2,3)])
  conv2<-chull(pca_comb$PCscores[spe=="plta",c(2,3)])
  points(pca_comb$PCscores[spe=="fles",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_comb$PCscores[spe=="plta",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("P. flesus","P. platessa"),fill=unique(as.vector(levels(col)))) #position of label can
switch to top/bottom+left/right

  plot(pca_ant$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.2,0.15))
```

```
  conv1<-chull(pca_ant$PCscores[spe=="fles",c(2,3)])
  conv2<-chull(pca_ant$PCscores[spe=="plta",c(2,3)])
  points(pca_ant$PCscores[spe=="fles",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_ant$PCscores[spe=="plta",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("P. flesus","P. platessa"),fill=unique(as.vector(levels(col)))) #position of label can
switch to top/bottom+left/right

  plot(pca_sin$PCscores[,2:3],asp=1,col=as.vector(col),pch=as.vector(shape),cex=2,cex.lab=2,cex.axis=1.5,xlim=c(-0.18,0.12))
  conv1<-chull(pca_sin$PCscores[spe=="fles",c(2,3)])
  conv2<-chull(pca_sin$PCscores[spe=="plta",c(2,3)])
  points(pca_sin$PCscores[spe=="fles",c(2,3)][c(conv1,conv1[1]),],lwd=2,type="l")
  points(pca_sin$PCscores[spe=="plta",c(2,3)][c(conv2,conv2[1]),],lwd=2,type="l")
  #legend("bottomleft",cex=1.3,legend=c("P. flesus","P. platessa"),fill=unique(as.vector(levels(col)))) #position of label can
switch to top/bottom+left/right
}

#Describe variation caused by each axis
pca_comb$Variance
pca_ant$Variance
pca_sin$Variance

# Wireframes deformation grids
SVc_PC1min_A<-twodvarshape(pca_comb,min(pca_comb$PCscores[,1]),1,1)
SVc_PC1max_A<-twodvarshape(pca_comb,max(pca_comb$PCscores[,1]),1,1)
SVc_PC2min_A<-twodvarshape(pca_comb,min(pca_comb$PCscores[,2]),2,1)
SVc_PC2max_A<-twodvarshape(pca_comb,max(pca_comb$PCscores[,2]),2,1)
SVc_PC1min_S<-twodvarshape(pca_comb,min(pca_comb$PCscores[,1]),1,2)
SVc_PC1max_S<-twodvarshape(pca_comb,max(pca_comb$PCscores[,1]),1,2)
SVc_PC2min_S<-twodvarshape(pca_comb,min(pca_comb$PCscores[,2]),2,2)
SVc_PC2max_S<-twodvarshape(pca_comb,max(pca_comb$PCscores[,2]),2,2)

if(vertebra_subset=="A"){
  wireframe_ant =
list(c(1,2),c(1,3),c(1,4),c(1,5),c(2,4),c(2,5),c(3,4),c(3,5),c(6,7),c(8,9),c(4,10),c(5,11),c(6,10),c(9,11),c(2,12),c(7,2),c(8,2))
  wireframe_sin = list(c(1,2),c(1,3),c(2,4),c(3,4),c(7,8),c(5,6),c(2,6),c(1,5),c(1,7))
} else if(vertebra_subset=="N"){
  wireframe_ant =
list(c(1,2),c(1,3),c(1,4),c(1,5),c(2,4),c(2,5),c(3,4),c(3,5),c(6,7),c(6,11),c(7,11),c(8,9),c(8,12),c(9,12),c(11,10),c(12,10),c(2,7),c(4,6
),c(8,2),c(9,5),c(2,10))
  wireframe_sin = list(c(1,2),c(1,3),c(2,3),c(4,5),c(4,6),c(5,6),c(6,7),c(7,8),c(1,6),c(3,4))
} else if(vertebra_subset=="P"){
  wireframe_ant =
list(c(1,2),c(1,3),c(1,4),c(1,5),c(2,4),c(2,5),c(3,4),c(3,5),c(6,7),c(8,9),c(4,6),c(3,7),c(3,8),c(5,9),c(10,11),c(10,15),c(11,15),c(12,16
),c(13,16),c(12,13),c(2,14),c(10,4),c(11,2),c(12,2),c(5,13))
  wireframe_sin = list(c(1,2),c(2,3),c(4,5),c(5,6),c(7,8),c(6,7),c(8,10),c(9,10),c(1,9),c(6,10),c(3,4))
} else if(vertebra_subset=="C"){
  wireframe_ant =
list(c(1,2),c(1,3),c(1,4),c(1,5),c(2,4),c(2,5),c(3,4),c(3,5),c(6,7),c(8,9),c(4,6),c(3,7),c(3,8),c(5,9),c(10,11),c(10,15),c(11,15),c(12,16
),c(13,16),c(12,13),c(2,14),c(10,4),c(11,2),c(12,2),c(5,13))
  wireframe_sin = list(c(1,2),c(2,3),c(4,5),c(5,6),c(7,8),c(6,7),c(8,10),c(9,10),c(1,9),c(6,10),c(3,4))
}

par(mfrow=c(2,2))
deformGrid2d(SVc_PC1min_A,SVc_PC1max_A,lines = TRUE,wireframe =
wireframe_ant,lwd=3,col1="#1B9E77",col2="#D95F02")
deformGrid2d(SVc_PC2min_A,SVc_PC2max_A,lines = TRUE,wireframe =
wireframe_ant,lwd=3,col1="#1B9E77",col2="#D95F02")
deformGrid2d(SVc_PC1min_S,SVc_PC1max_S,lines = TRUE,wireframe =
wireframe_sin,lwd=3,col1="#1B9E77",col2="#D95F02")
deformGrid2d(SVc_PC2min_S,SVc_PC2max_S,lines = TRUE,wireframe =
wireframe_sin,lwd=3,col1="#1B9E77",col2="#D95F02")

#######################################################
### Classification test - Linear Discriminant Analysis
#######################################################

# Function LDA
LDA_perm<-function(array1,array2=NULL,group,trainperc=0.7,varperc=99,perm=100){

  Accs<-NULL
```

```
  for(j in 1:perm){
    print(j)
    train_perc<-trainperc
    training_ids_pos<-NULL
    for(i in 1:nlevels(group)){
      sel_i<-which(as.vector(group)==levels(group)[[i]])
      sel_id<-sample(sel_i,(length(sel_i)*train_perc))
      training_ids_pos<-c(training_ids_pos,sel_id)
    }
    '%!in%' <- function(x,y)!('%in%'(x,y))
    training_ids_pos<-sort(training_ids_pos)
    testing_ids_pos<-which(c(1:length(as.vector(group)))%!in%training_ids_pos)


    trainset<-array1[,,training_ids_pos]
    testset<-array1[,,testing_ids_pos]
    testgro<-as.vector(group[training_ids_pos])

    if(!is.null(array2)){
      trainset2<-array2[,,training_ids_pos]
      testset2<-array2[,,testing_ids_pos]
    }

    if(is.null(array2)){
      PCA<-procSym(trainset)
      matref<-vecx(PCA$rotated)
      PCAref<-prcomp(matref,scale=FALSE,center = TRUE)
      PCscores<-PCAref$x
      colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
      eigv<-PCAref$sdev^2
      Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100
    }

    if(!is.null(array2)){
      gpa1<-procSym(trainset)
      gpa2<-procSym(trainset2)
      fact1<-sqrt(dim(gpa1$mshape)[1] * dim(gpa1$mshape)[2])
      fact2<-sqrt(dim(gpa2$mshape)[1] * dim(gpa2$mshape)[2])
      mat1<-vecx(gpa1$rotated)*fact1
      mat2<-vecx(gpa2$rotated)*fact2
      PCArefcomb<-prcomp(cbind(mat1,mat2),scale. = FALSE)
      PCscores<-PCArefcomb$x
      # plot(PCscores,pch=19,col=as.factor(group))
      colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
      eigv<-PCArefcomb$sdev^2
      Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100
    }
    boottrain<-data.frame(testgro,PCscores)
    colnames(boottrain)[1]<-"group"
    thr<-varperc
    form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                                  paste("PC",length(which(Variance[,3]<thr)),sep=""))))
    da=train(form,data=boottrain,method="lda")

    if(is.null(array2)){
      cootar<-t(apply(testset,3,function(x) rotonmat(x,x,PCA$mshape,scale=TRUE)))
      var_tar<-as.vector(group[testing_ids_pos])
      PCscores_tar<- predict(PCAref, newdata=cootar)
      colnames(PCscores_tar)<-paste("PC",1:dim(PCscores_tar)[2],sep="")
      trains_tar<-data.frame(var_tar,PCscores_tar)
      colnames(trains_tar)[1]<-"group"
      pred_tar<-predict(da,newdata=trains_tar)
      res_tar<-table(var_tar,pred_tar)
      accuracy_tar<-round(sum(diag(res_tar))/sum(res_tar),2)
    }

    if(!is.null(array2)){
      cootar1<-t(apply(testset,3,function(x) rotonmat(x,x,gpa1$mshape,scale=TRUE)))*fact1
      cootar2<-t(apply(testset2,3,function(x) rotonmat(x,x,gpa2$mshape,scale=TRUE)))*fact2
```

```
      var_tar<-as.vector(group[testing_ids_pos])
      PCscores_tar<- predict(PCArefcomb, newdata=cbind(cootar1,cootar2))
      colnames(PCscores_tar)<-paste("PC",1:dim(PCscores_tar)[2],sep="")
      trains_tar<-data.frame(var_tar,PCscores_tar)
      colnames(trains_tar)[1]<-"group"
      pred_tar<-predict(da,newdata=trains_tar)
      res_tar<-table(var_tar,pred_tar)
      accuracy_tar<-round(sum(diag(res_tar))/sum(res_tar),2)
    }

    Accs[j]<-accuracy_tar
  }

  return(Accs)

}

#Removing species from dataset
species_ex_sin<-
which(substr(dimnames(Sinview_outlier)[[3]],20,23)=="bosc"|substr(dimnames(Sinview_outlier)[[3]],20,23)=="punc"|substr(dimnames(Sinview_outlier)[[3]],20,23)=="regi"|substr(dimnames(Sinview_outlier)[[3]],20,23)=="lute"|substr(dimnames(Sinview_outlier)[[3]],20,23)=="hexo") #13,14 for family level; 16,18 for genus; 20,23 for species
species_ex_ant<-
which(substr(dimnames(Antview_outlier)[[3]],20,23)=="bosc"|substr(dimnames(Antview_outlier)[[3]],20,23)=="punc"|substr(dimnames(Antview_outlier)[[3]],20,23)=="regi"|substr(dimnames(Antview_outlier)[[3]],20,23)=="lute"|substr(dimnames(Antview_outlier)[[3]],20,23)=="hexo") #13,14 for family level; 16,18 for genus; 20,23 for species
if(length(species_ex_sin)>0){
Sinview_LDA<-Sinview_outlier[,,-species_ex_sin]
Antview_LDA<-Antview_outlier[,,-species_ex_ant]
} else if(length(species_ex_sin)==0){
  Sinview_LDA<-Sinview_outlier
  Antview_LDA<-Antview_outlier
}

##LDA
if(ID_level=="family"){
  fam<-substr(dimnames(Antview_LDA)[[3]],13,14)
  onlyAnt<-LDA_perm(array1=Antview_LDA,array2=NULL,group=as.factor(fam),perm=100)
  onlySin<-LDA_perm(array1=Sinview_LDA,array2=NULL,group=as.factor(fam),perm=100)
  AntSin<-LDA_perm(array1=Antview_LDA,array2=Sinview_LDA,group=as.factor(fam),perm=100)
} else {
  spe<-as.factor(substr(dimnames(Antview_LDA)[[3]],20,23))
  onlyAnt<-LDA_perm(array1=Antview_LDA,array2=NULL,group=as.factor(spe),perm=100)
  onlySin<-LDA_perm(array1=Sinview_LDA,array2=NULL,group=as.factor(spe),perm=100)
  AntSin<-LDA_perm(array1=Antview_LDA,array2=Sinview_LDA,group=as.factor(spe),perm=100)
}

boxplot(onlyAnt,onlySin,AntSin,names=c("Ant","Sin","Comb"))

mean(onlyAnt)
sd(onlyAnt)
mean(onlySin)
sd(onlySin)
mean(AntSin)
sd(AntSin)
```

Archaeological dataset (identification)

```
# Packages needed
library(geomorph)
library(Morpho)
library(caret)
library(MASS)
library(Arothron)
library(stringr)
library(e1071)
library(geometry)

# Data formatting: All TPS files need to follow this built-up of the name of the file; if not certain parts of the code should be changed to match the names of the files
# "xxxx_yyyy_V_FA_gen_spec.TPS" with x=unique file number; y=sample number; FA=family code; gen= genus code; spec=species code

# LM numbers:
 # Anterior all
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
  # LM in text: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17       18       19 20 21 22 23 24 25
 # Anterior atlas
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
  # LM in text: 1 2 3 4 5 6 7 8 9 10 11 12            13
 # Sinistral all
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13
  # LM in text: 1 2 3 4 5 6 7 8    9 10 11 12
 # Sinistral atlas
  # LM in TPS:  1 2 3 4 5 6 7 8 9 10 11 12 13 14
  # LM in text: 1       2 3 4 5 6  7  8  9

# Coding:
 # Vertebra type
  # N cervical; P precaudal, C caudal
 # Family
  # PL Pleuronectidae; SC Scophthalmidae; SO Soleidae
 # Genus
  # ple Pleuronectes; pla Platichthys; gly Glyptocephalus; hip Hippoglossus; hpe Hippoglossoides; mic Microstomus; lim Limanda;
  # sco Scophthalmus; zeu Zeugopterus; lep Lepidorhombus;
  # sol Solea; buglossidium; dic Dicologlossa;
  # cit Citharus; arn Arnoglossus
 # Species
  # plta platessa; fles flesus; cyno cynoglossus; hipp hippoglossus; plte platessoides; kitt kitt; lima limanda
  # maxi maximus; rhom rhombus; regi regius; punc punctatus; bosc boscii; whif whiffiagonis
  # sole solea; lasc lascaris; lute luteum; hexo hexophthalma
  # ling linguatula; late laterna

#######################

# Setting: These are to be changed

vertebra<-"normal"           # Choose vertebra type: normal or atlas
site<-"BSG"                  # Choose archaeological site: BSG (Barreau Saint-George) or COP (Coppergate)#

#######################

# Set selection
if(vertebra=="normal"){
  landmark_ant_nr<-29
  landmark_sin_nr<-13
  anterior_ref_file<-"Reference_anterior"
  sinistral_ref_file<-"Reference_sinistral"
  sel_ml_Ant<-c(1,2,3,18,19,21,22,24:29)
  sel_ml_Sin<-c(1,2,9)
} else if(vertebra=="atlas"){
  anterior_ref_file<-"Reference_anterior_atlas"
  sinistral_ref_file<-"Reference_sinistral_atlas"
  landmark_ant_nr<-17
```

```
  landmark_sin_nr<-14
  sel_ml_Ant<-c(1,13,14,15,16)
  sel_ml_Sin<-c(1,2,3,4,13,14)
}
length_ref_folder<-length(list.files(anterior_ref_file))
anterior_ref_file_cut<-print(paste0(anterior_ref_file,"/"))
sinistral_ref_file_cut<-print(paste0(sinistral_ref_file,"/"))

# Create empty arrays for archaelogical and reference sample
Sin_view_R<-array(NA,dim=c(landmark_sin_nr,2,length_ref_folder))
Ant_view_R<-array(NA,dim=c(landmark_ant_nr,2,length_ref_folder))
dimnames(Ant_view_R)[[3]]<-list.files(anterior_ref_file_cut)
dimnames(Sin_view_R)[[3]]<-list.files(sinistral_ref_file_cut)

# Fill the arrays
for(i in 1:length_ref_folder){
  path_ant_R<-paste(anterior_ref_file_cut,list.files(anterior_ref_file)[i],sep="")
  Ant_view_R[,,i]<-readallTPS(path_ant_R)$LM[[1]]

  path_sin_R<-paste(sinistral_ref_file_cut,list.files(sinistral_ref_file)[i],sep="")
  Sin_view_R[,,i]<-readallTPS(path_sin_R)$LM[[1]]
}

# Rearrange both arrays for reference and archaeological set so they match per sample
sel_ref_match<-match(substr(dimnames(Sin_view_R)[[3]],6,9),substr(dimnames(Ant_view_R)[[3]],6,9))
Ant_view_R<-Ant_view_R[,,sel_ref_match]

# Select landmarks
Ant_view<-Ant_view_R[-sel_ml_Ant,,]
Ant_view[which(Ant_view==-1,arr.ind = TRUE)]<-NA
Ant_view_est<-estimate.missing(Ant_view)
Sin_view<-Sin_view_R[-sel_ml_Sin,,]
Sin_view[which(Sin_view==-1,arr.ind = TRUE)]<-NA
Sin_view_est<-estimate.missing(Sin_view)
out_Ant<-procSym(Ant_view_est)
out_Sin<-procSym(Sin_view_est)

# If outliers
dists_ant<-apply(out_Ant$rotated,3,function(x) kendalldist(out_Ant$mshape,x))
qq_ant <- quantile(dists_ant, seq(0, 1, length.out = 4), names = FALSE)
r_ant<-qq_ant[3]+((qq_ant[3]-qq_ant[1])*1.5)
dists_sin<-apply(out_Sin$rotated,3,function(x)kendalldist(out_Sin$mshape,x))
qq_sin <- quantile(dists_sin, seq(0, 1, length.out = 4), names = FALSE)
r_sin<-qq_sin[3]+((qq_sin[3]-qq_sin[1])*1.5)
outliers<-unique(c(which(dists_ant>r_ant),which(dists_sin>r_sin)))
Antview_REF_outlier<-Ant_view_est[,,-outliers]
Sinview_REF_outlier<-Sin_view_est[,,-outliers]

# Removing species from dataset
species_ex_sin<-
which(substr(dimnames(Sinview_REF_outlier)[[3]],20,23)=="bosc"|substr(dimnames(Sinview_REF_outlier)[[3]],20,23)=="punc"|
substr(dimnames(Sinview_REF_outlier)[[3]],20,23)=="regi"|substr(dimnames(Sinview_REF_outlier)[[3]],20,23)=="lute"|substr(di
mnames(Sinview_REF_outlier)[[3]],20,23)=="hexo") #13,14 for family level; 16,18 for genus; 20,23 for species
Sinview_REF_outlier<-Sinview_REF_outlier[,,-species_ex_sin]
species_ex_ant<-
which(substr(dimnames(Antview_REF_outlier)[[3]],20,23)=="bosc"|substr(dimnames(Antview_REF_outlier)[[3]],20,23)=="punc"|
substr(dimnames(Antview_REF_outlier)[[3]],20,23)=="regi"|substr(dimnames(Antview_REF_outlier)[[3]],20,23)=="lute"|substr(di
mnames(Antview_REF_outlier)[[3]],20,23)=="hexo") #13,14 for family level; 16,18 for genus; 20,23 for species
Antview_REF_outlier<-Antview_REF_outlier[,,-species_ex_ant]

# Array for Archaeological samples
if(vertebra=="normal"){
  if(site=="COP"){
    anterior_arch_file<-"COP_anterior"
    sinistral_arch_file<-"COP_sinistral"
    folder_length<-49
  } else if(site=="BSG"){
    anterior_arch_file<-"BSG_anterior"
    sinistral_arch_file<-"BSG_sinistral"
    folder_length<-53
```

```
  }
  sel_ml_Ant_A<-c(1,2,3,18,19,21,22,24:29)
  sel_ml_Sin_A<-c(1,2,9)
  Sin_view_A<-array(NA,dim=c(13,2,folder_length))
  Ant_view_A<-array(NA,dim=c(29,2,folder_length))
} else if(vertebra=="atlas"){
    if(site=="COP"){
    anterior_arch_file<-"COP_anterior_atlas"
    sinistral_arch_file<-"COP_sinistral_atlas"
    folder_length<-0
    } else if(site=="BSG"){
    anterior_arch_file<-"BSG_anterior_atlas"
    sinistral_arch_file<-"BSG_sinistral_atlas"
    folder_length<-8
    }
  Sin_view_A<-array(NA,dim=c(14,2,folder_length))
  Ant_view_A<-array(NA,dim=c(17,2,folder_length))
  sel_ml_Ant_A<-c(1,13,14,15,16)
  sel_ml_Sin_A<-c(1,2,3,4,13,14)
}

anterior_arch_file_cut<-print(paste0(anterior_arch_file,"/"))
sinistral_arch_file_cut<-print(paste0(sinistral_arch_file,"/"))
dimnames(Ant_view_A)[[3]]<-list.files(anterior_arch_file_cut)
dimnames(Sin_view_A)[[3]]<-list.files(sinistral_arch_file_cut)

for(i in 1:folder_length){
  path_sin_A<-paste(sinistral_arch_file_cut,list.files(sinistral_arch_file)[i],sep="")
  Sin_view_A[,,i]<-readallTPS(path_sin_A)$LM[[1]]
}

for(i in 1:folder_length){
  path_ant_A<-paste(anterior_arch_file_cut,list.files(anterior_arch_file)[i],sep="")
  Ant_view_A[,,i]<-readallTPS(path_ant_A)$LM[[1]]
}

sel_arch_match<-match(substr(dimnames(Sin_view_A)[[3]],6,9),substr(dimnames(Ant_view_A)[[3]],6,9))
Ant_view_A<-Ant_view_A[,,sel_arch_match]

#select landmarks archaeological
Ant_view_A_est<-Ant_view_A[-sel_ml_Ant_A,,]
Sin_view_A_est<-Sin_view_A[-sel_ml_Sin_A,,]

sample<-substr(list.files(sinistral_arch_file),20,23)

#create empty tables
result_tax_ant<-data.frame(sample=sample,family=NA,probfam=NA,genus=NA,probgen=NA,LMused=NA)
result_tax_sin<-data.frame(sample=sample,family=NA,probfam=NA,genus=NA,probgen=NA,LMused=NA)
result_tax_com<-data.frame(sample=sample,family=NA,probfam=NA,genus=NA,probgen=NA,LMused=NA)

#Run identification of archaeological dataset anterior
for(j in 1:folder_length){
  #load the specimen j
  Ant_A_J_temp<-Ant_view_A_est[,,j]
  print(j)

  #Vertebra type
  Ant_R_vert_type<-which(substr(dimnames(Antview_REF_outlier)[[3]],11,11)==substr(list.files(anterior_arch_file)[j],11,11))
  Ant_view_R_temp<-Antview_REF_outlier[,,Ant_R_vert_type]
  vert_type<-substr(list.files(anterior_arch_file)[j],11,11)
  fam<-substr(list.files("Reference_anterior"),13,14)[Ant_R_vert_type]

  #Family level
  #Missing landmarks
  if(vert_type=="N"){
    sel_ml_ant<-c(6,7,8,9,which(Ant_A_J_temp[,1]==-1))
    LM_set_ant<-as.vector(1:16)
  } else {
    sel_ml_ant<-c(which(Ant_A_J_temp[,1]==-1))
    LM_set_ant<-as.vector(1:16)
```

```
  }

  if(length(sel_ml_ant)>0){
    Ant_A_J<-Ant_A_J_temp[-sel_ml_ant,]
    Ant_view_R_J<-Ant_view_R_temp[-sel_ml_ant,,]
    LM_used_ant<-LM_set_ant[-sel_ml_ant]
  } else {
    Ant_A_J<-Ant_A_J_temp
    Ant_view_R_J<-Ant_view_R_temp
    LM_used_ant<-LM_set_ant
  }

  #unique array with archaeological specimen and reference sample
  all_specs<-bindArr(Ant_A_J,Ant_view_R_J,along=3)
  fam<-substr(dimnames(Ant_view_R_J)[[3]],13,14)
  group<-c("ArchSam",fam) #change fam,gen,spe of reference group

  gpa<-procSym(all_specs)

  train<-data.frame(group[-1],gpa$PCscores[-1,])
  colnames(train)[1]<-"group"

  matref<-vecx(gpa$rotated)
  gparef<-prcomp(matref,scale=FALSE,center = TRUE)
  PCscores<-gparef$x
  colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
  eigv<-gparef$sdev^2
  Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100

  thr<-99
  form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                        paste("PC",length(which(Variance[,3]<thr)),sep=""))))


  da=train(form,data=train,method="lda")



  #we create a table only for the archaeological specimen
  tobe_fam<-t(gpa$PCscores[1,])
  colnames(tobe_fam)
  #we predict its taxonomy
  pred_fam<-predict(da,newdata =tobe_fam,type = "prob")

  Class_fam<-names(which.max(pred_fam))
  Prob_fam<-max(pred_fam)

  result_tax_ant[j,2]<-Class_fam
  result_tax_ant[j,3]<-Prob_fam


  #Species level
  if (Class_fam=="BO"|Class_fam=="CI"){
    Class_spe<-"NA"
    Prob_spe<-"NA"
  } else {

    Ant_R_gen<-
which(substr(dimnames(Antview_REF_outlier)[[3]],13,14)==Class_fam&substr(dimnames(Antview_REF_outlier)[[3]],11,11)==s
ubstr(list.files(anterior_arch_file)[j],11,11))
    Ant_view_R_gen_temp<-Antview_REF_outlier[,,Ant_R_gen]
    spe<-substr(dimnames(Antview_REF_outlier)[[3]],20,23)[Ant_R_gen]

    #Missing landmarks
    if(vert_type=="N"){
      sel_ml_ant<-c(6,7,8,9,which(Ant_A_J_temp[,1]==-1))
      LM_set_ant<-as.vector(1:16)
    } else {
      sel_ml_ant<-c(which(Ant_A_J_temp[,1]==-1))
```

```
      LM_set_ant<-as.vector(1:16)
    }

    if(length(sel_ml_ant)>0){
      Ant_A_J<-Ant_A_J_temp[-sel_ml_ant,]
      Ant_view_R_J<-Ant_view_R_gen_temp[-sel_ml_ant,,]
    } else {
      Ant_A_J<-Ant_A_J_temp
      Ant_view_R_J<-Ant_view_R_gen_temp
    }

    #unique array with archeological specimen and reference sample
    all_specs<-bindArr(Ant_A_J,Ant_view_R_J[,,],along=3)
    group<-c("ArchSam",spe)

    gpa<-procSym(all_specs)

    train<-data.frame(group[-1],gpa$PCscores[-1,])
    colnames(train)[1]<-"group"

    matref<-vecx(gpa$rotated)
    gparef<-prcomp(matref,scale=FALSE,center = TRUE)
    PCscores<-gparef$x
    colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
    eigv<-gparef$sdev^2
    Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100

    thr<-99
    form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                                  paste("PC",length(which(Variance[,3]<thr)),sep=""))))


    da=train(form,data=train,method="lda")
    #we create a table only for the archaeological specimen
    tobe_fam<-t(gpa$PCscores[1,])
    colnames(tobe_fam)
    #we predict its taxonomy
    pred_spe<-predict(da,newdata =tobe_fam,type = "prob")

    Class_spe<-names(which.max(pred_spe))
    Prob_spe<-max(pred_spe)

    result_tax_ant[j,4]<-Class_spe
    result_tax_ant[j,5]<-Prob_spe

    #result_tax_ant[j,6]<-toString(LM_used_ant) Doesnt work because we remove LMs in beginning and nrs are mixed up
  }
}
result_tax_ant

#Run identification of archaeological dataset sinistral
for(j in 1:folder_length){
  #load the specimen j
  Sin_A_J_temp<-Sin_view_A_est[,,j]
  print(j)

  #Vertebra type
  Sin_R_vert_type<-which(substr(dimnames(Sinview_REF_outlier)[[3]],11,11)==substr(list.files(sinistral_arch_file)[j],11,11))
  Sin_view_R_temp<-Sinview_REF_outlier[,,Sin_R_vert_type]
  vert_type<-substr(list.files(sinistral_arch_file)[j],11,11)
  fam<-substr(list.files("Reference_sinistral"),13,14)[Sin_R_vert_type]

  #Family level
  #Missing landmarks
  if(vert_type=="N"){
    sel_ml_sin<-c(6,7,8,9,which(Sin_A_J_temp[,1]==-1))
    LM_set_sin<-as.vector(1:16)
  } else {
    sel_ml_sin<-c(which(Sin_A_J_temp[,1]==-1))
```

```
  LM_set_sin<-as.vector(1:16)
 }

 if(length(sel_ml_sin)>0){
  Sin_A_J<-Sin_A_J_temp[-sel_ml_sin,]
  Sin_view_R_J<-Sin_view_R_temp[-sel_ml_sin,,]
  LM_used_sin<-LM_set_sin[-sel_ml_sin]
 } else {
  Sin_A_J<-Sin_A_J_temp
  Sin_view_R_J<-Sin_view_R_temp
  LM_used_sin<-LM_set_sin
 }

 #unique array with archaeological specimen and reference sample
 all_specs<-bindArr(Sin_A_J,Sin_view_R_J,along=3)
 fam<-substr(dimnames(Sin_view_R_J)[[3]],13,14)
 group<-c("ArchSam",fam) #change fam,gen,spe of reference group

 gpa<-procSym(all_specs)

 train<-data.frame(group[-1],gpa$PCscores[-1,])
 colnames(train)[1]<-"group"

 matref<-vecx(gpa$rotated)
 gparef<-prcomp(matref,scale=FALSE,center = TRUE)
 PCscores<-gparef$x
 colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
 eigv<-gparef$sdev^2
 Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100

 thr<-99
 form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                paste("PC",length(which(Variance[,3]<thr)),sep=""))))


 da=train(form,data=train,method="lda")
 #we create a table only for the archaeological specimen
 tobe_fam<-t(gpa$PCscores[1,])
 colnames(tobe_fam)
 #we predict its taxonomy
 pred_fam<-predict(da,newdata =tobe_fam,type = "prob")

 Class_fam<-names(which.max(pred_fam))
 Prob_fam<-max(pred_fam)

 result_tax_sin[j,2]<-Class_fam
 result_tax_sin[j,3]<-Prob_fam



 #Species level
 if (Class_fam=="BO"|Class_fam=="CI"){
  Class_spe<-"NA"
  Prob_spe<-"NA"
 } else {

  Sin_R_gen<-
which(substr(dimnames(Sinview_REF_outlier)[[3]],13,14)==Class_fam&substr(dimnames(Sinview_REF_outlier)[[3]],11,11)==s
ubstr(list.files(sinistral_arch_file)[j],11,11))
  Sin_view_R_gen_temp<-Sinview_REF_outlier[,,Sin_R_gen]
  spe<-substr(dimnames(Sinview_REF_outlier)[[3]],20,23)[Sin_R_gen]

  #Missing landmarks
  if(vert_type=="N"){
   sel_ml_sin<-c(6,7,8,9,which(Sin_A_J_temp[,1]==-1))
   LM_set_sin<-as.vector(1:16)
  } else {
   sel_ml_sin<-c(which(Sin_A_J_temp[,1]==-1))
   LM_set_sin<-as.vector(1:16)
```

```
    }
    if(length(sel_ml_sin)>0){
      Sin_A_J<-Sin_A_J_temp[-sel_ml_sin,]
      Sin_view_R_J<-Sin_view_R_gen_temp[-sel_ml_sin,,]
    } else {
      Sin_A_J<-Sin_A_J_temp
      Sin_view_R_J<-Sin_view_R_gen_temp
    }

    #unique array with archeological specimen and reference sample
    all_specs<-bindArr(Sin_A_J,Sin_view_R_J[,,],along=3)
    group<-c("ArchSam",spe)

    gpa<-procSym(all_specs)

    train<-data.frame(group[-1],gpa$PCscores[-1,])
    colnames(train)[1]<-"group"

    matref<-vecx(gpa$rotated)
    gparef<-prcomp(matref,scale=FALSE,center = TRUE)
    PCscores<-gparef$x
    colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
    eigv<-gparef$sdev^2
    Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100

    thr<-99
    form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                                  paste("PC",length(which(Variance[,3]<thr)),sep=""))))


    da=train(form,data=train,method="lda")
    #we create a table only for the archaeological specimen
    tobe_fam<-t(gpa$PCscores[1,])
    colnames(tobe_fam)
    #we predict its taxonomy
    pred_spe<-predict(da,newdata =tobe_fam,type = "prob")

    Class_spe<-names(which.max(pred_spe))
    Prob_spe<-max(pred_spe)

    result_tax_sin[j,4]<-Class_spe
    result_tax_sin[j,5]<-Prob_spe

    #result_tax_ant[j,6]<-toString(LM_used_ant) Doesnt work because we remove LMs in beginning and nrs are mixed up
  }
}
result_tax_sin

#Run identification of archaeological dataset combined
for(j in 1:folder_length){
  #load the specimen j
  Sin_A_J_temp<-Sin_view_A_est[,,j]
  Ant_A_J_temp<-Ant_view_A_est[,,j]
  print(j)

  #Vertebra type
  Ant_R_vert_type<-which(substr(dimnames(Antview_REF_outlier)[[3]],11,11)==substr(list.files(anterior_arch_file)[j],11,11))
  Ant_view_R_temp<-Antview_REF_outlier[,,Ant_R_vert_type]

  Sin_R_vert_type<-which(substr(dimnames(Sinview_REF_outlier)[[3]],11,11)==substr(list.files(sinistral_arch_file)[j],11,11))
  Sin_view_R_temp<-Sinview_REF_outlier[,,Sin_R_vert_type]

  vert_type<-substr(list.files(sinistral_arch_file)[j],11,11)

  #Family level
  #Missing landmarks
  if(vert_type=="N"){
    sel_ml_sin<-c(6,7,8,9,which(Sin_A_J_temp[,1]==-1))
    LM_set_sin<-as.vector(1:16)
```

```
  } else {
    sel_ml_sin<-c(which(Sin_A_J_temp[,1]==-1))
    LM_set_sin<-as.vector(1:16)
  }

  if(vert_type=="N"){
    sel_ml_ant<-c(6,7,8,9,which(Ant_A_J_temp[,1]==-1))
    LM_set_ant<-as.vector(1:16)
  } else {
    sel_ml_ant<-c(which(Ant_A_J_temp[,1]==-1))
    LM_set_ant<-as.vector(1:16)
  }

  if(length(sel_ml_sin)>0){
    Sin_A_J<-Sin_A_J_temp[-sel_ml_sin,]
    Sin_view_R_J<-Sin_view_R_temp[-sel_ml_sin,,]
    LM_used_sin<-LM_set_sin[-sel_ml_sin]
  } else {
    Sin_A_J<-Sin_A_J_temp
    Sin_view_R_J<-Sin_view_R_temp
    LM_used_sin<-LM_set_sin
  }

  if(length(sel_ml_ant)>0){
    Ant_A_J<-Ant_A_J_temp[-sel_ml_ant,]
    Ant_view_R_J<-Ant_view_R_temp[-sel_ml_ant,,]
    LM_used_ant<-LM_set_ant[-sel_ml_ant]
  } else {
    Ant_A_J<-Ant_A_J_temp
    Ant_view_R_J<-Ant_view_R_temp
    LM_used_ant<-LM_set_ant
  }

  #unique array with archaeological specimen and reference sample
  all_specs_sin<-bindArr(Sin_A_J,Sin_view_R_J,along=3)
  all_specs_ant<-bindArr(Ant_A_J,Ant_view_R_J,along=3)

  fam<-substr(dimnames(Sin_view_R_J)[[3]],13,14)
  group<-c("ArchSam",fam) #change fam,gen,spe of reference group

  listviews<-list("sinistral"=array2list(all_specs_sin),"anterior"=array2list(all_specs_ant))

  gpa_sin<-procSym(all_specs_sin)
  gpa_ant<-procSym(all_specs_ant)
  fact1<-sqrt(dim(gpa_sin$mshape)[1] * dim(gpa_sin$mshape)[2])
  fact2<-sqrt(dim(gpa_ant$mshape)[1] * dim(gpa_ant$mshape)[2])
  mat1<-vecx(gpa_sin$rotated)*fact1
  mat2<-vecx(gpa_ant$rotated)*fact2
  PCArefcomb<-prcomp(cbind(mat1,mat2),scale. = FALSE)
  PCscores<-PCArefcomb$x
  # plot(PCscores,pch=19,col=as.factor(group))
  colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
  eigv<-PCArefcomb$sdev^2
  Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100

  train<-data.frame(group[-1],PCscores[-1,])
  colnames(train)[1]<-"group"
  thr<-99
  form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                              paste("PC",length(which(Variance[,3]<thr)),sep=""))))

  da=train(form,data=train,method="lda")
  #we create a table only for the archaeological specimen
  pca_comb<-twodviews(listviews, scale = TRUE, vector = c(1:2))

  tobe_fam<-t(pca_comb$PCscores[1,])
  colnames(tobe_fam)
  #we predict its taxonomy
  pred_fam<-predict(da,newdata =tobe_fam,type = "prob")
```

```
  Class_fam<-names(which.max(pred_fam))
  Prob_fam<-max(pred_fam)

  result_tax_com[j,2]<-Class_fam
  result_tax_com[j,3]<-Prob_fam



  #Species level
  if (Class_fam=="BO"|Class_fam=="CI"){
    Class_spe<-"NA"
    Prob_spe<-"NA"
  } else {

    Sin_R_gen<-which(substr(dimnames(Sinview_REF_outlier)[[3]],13,14)==Class_fam&substr(dimnames(Sinview_REF_outlier)[[3]],11,11)==substr(list.files(sinistral_arch_file)[j],11,11))
    Sin_view_R_gen_temp<-Sinview_REF_outlier[,,Sin_R_gen]

    Ant_R_gen<-which(substr(dimnames(Antview_REF_outlier)[[3]],13,14)==Class_fam&substr(dimnames(Antview_REF_outlier)[[3]],11,11)==substr(list.files(anterior_arch_file)[j],11,11))
    Ant_view_R_gen_temp<-Antview_REF_outlier[,,Sin_R_gen]

    #spe<-substr(dimnames(Sinview_REF_outlier)[[3]],20,23)[Sin_R_gen]

    #Missing landmarks
    if(vert_type=="N"){
      sel_ml_sin<-c(6,7,8,9,which(Sin_A_J_temp[,1]==-1))
      LM_set_sin<-as.vector(1:16)
    } else {
      sel_ml_sin<-c(which(Sin_A_J_temp[,1]==-1))
      LM_set_sin<-as.vector(1:16)
    }

    if(vert_type=="N"){
      sel_ml_ant<-c(6,7,8,9,which(Ant_A_J_temp[,1]==-1))
      LM_set_ant<-as.vector(1:16)
    } else {
      sel_ml_ant<-c(which(Ant_A_J_temp[,1]==-1))
      LM_set_ant<-as.vector(1:16)
    }

    if(length(sel_ml_sin)>0){
      Sin_A_J<-Sin_A_J_temp[-sel_ml_sin,]
      Sin_view_R_J<-Sin_view_R_gen_temp[-sel_ml_sin,,]
    } else {
      Sin_A_J<-Sin_A_J_temp
      Sin_view_R_J<-Sin_view_R_gen_temp
    }

    if(length(sel_ml_ant)>0){
      Ant_A_J<-Ant_A_J_temp[-sel_ml_ant,]
      Ant_view_R_J<-Ant_view_R_gen_temp[-sel_ml_ant,,]
    } else {
      Ant_A_J<-Ant_A_J_temp
      Ant_view_R_J<-Ant_view_R_gen_temp
    }

    #unique array with archeological specimen and reference sample
    all_specs_sin<-bindArr(Sin_A_J,Sin_view_R_J,along=3)
    all_specs_ant<-bindArr(Ant_A_J,Ant_view_R_J,along=3)

    spe<-substr(dimnames(Sin_view_R_J)[[3]],20,23)
    group<-c("ArchSam",spe) #change fam,gen,spe of reference group

    listviews<-list("sinistral"=array2list(all_specs_sin),"anterior"=array2list(all_specs_ant))

    gpa_sin<-procSym(all_specs_sin)
```

```
    gpa_ant<-procSym(all_specs_ant)
    fact1<-sqrt(dim(gpa_sin$mshape)[1] * dim(gpa_sin$mshape)[2])
    fact2<-sqrt(dim(gpa_ant$mshape)[1] * dim(gpa_ant$mshape)[2])
    mat1<-vecx(gpa_sin$rotated)*fact1
    mat2<-vecx(gpa_ant$rotated)*fact2
    PCArefcomb<-prcomp(cbind(mat1,mat2),scale. = FALSE)
    PCscores<-PCArefcomb$x
    # plot(PCscores,pch=19,col=as.factor(group))
    colnames(PCscores)<-paste("PC",1:dim(PCscores)[2],sep="")
    eigv<-PCArefcomb$sdev^2
    Variance <- cbind(sqrt(eigv), eigv/sum(eigv), cumsum(eigv)/sum(eigv)) * 100

    train<-data.frame(group[-1],PCscores[-1,])
    colnames(train)[1]<-"group"
    thr<-99
    form= as.formula(c("group~",c(paste(paste("PC",(which(Variance[,3]<thr)[1:(length(which(Variance[,3]<thr))-
1)]),sep=""),"+",sep=""),
                              paste("PC",length(which(Variance[,3]<thr)),sep=""))))

    da=train(form,data=train,method="lda")
    #we create a table only for the archaeological specimen
    pca_comb<-twodviews(listviews, scale = TRUE, vector = c(1:2))

    tobe_fam<-t(pca_comb$PCscores[1,])
    colnames(tobe_fam)
    #we predict its taxonomy
    pred_spe<-predict(da,newdata =tobe_fam,type = "prob")

    Class_spe<-names(which.max(pred_spe))
    Prob_spe<-max(pred_spe)

    result_tax_com[j,4]<-Class_spe
    result_tax_com[j,5]<-Prob_spe

  }
}
result_tax_com
```

Appendix D – Chapter 5. Peptide mass fingerprinting of preserved collagen in archaeological fish bones for identification of flatfish in European waters

Part D1. Peptide mass fingerprints of species

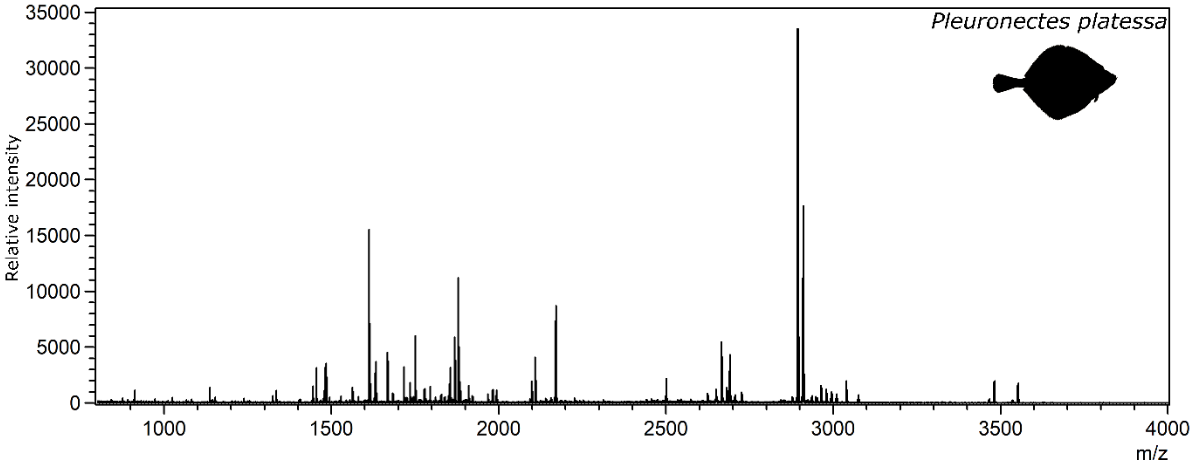

Figure D1. Collagen fingerprint of modern *Pleuronectes platessa* (RBINS 23806).

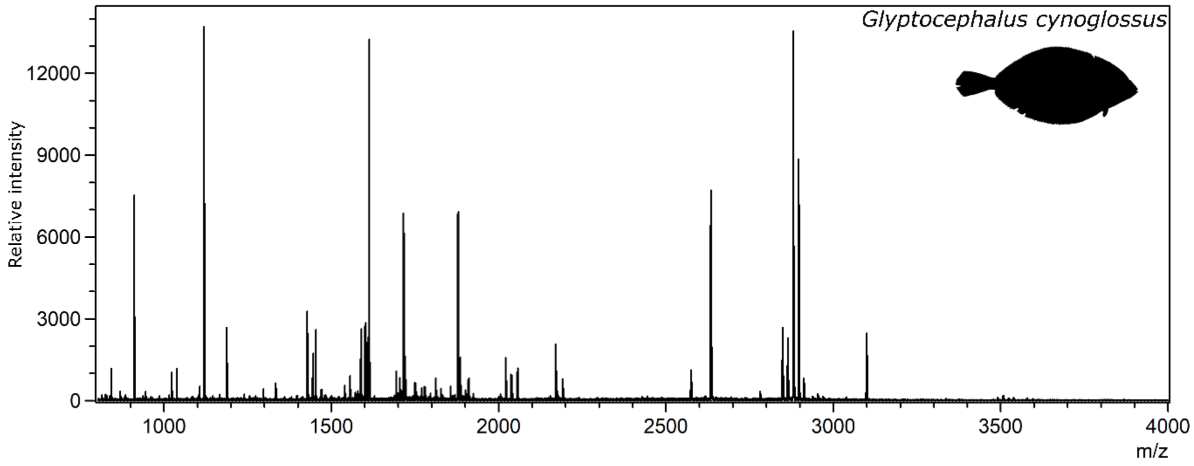

Figure D2. Collagen fingerprint of modern *Glyptocephalus cynoglossus* (RBINS DCB359).

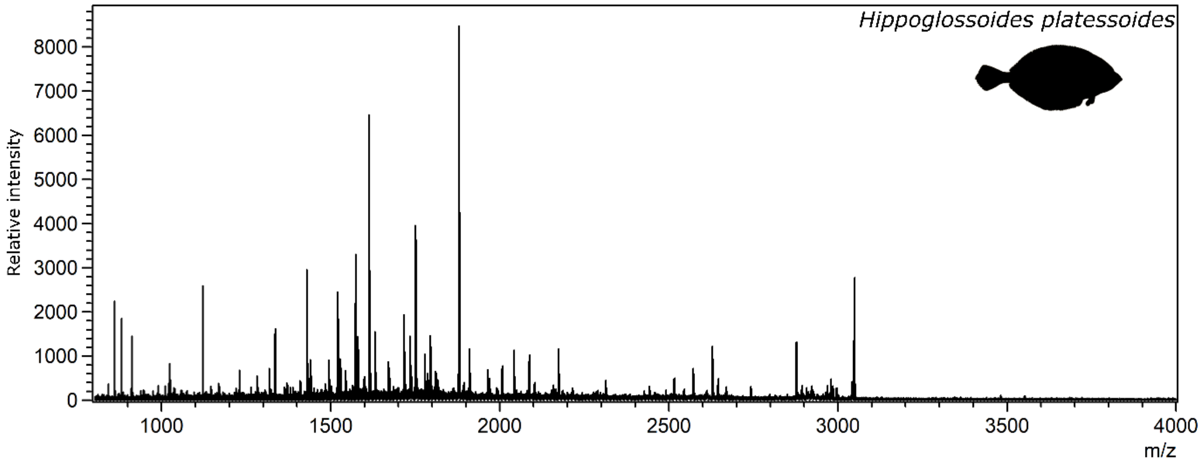

Figure D3. Collagen fingerprint of modern *Hippoglossoides platessoides* (RBINS 91-017-P-142).

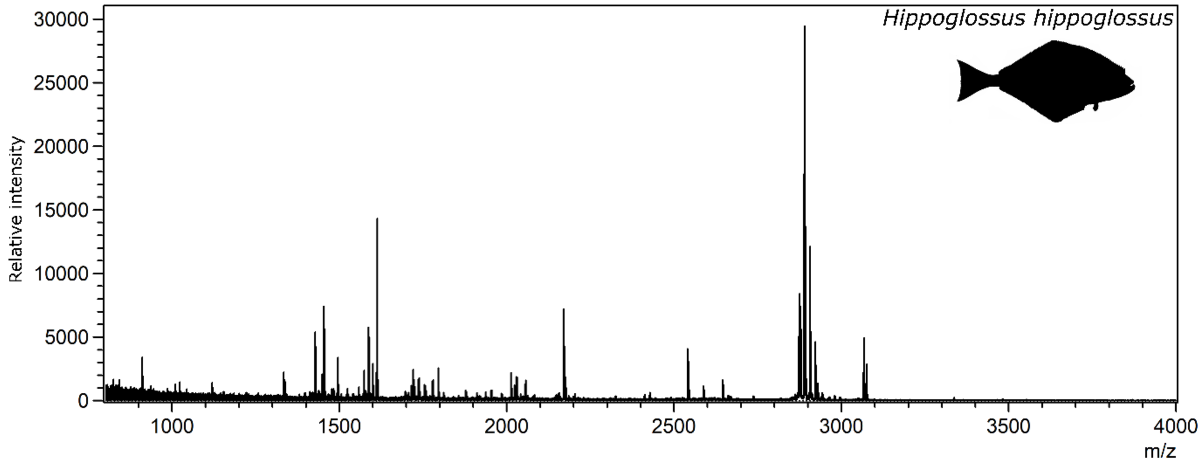

Figure D4. Collagen fingerprint of modern *Hippoglossus hippoglossus* (RBINS 91-017-P-2).

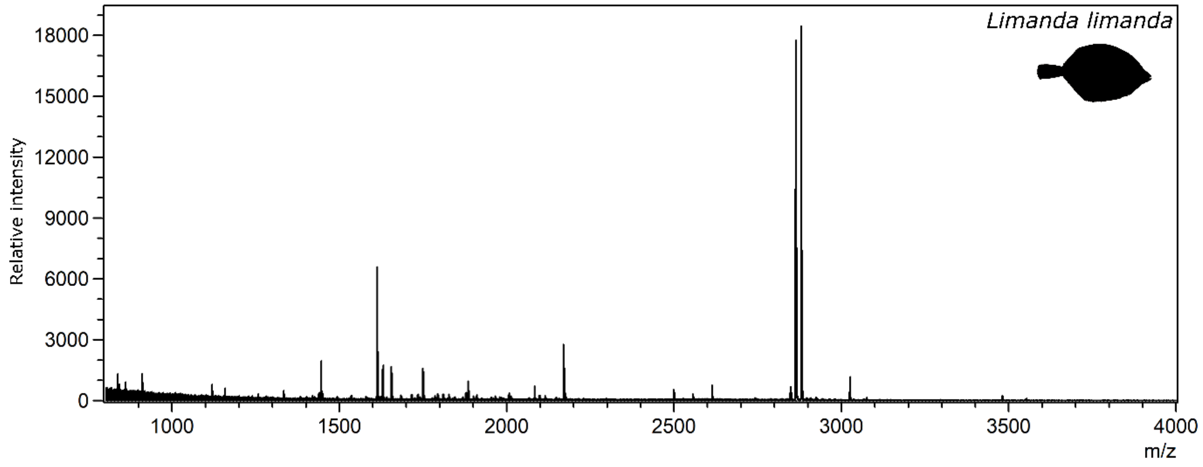

Figure D5. Collagen fingerprint of modern *Limanda limanda* (RBINS A4-002-P-0061).

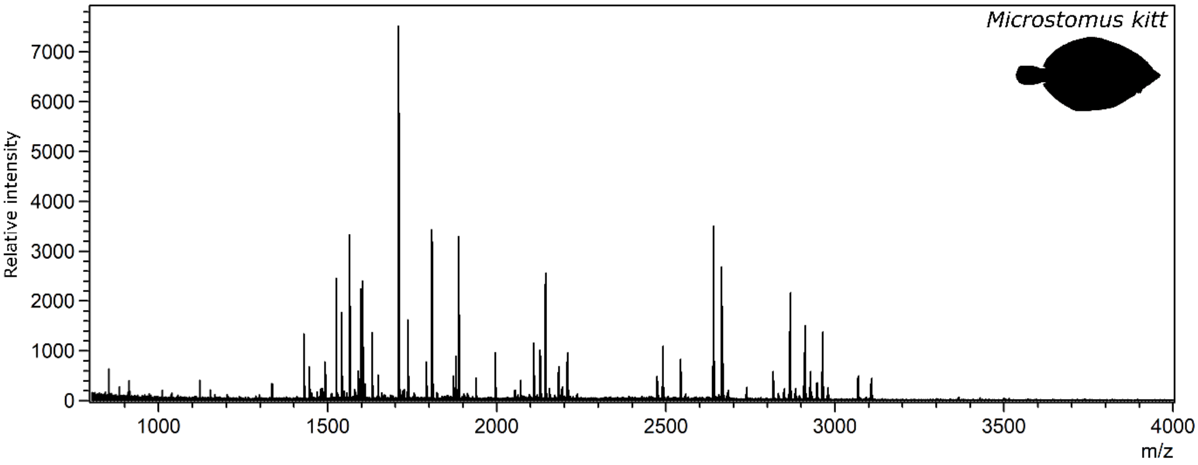

Figure D6. Collagen fingerprint of modern *Microstomus kitt* (YZL 1963).

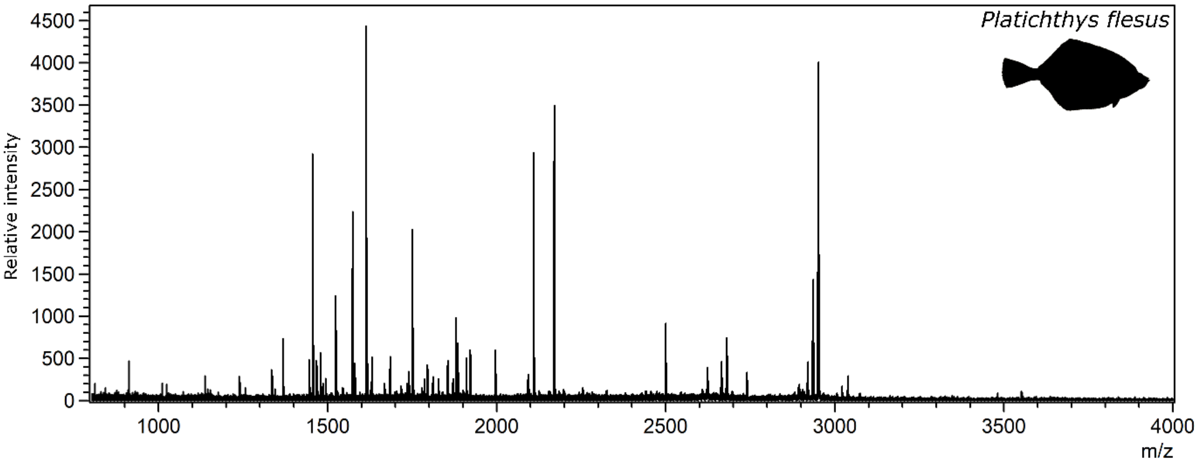

Figure D7. Collagen fingerprint of modern *Platichthys flesus* (RBINS A4-001-P-36).

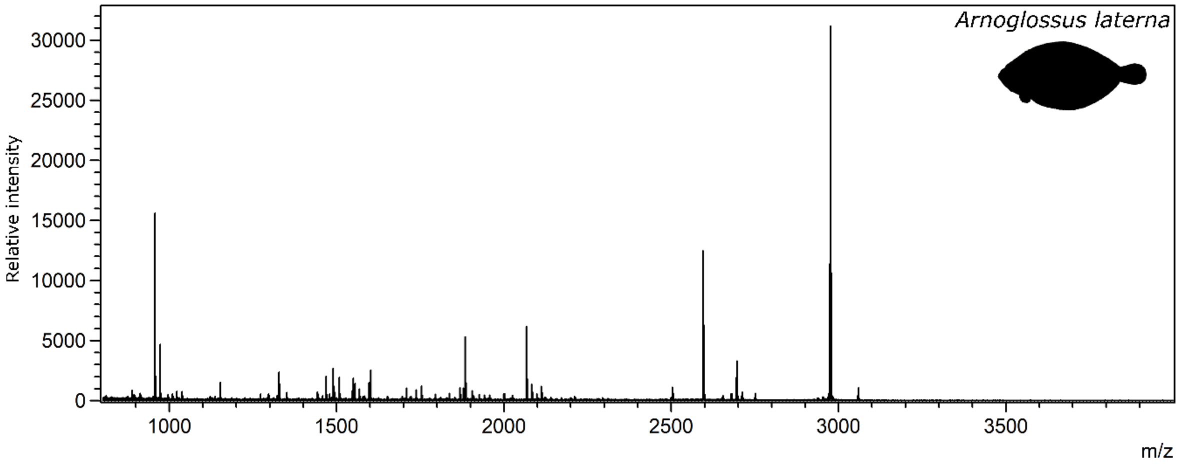

Figure D8. Collagen fingerprint of modern *Arnoglossus laterna* (RBINS A2-038-P-18).

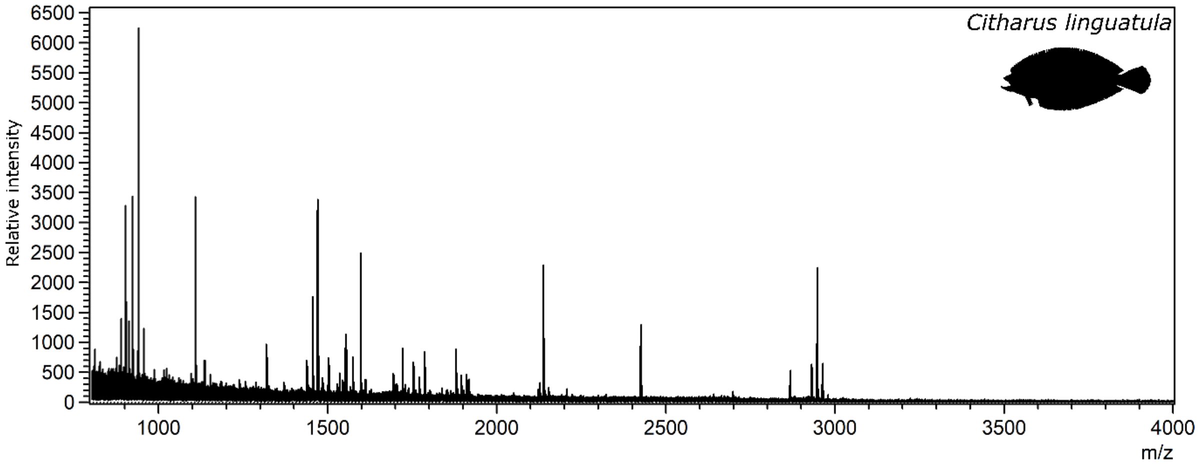

Figure D9. Collagen fingerprint of modern *Citharus linguatula* (RBINS 24631).

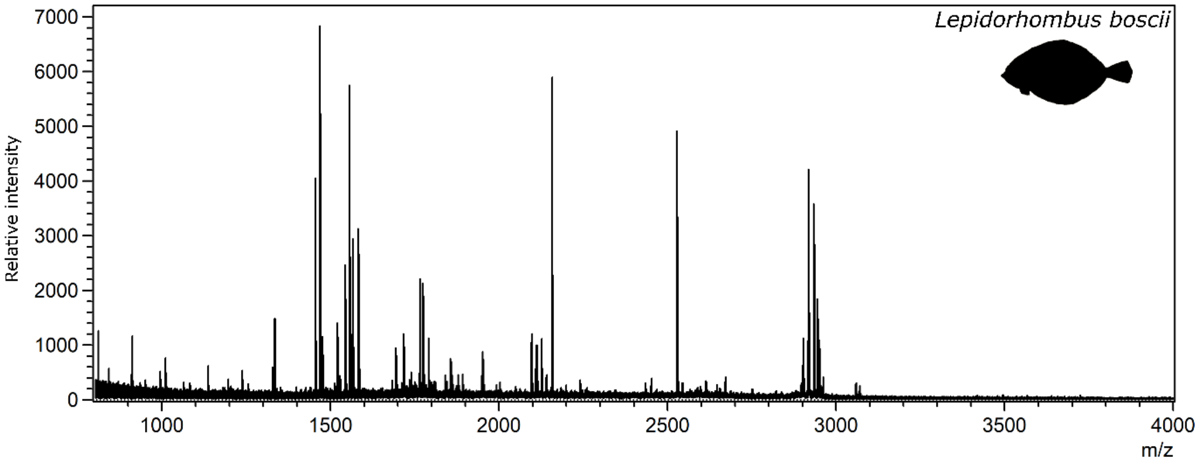

Figure D10. Collagen fingerprint of modern *Lepidorhombus boscii* (RBINS DCB773).

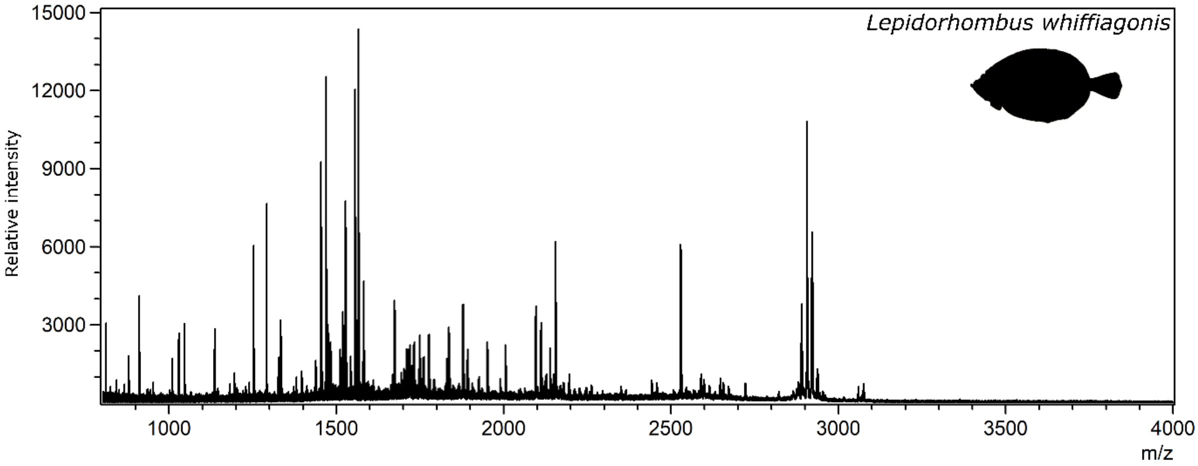

Figure D11. Collagen fingerprint of modern *Lepidorhombus whiffiagonis* (RBINS 91-017-P-14).

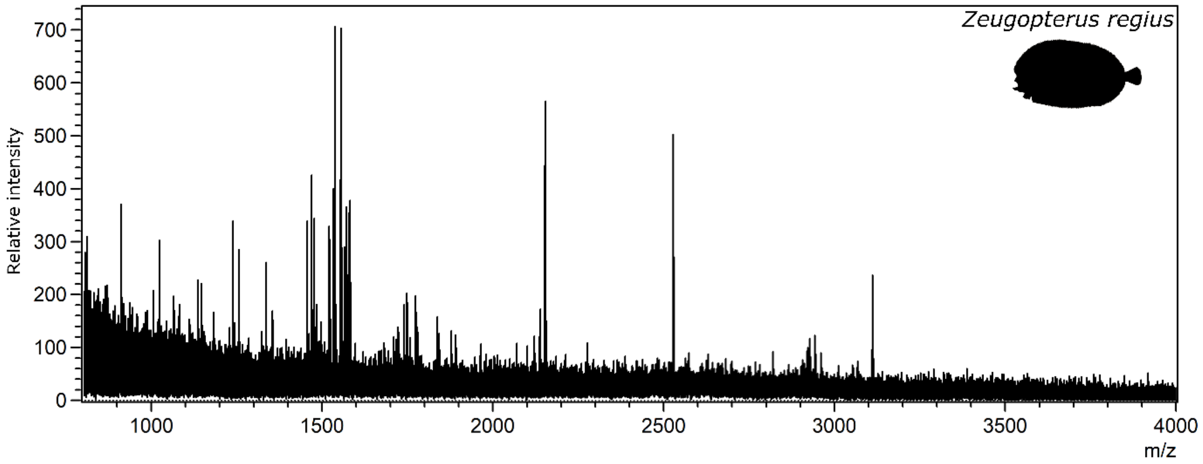

Figure D12. Collagen fingerprint of modern *Zeugopterus regius* (RBINS A2-019-P-0030).

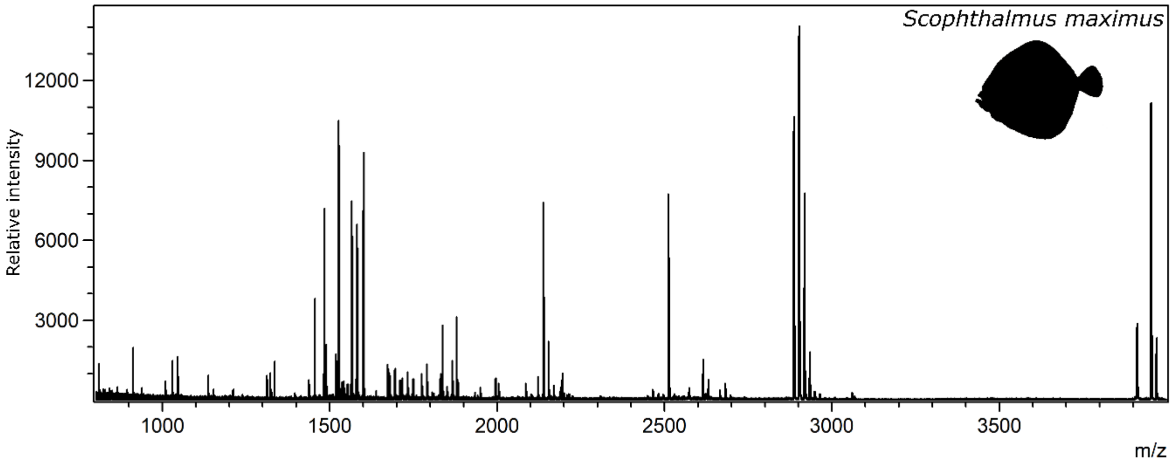

Figure D13. Collagen fingerprint of modern *Scophthalmus maximus* (RBINS A2-052-P-0012).

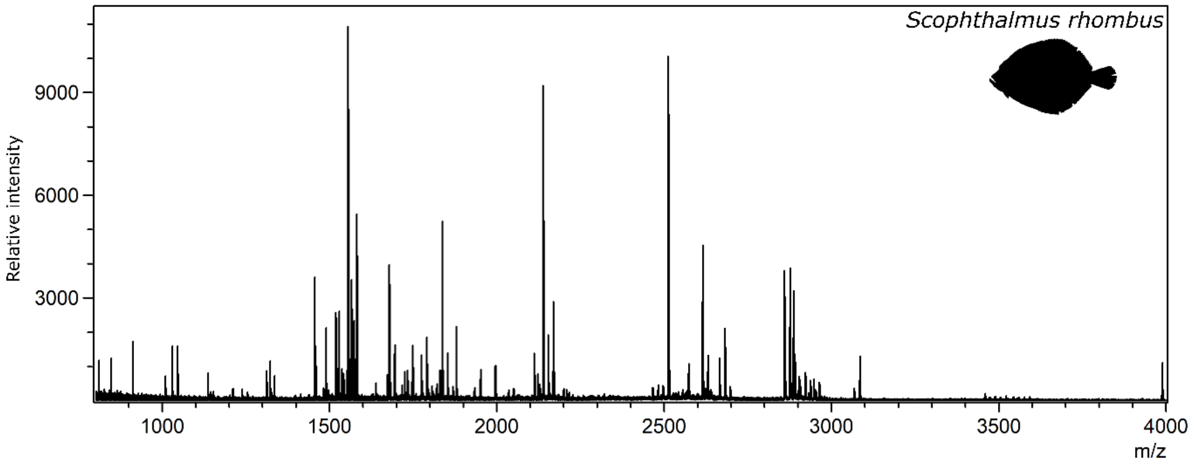

Figure D14. Collagen fingerprint of modern *Scophthalmus rhombus* (RBINS 23771).

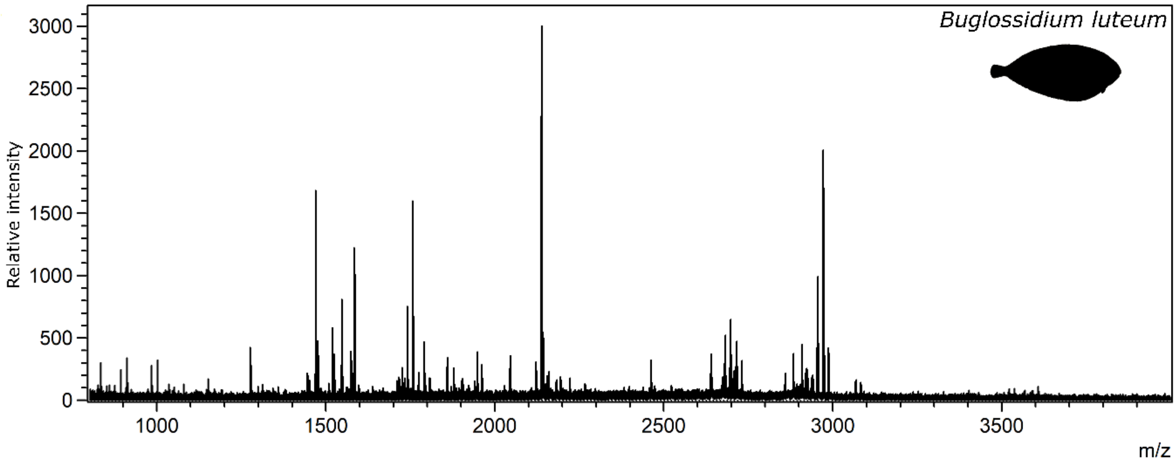

Figure D15. Collagen fingerprint of modern *Buglossidium luteum* (RBINS 91-017-P-138).

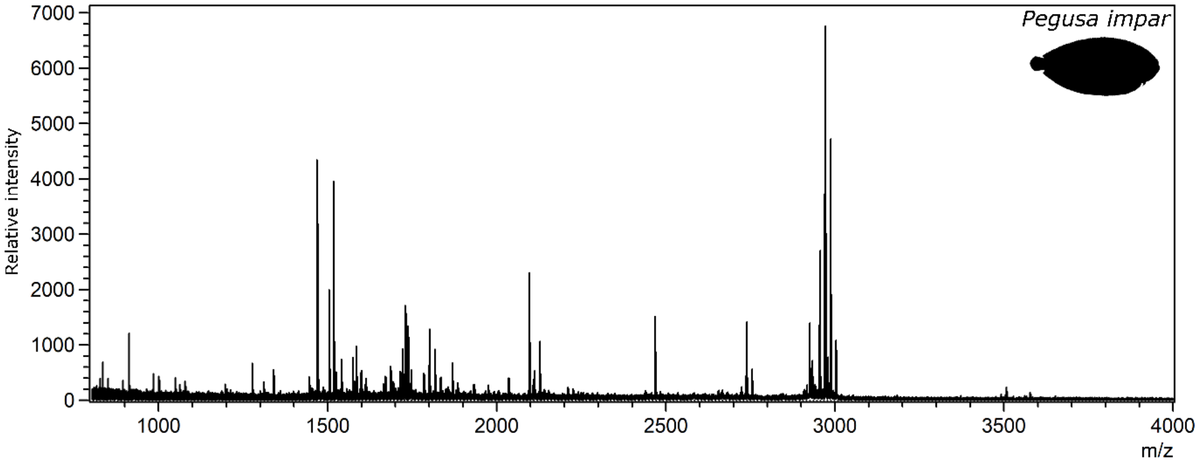

Figure D16. Collagen fingerprint of modern *Pegusa impar* (RBINS DCB915).

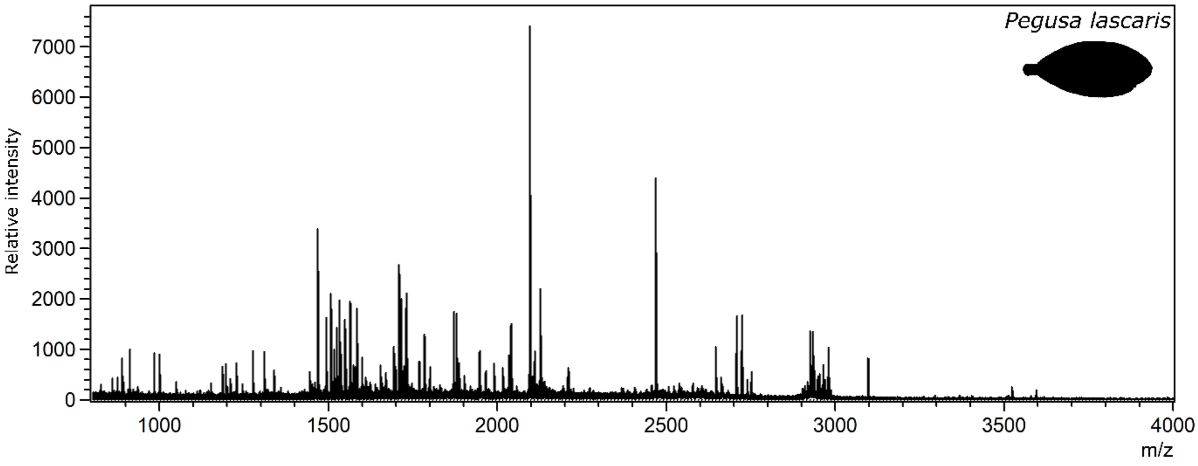

Figure D17. Collagen fingerprint of modern *Pegusa lascaris* (RBINS A2-057-P-0051).

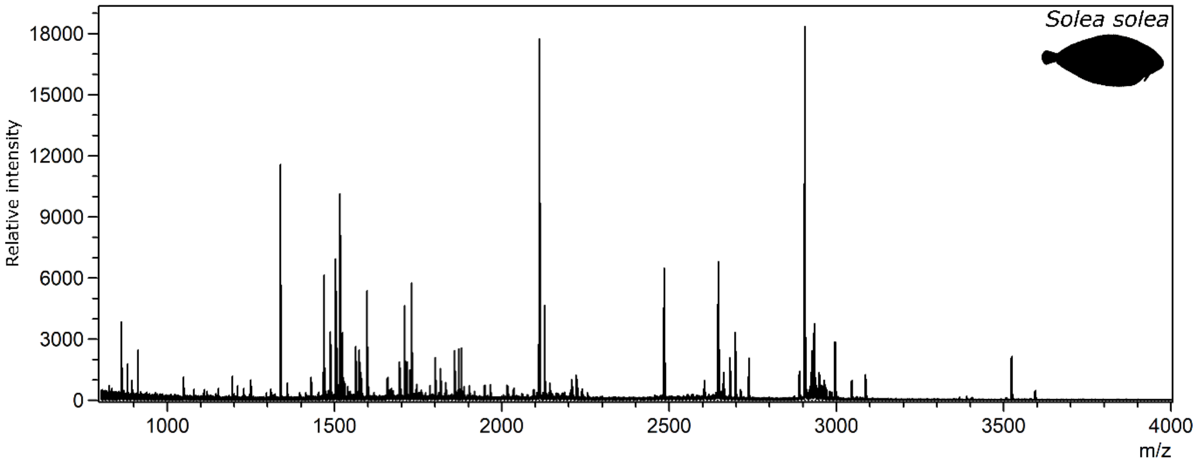

Figure D18. Collagen fingerprint of modern *Solea solea* (RBINS 24857).

Part D2. Ion spectra

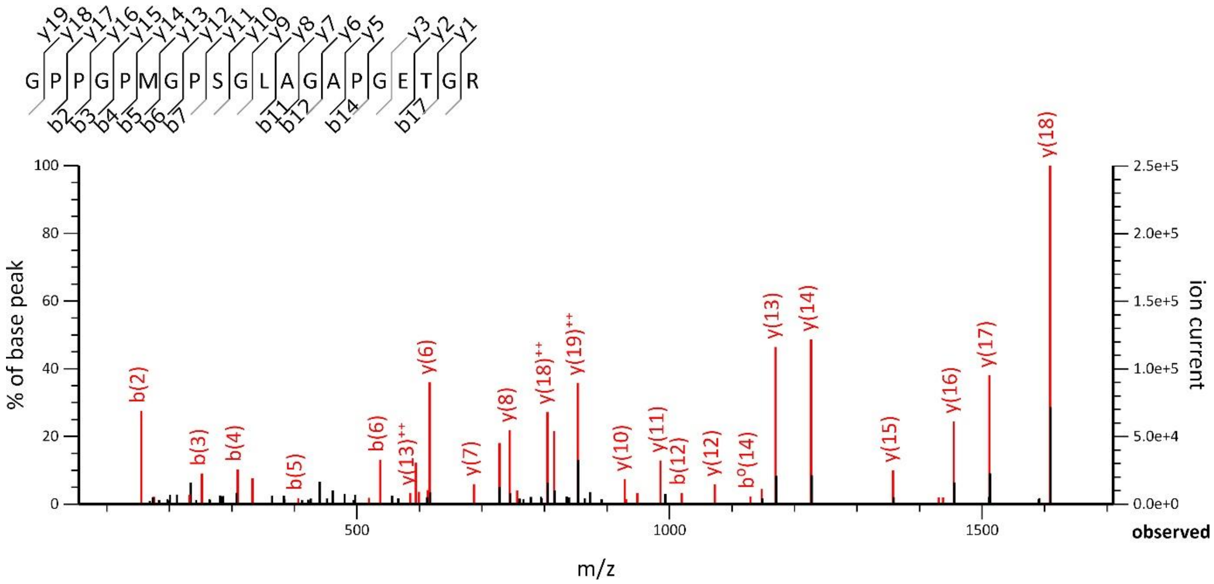

Figure D19. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Pleuronectes platessa*.

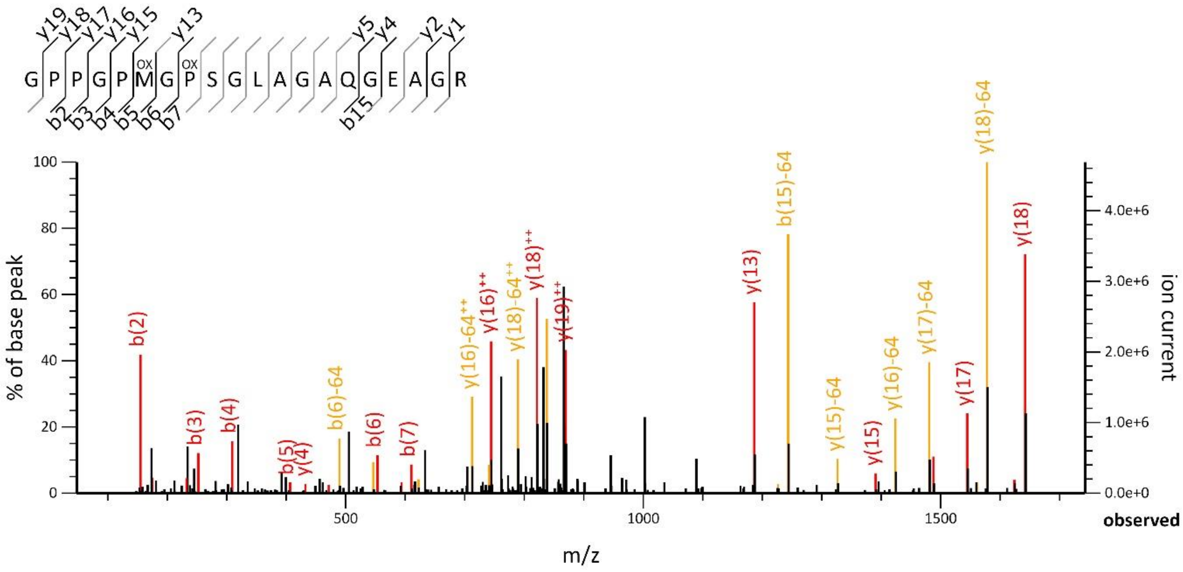

Figure D20. Ion spectrum of the COL1ɑ1 817 – 836 peptide marker of *Glyptocephalus cynoglossus*.

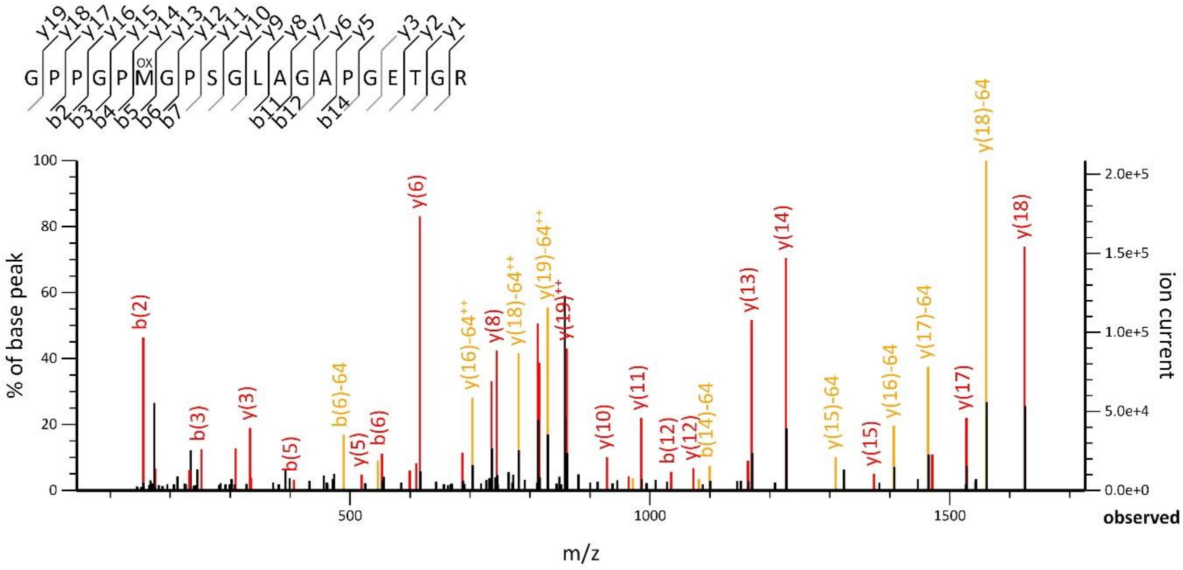

Figure D21. Ion spectrum of the COL1ɑ1 817 – 836 peptide marker of *Hippoglossoides platessoides*.

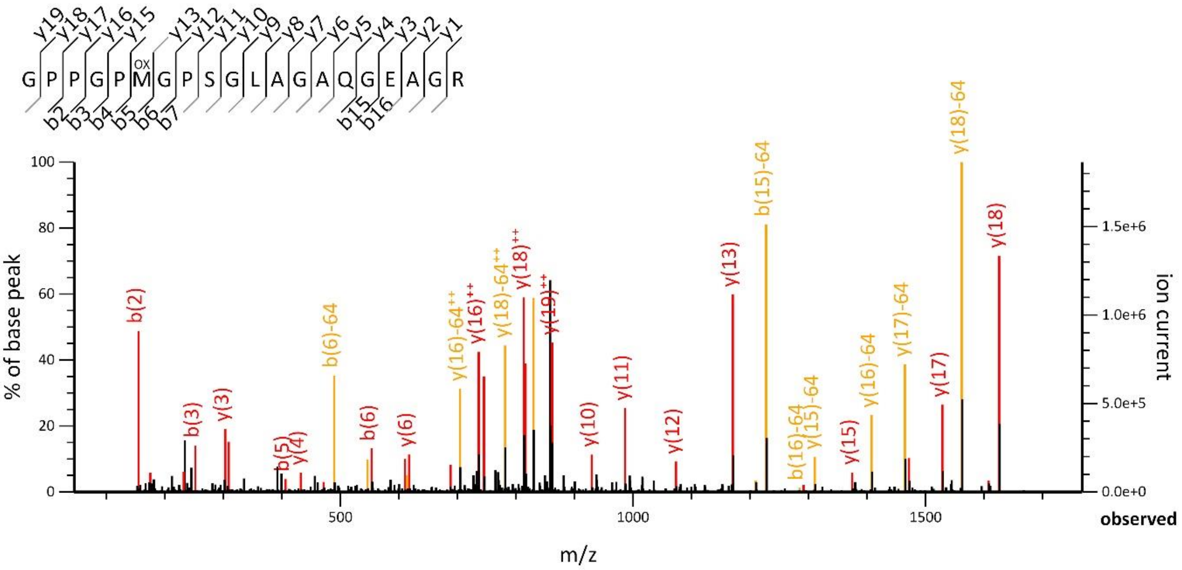

Figure D2. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Hippoglossus hippoglossus*.

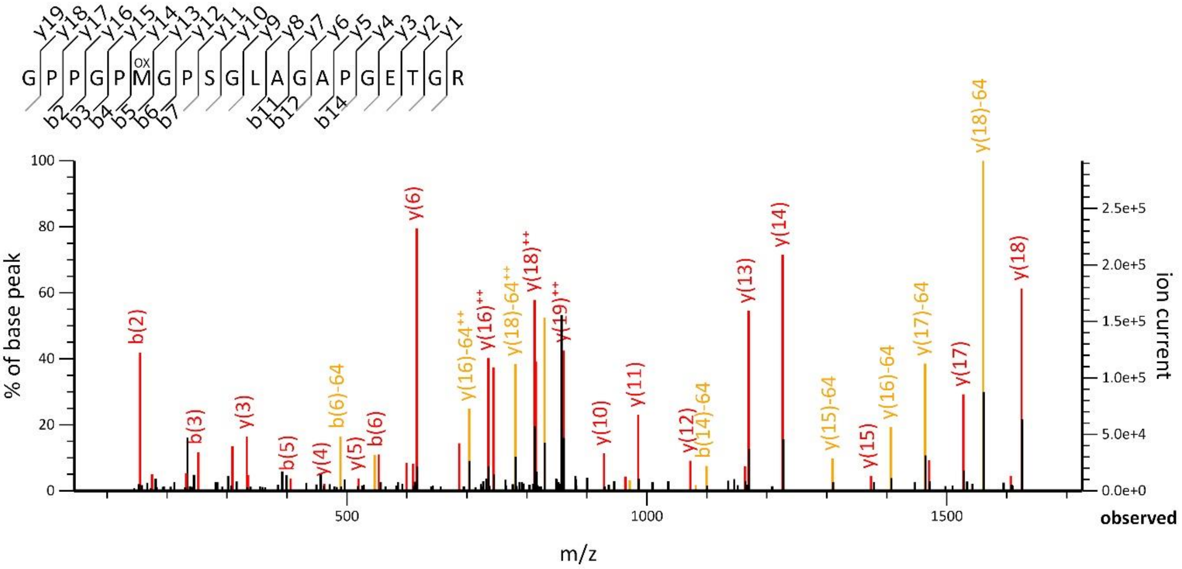

Figure D23. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Limanda limanda*.

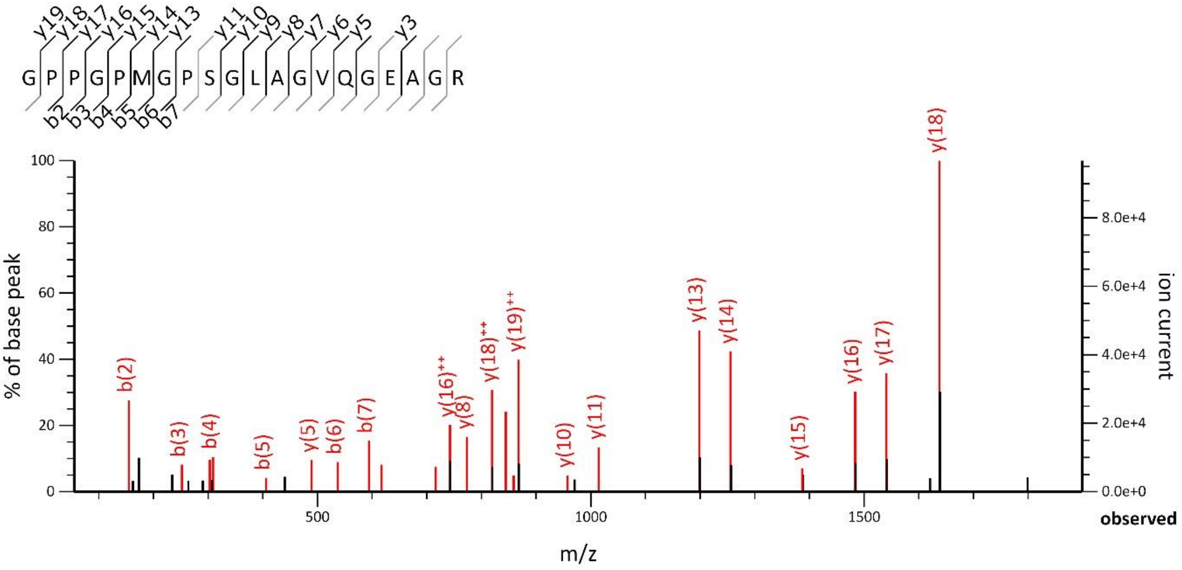

Figure D24. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Microstomus kitt*.

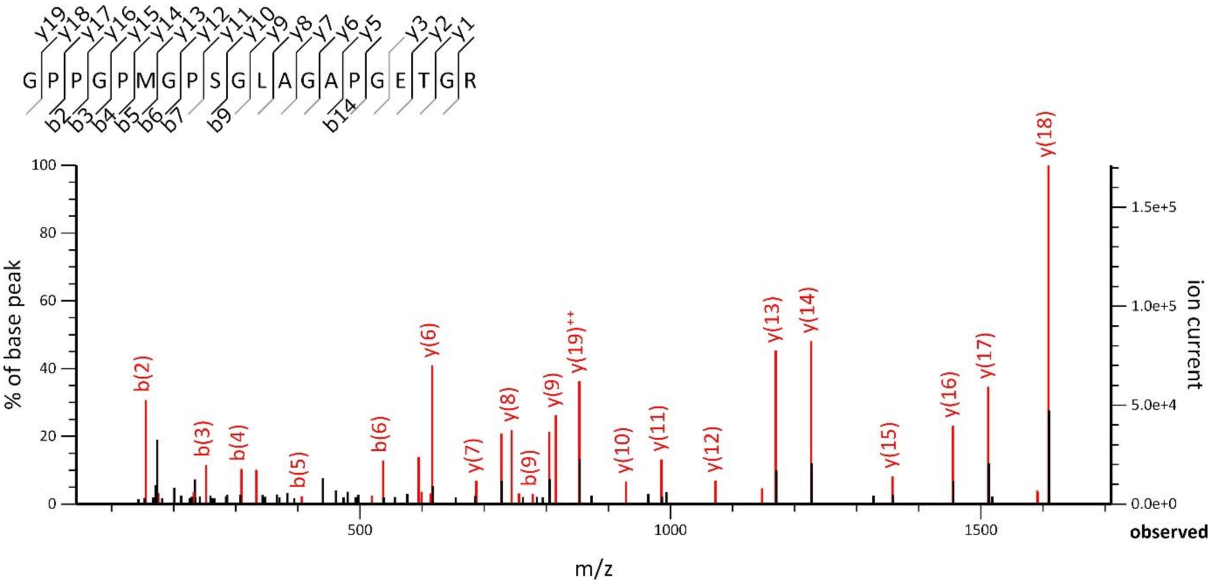

Figure D25. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Platichthys flesus*.

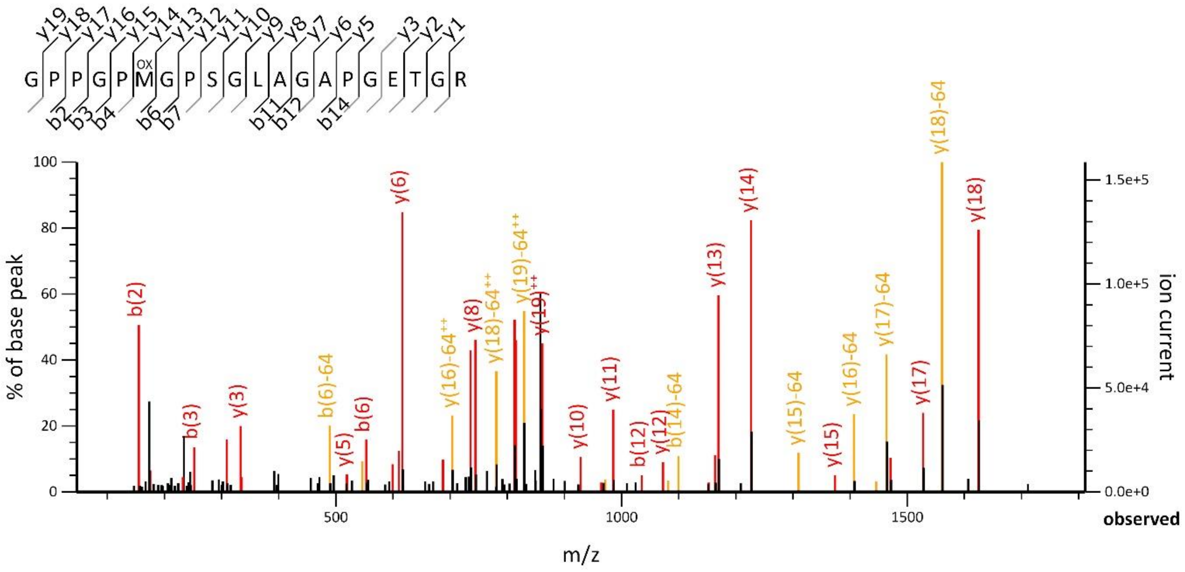

Figure D26. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Arnoglossus laterna*.

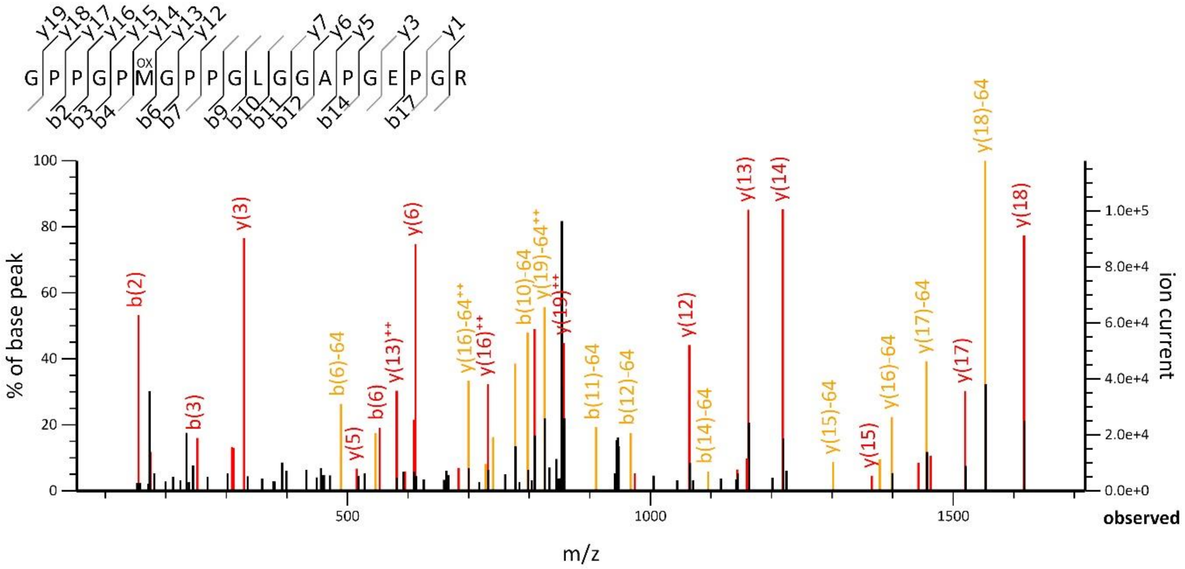

Figure D27. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Citharus linguatula*.

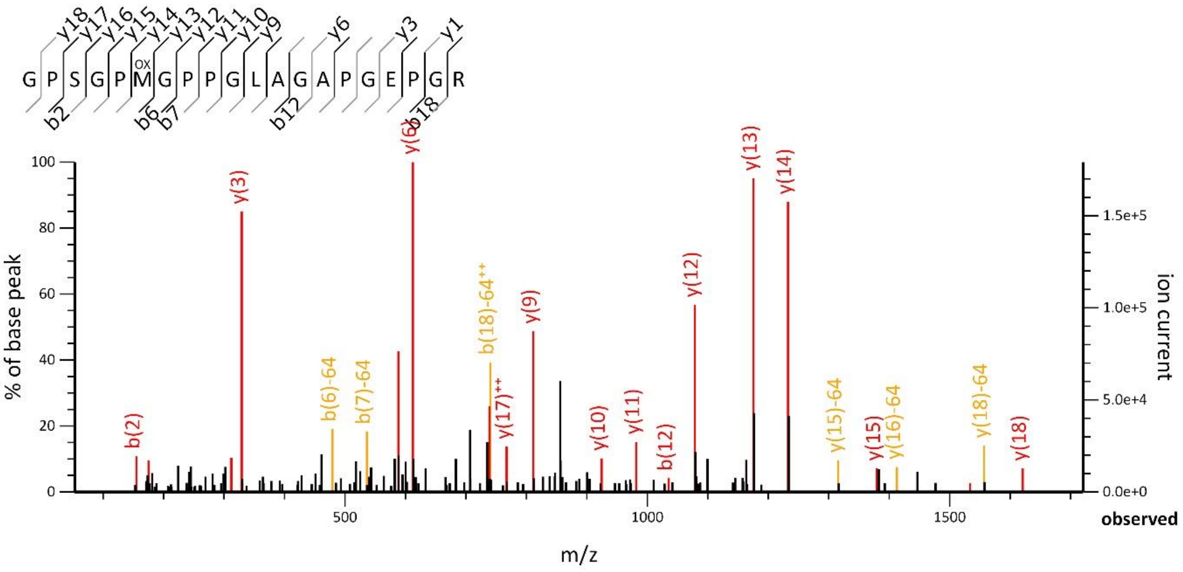

Figure D28. Ion spectrum of the COL1ɑ1 817 – 836 peptide marker of *Lepidorhombus boscii*.

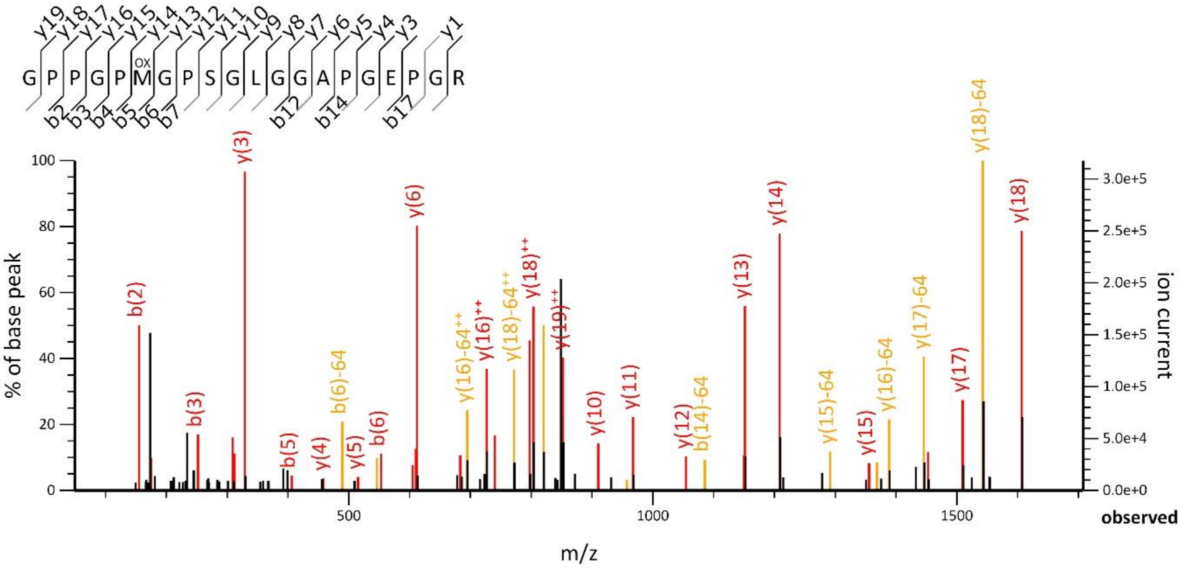

Figure D29. Ion spectrum of the COL1ɑ1 817 – 836 peptide marker of *Lepidorhombus whiffiagonis*.

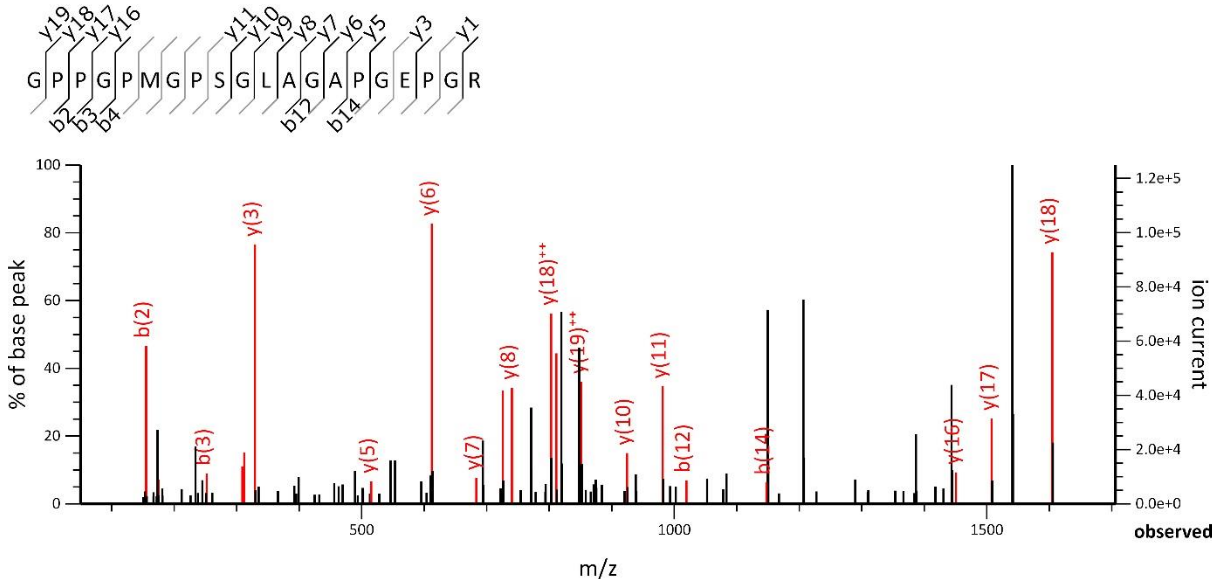

Figure D30. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Zeugopterus regius*.

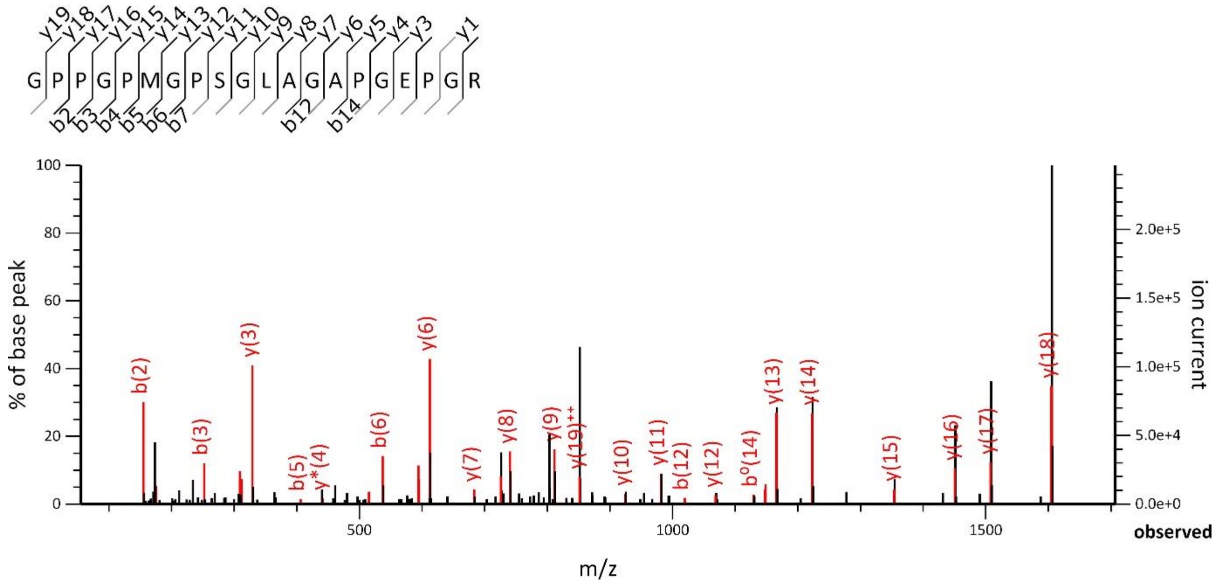

Figure D31. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Scophthalmus maximus*.

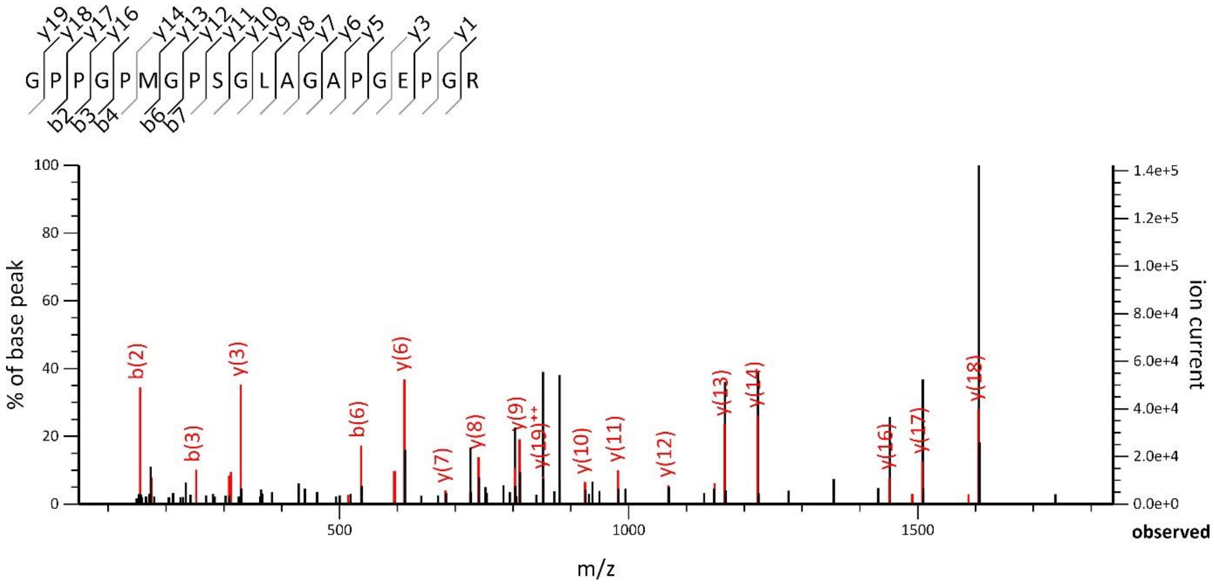

Figure D32. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Scophthalmus rhombus*.

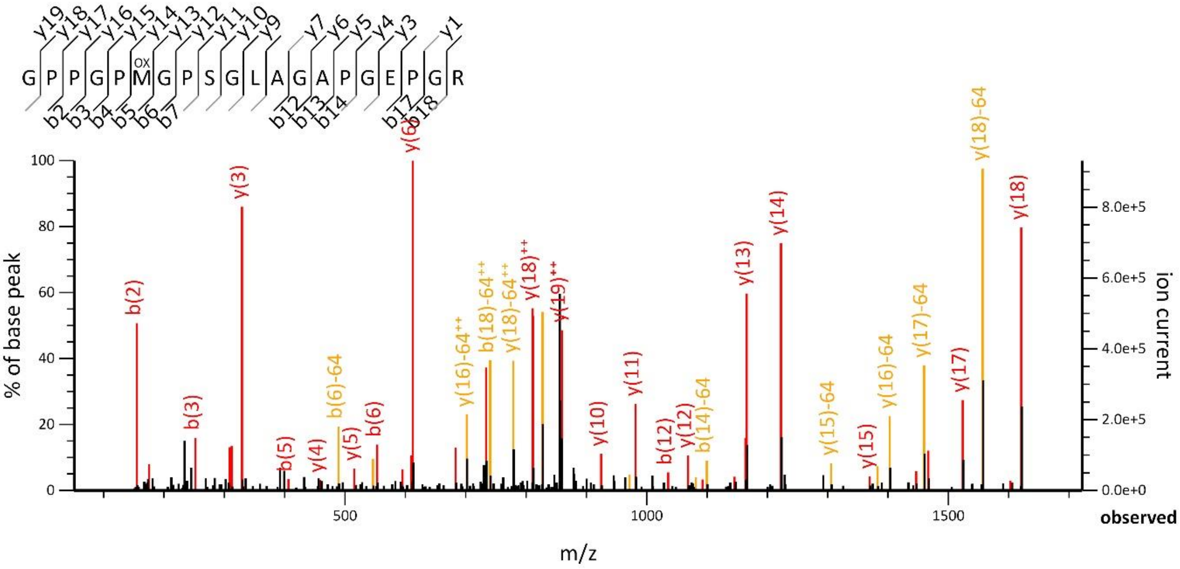

Figure D33. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Buglossidium luteum*.

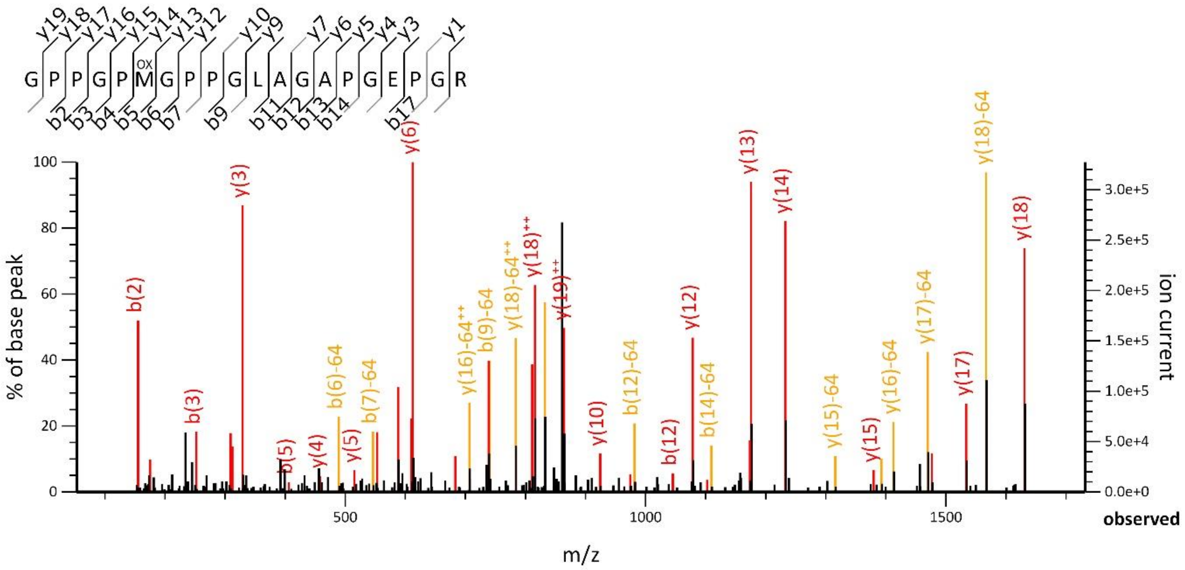

Figure D34. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Pegusa impar*.

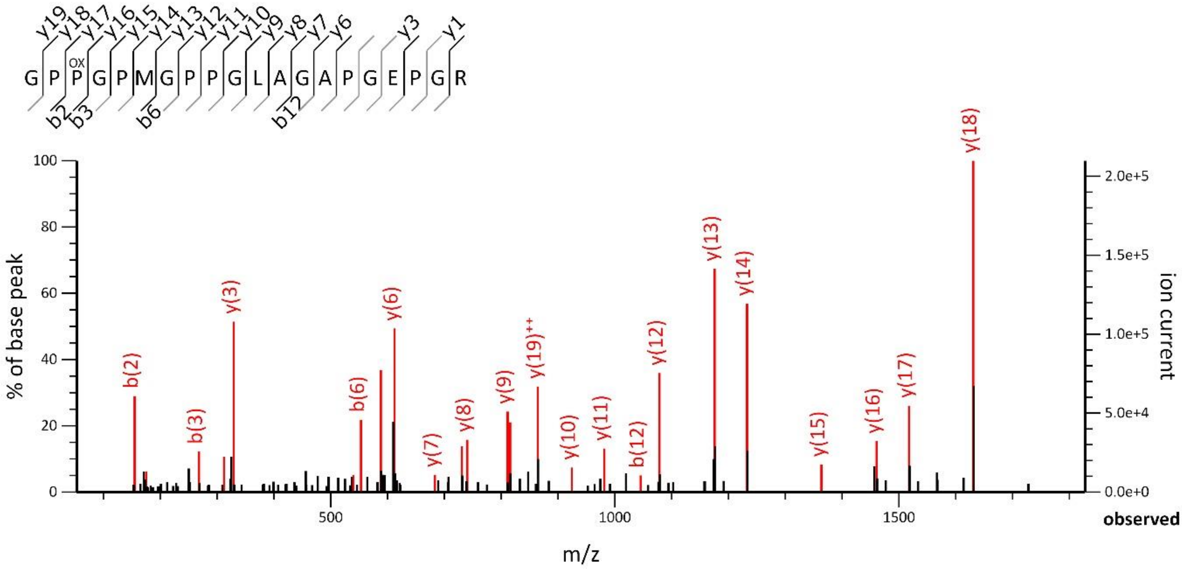

Figure D35. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Pegusa lascaris*.

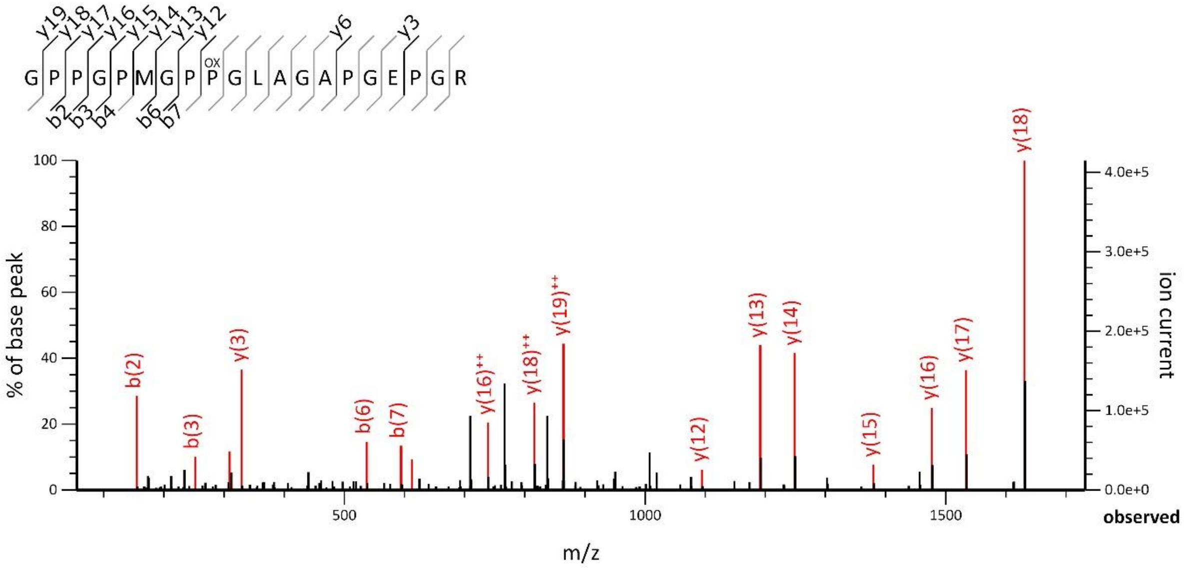

Figure D36. Ion spectrum of the COL1α1 817 – 836 peptide marker of *Solea solea*.

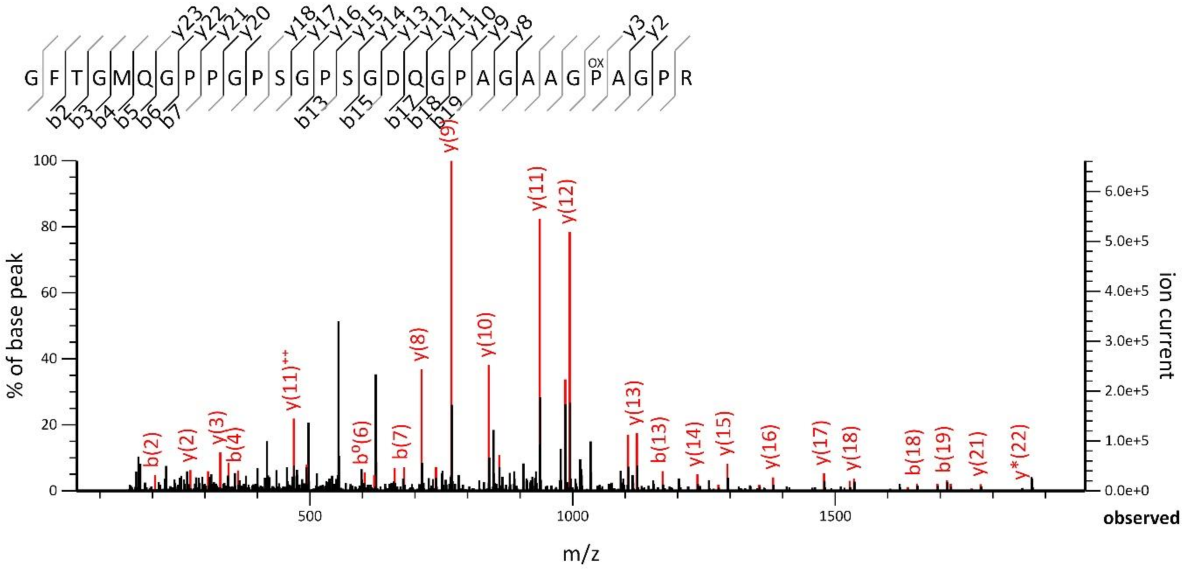

Figure D37. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Pleuronectes platessa*.

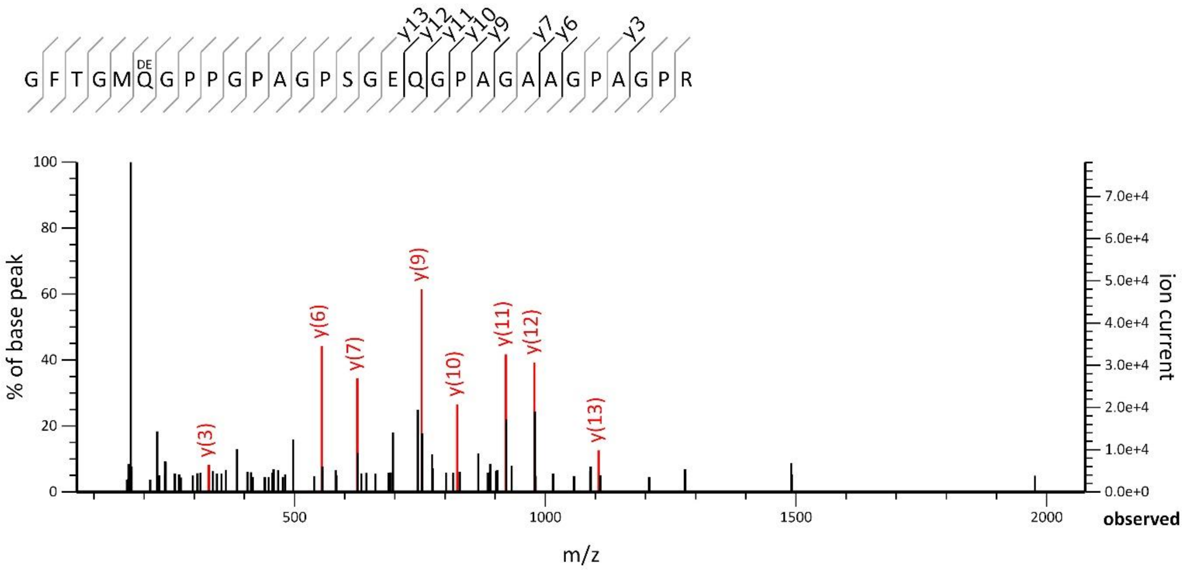

Figure D38. Ion spectrum of the COL1ɑ1 934 – 963 peptide marker of *Glyptocephalus cynoglossus*.

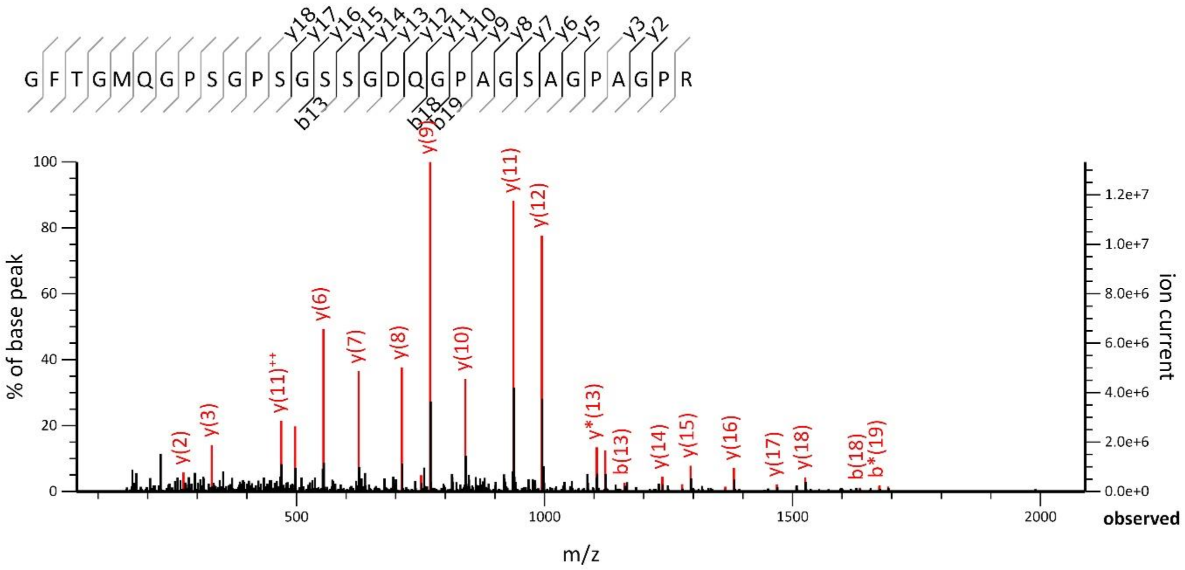

Figure D39. Ion spectrum of the COL1ɑ1 934 – 963 peptide marker of *Hippoglossoides platessoides*.

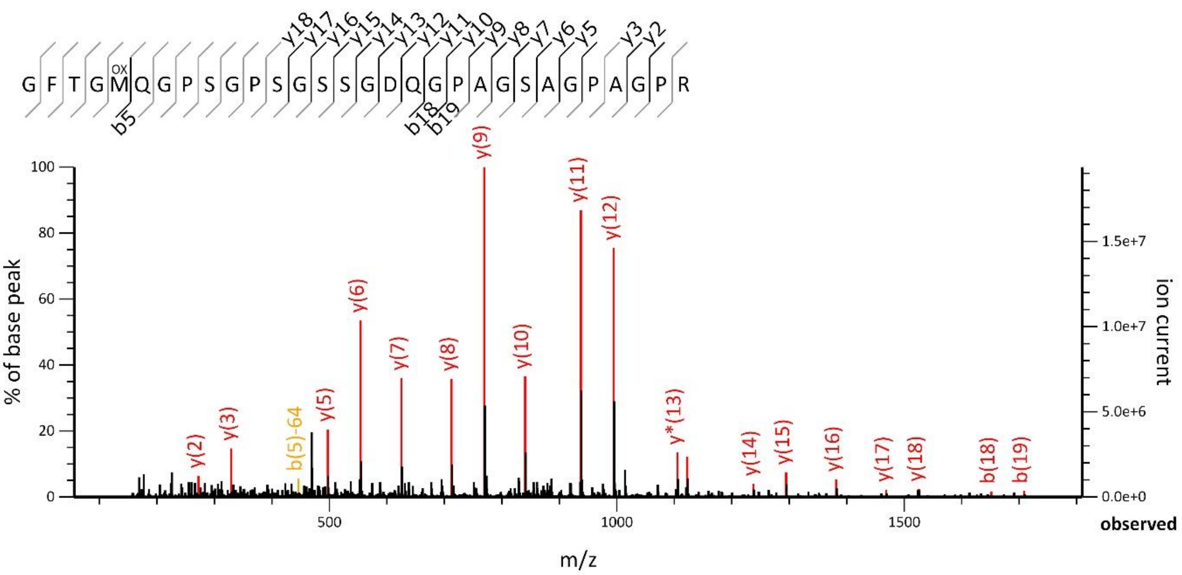

Figure D40. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Hippoglossus hippoglossus*.

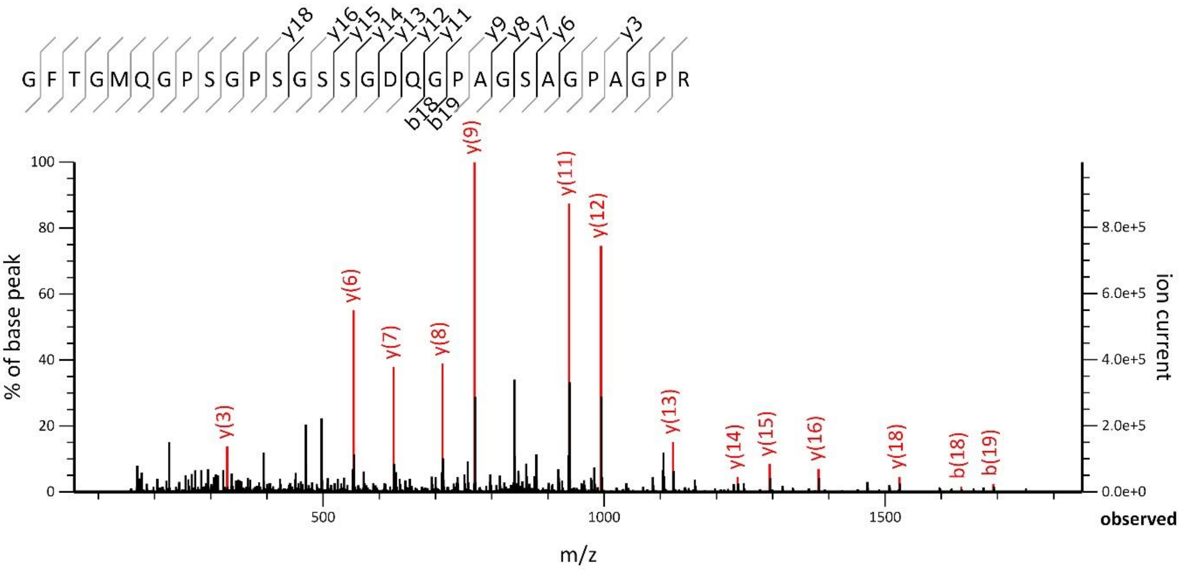

Figure D41. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Limanda limanda*.

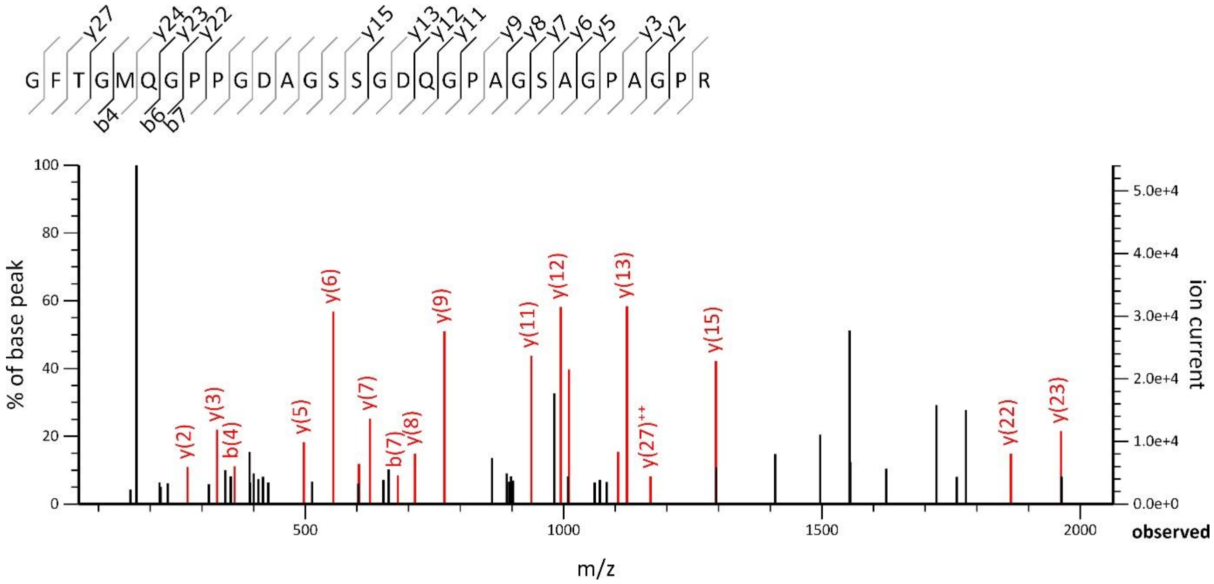

Figure D42. Ion spectrum of the COL1ɑ1 934 – 963 peptide marker of *Microstomus kitt*.

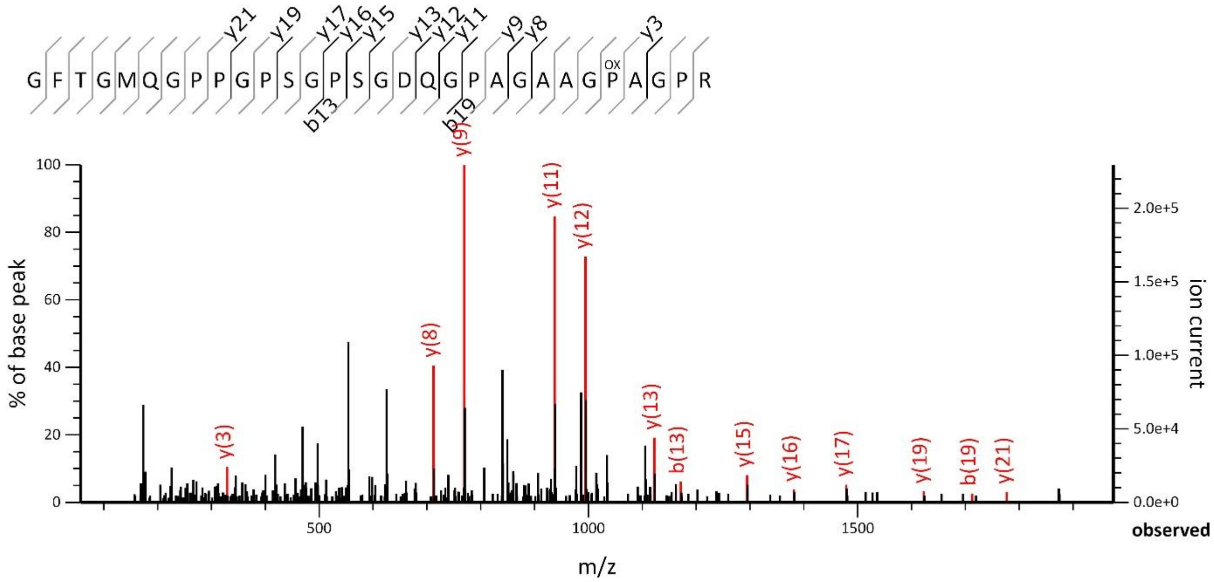

Figure D43. Ion spectrum of the COL1ɑ1 934 – 963 peptide marker of *Platichthys flesus*.

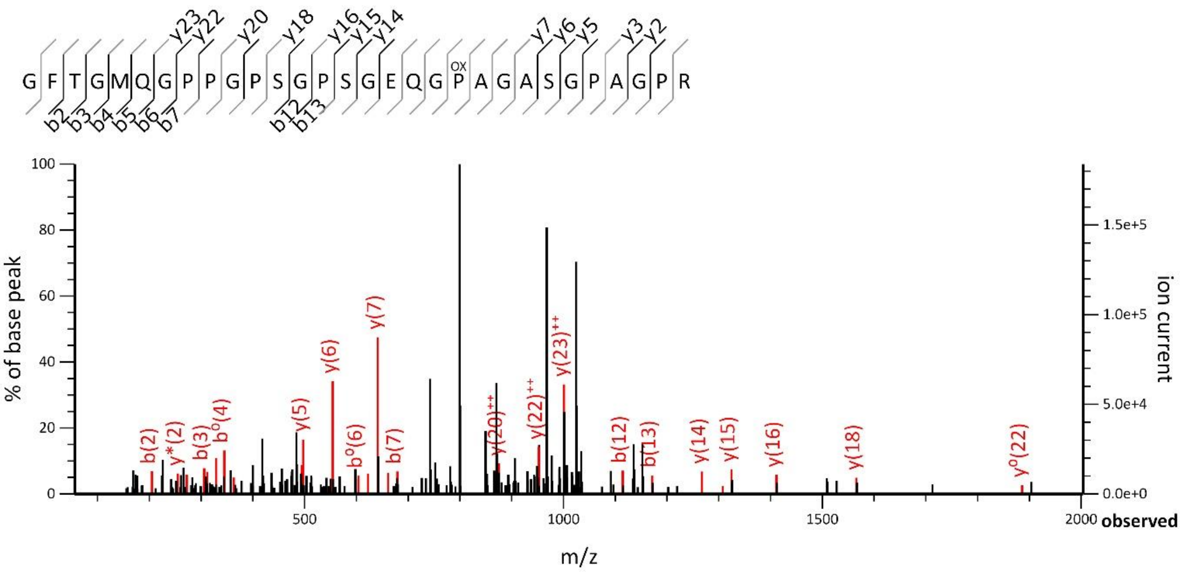

Figure D44. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Arnoglossus laterna*.

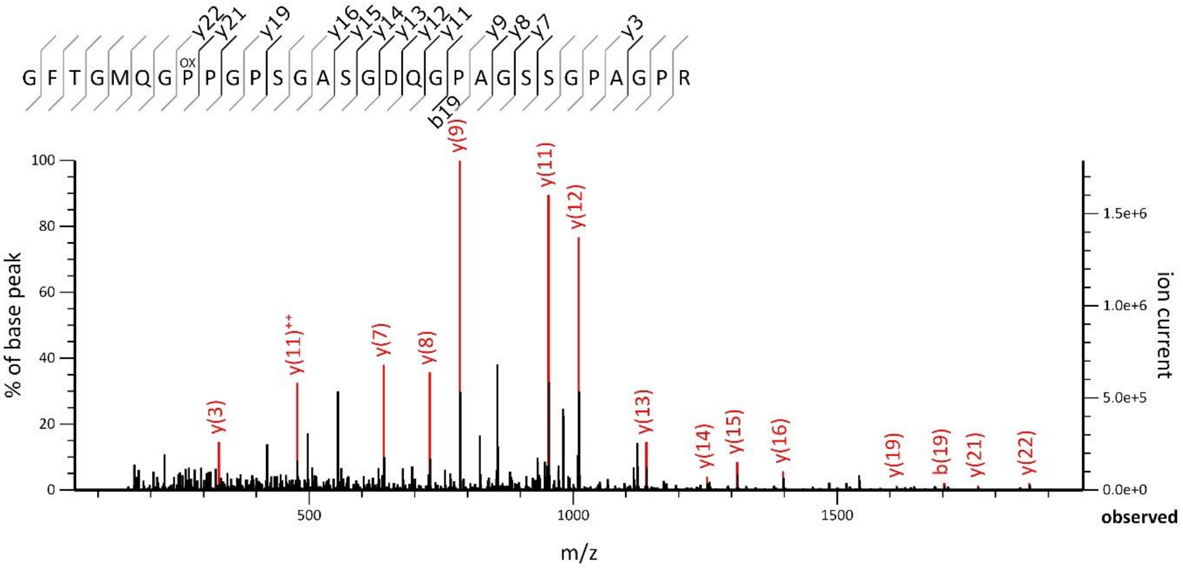

Figure D45. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Lepidorhombus boscii*.

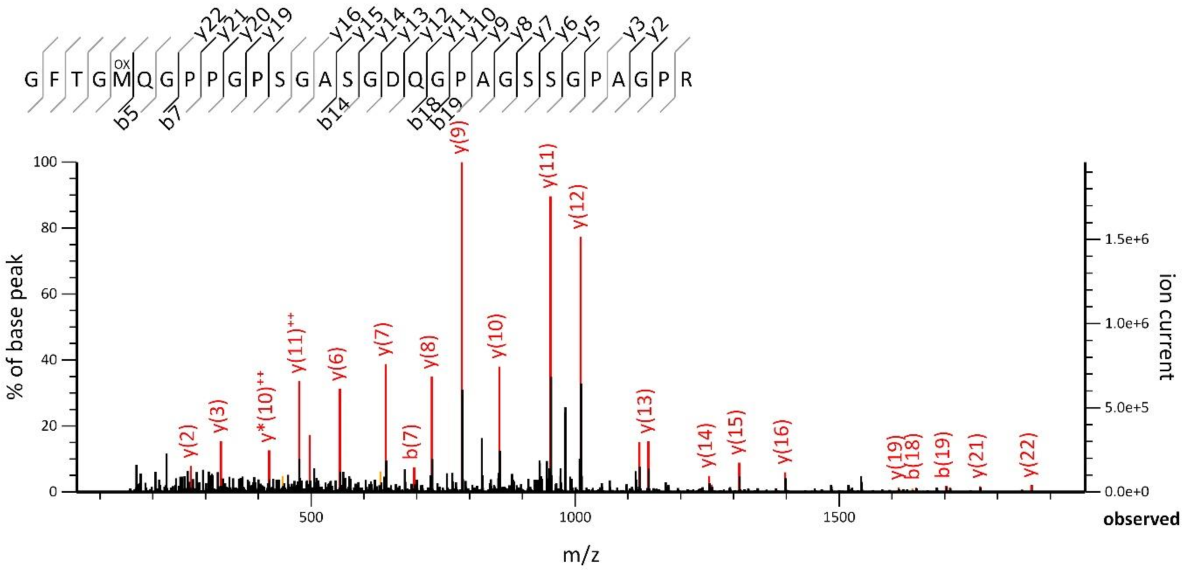

Figure D46. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Lepidorhombus whiffiagonis*.

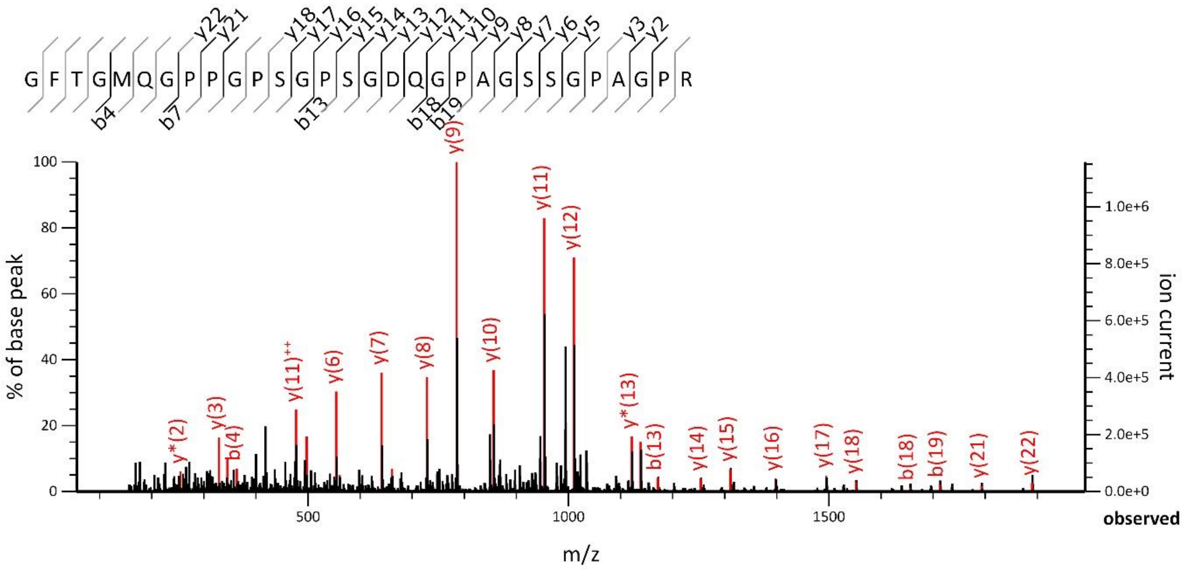

Figure D47. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Scophthalmus maximus*.

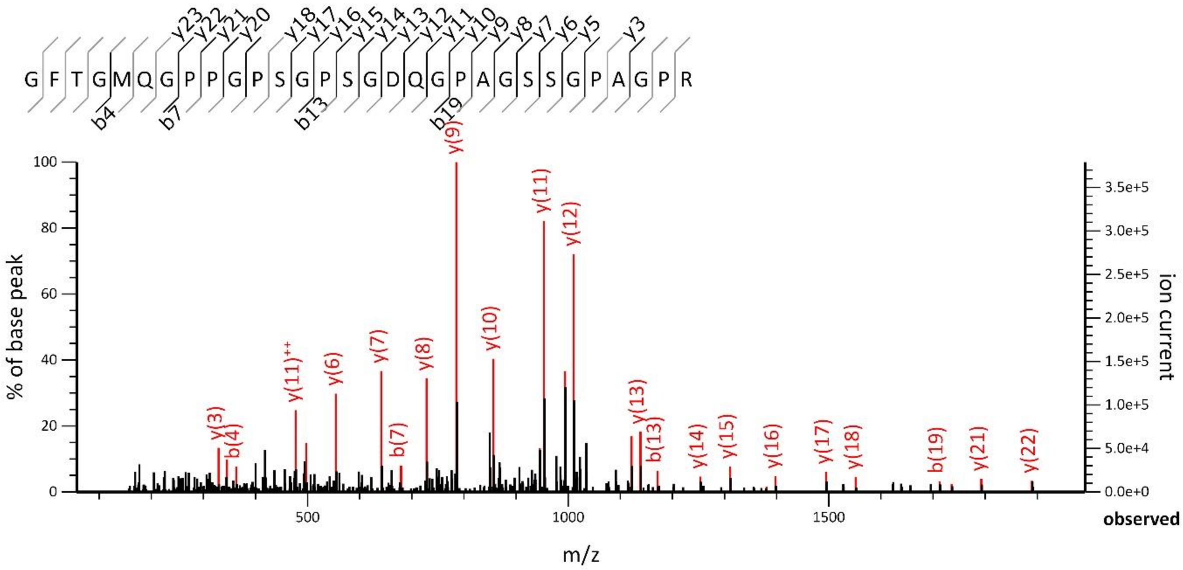

Figure D48. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Scophthalmus rhombus*.

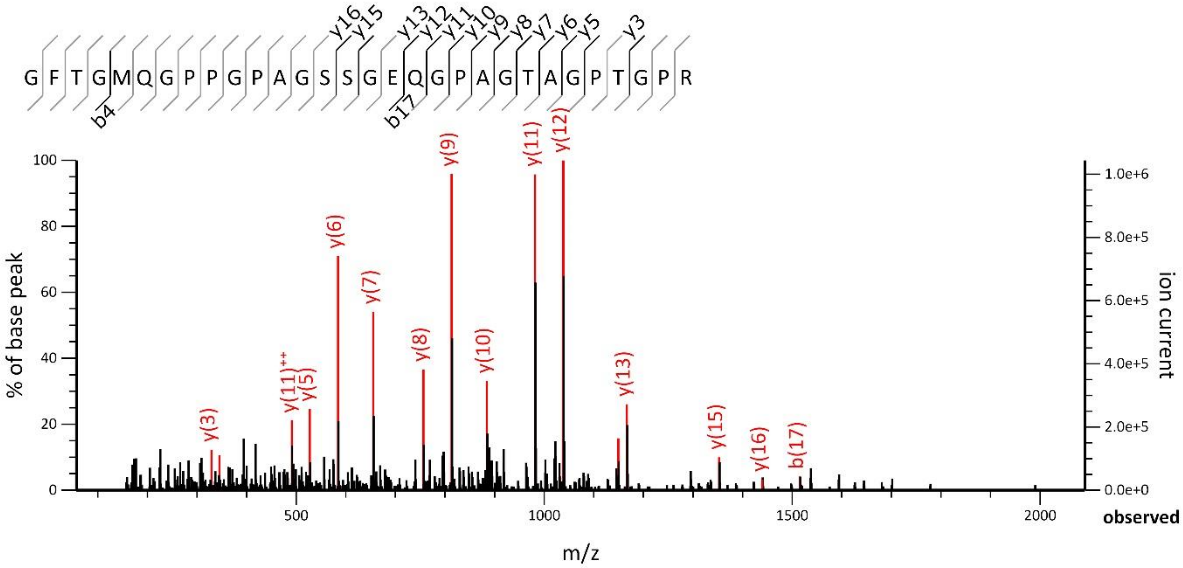

Figure D49. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Buglossidium luteum*.

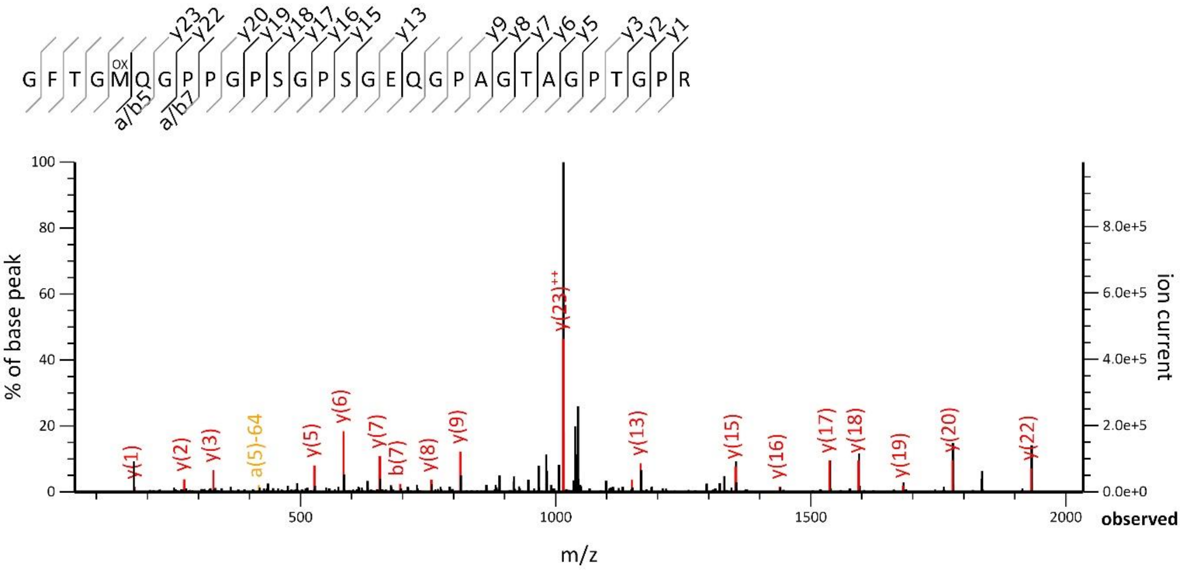

Figure D50. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Pegusa impar*.

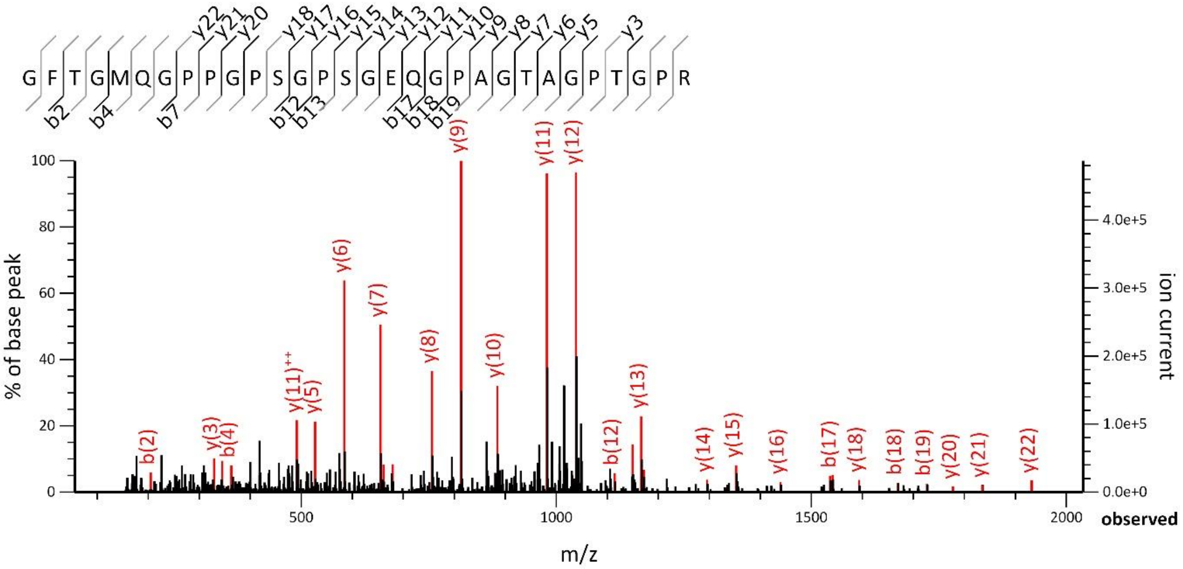

Figure D51. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Pegusa lascaris*.

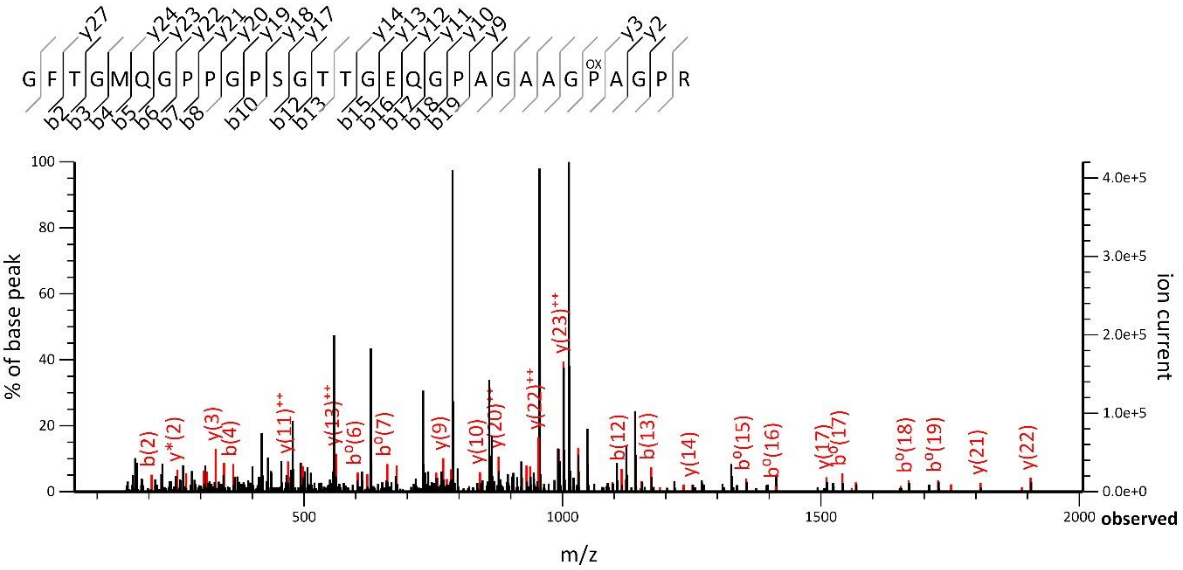

Figure D52. Ion spectrum of the COL1α1 934 – 963 peptide marker of *Solea solea*.

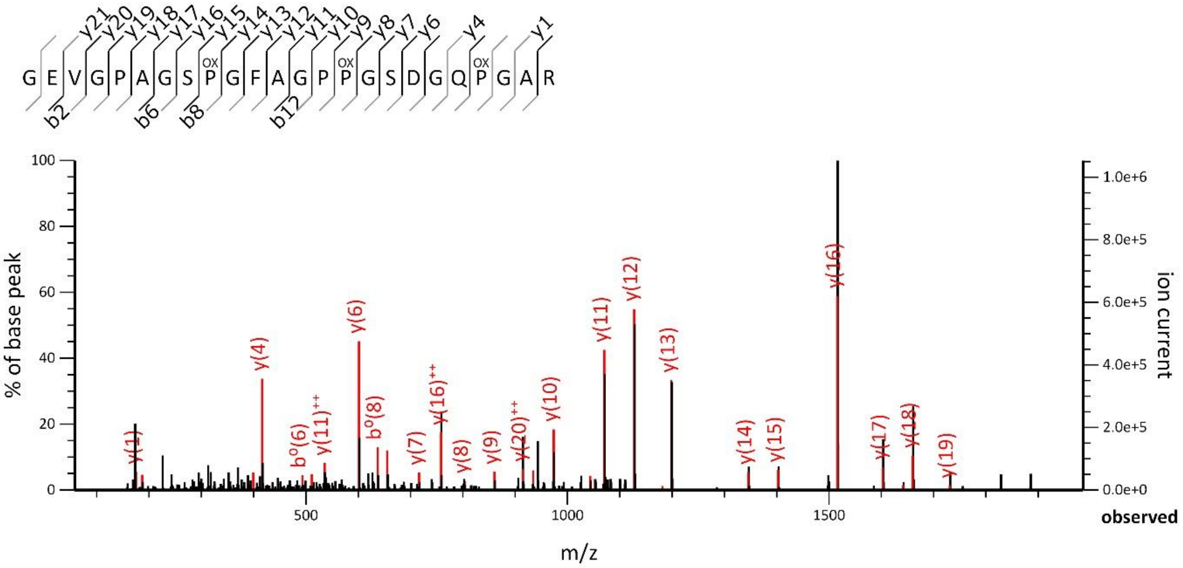

Figure D53. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Pleuronectes platessa*.

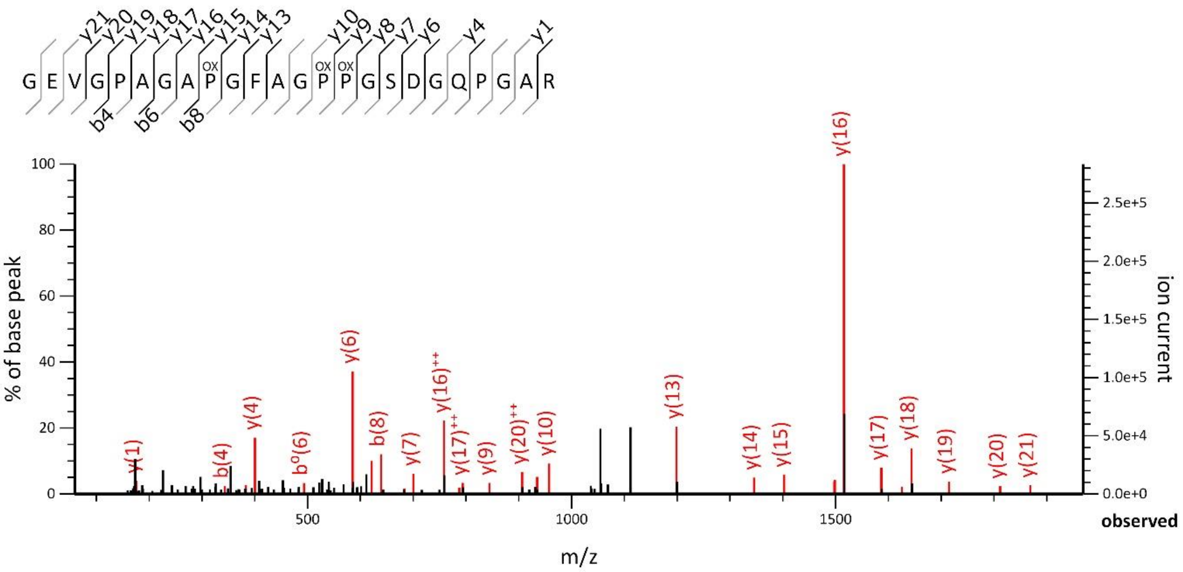

Figure D54. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Glyptocephalus cynoglossus*.

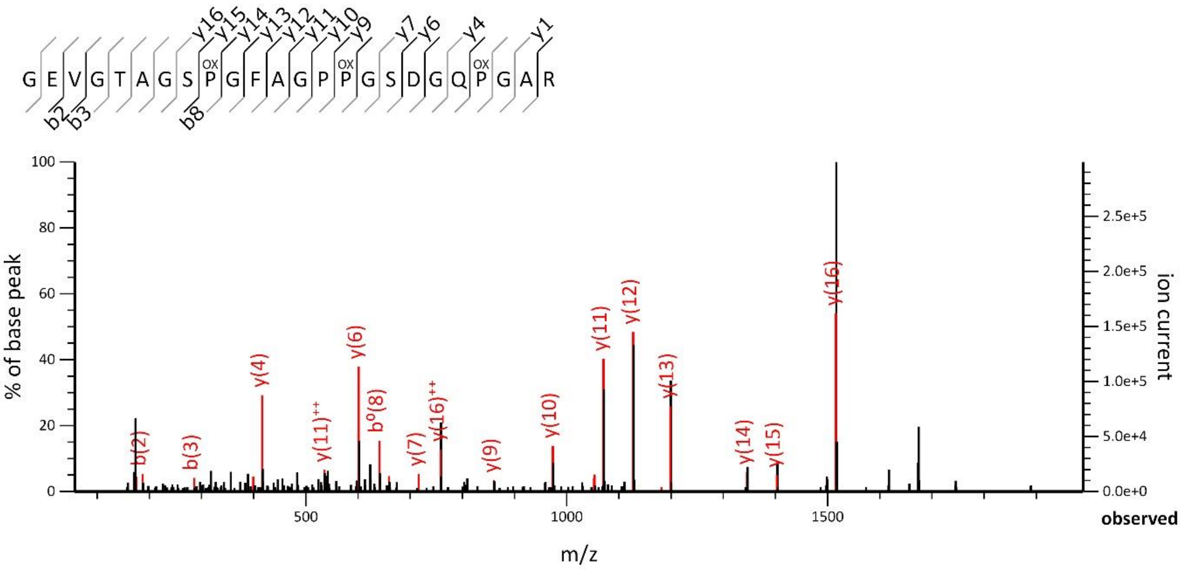

Figure D55. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Hippoglossoides platessoides*.

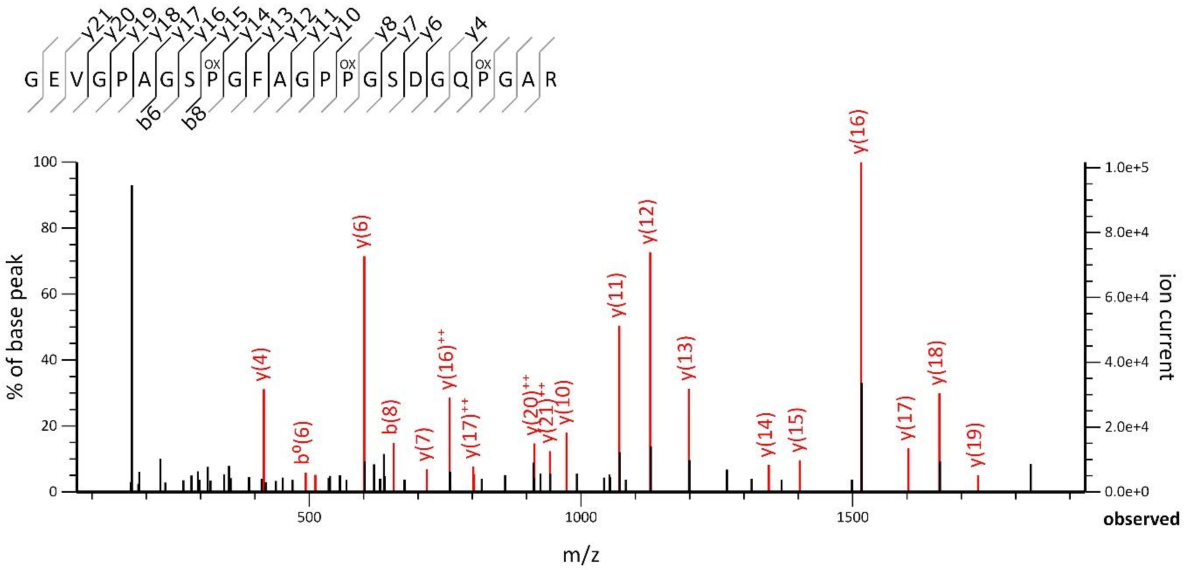

Figure D56. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Hippoglossus hippoglossus*.

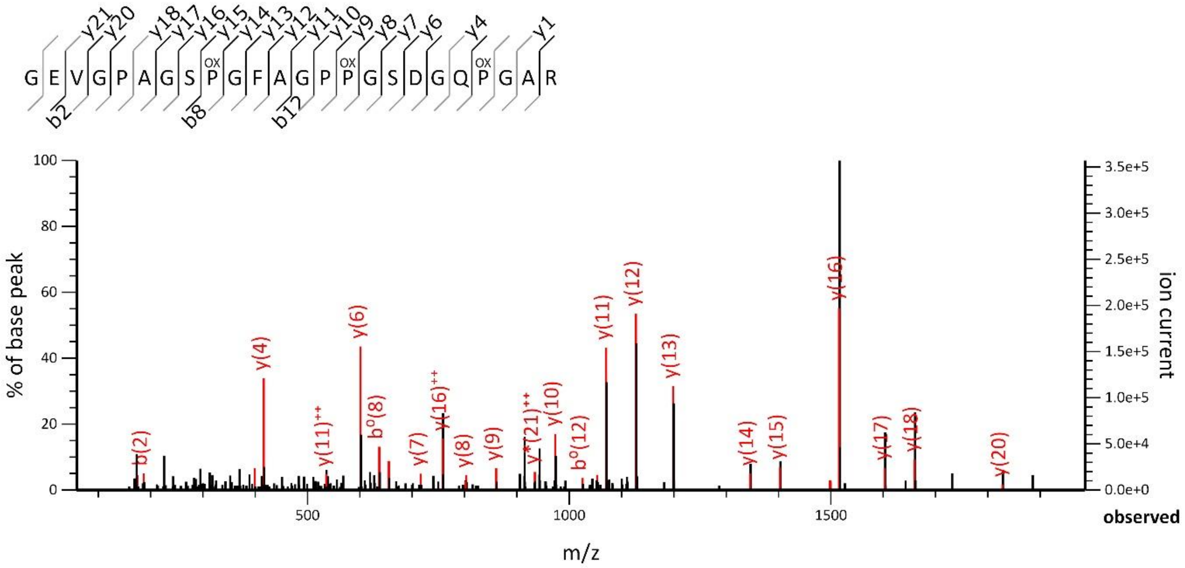

Figure D57. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Limanda limanda*.

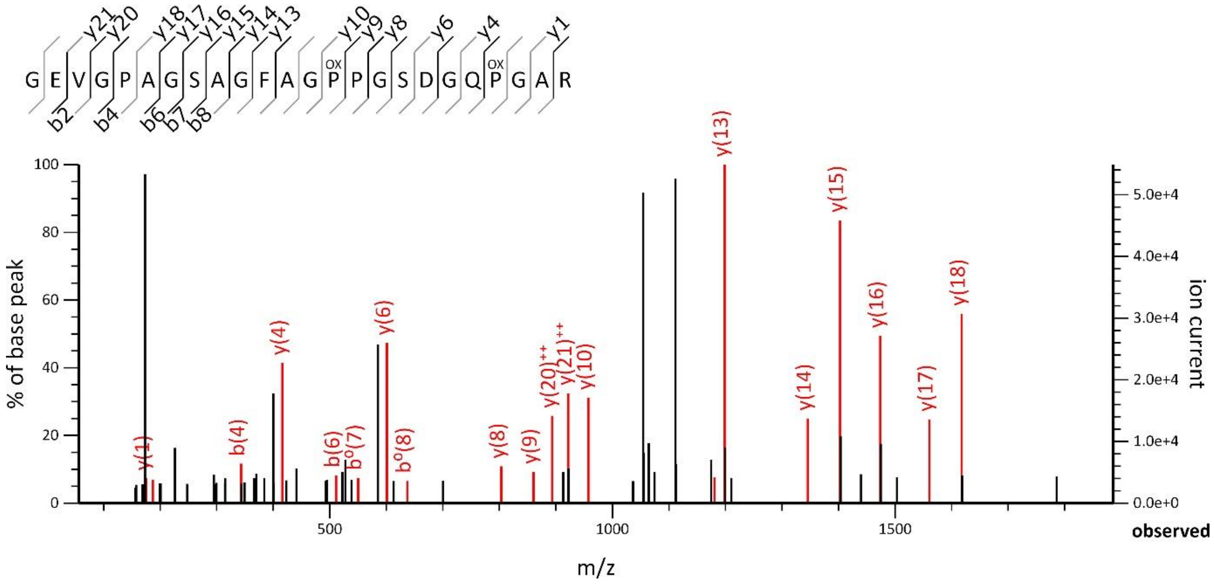

Figure D58. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Microstomus kitt*.

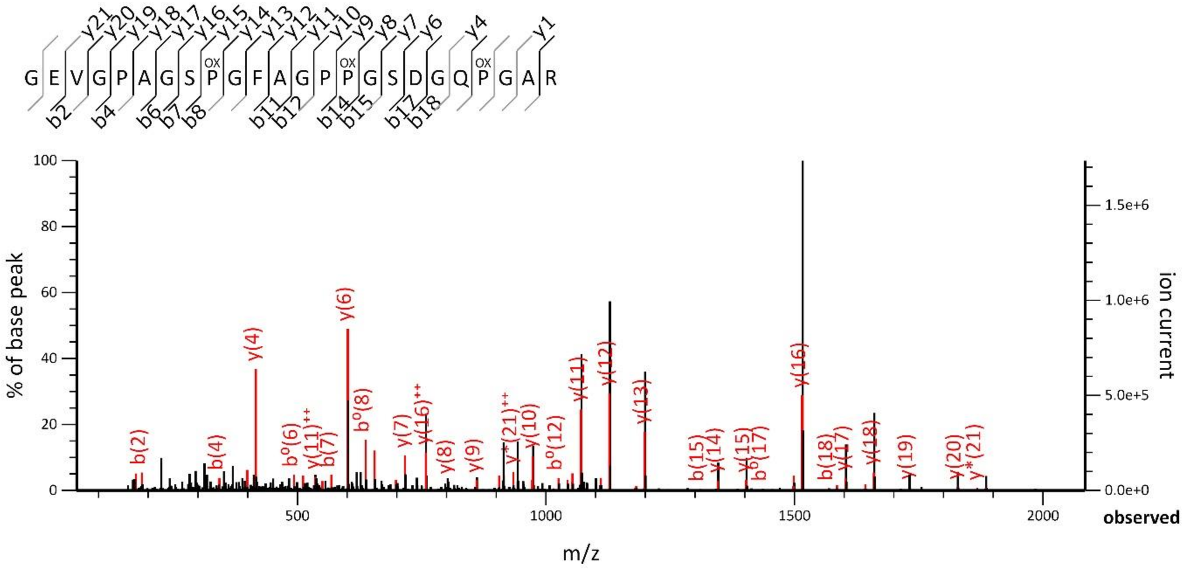

Figure D59. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Platichthys flesus*.

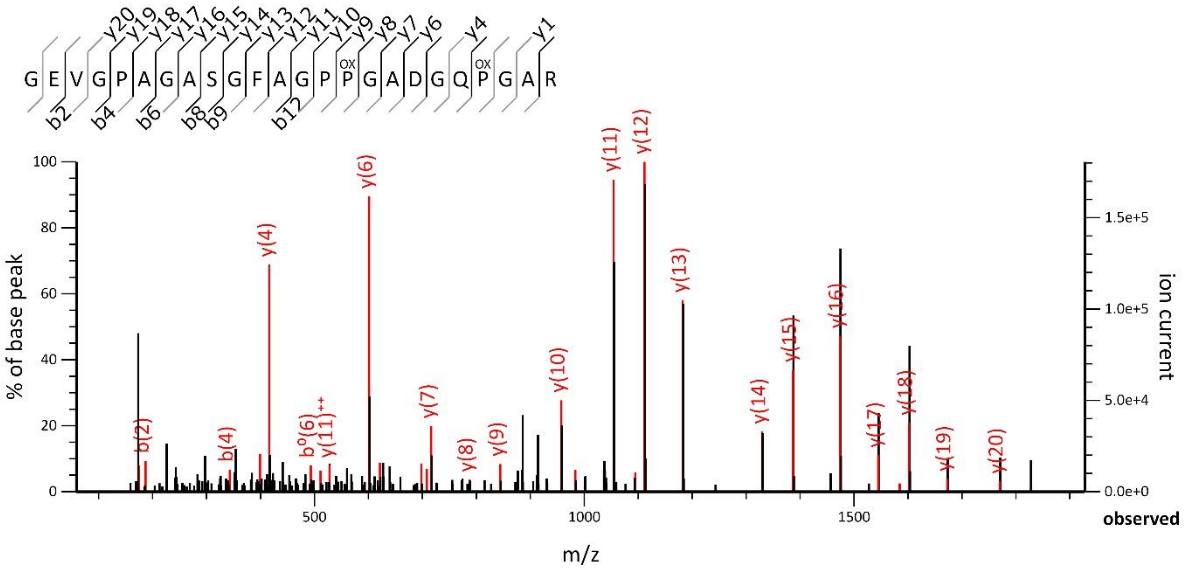

Figure D60. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Arnoglossus laterna*.

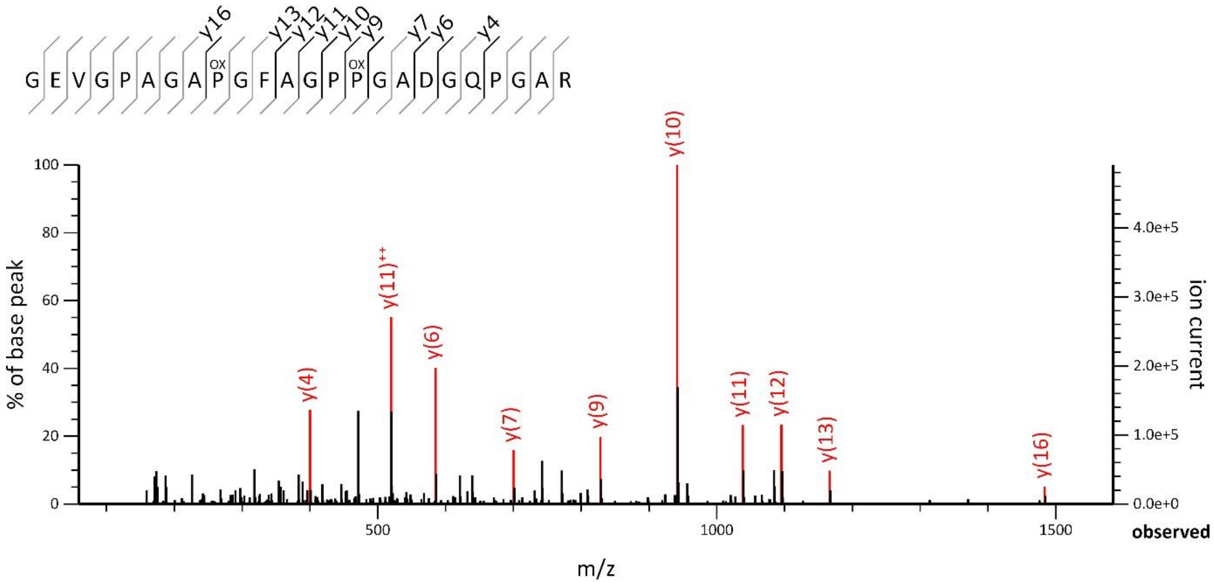

Figure D61. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Citharus linguatula*.

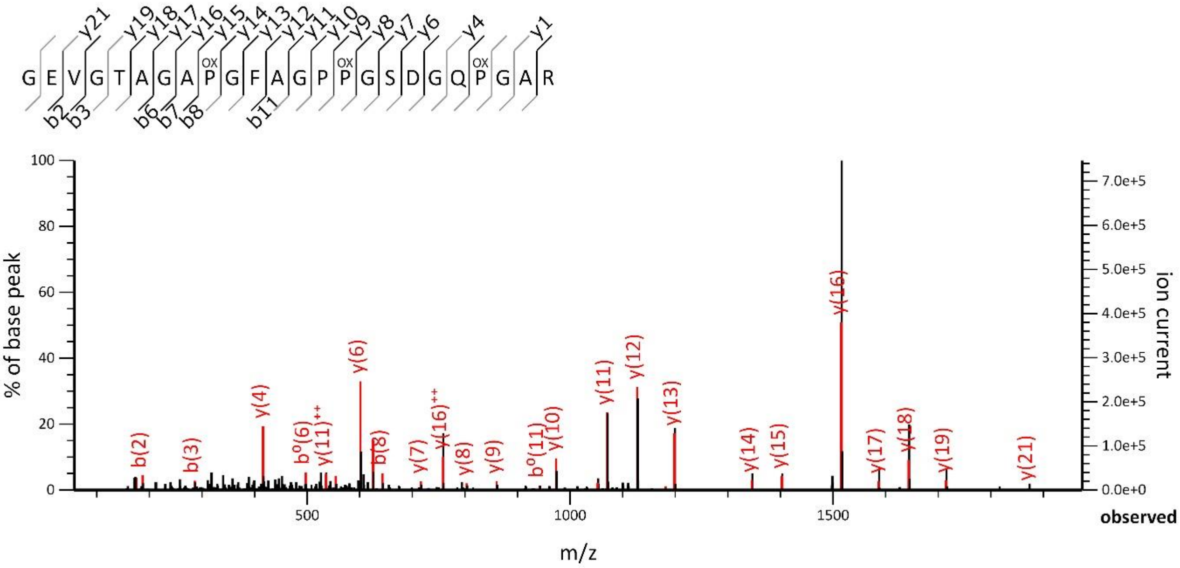

Figure D62. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Lepidorhombus boscii*.

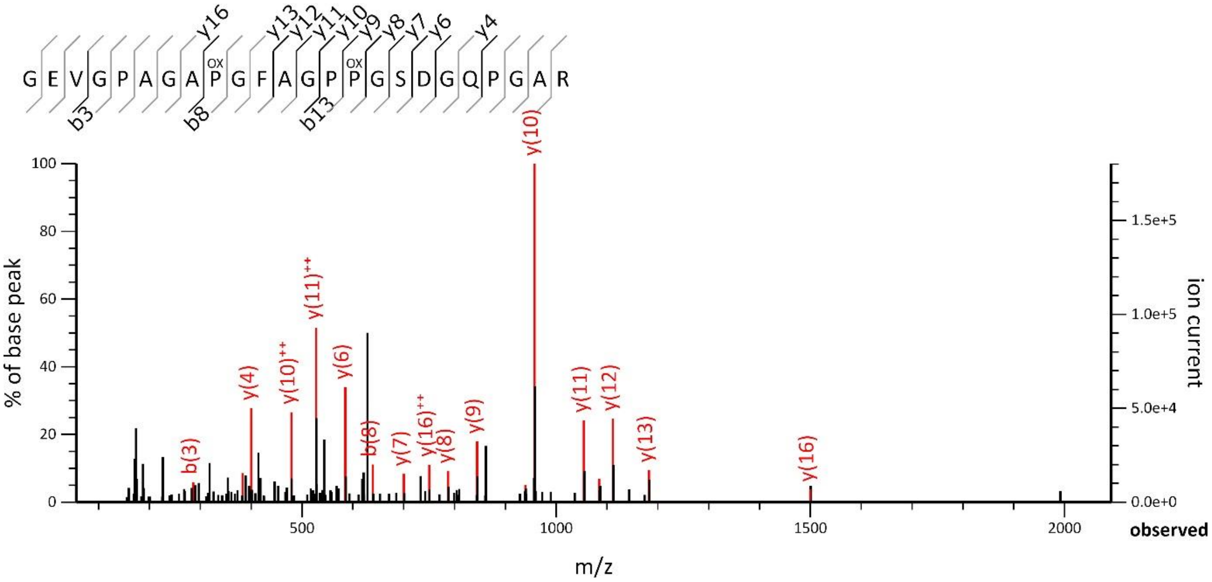

Figure D63. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Lepidorhombus whiffiagonis*.

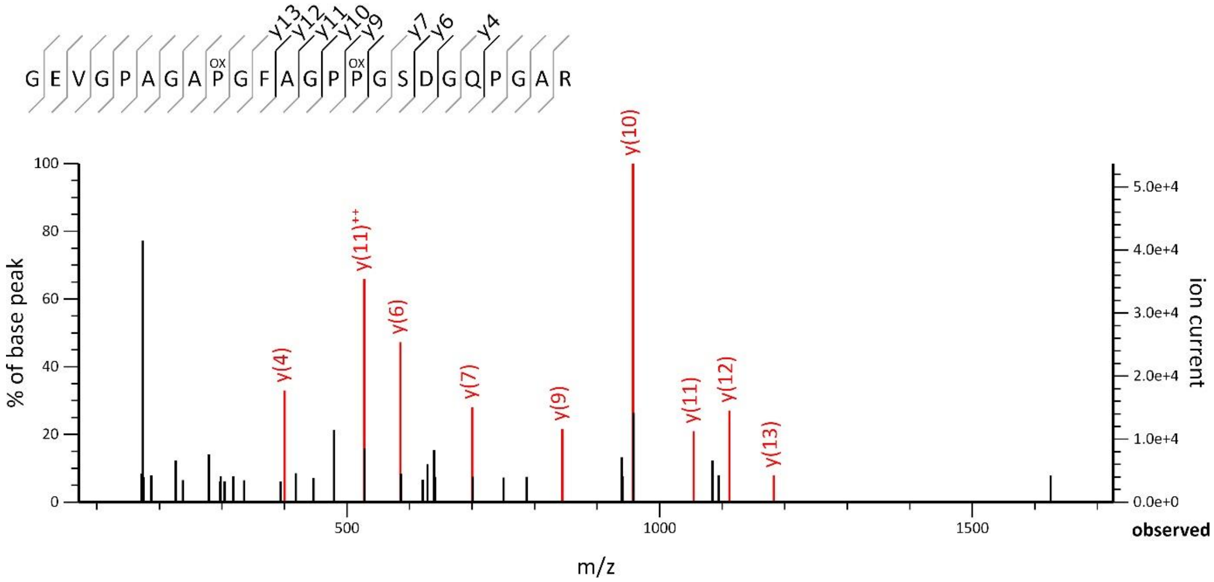

Figure D64. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Zeugopterus regius*.

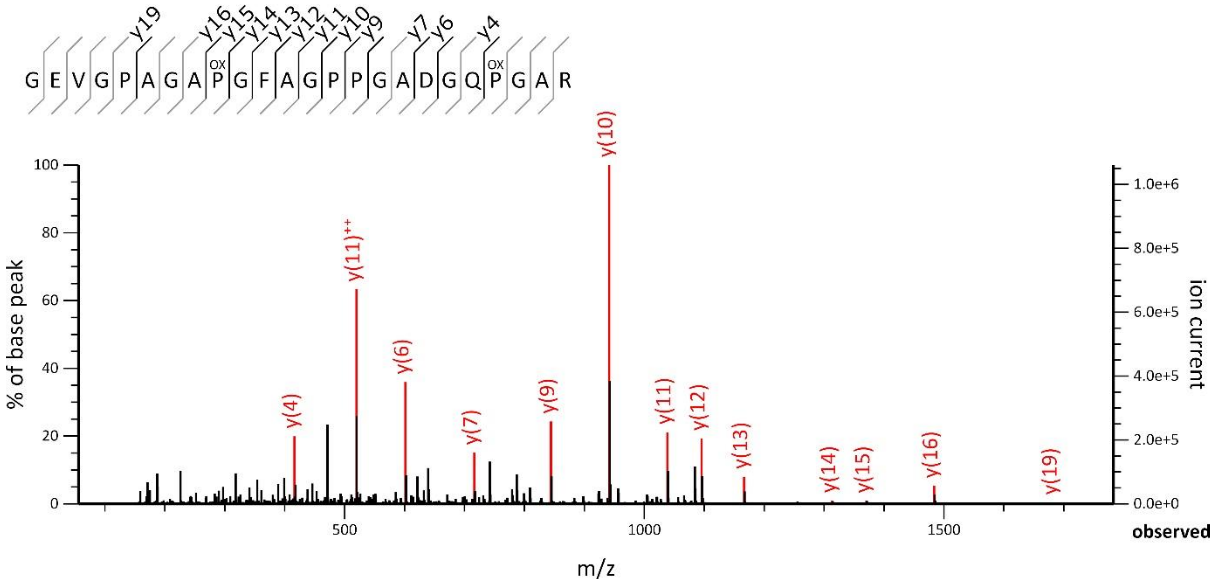

Figure D65. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Scophthalmus maximus*.

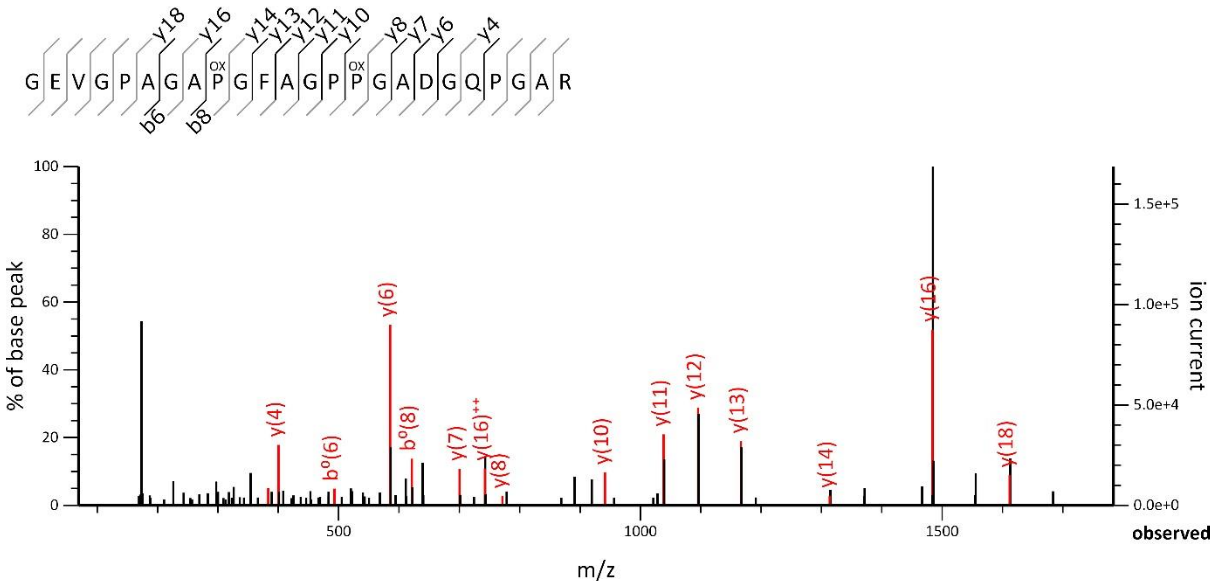

Figure D66. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Scophthalmus rhombus*.

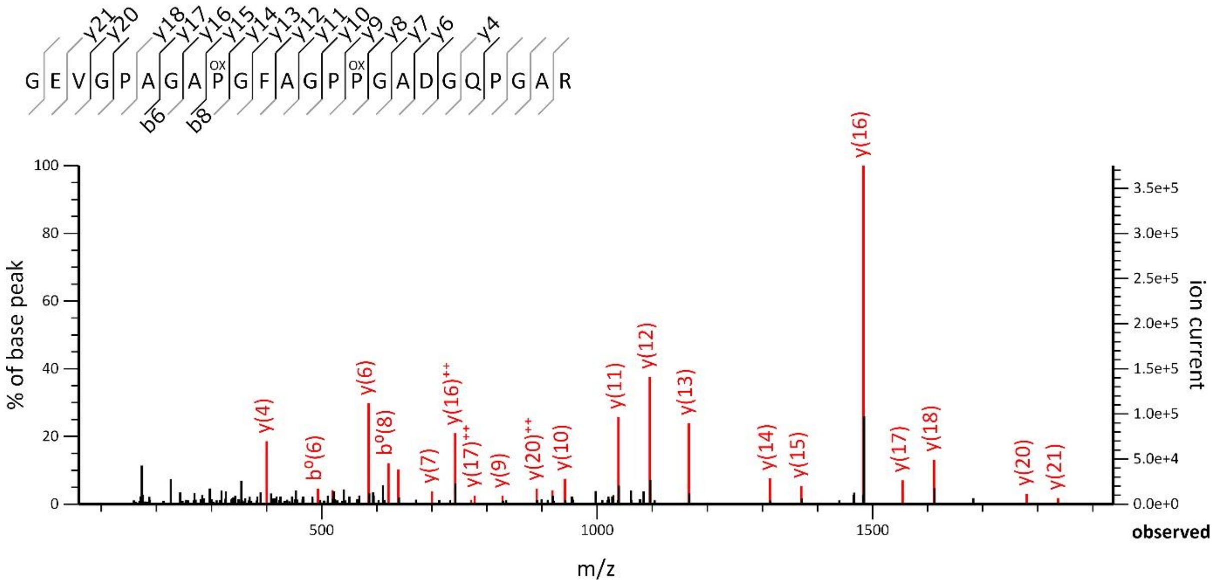

Figure D67. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Buglossidium luteum*.

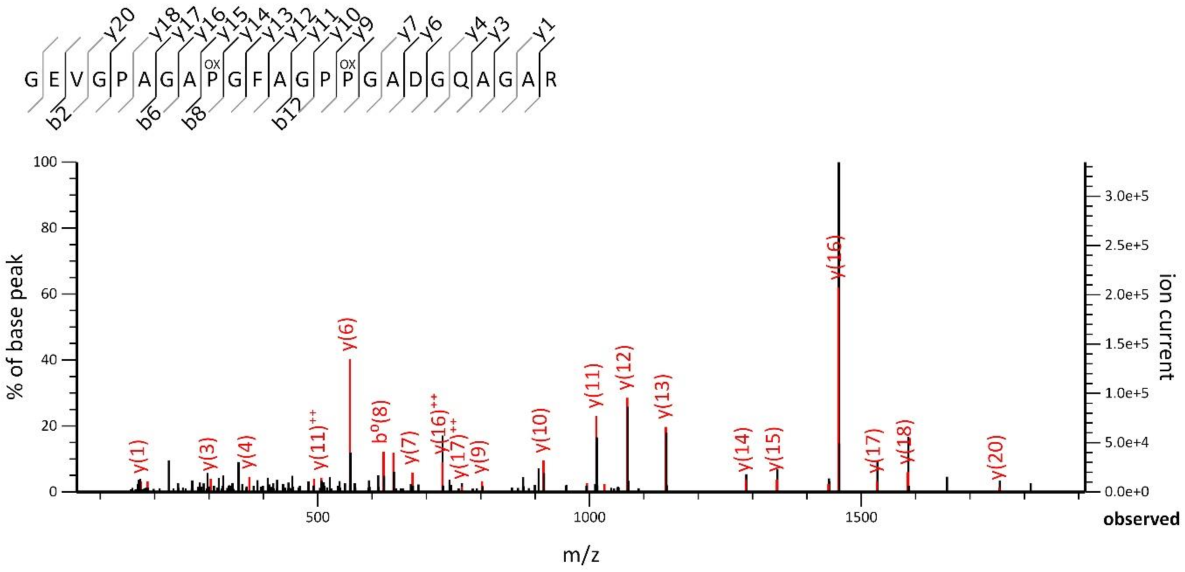

Figure D68. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Pegusa impar*.

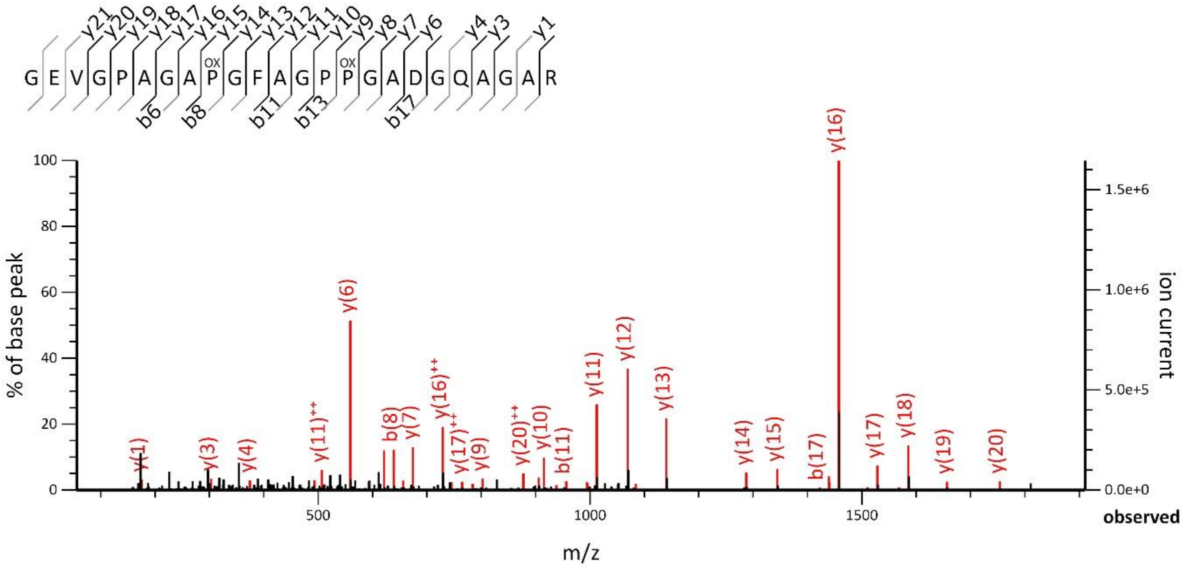

Figure D69. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Pegusa lascaris*.

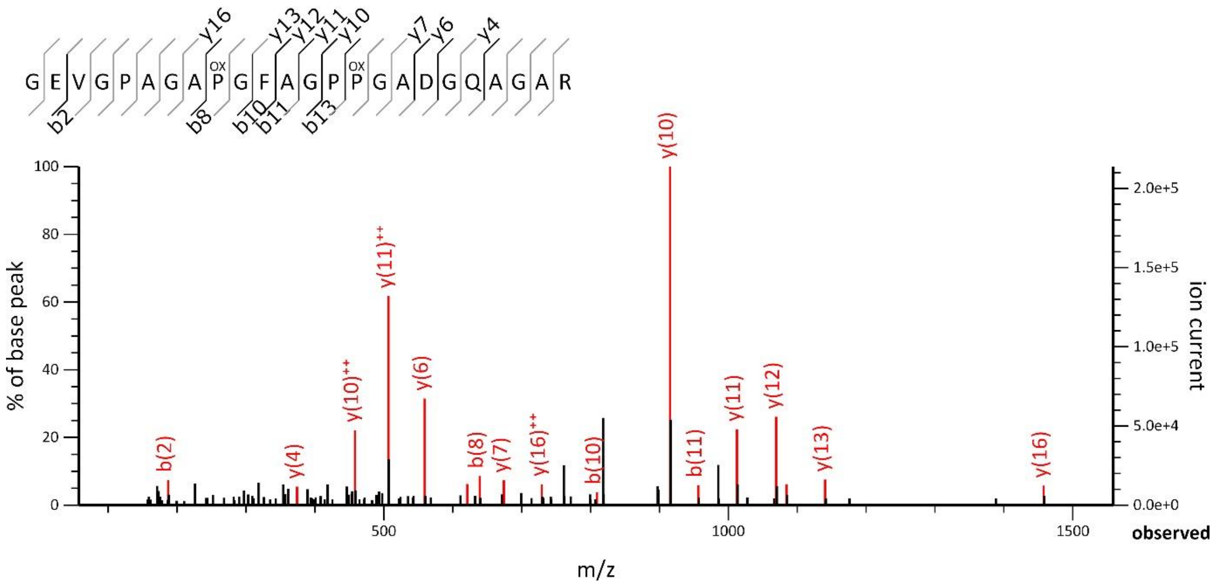

Figure D70. Ion spectrum of the COL1α2 625 – 648 peptide marker of *Solea solea*.

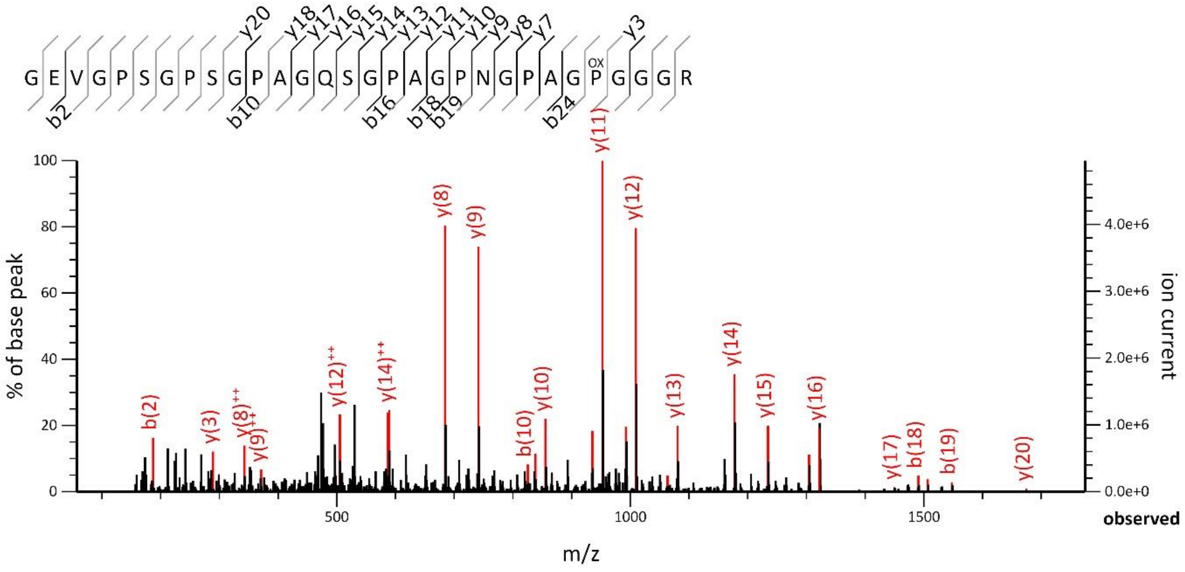

Figure D71. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Pleuronectes platessa*.

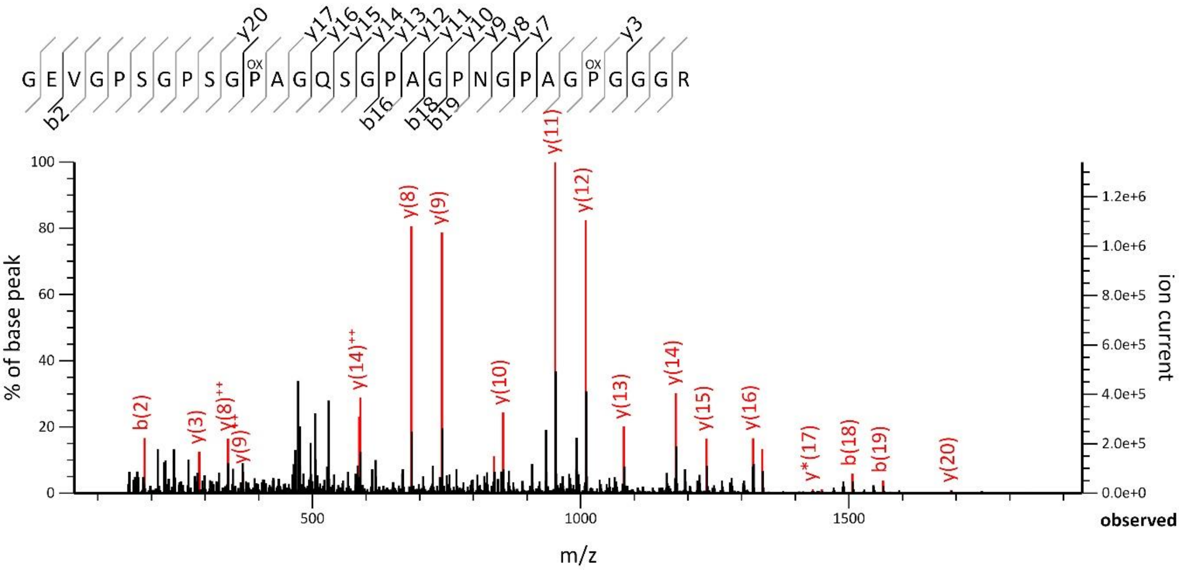

Figure D72. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Hippoglossoides platessoides*.

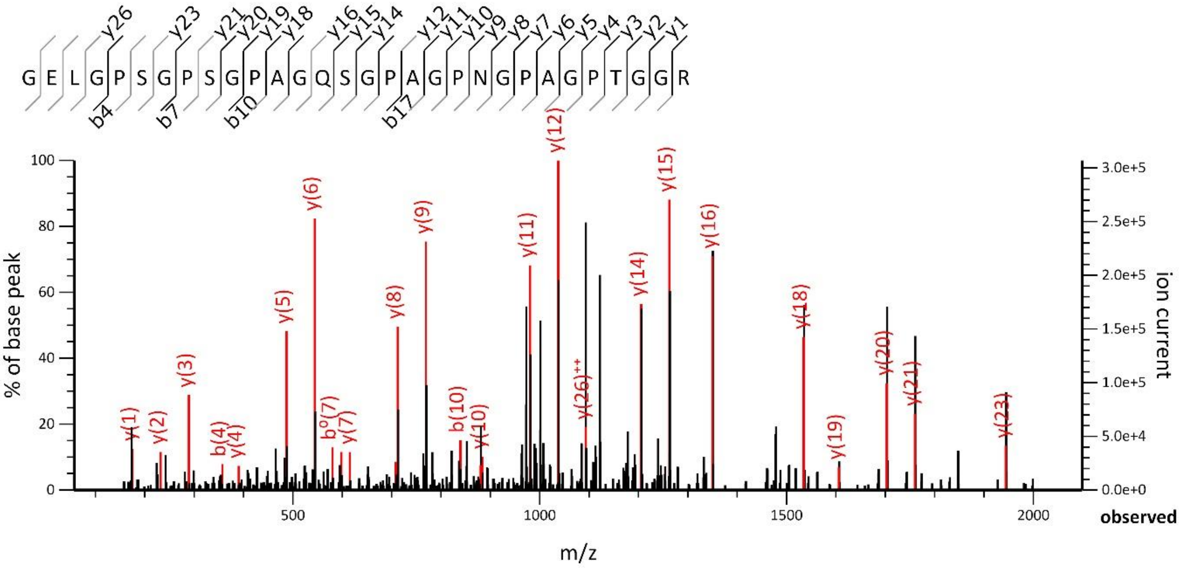

Figure D73. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Hippoglossus hippoglossus*.

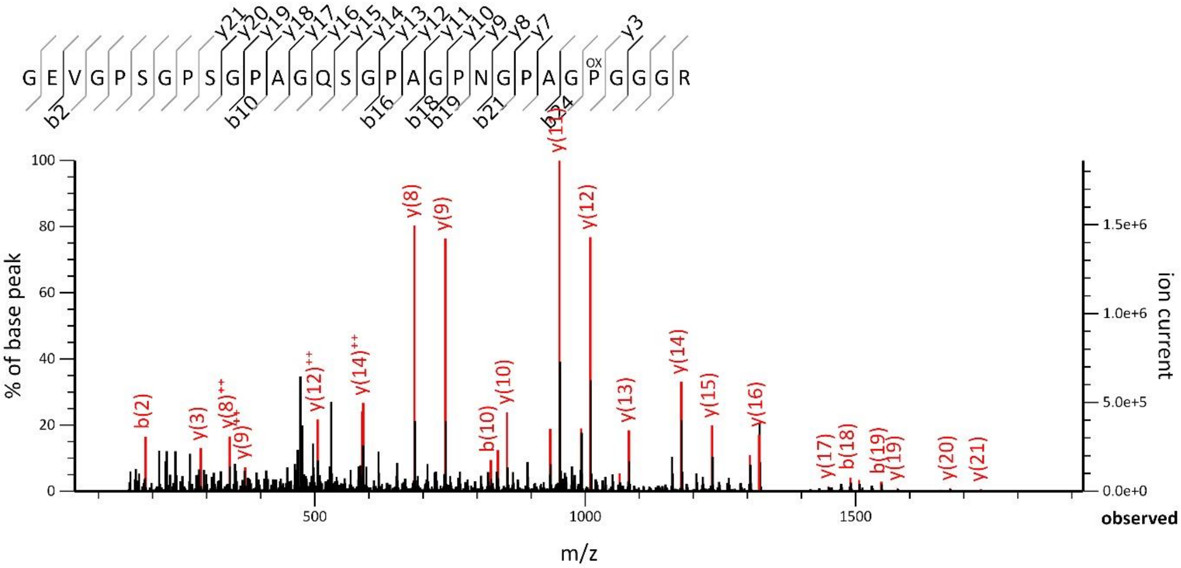

Figure D74. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Limanda limanda*.

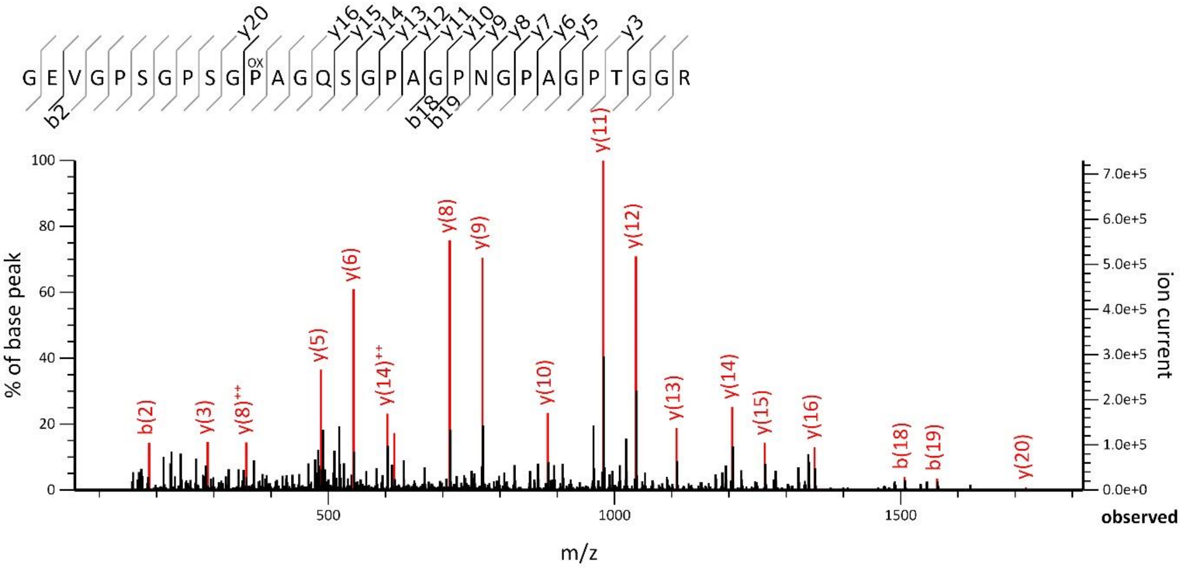

Figure D75. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Microstomus kitt*.

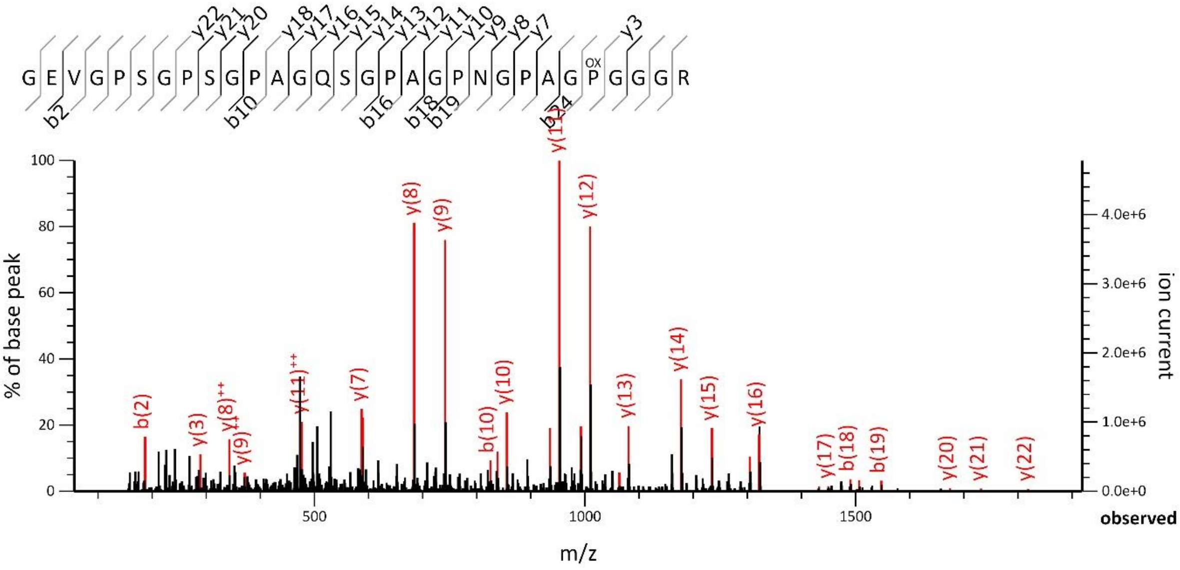

Figure D76. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Platichthys flesus*.

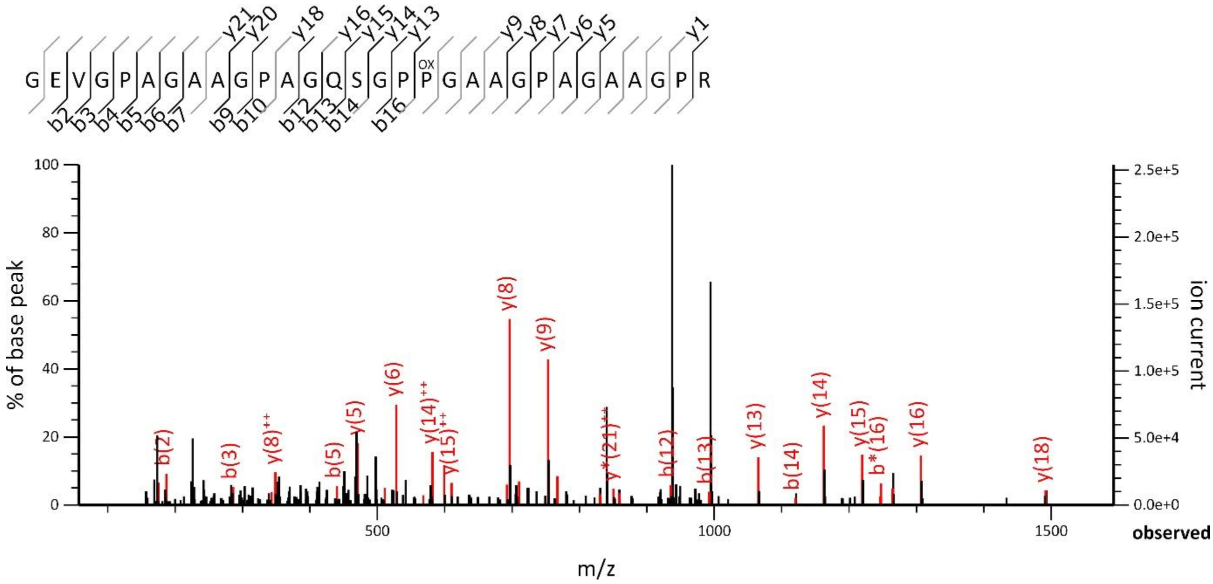

Figure D77. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Citharus linguatula*.

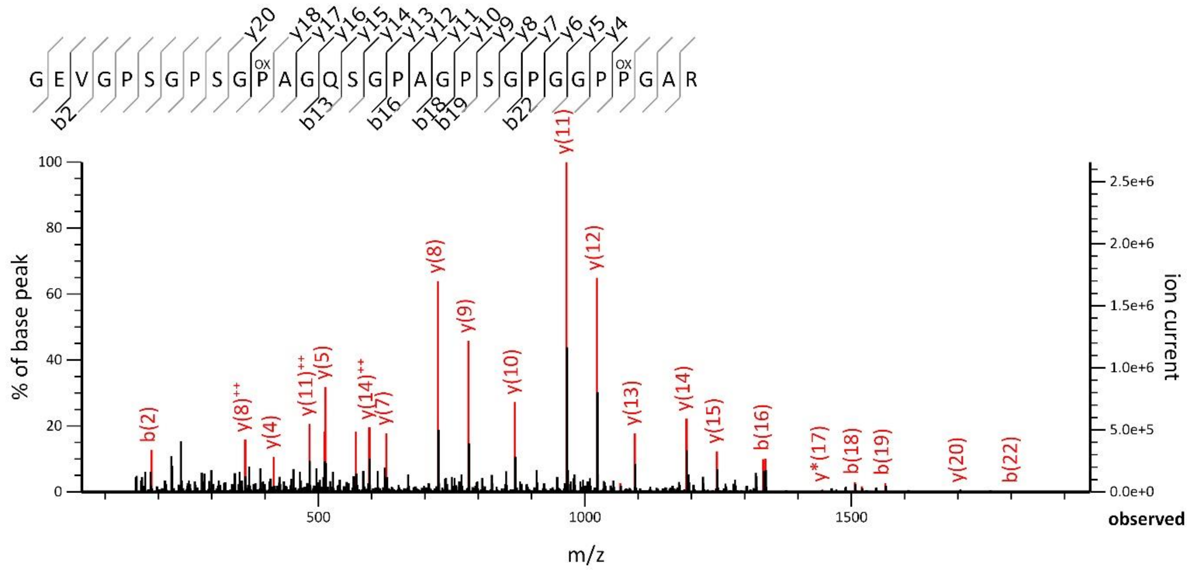

Figure D78. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Lepidorhombus boscii*.

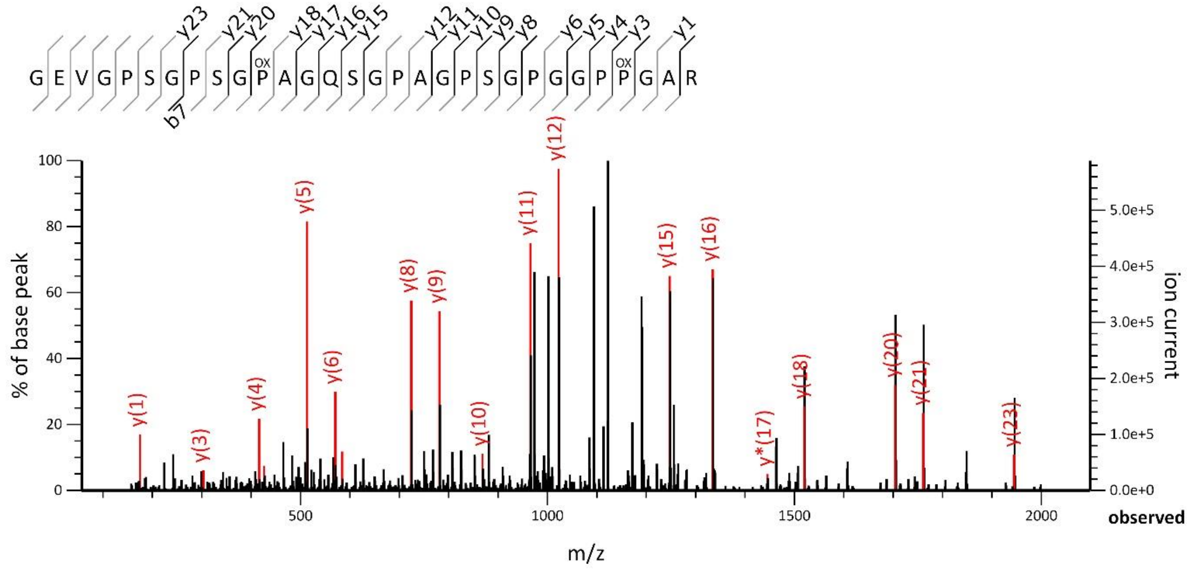

Figure D79. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Lepidorhombus whiffiagonis*.

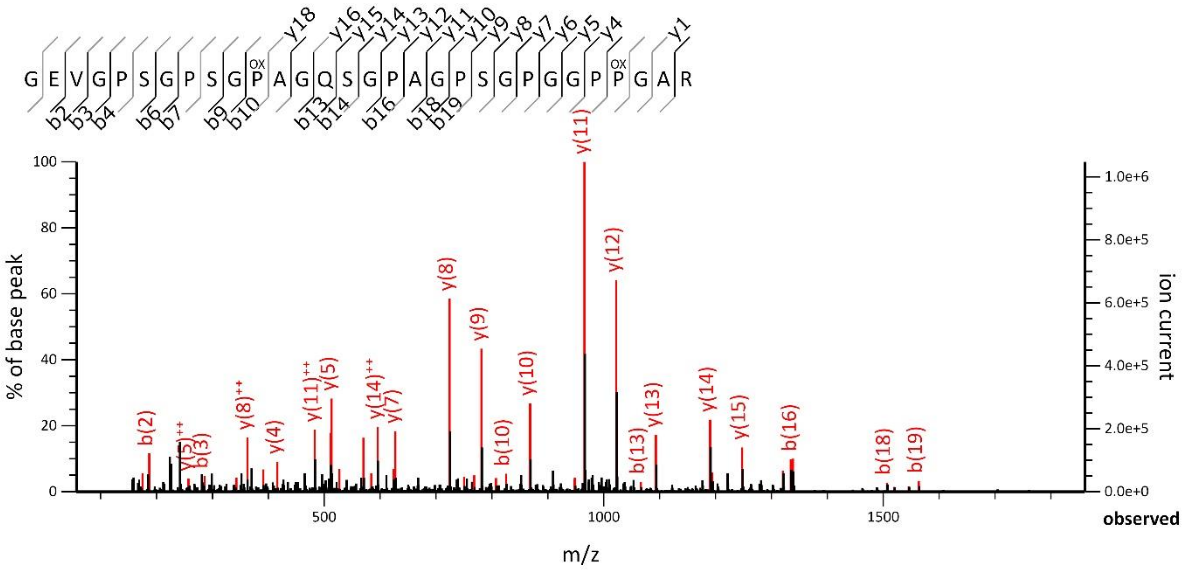

Figure D80. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Zeugopterus regius*.

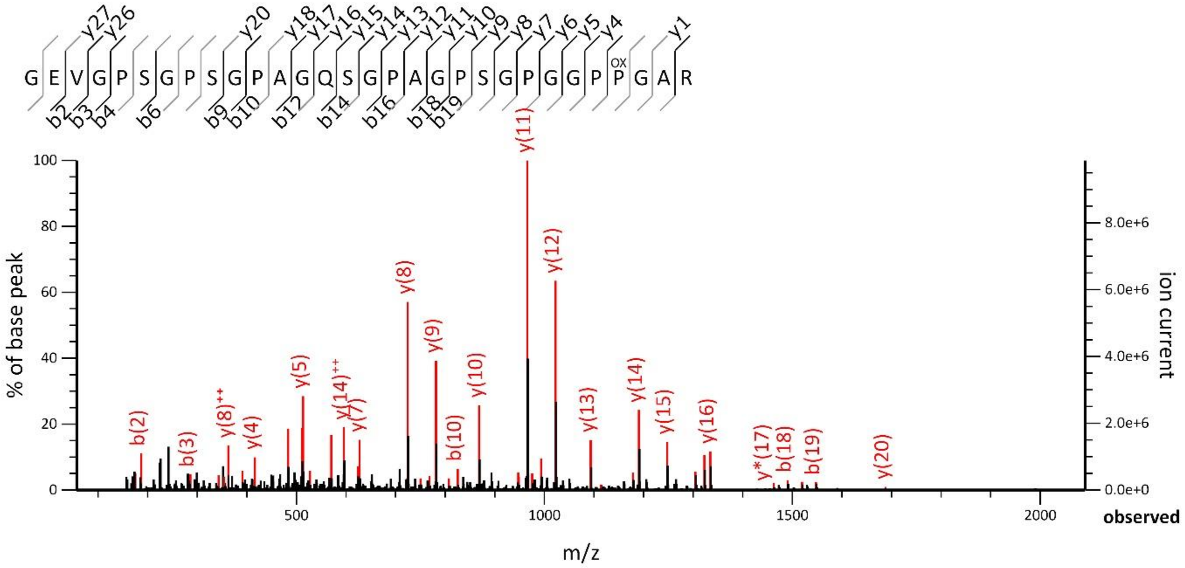

Figure D81. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Scophthalmus maximus*.

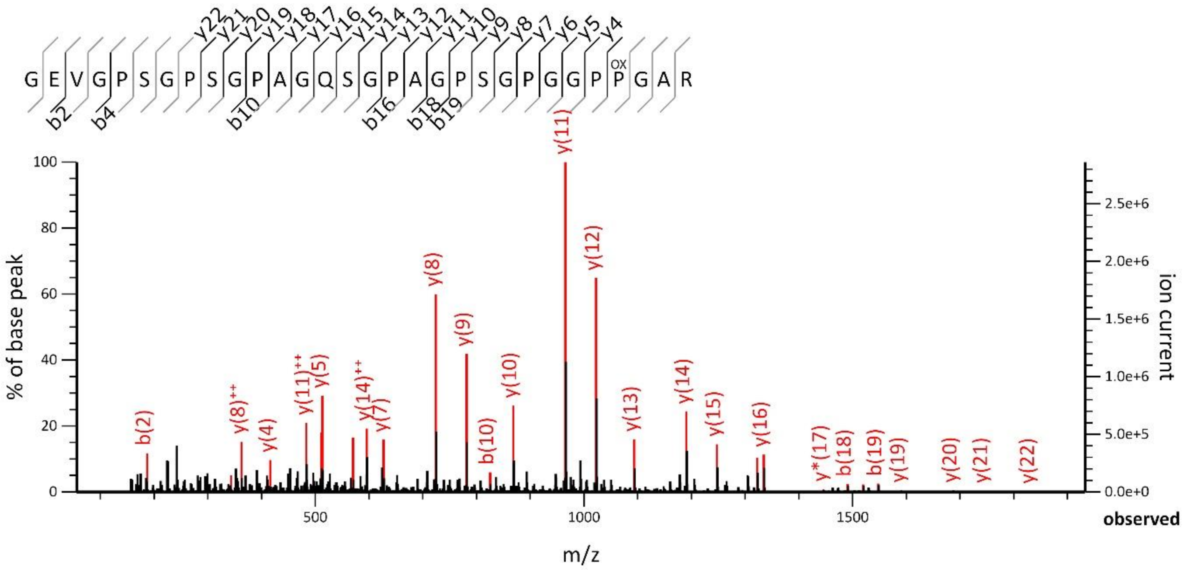

Figure D82. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Scophthalmus rhombus*.

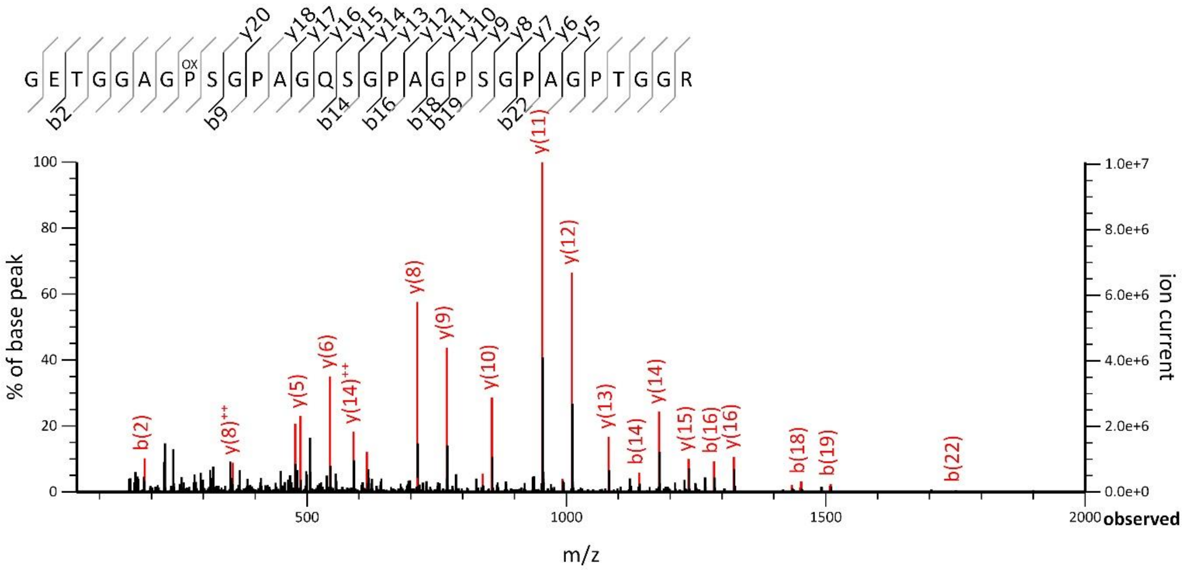

Figure D83. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Buglossidium luteum*.

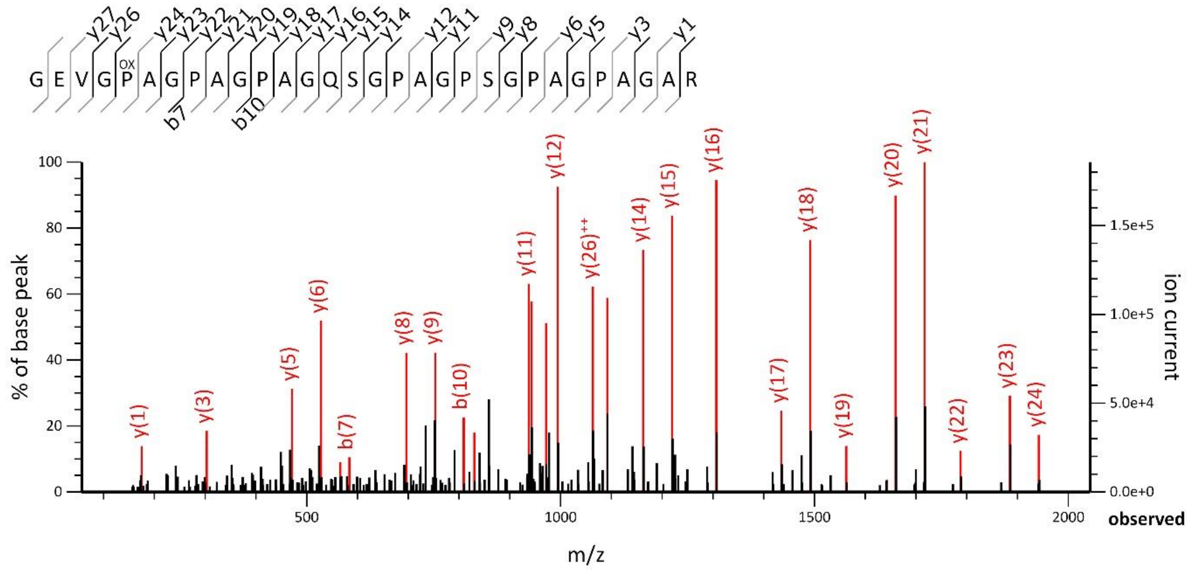

Figure D84. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Pegusa impar*.

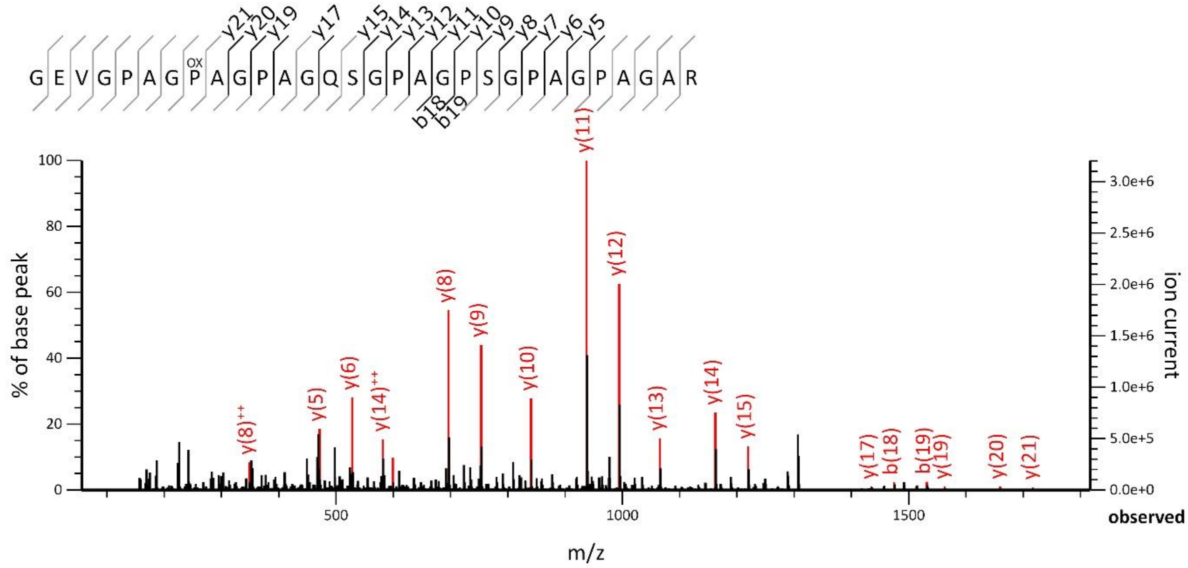

Figure D85. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Pegusa lascaris*.

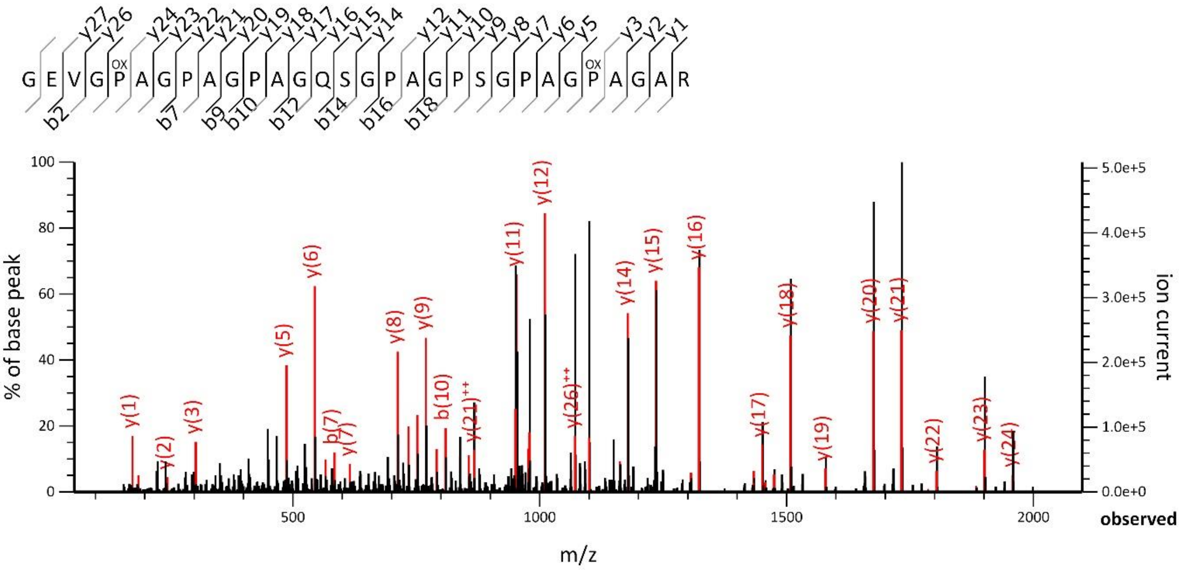

Figure D86. Ion spectrum of the COL1α2 658 – 687 peptide marker of *Solea solea*.

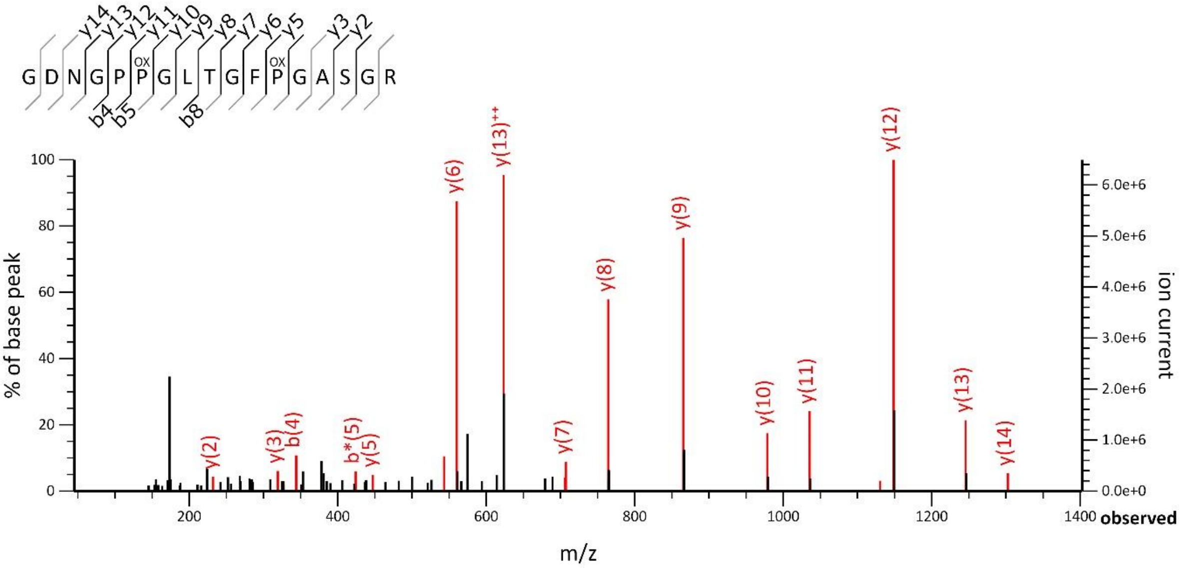

Figure D87. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Glyptocephalus cynoglossus*.

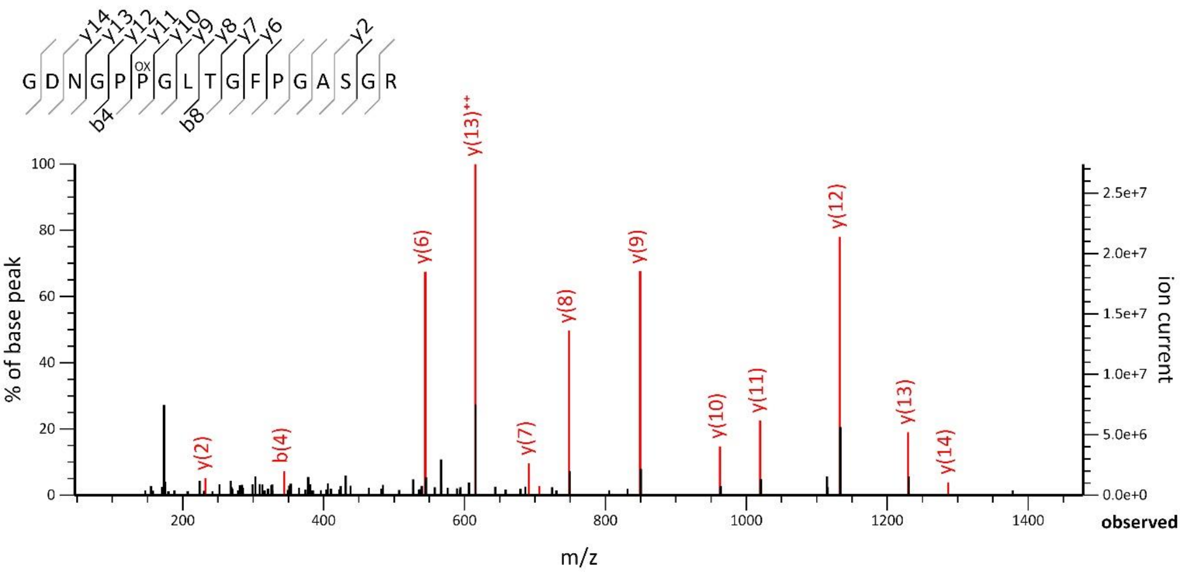

Figure D88. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Hippoglossoides platessoides*.

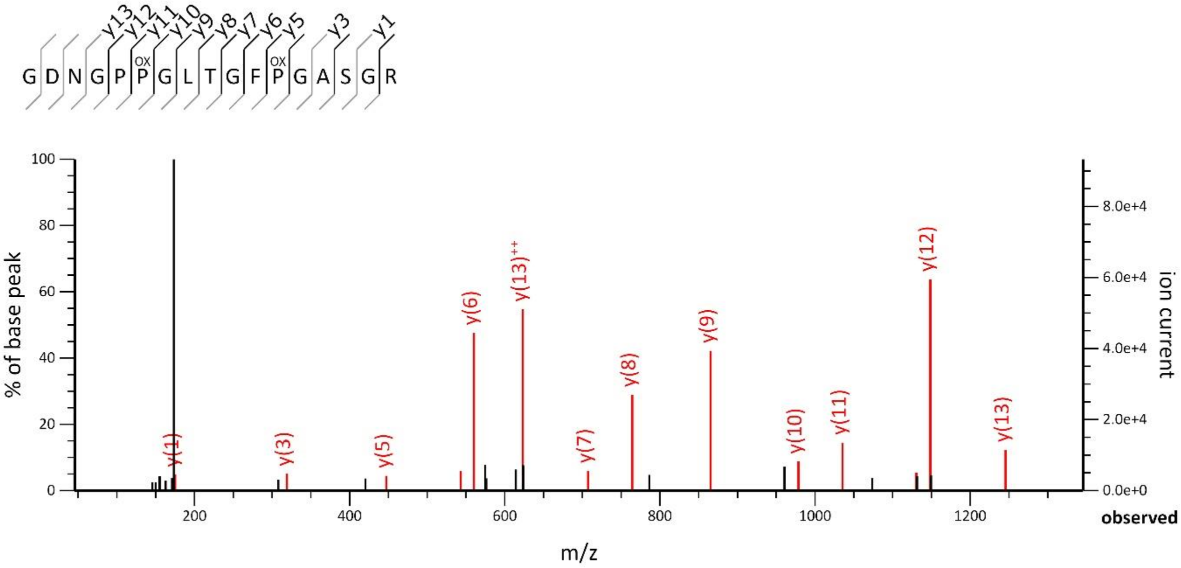

Figure D89. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Hippoglossus hippoglossus*.

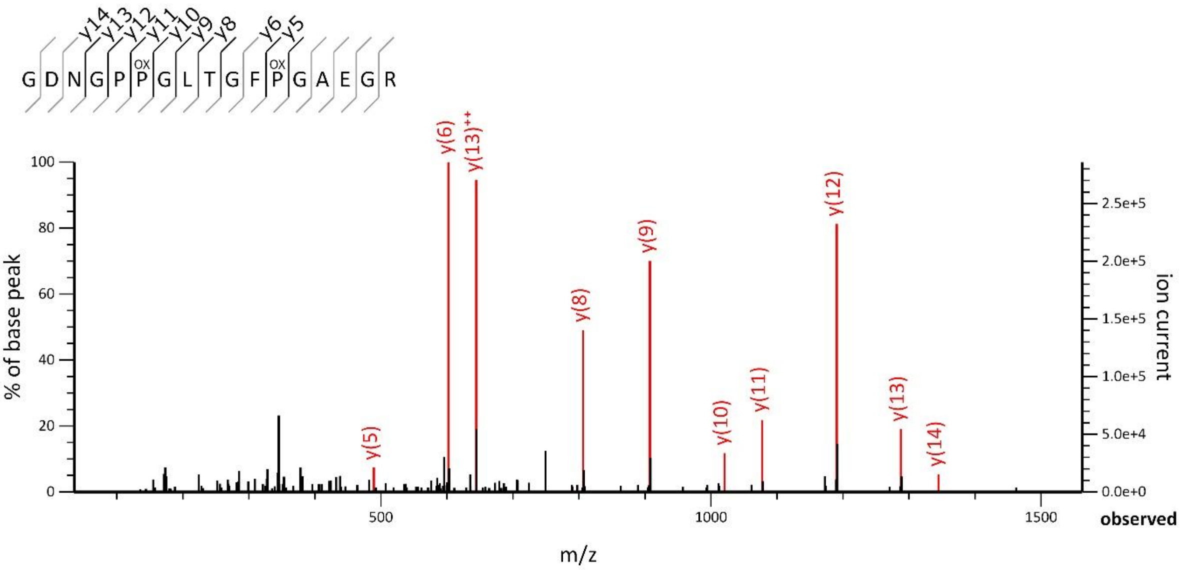

Figure D90. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Limanda limanda*.

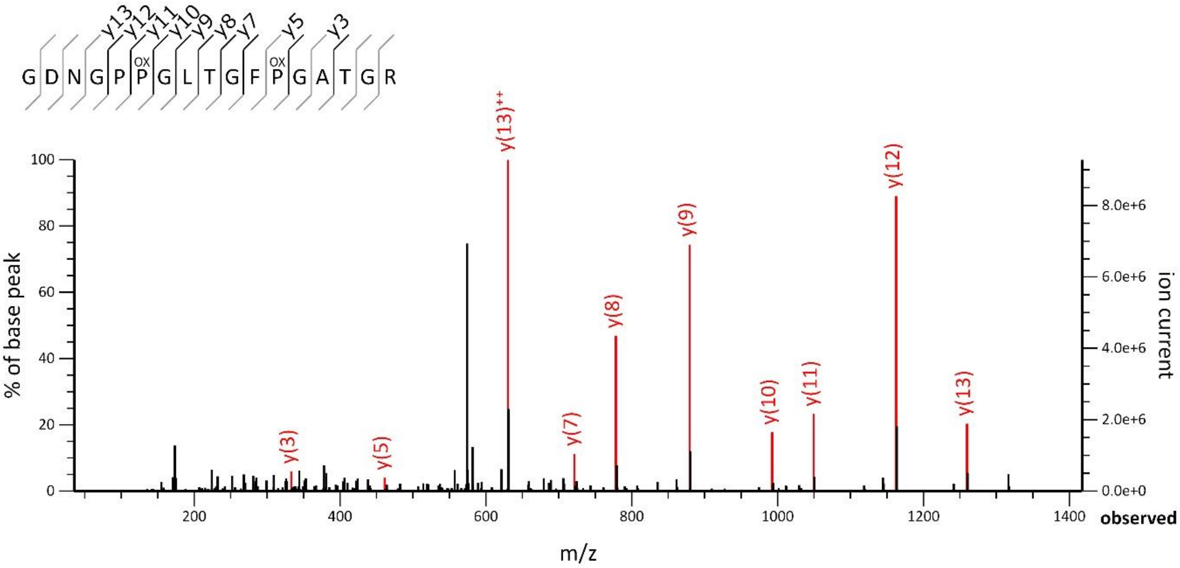

Figure D91. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Microstomus kitt*.

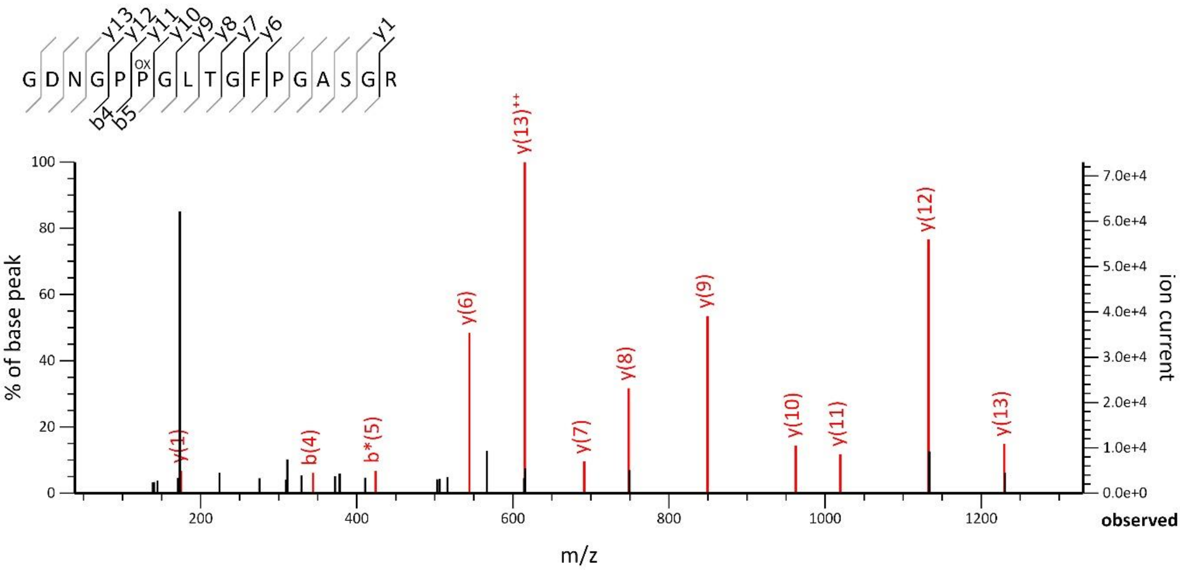

Figure D92. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Platichthys flesus*.

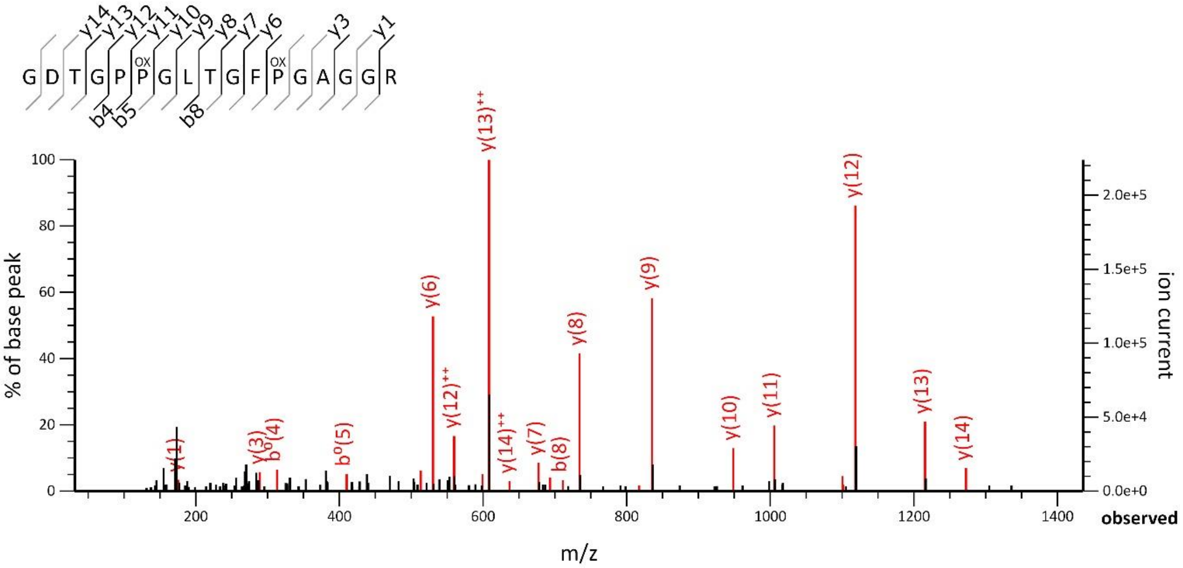

Figure D93. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Arnoglossus laterna*.

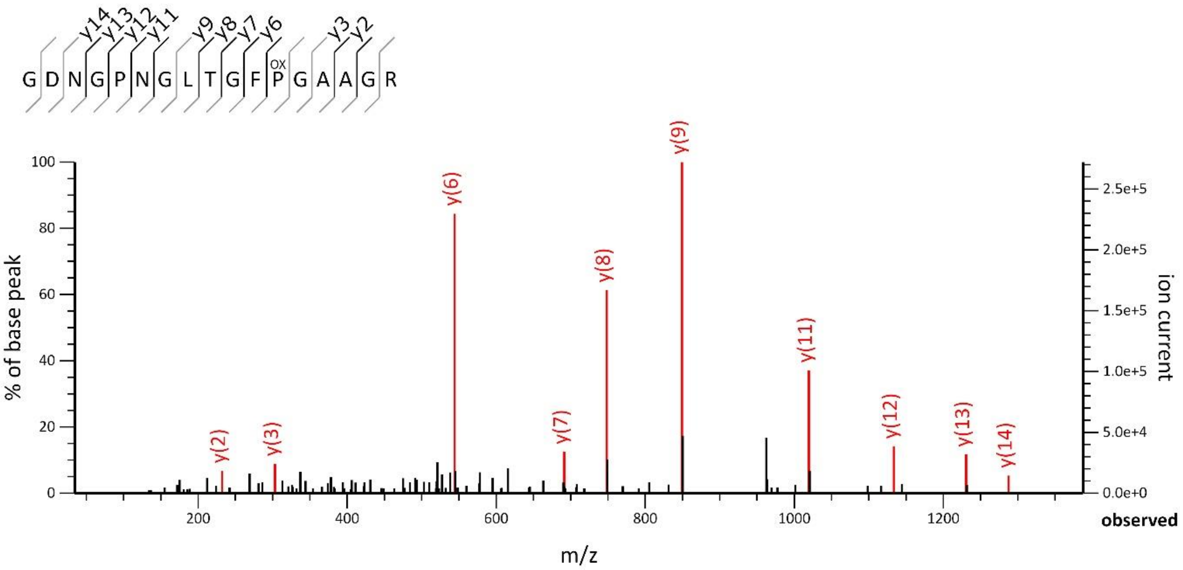

Figure D94. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Citharus linguatula*.

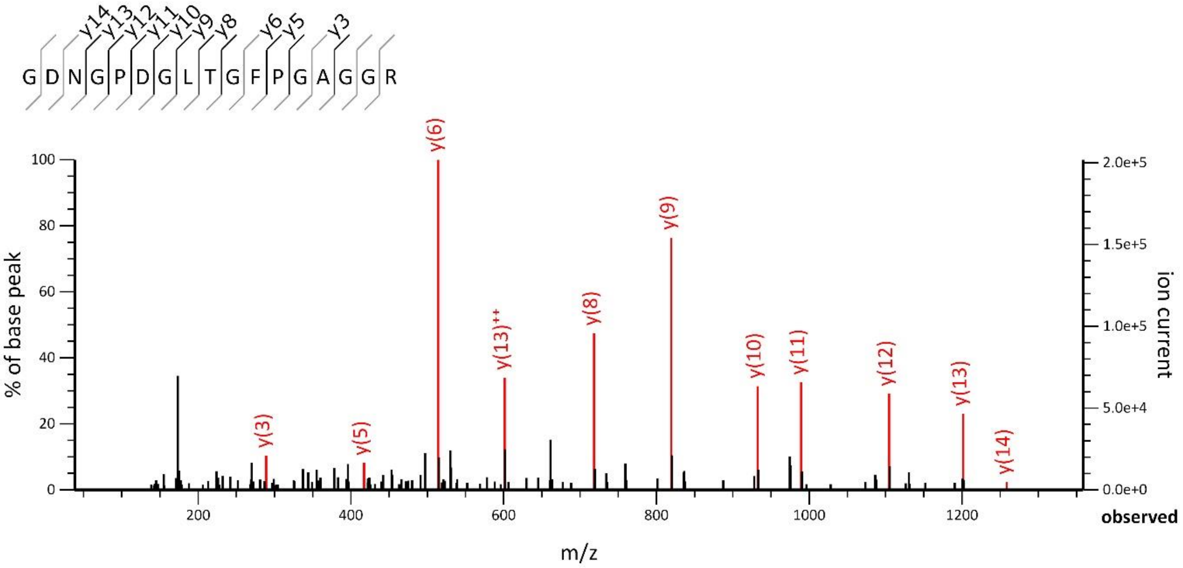

Figure D95. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Lepidorhombus boscii*.

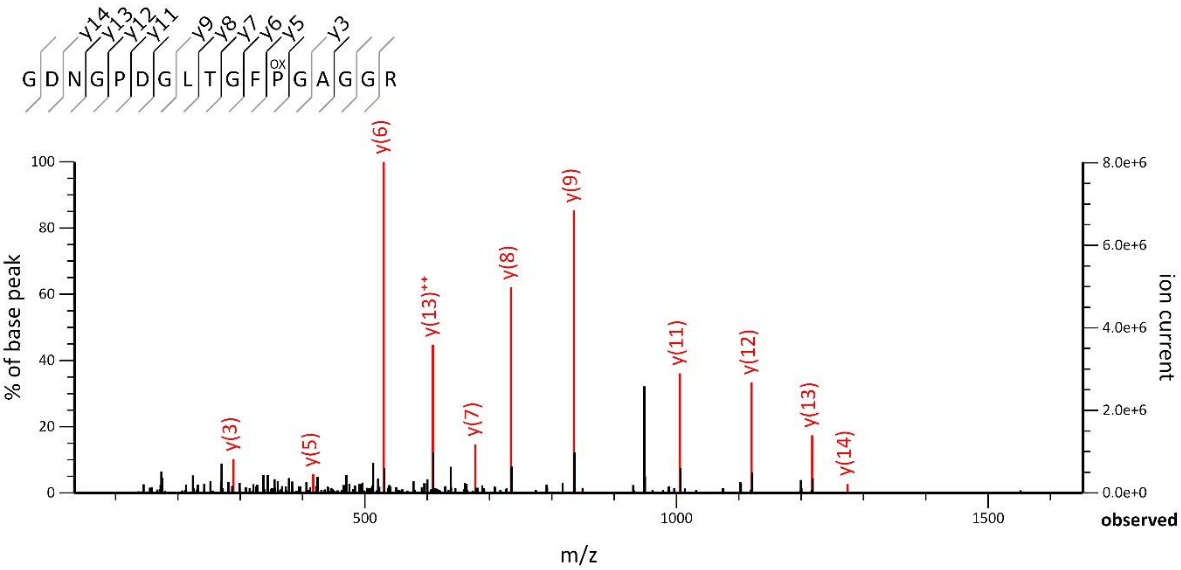

Figure D96. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Lepidorhombus whiffiagonis*.

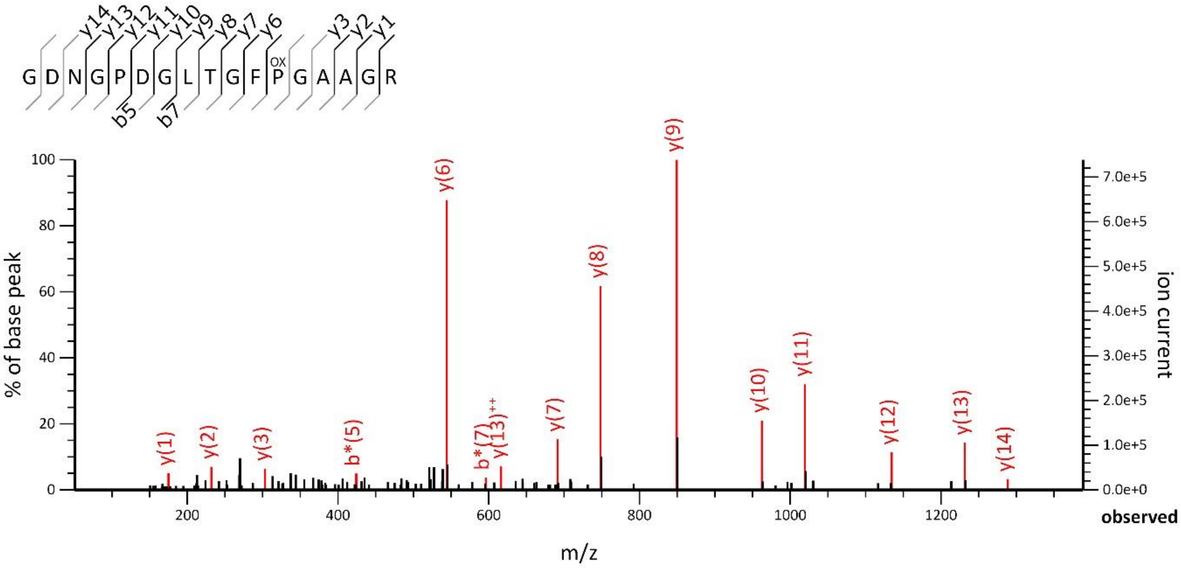

Figure D97. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Zeugopterus regius*.

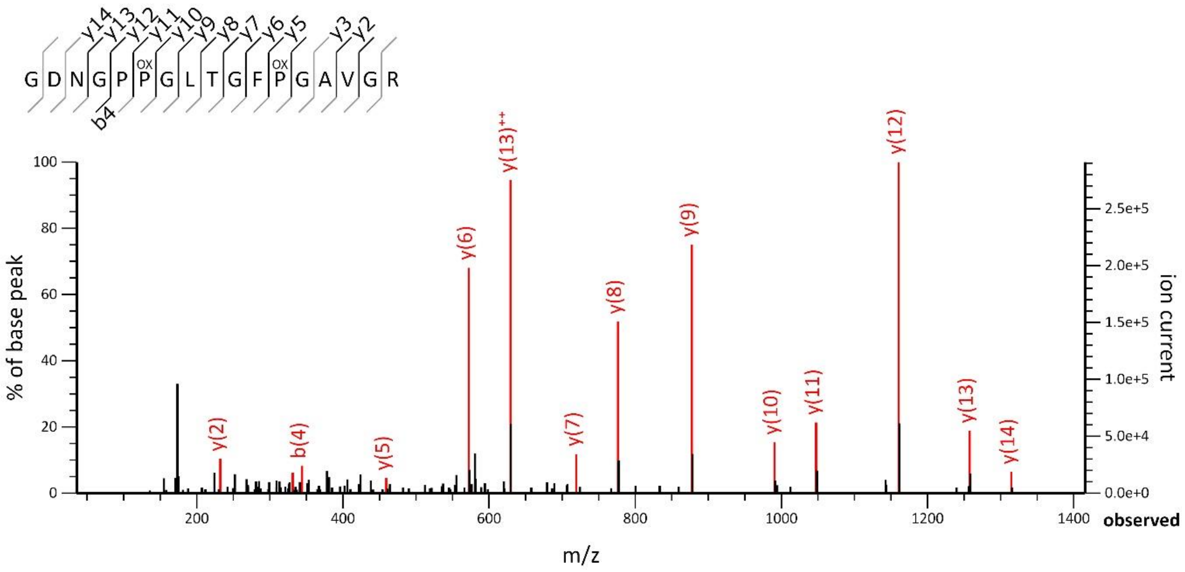

Figure D98. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Scophthalmus maximus*.

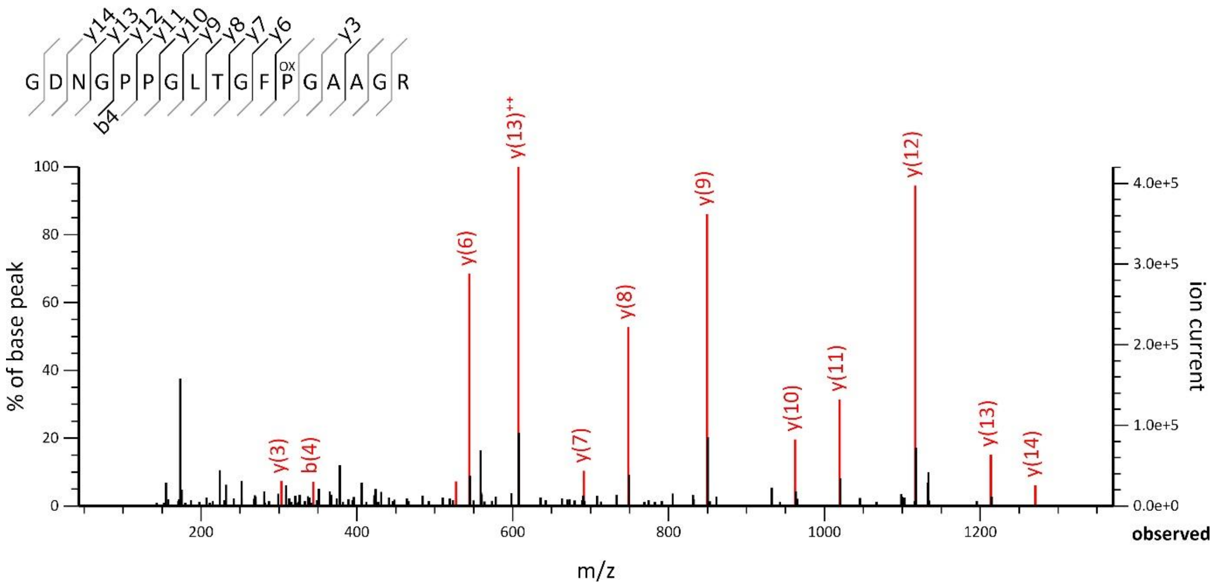

Figure D99. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Scophthalmus rhombus*.

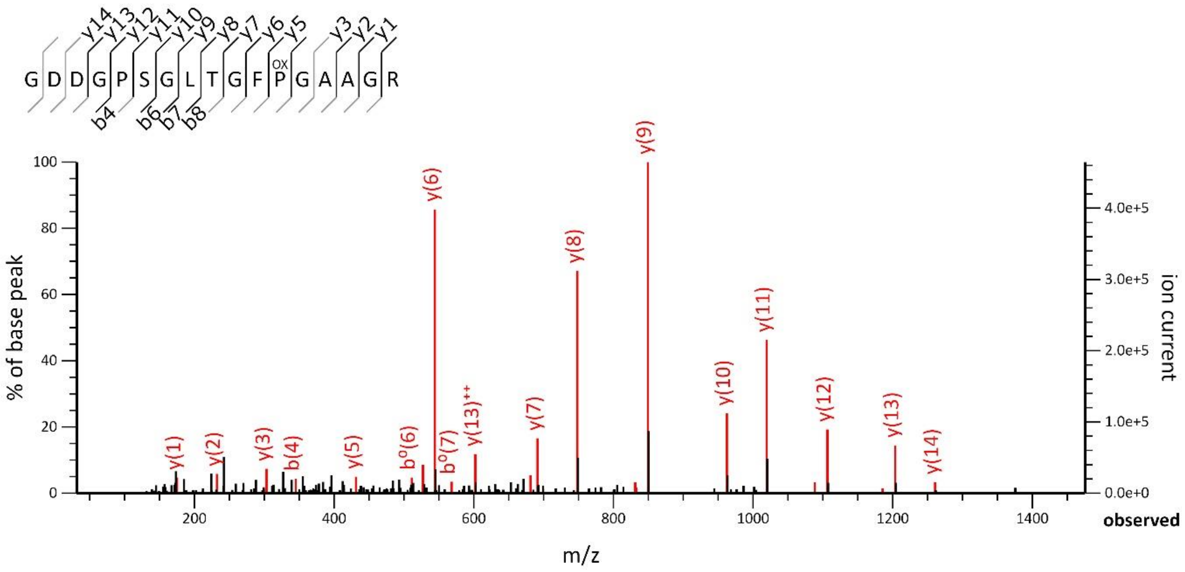

Figure D100. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Buglossidium luteum*.

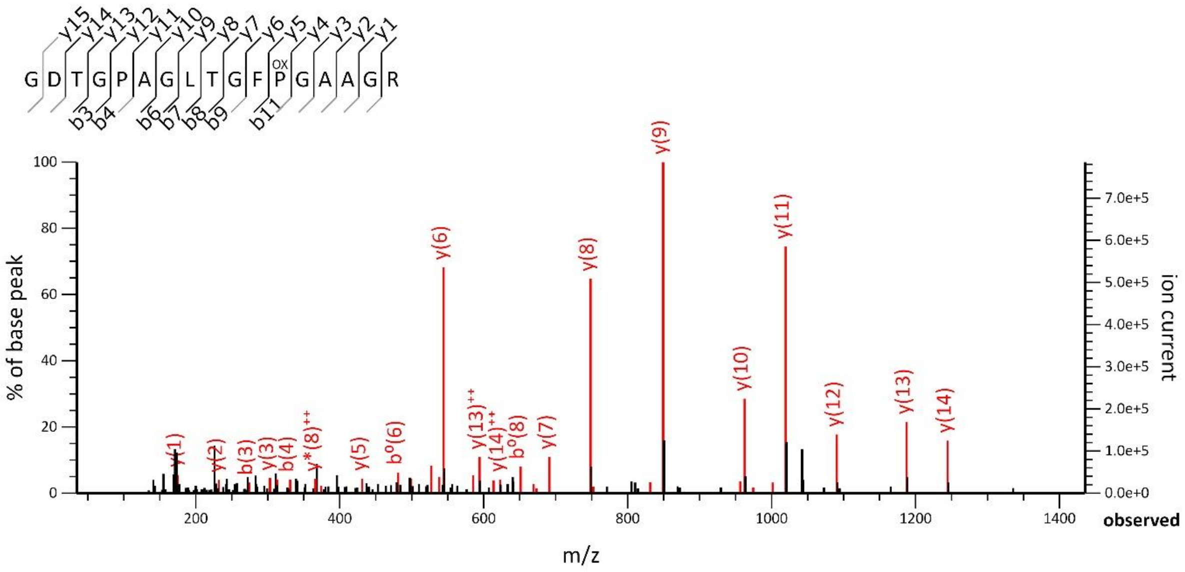

Figure D101. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Pegusa impar*.

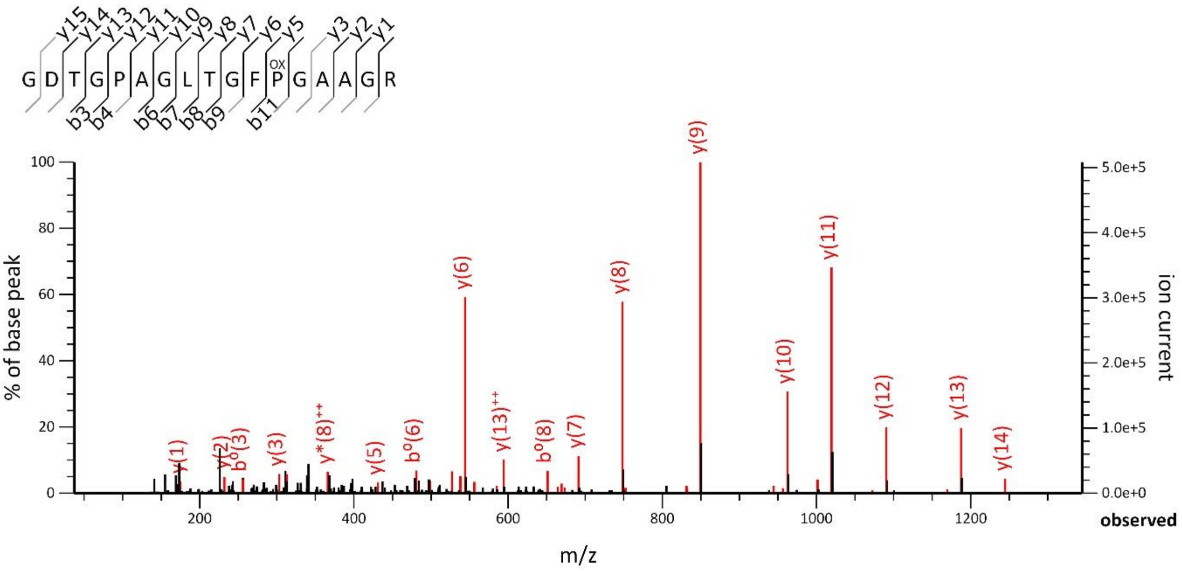

Figure D102. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Pegusa lascaris*.

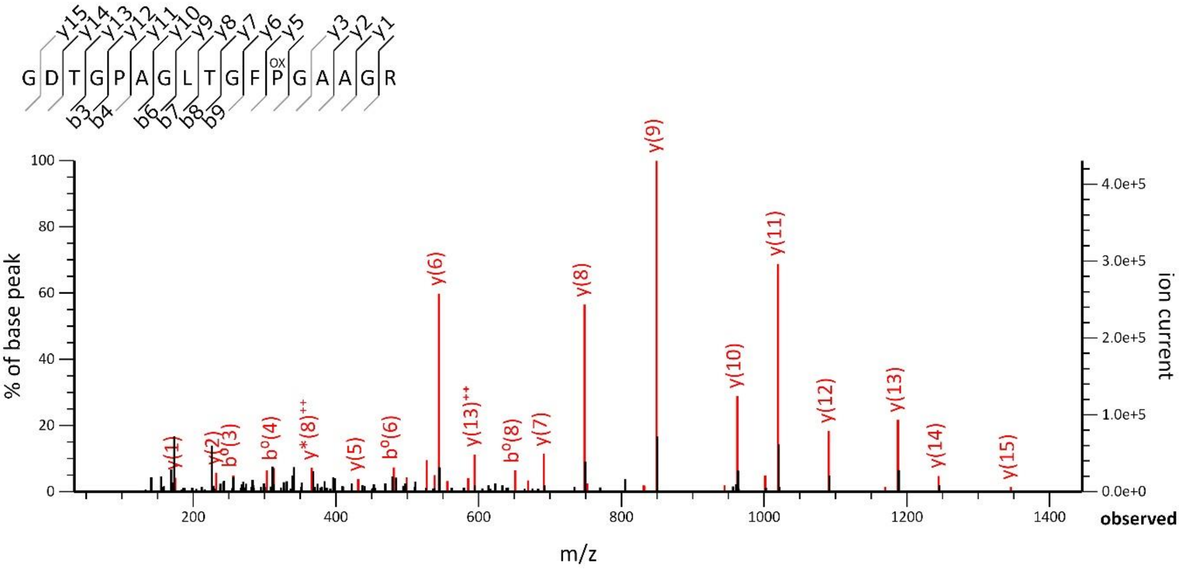

Figure D103. Ion spectrum of the COL1α2 688 – 704 peptide marker of *Solea solea*.

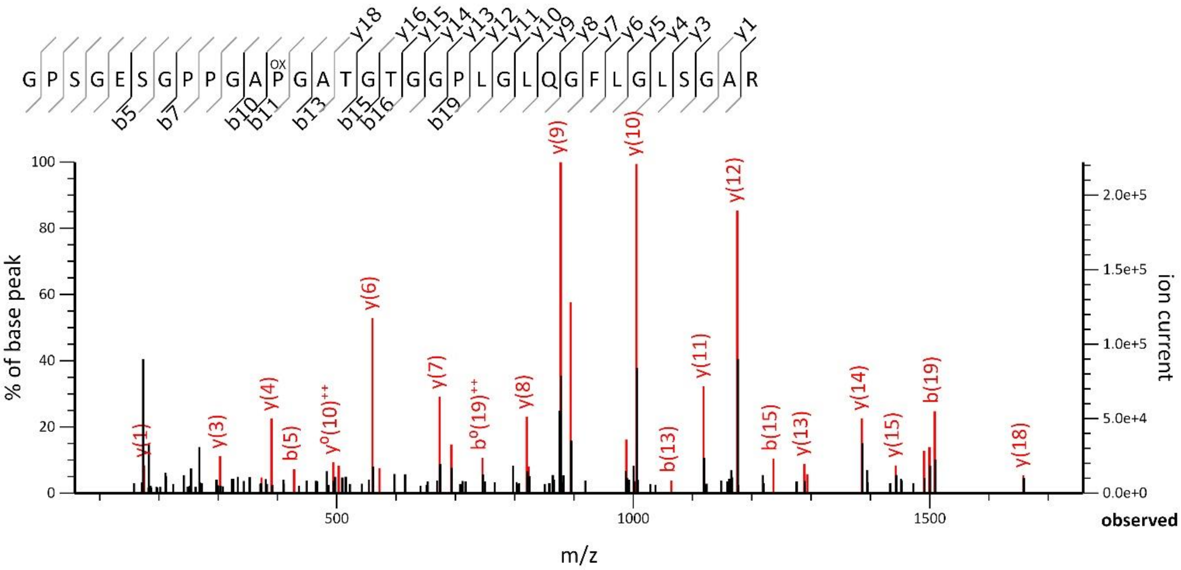

Figure D104. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Pleuronectes platessa*.

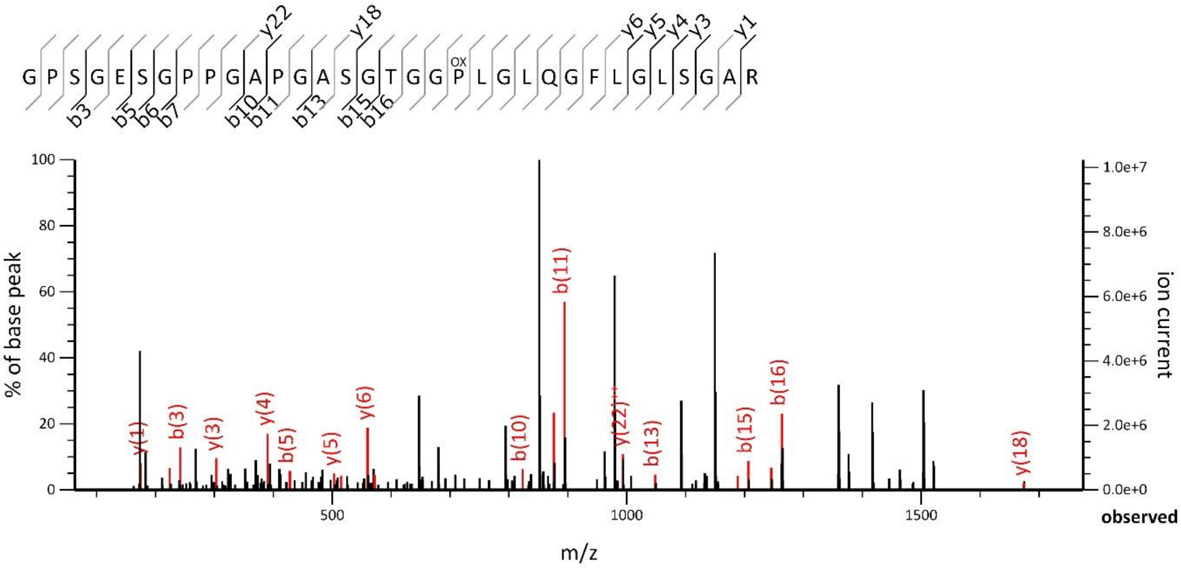

Figure D105. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Glyptocephalus cynoglossus*.

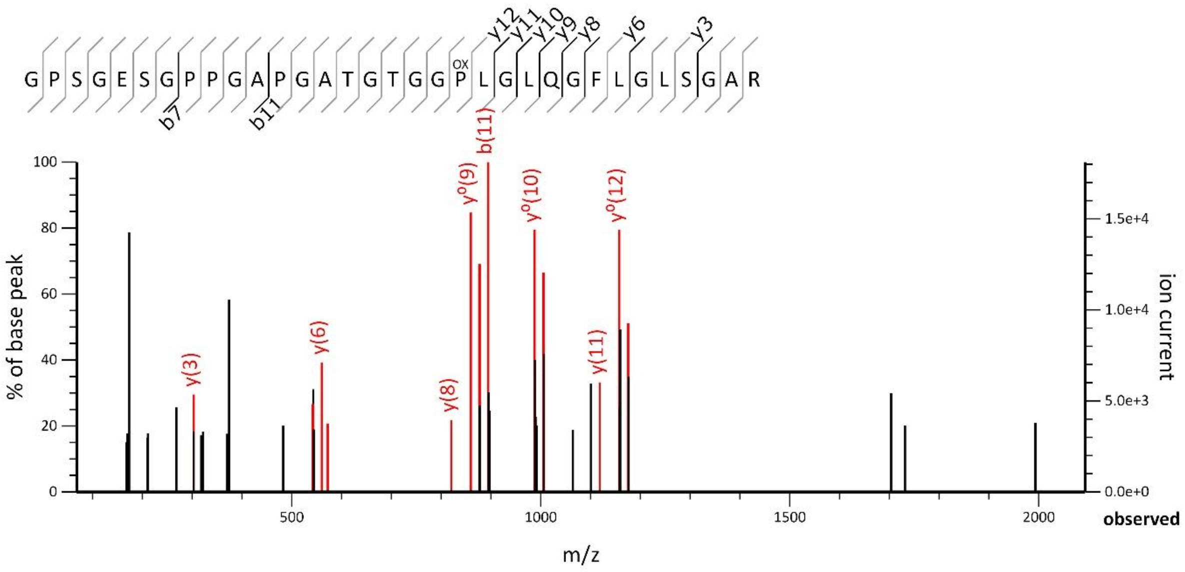

Figure D106. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Hippoglossoides platessoides*.

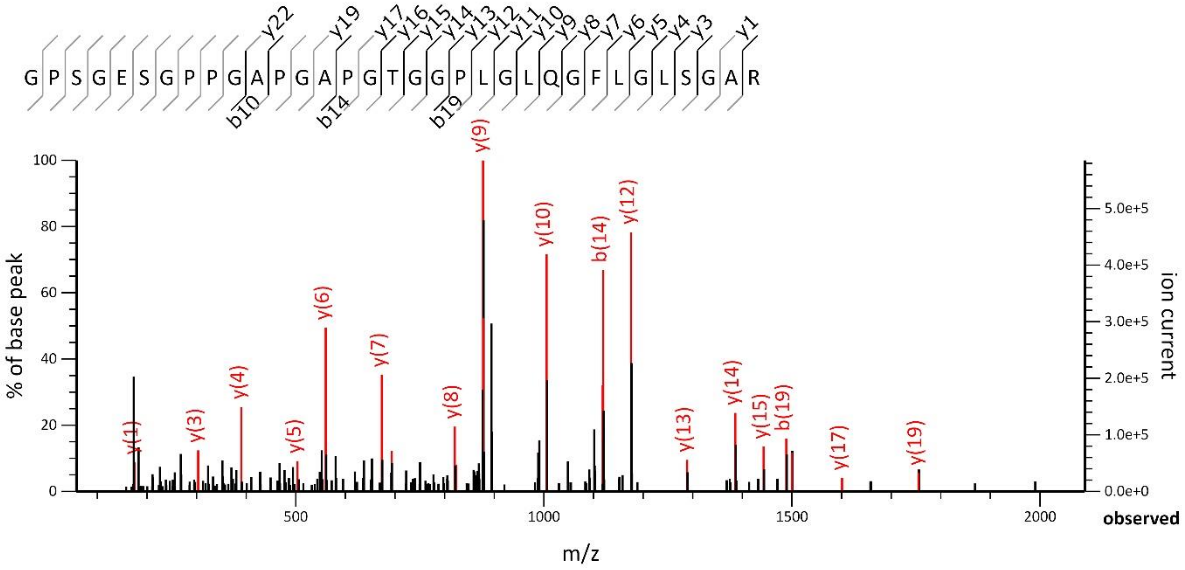

Figure D107. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Hippoglossus hippoglossus*.

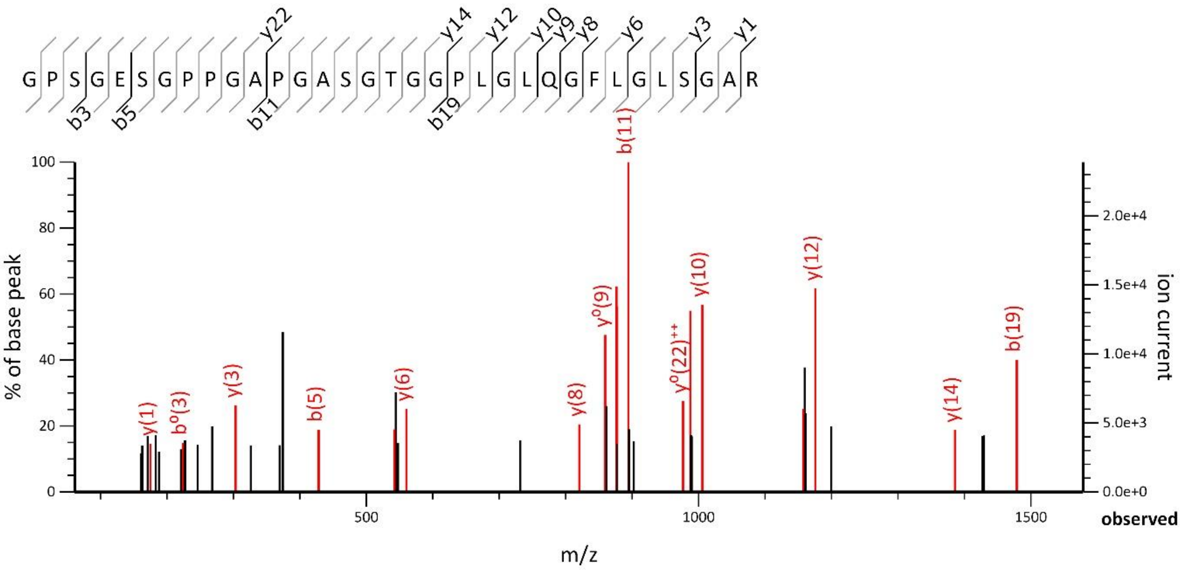

Figure D108. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Limanda limanda*.

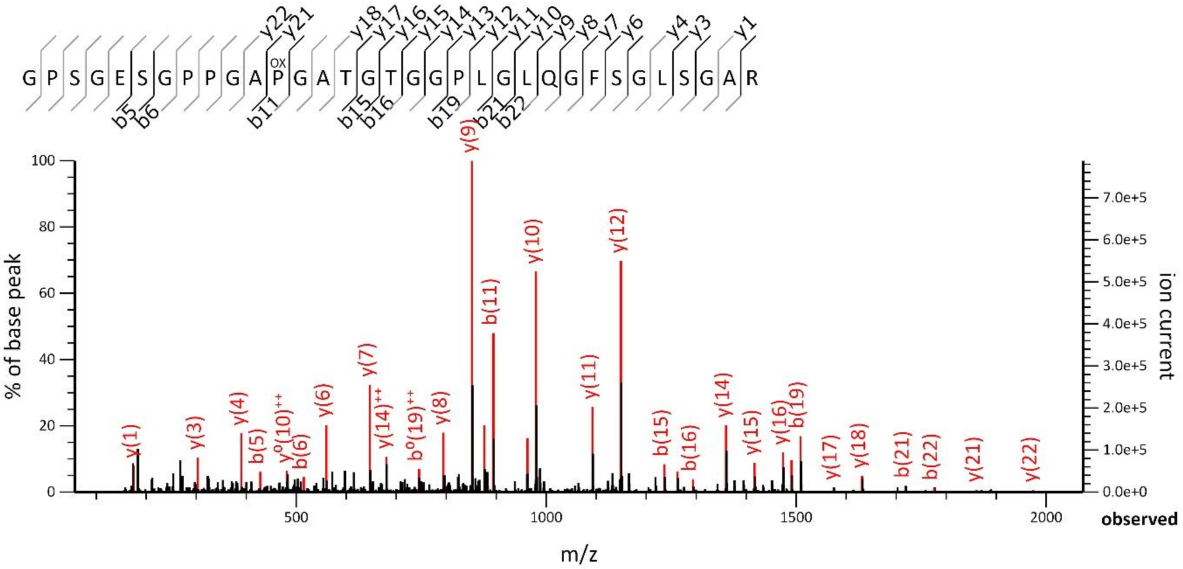

Figure D109. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Microstomus kitt*.

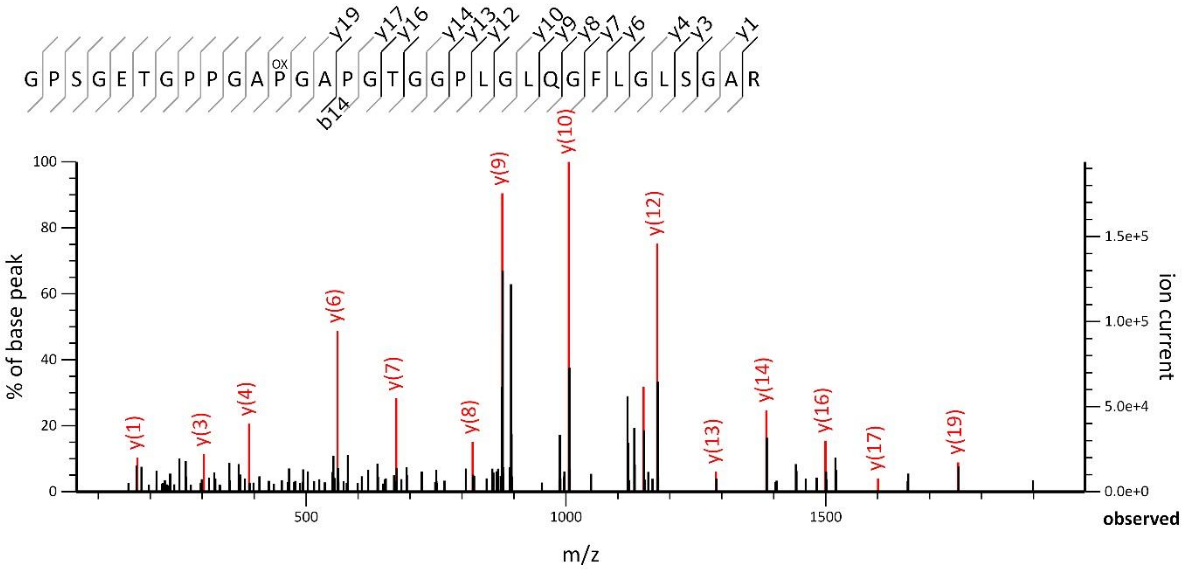

Figure D110. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Platichthys flesus*.

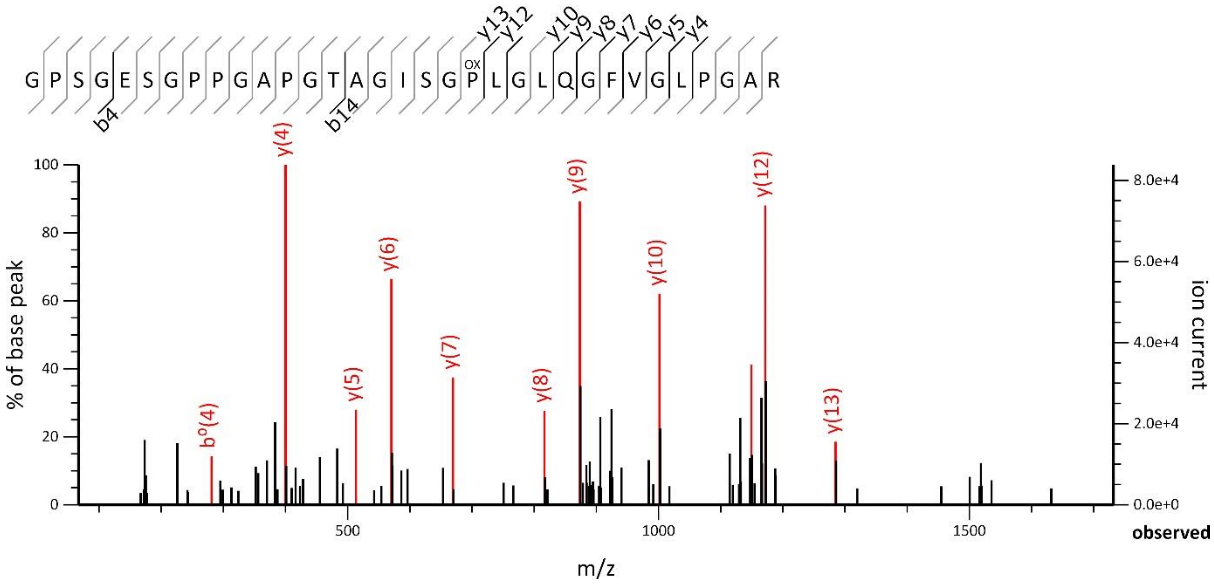

Figure D111. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Citharus linguatula*.

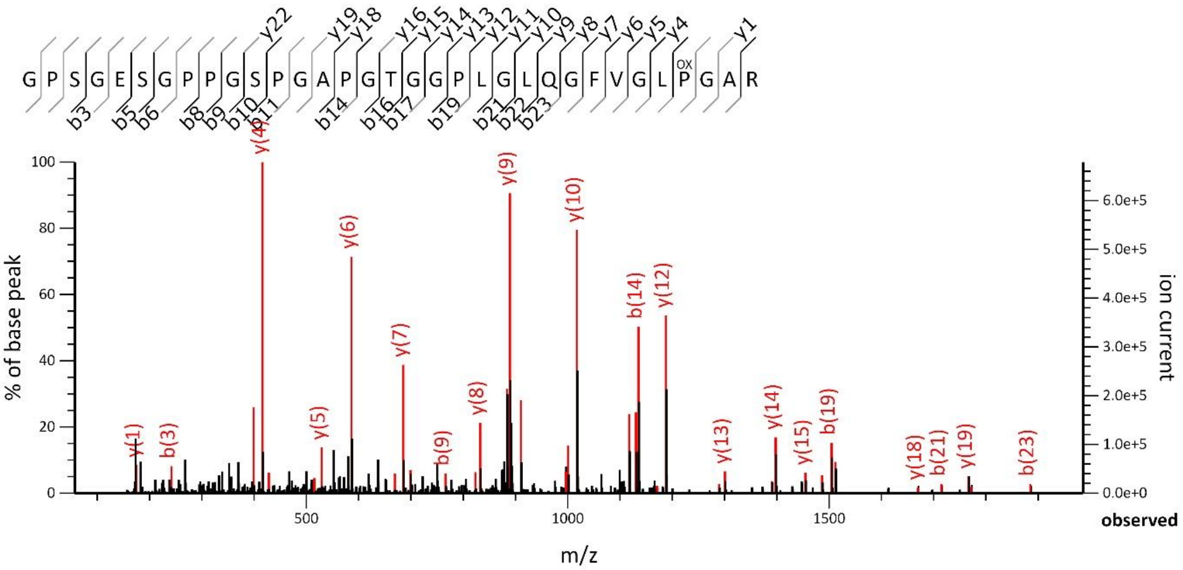

Figure D112. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Lepidorhombus boscii*.

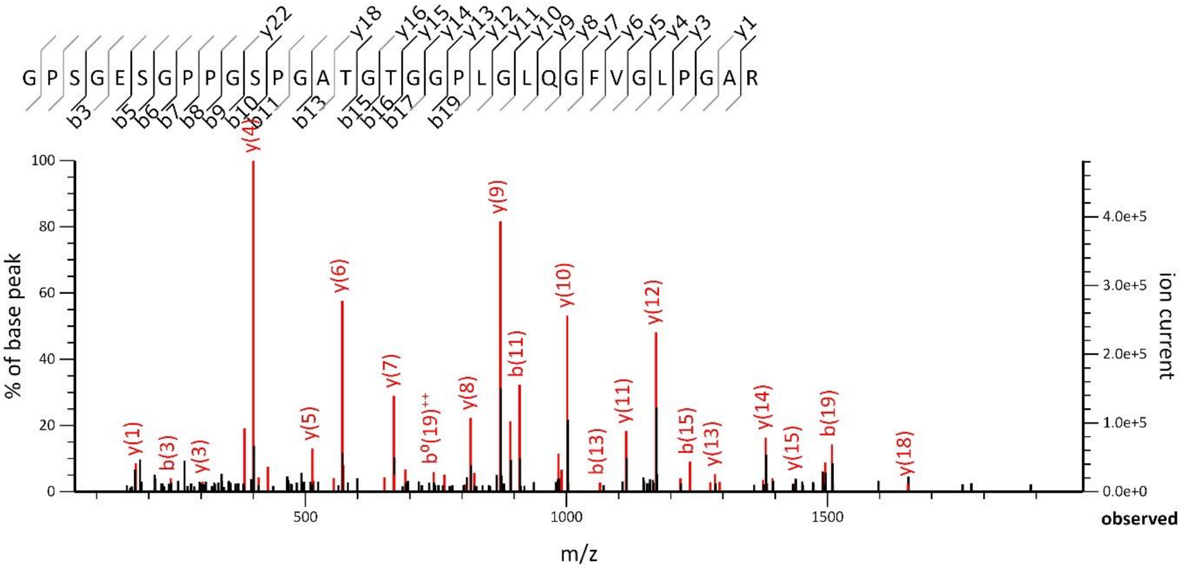

Figure D113. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Lepidorhombus whiffiagonis*.

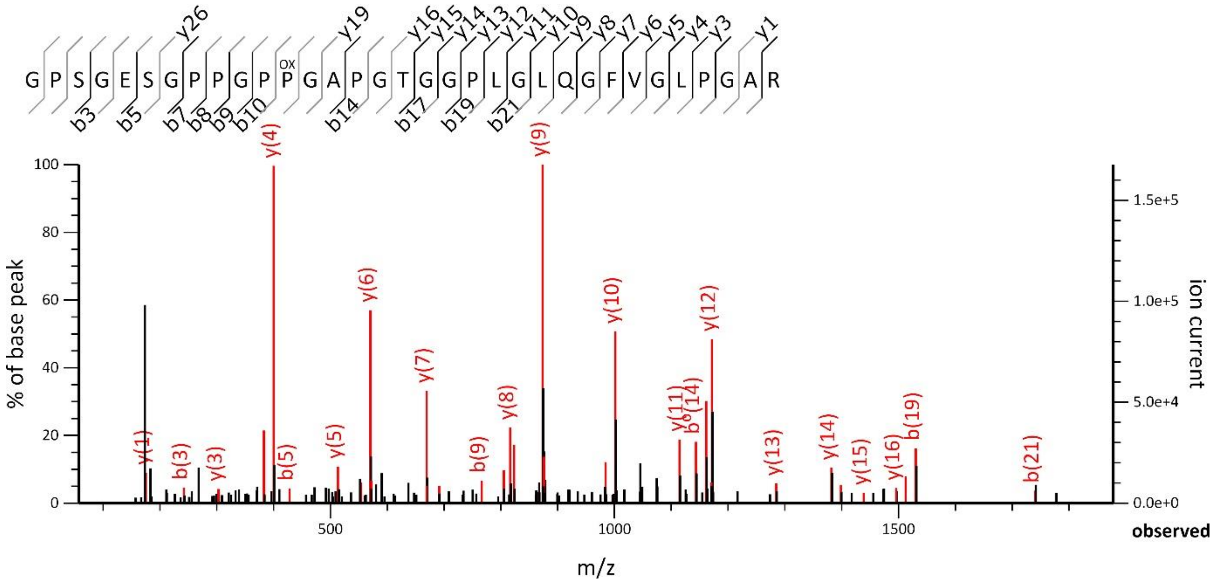

Figure D114. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Zeugopterus regius*.

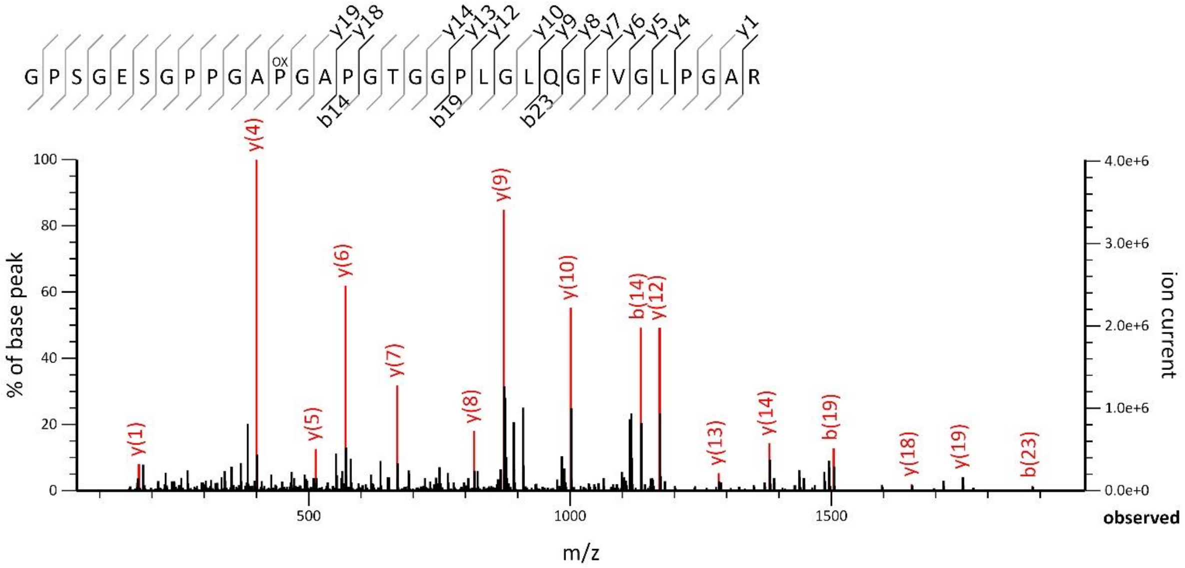

Figure D115. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Scophthalmus maximus*.

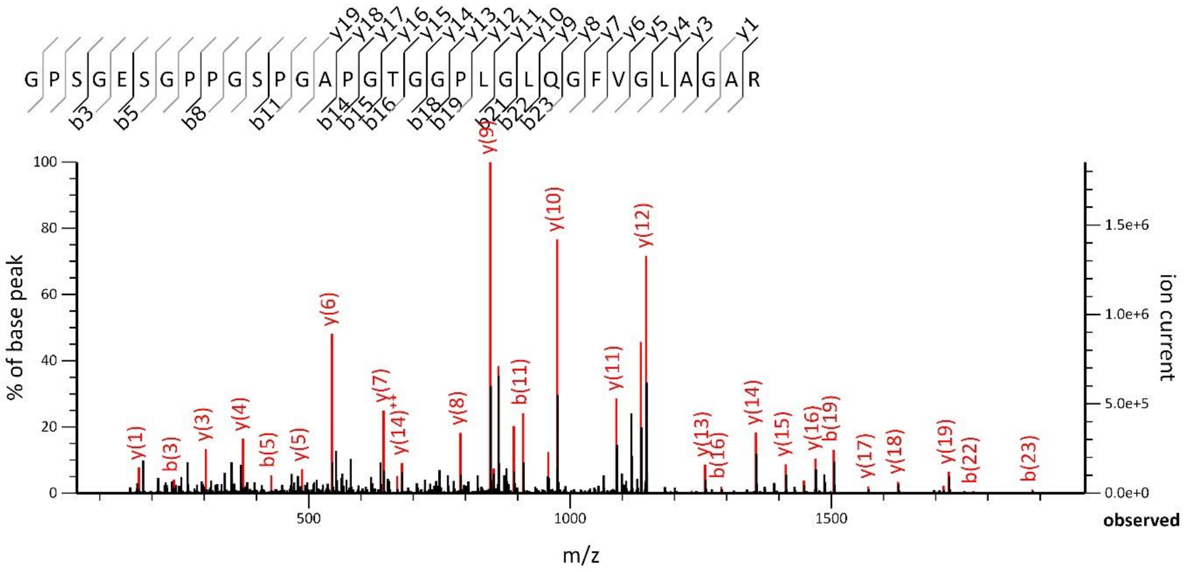

Figure D116. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Scophthalmus rhombus*.

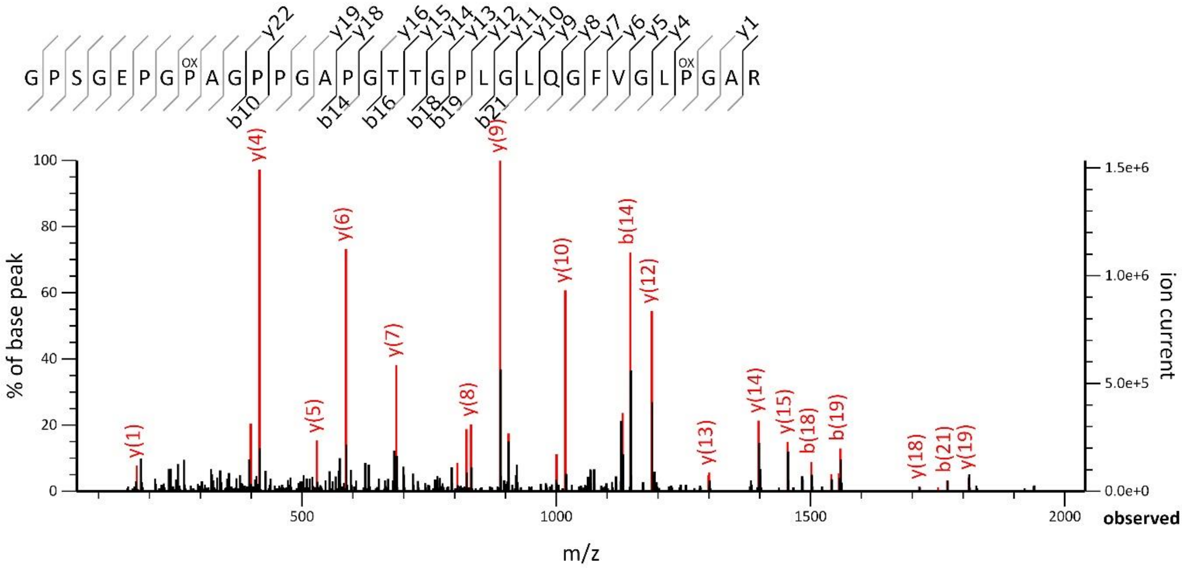

Figure D117. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Buglossidium luteum*.

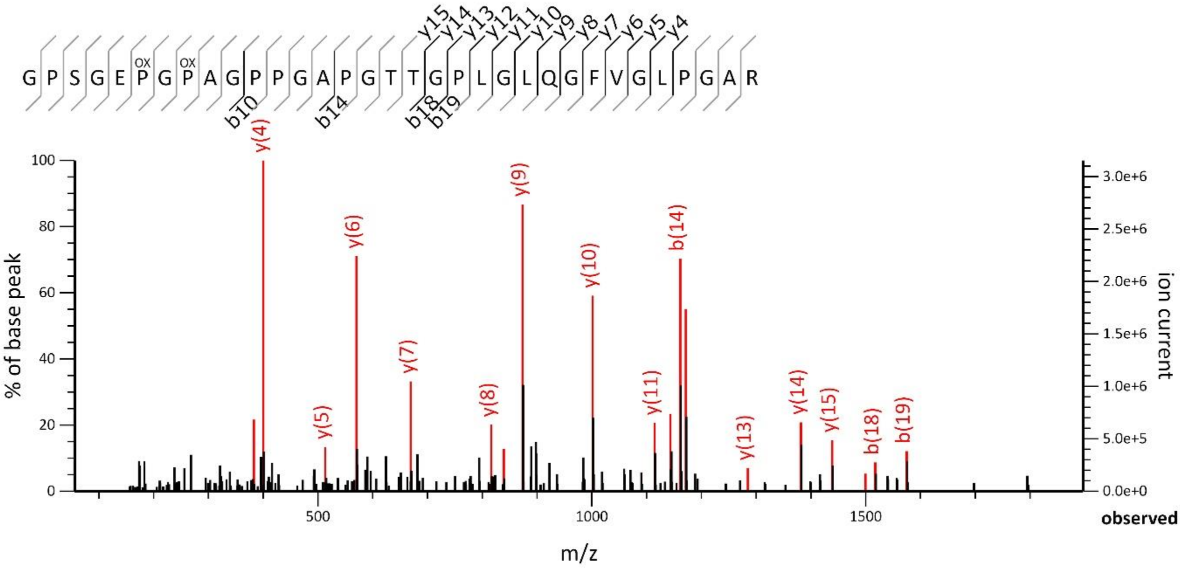

Figure D118. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Pegusa impar*.

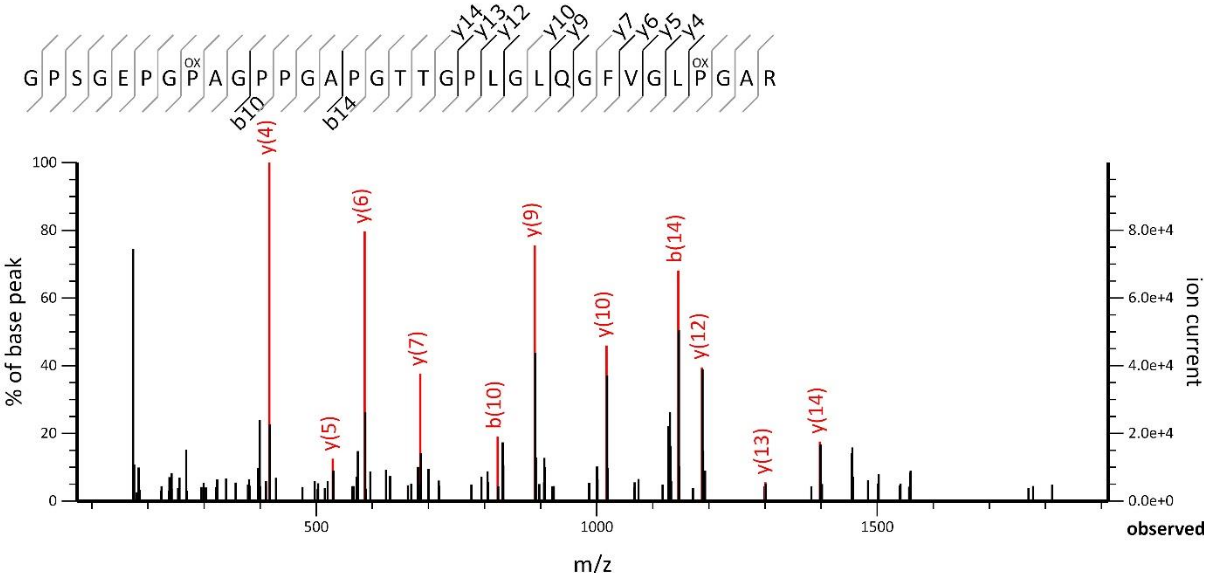

Figure D119. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Pegusa lascaris*.

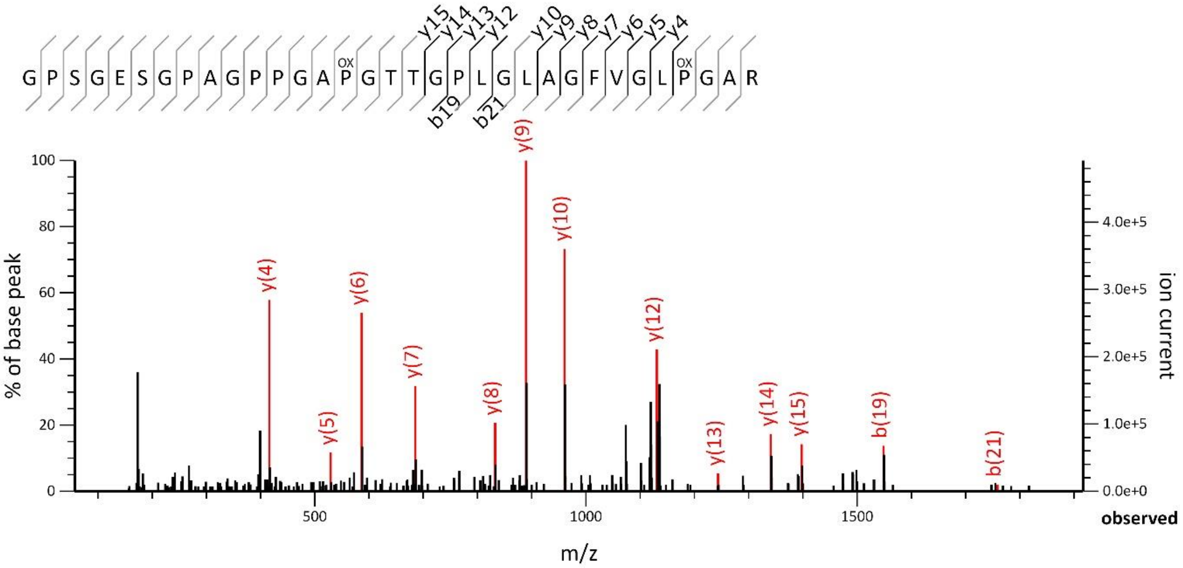

Figure D120. Ion spectrum of the COL1α2 757 – 789 peptide marker of *Solea solea*.

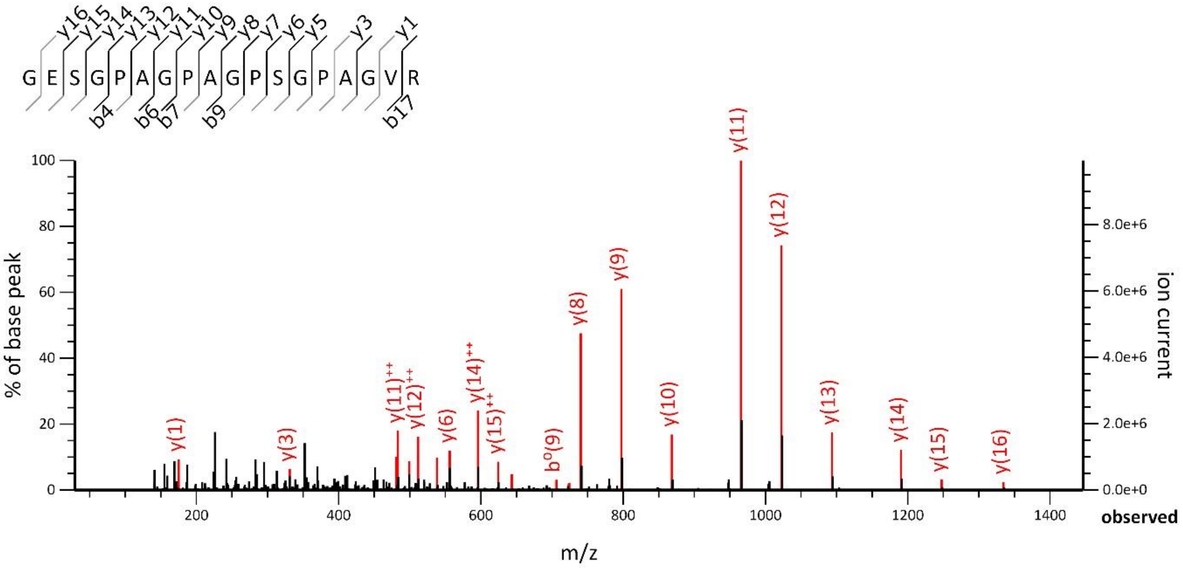

Figure D121. Ion spectrum of the COL1α3 889 – 909 peptide marker of *Lepidorhombus boscii*.

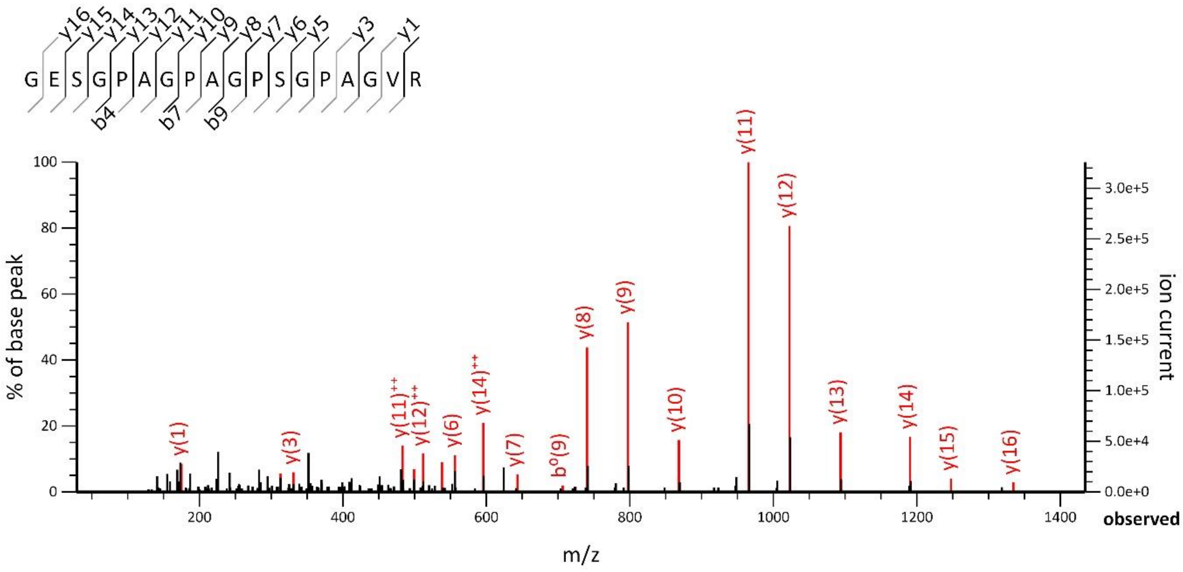

Figure D122. Ion spectrum of the COL1α3 889 – 909 peptide marker of *Lepidorhombus whiffiagonis*.

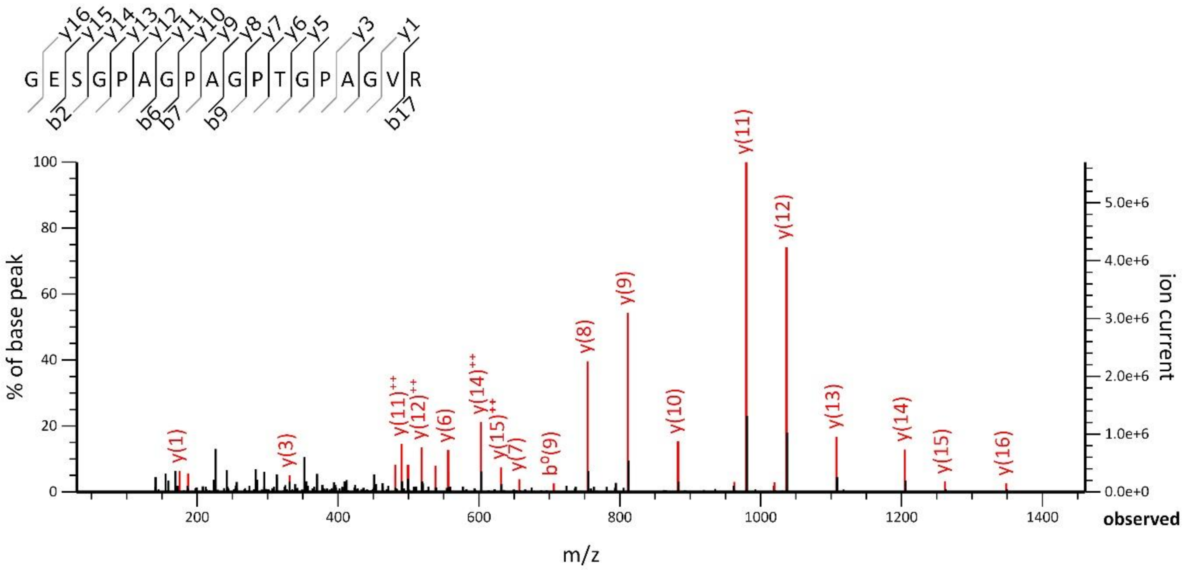

Figure D123. Ion spectrum of the COL1α3 889 – 909 peptide marker of *Zeugopterus regius*.

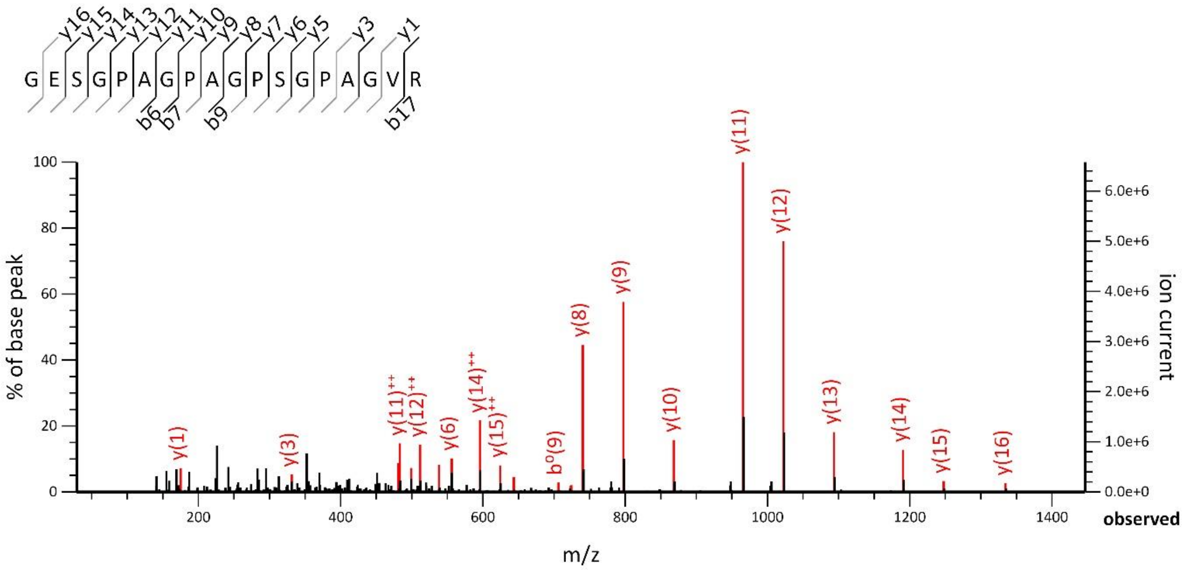

Figure D124. Ion spectrum of the COL1α3 889 – 909 peptide marker of *Scophthalmus maximus*.

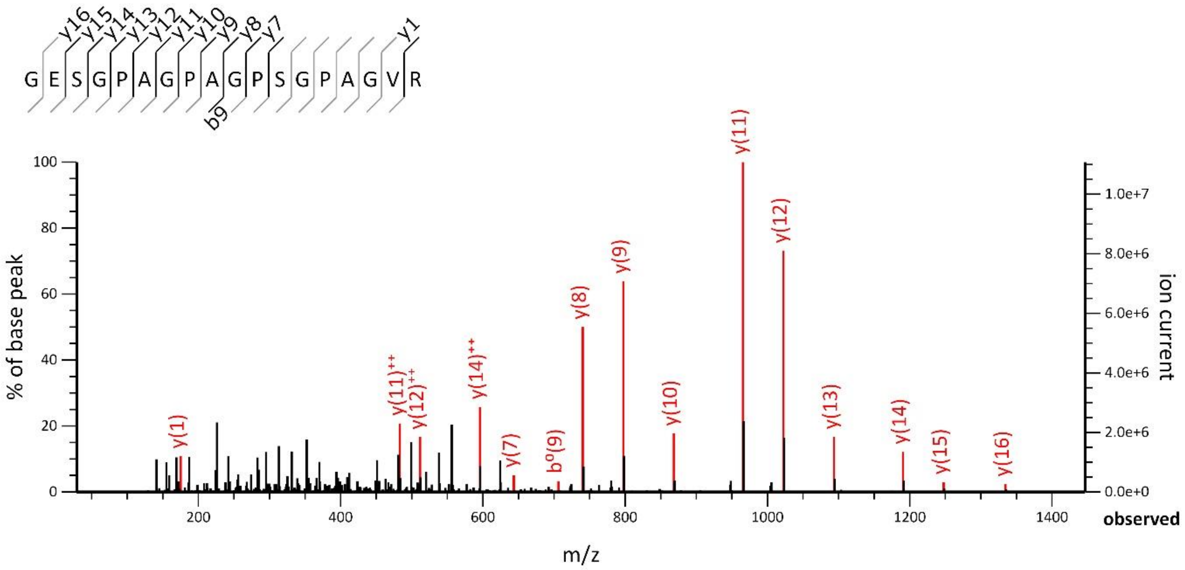

Figure D125. Ion spectrum of the COL1α3 889 – 909 peptide marker of *Scophthalmus rhombus*.

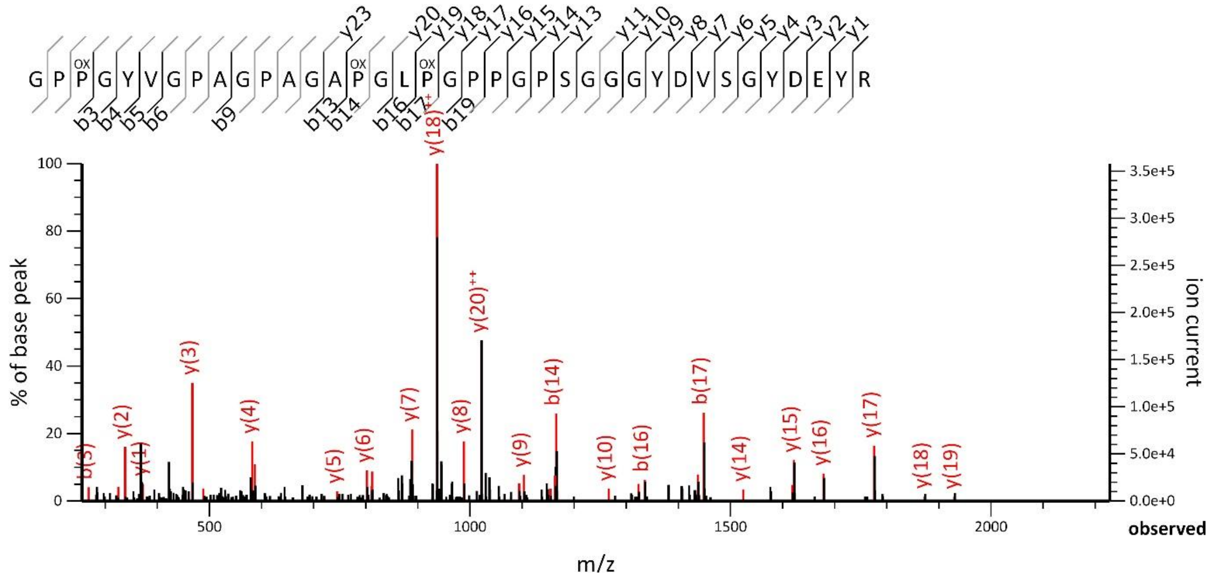

Figure D126. Ion spectrum of the COL1α2 991 – 1027 peptide marker of *Pegusa impar*.

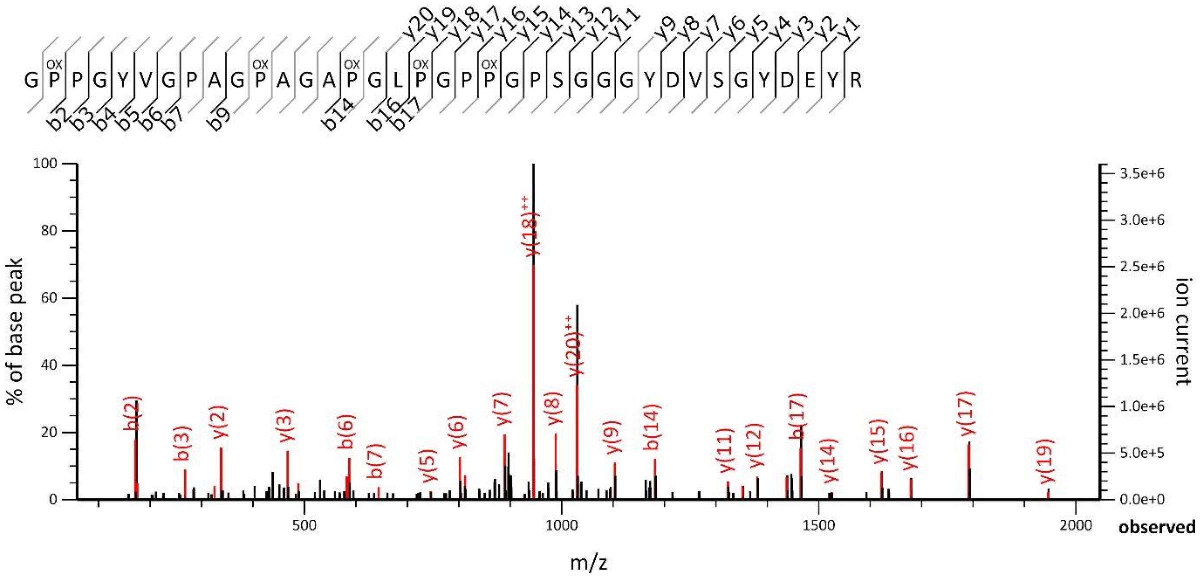

Figure D127. Ion spectrum of the COL1α2 991 – 1027 peptide marker of *Pegusa lascaris*.

Part D3. Peptide biomarkers details

Table D1. Details of peptide biomarker α1 817.

Family	Genus	Species	Mass	Sequence α1 817																					PTM
Pleuronectidae	*Pleuronectes*	*platessa*	1762	R.GPPGPMGPSGLAGAPGETGR.E	G	P	P	G	P	M	G	P	S	G	L	A	G	A	P	G	E	T	G	R	
Pleuronectidae	*Glyptocephalus*	*cynoglossus*	1795	R.GPPGPMGPSGLAGAQGEAGR.E															Q			A			Oxidation M6, P8; low support for sequence
Pleuronectidae	*Hippoglossoides*	*platessoides*	1778	R.GPPGPMGPSGLAGAPGETGR.E																					Oxidation M6
Pleuronectidae	*Hippoglossus*	*hippoglossus*	1779	R.GPPGPMGPSGLAGAQGEAGR.E															Q			A			Oxidation M6
Pleuronectidae	*Limanda*	*limanda*	1778	R.GPPGPMGPSGLAGAPGETGR.E																					Oxidation M6
Pleuronectidae	*Microstomus*	*kitt*	1791	R.GPPGPMGPSGLAGVQGEAGR.E														V	Q			A			
Pleuronectidae	*Platichthys*	*flesus*	1762	R.GPPGPMGPSGLAGAPGETGR.E																					
Bothidae	*Arnoglossus*	*laterna*	1778	R.GPPGPMGPSGLAGAPGETGR.E																					Oxidation M6
Citharidae	*Citharus*	*linguatula*	1770	R.GPPGPMGPPGLGGAPGEPGR.E									P			G						P			Oxidation M6
Scophthalmidae	*Lepidorhombus*	*boscii*	1774	R.GPSGPMGPPGLAGAPGEPGR.E			S						P									P			Oxidation M6
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	1760	R.GPPGPMGPSGLGGAPGEPGR.E												G						P			Oxidation M6
Scophthalmidae	*Zeugopterus*	*regius*	1758	R.GPPGPMGPSGLAGAPGEPGR.E																		P			
Scophthalmidae	*Scophthalmus*	*maximus*	1758	R.GPPGPMGPSGLAGAPGEPGR.E																		P			
Scophthalmidae	*Scophthalmus*	*rhombus*	1758	R.GPPGPMGPSGLAGAPGEPGR.E																		P			
Soleidae	*Buglossidium*	*luteum*	1774	R.GPPGPMGPSGLAGAPGEPGR.E																		P			Oxidation M6
Soleidae	*Pegusa*	*impar*	1784	R.GPPGPMGPPGLAGAPGEPGR.E									P									P			Oxidation M6
Soleidae	*Pegusa*	*lascaris*	1784	R.GPPGPMGPPGLAGAPGEPGR.E									P									P			Oxidation P3
Soleidae	*Solea*	*solea*	1784	GPPGPMGPPGLAGAPGEPGR									P									P			Oxidation P9; low support for sequence

Table D2. Details of peptide biomarker α1 934.

Family	**Genus**	**Species**	**Mass**	**Sequence α1 934**																															**PTM**
Pleuronectidae	*Pleuronectes*	*platessa*	2649	R.GFTGMQGPPGPSGPSGDQGPAGAAGPAGPR.G	G	F	T	G	M	Q	G	P	P	G	P	S	G	P	S	G	D	Q	G	P	A	G	A	A	G	P	A	G	P	R	Oxidation P26
Pleuronectidae	*Glyptocephalus*	*cynoglossus*	2632	R.GFTGMQGPPGPAGPSGEQGPAGAAGPAGPR.G												A					E														Deamidated Q6
Pleuronectidae	*Hippoglossoides*	*platessoides*	2629	R.GFTGMQGPSGPSGSSGDQGPAGSAGPAGPR.G									S					S									S								
Pleuronectidae	*Hippoglossus*	*hippoglossus*	2645	R.GFTGMQGPSGPSGSSGDQGPAGSAGPAGPR.G									S					S									S								Oxidation M5
Pleuronectidae	*Limanda*	*limanda*	2629	R.GFTGMQGPSGPSGSSGDQGPAGSAGPAGPR.G									S					S									S								
Pleuronectidae	*Microstomus*	*kitt*	2641	R.GFTGMQGPPGDAGSSGDQGPAGSAGPAGPR.G											D	A		S									S								
Pleuronectidae	*Platichthys*	*flesus*	2649	R.GFTGMQGPPGPSGPSGDQGPAGAAGPAGPR.G																															Oxidation P26
Bothidae	*Arnoglossus*	*laterna*	2679	R.GFTGMQGPPGPSGPSGEQGPAGASGPAGPR.G																	E							S							Oxidation P20
Citharidae	*Citharus*	*linguatula*																																	
Scophthalmidae	*Lepidorhombus*	*boscii*	2655	R.GFTGMQGPPGPSGASGDQGPAGSSGPAGPR.G														A									S	S							Oxidation P8
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	2655	R.GFTGMQGPPGPSGASGDQGPAGSSGPAGPR.G														A									S	S							Oxidation M5
Scophthalmidae	*Zeugopterus*	*regius*																																	
Scophthalmidae	*Scophthalmus*	*maximus*	2665	R.GFTGMQGPPGPSGPSGDQGPAGSSGPAGPR.G																							S	S							
Scophthalmidae	*Scophthalmus*	*rhombus*	2665	R.GFTGMQGPPGPSGPSGDQGPAGSSGPAGPR.G																							S	S							
Soleidae	*Buglossidium*	*luteum*	2681	R.GFTGMQGPPGPAGSSGEQGPAGTAGPTGPR.G												A		S			E						T				T				
Soleidae	*Pegusa*	*impar*	2723	R.GFTGMQGPPGPSGPSGEQGPAGTAGPTGPR.G																	E						T				T				Oxidation M5
Soleidae	*Pegusa*	*lascaris*	2707	R.GFTGMQGPPGPSGPSGEQGPAGTAGPTGPR.G																	E						T				T				
Soleidae	*Solea*	*solea*	2681	R.GFTGMQGPPGPSGTTGEQGPAGAAGPAGPR.G														T	T		E														Oxidation P26

Table D3. Details of peptide biomarker α2 625.

Family	Genus	Species	Mass	Sequence α2 625																									PTM
Pleuronectidae	*Pleuronectes*	*platessa*	2169	R.GEVGPAGSPGFAGPPGSDGQPGAR.G	G	E	V	G	P	A	G	S	P	G	F	A	G	P	P	G	S	D	G	Q	P	G	A	R	Oxidation P9, P15, P21
Pleuronectidae	*Glyptocephalus*	*cynoglossus*	2153	R.GEVGPAGAPGFAGPPGSDGQPGAR.G								A																	Oxidation P9, P14, P15
Pleuronectidae	*Hippoglossoides*	*platessoides*	2173	R.GEVGTAGSPGFAGPPGSDGQPGAR.G					T																				Oxidation P9, P15, P21
Pleuronectidae	*Hippoglossus*	*hippoglossus*	2169	R.GEVGPAGSPGFAGPPGSDGQPGAR.G																									Oxidation P9, P15, P21
Pleuronectidae	*Limanda*	*limanda*	2169	R.GEVGPAGSPGFAGPPGSDGQPGAR.G																									Oxidation P9, P15, P21
Pleuronectidae	*Microstomus*	*kitt*	2127	R.GEVGPAGSAGFAGPPGSDGQPGAR.G									A																Oxidation P14, P21
Pleuronectidae	*Platichthys*	*flesus*	2169	R.GEVGPAGSPGFAGPPGSDGQPGAR.G																									Oxidation P9, P15, P21
Bothidae	*Arnoglossus*	*laterna*	2111	R.GEVGPAGASGFAGPPGADGQPGAR.G								A	S								A								Oxidation P15, P21
Citharidae	*Citharus*	*linguatula*	2121	R.GEVGPAGAPGFAGPPGADGQPGAR.G								A									A								Oxidation P9, P15
Scophthalmidae	*Lepidorhombus*	*boscii*	2157	R.GEVGTAGAPGFAGPPGSDGQPGAR.G					T			A																	Oxidation P9, P15, P21
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	2137	R.GEVGPAGAPGFAGPPGSDGQPGAR.G								A																	Oxidation P9, P15; low support for sequence
Scophthalmidae	*Zeugopterus*	*regius*	2137	R.GEVGPAGAPGFAGPPGSDGQPGAR.G								A																	Oxidation P9, P15
Scophthalmidae	*Scophthalmus*	*maximus*	2121	R.GEVGPAGAPGFAGPPGADGQPGAR.G								A									A								Oxidation P9, P21
Scophthalmidae	*Scophthalmus*	*rhombus*	2121	R.GEVGPAGAPGFAGPPGADGQPGAR.G								A									A								Oxidation P9, P15
Soleidae	*Buglossidium*	*luteum*	2121	R.GEVGPAGAPGFAGPPGADGQPGAR.G								A									A								Oxidation P9, P15
Soleidae	*Pegusa*	*impar*	2095	R.GEVGPAGAPGFAGPPGADGQAGAR.G								A									A				A				Oxidation P9, P15
Soleidae	*Pegusa*	*lascaris*	2095	R.GEVGPAGAPGFAGPPGADGQAGAR.G								A									A				A				Oxidation P9, P15
Soleidae	*Solea*	*solea*	2095	R.GEVGPAGAPGFAGPPGADGQAGAR.G								A									A				A				Oxidation P9, P15; low support for sequence

Table D4. Details of peptide biomarker α2 658.

Family	Genus	Species	Mass	Sequence α2 658																															PTM
Pleuronectidae	*Pleuronectes*	*platessa*	2499	K.GEVGPSGPSGPAGQSGPAGPNGPAGPGGGR.G	G	E	V	G	P	S	G	P	S	G	P	A	G	Q	S	G	P	A	G	P	N	G	P	A	G	P	G	G	G	R	Oxidation P26
Pleuronectidae	*Glyptocephalus*	*cynoglossus*																																	
Pleuronectidae	*Hippoglossoides*	*platessoides*	2515	K.GEVGPSGPSGPAGQSGPAGPNGPAGPGGGR.G																															Oxidation P11, P26
Pleuronectidae	*Hippoglossus*	*hippoglossus*	2541	K.GELGPSGPSGPAGQSGPAGPNGPAGPTGGR.G			L																								T				
Pleuronectidae	*Limanda*	*limanda*	2499	K.GEVGPSGPSGPAGQSGPAGPNGPAGPGGGR.G																															Oxidation P26
Pleuronectidae	*Microstomus*	*kitt*	2543	K.GEVGPSGPSGPAGQSGPAGPNGPAGPTGGR.G																											T				Oxidation P11
Pleuronectidae	*Platichthys*	*flesus*	2499	K.GEVGPSGPSGPAGQSGPAGPNGPAGPGGGR.G																															Oxidation P26
Bothidae	*Arnoglossus*	*laterna*																																	
Citharidae	*Citharus*	*linguatula*	2426	K.GEVGPAGAAGPAGQSGPPGAAGPAGAAGPR.G						A		A	A									P		A	A					A	A		P		Oxidation P18
Scophthalmidae	*Lepidorhombus*	*boscii*	2528	K.GEVGPSGPSGPAGQSGPAGPSGPGGPPGAR.G																					S			G			P		A		Oxidation P11, P27
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	2528	K.GEVGPSGPSGPAGQSGPAGPSGPGGPPGAR.G																					S			G			P		A		Oxidation P11, P27
Scophthalmidae	*Zeugopterus*	*regius*	2528	K.GEVGPSGPSGPAGQSGPAGPSGPGGPPGAR.G																					S			G			P		A		Oxidation P11, P27
Scophthalmidae	*Scophthalmus*	*maximus*	2512	K.GEVGPSGPSGPAGQSGPAGPSGPGGPPGAR.G																					S			G			P		A		Oxidation P27
Scophthalmidae	*Scophthalmus*	*rhombus*	2512	K.GEVGPSGPSGPAGQSGPAGPSGPGGPPGAR.G																					S			G			P		A		Oxidation P27
Soleidae	*Buglossidium*	*luteum*	2462	K.GETGGAGPSGPAGQSGPAGPSGPAGPTGGR.G			T		G	A															S						T				Oxidation P8
Soleidae	*Pegusa*	*impar*	2468	K.GEVGPAGPAGPAGQSGPAGPSGPAGPAGAR.G						A			A												S						A		A		Oxidation P5
Soleidae	*Pegusa*	*lascaris*	2468	K.GEVGPAGPAGPAGQSGPAGPSGPAGPAGAR.G						A			A												S						A		A		Oxidation P8
Soleidae	*Solea*	*solea*	2484	K.GEVGPAGPAGPAGQSGPAGPSGPAGPAGAR.G						A			A												S						A		A		Oxidation P5, P26

Table D5. Details of peptide biomarker α2 688.

Family	**Genus**	**Species**	**Mass**	**Sequence α2 688**																		**PTM**
Pleuronectidae	*Pleuronectes*	*platessa*																				
Pleuronectidae	*Glyptocephalus*	*cynoglossus*	1588	R.GDNGPPGLTGFPGASGR.V																		Oxidation P6, P12
Pleuronectidae	*Hippoglossoides*	*platessoides*	1572	R.GDNGPPGLTGFPGASGR.V																		Oxidation P6
Pleuronectidae	*Hippoglossus*	*hippoglossus*	1588	R.GDNGPPGLTGFPGASGR.V																		Oxidation P6, P12
Pleuronectidae	*Limanda*	*limanda*	1630	R.GDNGPPGLTGFPGAEGR.V															E			Oxidation P6, P12
Pleuronectidae	*Microstomus*	*kitt*	1602	R.GDNGPPGLTGFPGATGR.V															T			Oxidation P6, P12
Pleuronectidae	*Platichthys*	*flesus*	1572	R.GDNGPPGLTGFPGASGR.V	G	D	N	G	P	P	G	L	T	G	F	P	G	A	S	G	R	Oxidation P6
Bothidae	*Arnoglossus*	*laterna*	1545	R.GDTGPPGLTGFPGAGGR.V			T												G			Oxidation P6, P12
Citharidae	*Citharus*	*linguatula*	1573	R.GDNGPNGLTGFPGAAGR.V						N									A			Oxidation P12
Scophthalmidae	*Lepidorhombus*	*boscii*	1544	R.GDNGPDGLTGFPGAGGR.V						D									G			
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	1560	R.GDNGPDGLTGFPGAGGR.V						D									G			Oxidation P12
Scophthalmidae	*Zeugopterus*	*regius*	1574	R.GDNGPDGLTGFPGAAGR.V						D									A			Oxidation P12
Scophthalmidae	*Scophthalmus*	*maximus*	1600	R.GDNGPPGLTGFPGAVGR.M															V			Oxidation P6, P12
Scophthalmidae	*Scophthalmus*	*rhombus*	1556	R.GDNGPPGLTGFPGAAGR.V															A			Oxidation P12
Soleidae	*Buglossidium*	*luteum*	1547	R.GDDGPSGLTGFPGAAGR.V			D			S									A			Oxidation P12
Soleidae	*Pegusa*	*impar*	1517	R.GDTGPAGLTGFPGAAGR.V			T			A									A			Oxidation P12
Soleidae	*Pegusa*	*lascaris*	1517	R.GDTGPAGLTGFPGAAGR.V			T			A									A			Oxidation P12
Soleidae	*Solea*	*solea*	1517	R.GDTGPAGLTGFPGAAGR.V			T			A									A			Oxidation P12

Table D6. Details of peptide biomarker α2 757.

Family	Genus	Species	Mass	Sequence α2 757																																		PTM
Pleuronectidae	*Pleuronectes*	*platessa*	2893	K.GPSGESGPPGAPGATGTGGPLGLQGFLGLSGAR.G	G	P	S	G	E	S	G	P	P	G	A	P	G	A	T	G	T	G	G	P	L	G	L	Q	G	F	L	G	L	S	G	A	R	Oxidation P12
Pleuronectidae	*Glyptocephalus*	*cynoglossus*	2879	K.GPSGESGPPGAPGASGTGGPLGLQGFLGLSGAR.G															S																			Oxidation P20; low support for sequence
Pleuronectidae	*Hippoglossoides*	*platessoides*	2893	K.GPSGESGPPGAPGATGTGGPLGLQGFLGLSGAR.G																																		Oxidation P20; low support for sequence
Pleuronectidae	*Hippoglossus*	*hippoglossus*	2873	K.GPSGESGPPGAPGAPGTGGPLGLQGFLGLSGAR.G															P																			
Pleuronectidae	*Limanda*	*limanda*	2863	K.GPSGESGPPGAPGASGTGGPLGLQGFLGLSGAR.G															S																			low support for sequence
Pleuronectidae	*Microstomus*	*kitt*	2867	K.GPSGESGPPGAPGATGTGGPLGLQGFSGLSGAR.G																											S							Oxidation P12
Pleuronectidae	*Platichthys*	*flesus*	2903	K.GPSGETGPPGAPGAPGTGGPLGLQGFLGLSGAR.G						T									P																			Oxidation P12
Bothidae	*Arnoglossus*	*laterna*																																				
Citharidae	*Citharus*	*linguatula*	2931	K.GPSGESGPPGAPGTAGISGPLGLQGFVGLPGAR.G														T	A		I	S									V			P				Oxidation P20
Scophthalmidae	*Lepidorhombus*	*boscii*	2901	K.GPSGESGPPGSPGAPGTGGPLGLQGFVGLPGAR.G											S				P												V			P				Oxidation P30
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	2889	K.GPSGESGPPGSPGATGTGGPLGLQGFVGLPGAR.G											S																V			P				
Scophthalmidae	*Zeugopterus*	*regius*	2911	K.GPSGESGPPGPPGAPGTGGPLGLQGFVGLPGAR.G											P				P												V			P				Oxidation P12
Scophthalmidae	*Scophthalmus*	*maximus*	2885	K.GPSGESGPPGAPGAPGTGGPLGLQGFVGLPGAR.G															P												V			P				Oxidation P12
Scophthalmidae	*Scophthalmus*	*rhombus*	2859	K.GPSGESGPPGSPGAPGTGGPLGLQGFVGLAGAR.G															P												V			A				
Soleidae	*Buglossidium*	*luteum*	2955	K.GPSGEPGPAGPPGAPGTTGPLGLQGFVGLPGAR.G						P			A		P				P			T									V			P				Oxidation P8, P30
Soleidae	*Pegusa*	*impar*	2955	K.GPSGEPGPAGPPGAPGTTGPLGLQGFVGLPGAR.G						P			A		P				P			T									V			P				Oxidation P6, P8
Soleidae	*Pegusa*	*lascaris*	2955	K.GPSGEPGPAGPPGAPGTTGPLGLQGFVGLPGAR.G						P			A		P				P			T									V			P				Oxidation P8, P30; low support for sequence
Soleidae	*Solea*	*solea*	2888	K.GPSGESGPAGPPGAPGTTGPLGLAGFVGLPGAR.G									A		P				P			T						A			V			P				Oxidation P15, P30

Table D7. Details of peptide biomarker α3 889.

Family	Genus	Species	Mass	Sequence α3 889																			PTM
Scophthalmidae	*Lepidorhombus*	*boscii*	1520	R.GESGPAGPAGPSGPAGVR.G																			
Scophthalmidae	*Lepidorhombus*	*whiffiagonis*	1520	R.GESGPAGPAGPSGPAGVR.G																			
Scophthalmidae	*Zeugopterus*	*regius*	1534	R.GESGPAGPAGPTGPAGVR.G												T							
Scophthalmidae	*Scophthalmus*	*maximus*	1520	R.GESGPAGPAGPSGPAGVR.G	G	E	S	G	P	A	G	P	A	G	P	S	G	P	A	G	V	R	

Table D8. Details of peptide biomarker α2 991.

Family	Genus	Species	Mass	Sequence α2 991																																						PTM
Soleidae	*Pegusa*	*impar*	3490	GPPGYVGPAGPAGAPGLPGPPGPSGGGYDVSGYDEYR	G	P	P	G	Y	V	G	P	A	G	P	A	G	A	P	G	L	P	G	P	P	G	P	S	G	G	G	Y	D	V	S	G	Y	D	E	Y	R	Oxidation P3, P15, P18
Soleidae	*Pegusa*	*lascaris*	3522	GPPGYVGPAGPAGAPGLPGPPGPSGGGYDVSGYDEYR																																						Oxidation P2, P11, P15, P18, P21

Part D4. Collagen sequences

Pleuronectes platessa

>GPMGPMGPRGPPGPAGSSGPQGFTGPPGEPGEAGSTGPMGPRGAAGPPGKNGEDGESGKPGRGGERGPS
GPQGARGFPGTPGLPGIKGHRGFSGLDGSKGESGPAGPKGESGTAGENGTPGAMGPRGLPGERGRTGASGS
AGARGNDGAAGAAGPPGPTGPAGPPGFPGGPGSKGEGGAQGSRGPEGPAGTRGEPGNPGPAGAAGPSGNS
GTDGAPGAKGLPGSAGVAGAPGFPGPRGPPGAQGAAGATGSKGNTGEAGGPGSKGEHGAKGESGVAGLQGP
PGPSGEEGKRGARGEPGTAGGRGSPGERGGPGGRGFPGSDGSAGAKGAPGERGGPGLLGPKGSTGESGRT
GEAGLPGAKGMTGSPGSPGPDGKMGSSGAPGQDGRPGPPGAVGARGQPGVMGFPGPKGAAGEGGKPGER
GVMGPTGPVGAPGKDGDLGAQGPSGPSGPAGERGEQGAAGGPGFQGLPGPQGAAGETGKPGEQGLSGEAG
AVGPGGSRGDRGFPGERGAPGALGPAGARGSPGASGNDGAKGDAGASGAPGAQGPPGLQGMPGERGSAGL
PGLRGDRGDQGGKGGDGAPGKDGVRGLTGPIGLPGSAGATGDKGESGAPGIVGPAGARGGPGERGESGPPG
PAGFAGPPGGDGQPGAKGESGDNGAKGDAGPPGASGPTGAAGPAGPVGNTGAKGARGPAGPPGATGFPGG
AGRVGPPGPSGDSGPPGPSGGVGKEGPKGNRGETGPAGRPGEMGASGPPGASGEKGSAGSEGASGSSGIPG
PQGIAGGRGIVGLPGQRGERGFPGLPGPSGELGKQGSSGPGGERGPPGPMGPSGLAGAPGETGREGSPGNE
GSSGRDGPAGPKGDRGESGPAGGAGAPGPPGAPGPVGPAGKSGDRGETGPAGAAGSAGPSGPRGPAGAVG
ARGDKGESGEAGERGMKGHRGFTGMQGPPGPSGPSGDQGPAGAAGPAGPRGPSGAAGSAGKDGMSGLPG
PTGPPGTRGRSGEMGPSGPPGPPGPAGAPGAPGGGFDLGFIAQPQEKAPDPFRFAAQYEGAKGPDAGPGPM
GMSGPRGPPGPPGSPGPQGHTGHAGEPGEPGQSGALGPRGPPGPPGKAGDDGNNGRPGKPGDRGTAGVQ
GARGFPGTPGLPGMKGHRGYTGLDGRKGEAGTSGAKGESGAHGASGSPGLAGSRGMAGERGRAGPAGVAG
ARGADGNVGPSGPSGPLGAAGPPGFPGGPGPKGELGAAGANGPSGAQGSRGEPGSNGAGGPLGPAGNPGA
NGLNGAKGAAGTPGVSGTPGFPGPRGGPGPQGPQGSAGPRGLAGDPGTQGVKGDGGPKGEPGNSGAQGSP
GPNGEEGKRGPTGELGATGPGGVRGARGAAGSRGMPGSEGRTGPIGMPGARGSTGSGGPRGPPGDAGRAG
EPGSAGLRGLPGSPGSSGPPGKEGLAGPAGQDGRSGPPGPTGPRGQPGNIGFPGPKGASGEGGKPGDKGAT
GPTGMRGTPGSDGNNGGTGAMGPAGGSGEKGEQGPSGAPGFQGLPGPAGAGGEGGKPGDRGIPGDQGLGG
PAGSKGERGNPGAAGASGAQGGIGARGPAGAPGPDGGKGEPGVAGAAGGPGHQGPGGMPGERGIAGGPGG
KGEKGEGGHRGPEGNSGRDGARGMPGPAGPPGPTGANGDKGESGSFGPAGPAGARGASGERGEVGPAGSP
GFAGPPGSDGQPGARGERGPGGIKGEVGPSGPSGPAGQSGPAGPNGPAGPGGGRGDTGPPGLTGFPGAAG
RVGVSGPAGIVGPPGPAGSAGKDGPRGLRGDVGPAGSSGEQGMVGPPGVIGEKGPSGESGPPGAPGATGTG
GPLGLQGFLGLSGARGDRGTPGGAGGLGEAGRVGPAGPPGSRGPSGNIGMPGMTGPQGEAGREGNPGNDG
PPGRPGTAGFKGDRGEPGSAGSMGLAGSPGPAGPSGAVGRPGNRGESGPGGANGPAGAPGARGAAGPSGT
RGEKGVGGEKGERGMKGLRGHPGLQGMPGPSGPSGDTGASGASGASGNRGPSGPHGPAGKDGRAGGHGTI
GSPGARGPPGYVGPAGPAGSPGLPGPAGPSGGGYDVSQYDEYRMSYTDHSKSSGPPVPGPMGPMGARGPP
GPSGSSGPQGFTGPSGEPGEPGAAGPMGPRGPGGPNGKNGDDGEPGKPGRPGERGAAGSQGARGFPGTPG
LPGIKGHRGFSGLDGAKGDGGPAGPKGEPGSSGENGIPGAMGARGLPGERGRPGPPGPAGARGNDGNSGGS
GPPGPTGPAGPPGFPGGAGAKGETGPQGGRGSEGPQGSRGEPGNPGSAGSAGPAGNPGSDGAPGNKGGPG
SAGIAGAPGFPGTRGPSGAQGAVGAPGPKGNNGDHGPSGPKGEPGAKGDGGPAGVQGLPGLSGEEGKRGGR
GEPGGAGARGPSGERGGPGARGFPGADGAAGGKGGPGERGAPGAMGSQGATGESGNSGAPGAPGSKGVT
GSPGSPGPDGKAGPTGTPGQDGRSGPAGSLGSRGQPGVMGFPGPKGPGGESGKPGERGPAGATGALGAPG
KDGDVGAPGPSGIAGPAGEKGEQGPGGSSGFQGLPGPQGSTGETGKPGEQGVNGESGPPGPFGPRGDRGFP
GERGTSGIVGPTGARGAPGPGGNDGAKGEAGVNGAPGVNGSPGMQGMPGERGASGLSGAKGERGDAGAKG
VDGALGKDGSRGMSGGIGVPGPPGAQGEKGEGGAPGVSGASGPRGSPGERGEAGPSGPAGFAGPPGTDGQ
PGAKGEAGDSGPKGDAGAPGPGGPVGAAGPQGPSGPSGPKGSRGGAGPPGATGFPGPAGRVGPPGPSGVS
GPAGPGGPLGKDGARGGRGETGPAGRPGEAGSSGAPGMNGEKGSAGSDGAPGTSGIPGPQGIAGGRGMVGL
PGQRGERGFSGLPGPSGEPGKQGSSGLHGERGPPGPSGPPGLSGATGEAGREGSAGHDGAPGRDGVAGPK
GDRGESGNAGSPGAPGAPGAPGAFGPSGKNGDRGESGAAGPAGPSGPAGVRGPAGPAGAKGDRGEAGDAG
DRGHKGHRGFTGMQGLPGTAGTSGERGPAGTSGPAGPRGPAGSNGSPGKDGMNGLPGPIGPPGPRGRNGE
MGPSGPPGPPGPAGPPGSPGGGFDFISQPSQEKAPDPFRGGGYR

Glyptocephaluss cynoglossus

>GPMGPMGPRGPPGPAGSSGPQGFTGPAGEPGEAGSSGPMGPRGAAGPPGKNGEDGESGKPGRGGERGPS
GPQGARGFPGTPGLPGIKGHRGFSGLDGSKGESGPAGPKGESGTAGENGTPGAMGPRGLPGERGRTGASGS
AGARGNDGAAGAGGPNGPTGPAGPPGFPGGPGSKGEGGAQGSRGPEGPAGTRGEPGNPGPAGAAGPSGNS
GTDGAPGAKGLPGSAGVAGAPGFPGPRGPPGAQGAAGATGSKGNTGEAGGPGSKGEHGAKGESGVPGLQGP
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Lepidorhombus whiffiagonis
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Zeugopterus regius
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Scophthalmus maximus
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Pegusa impar
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Pegusa lascaris

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Solea solea

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Part D5. Archaeological spectra examples

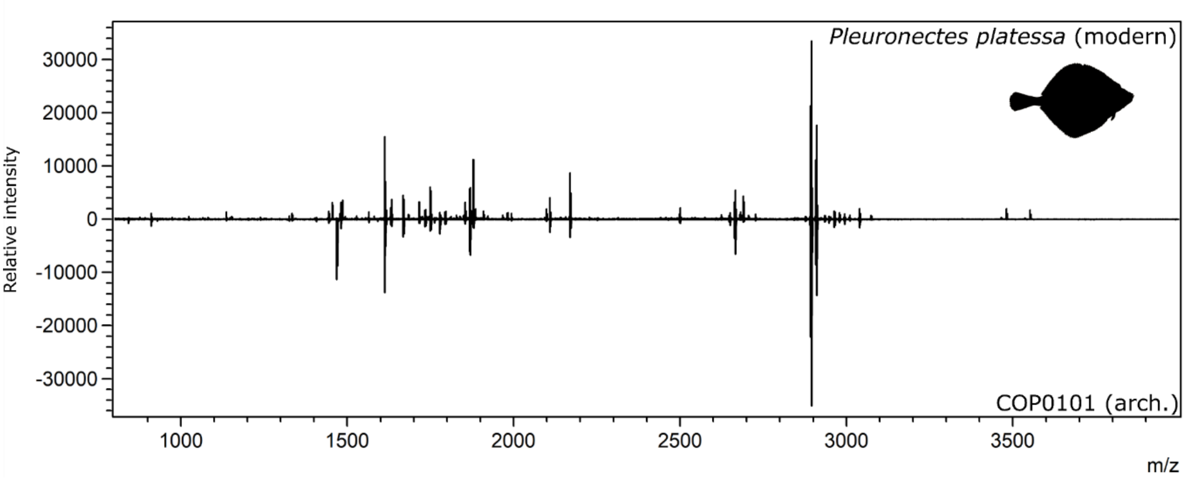

Figure D128. Collagen fingerprints of modern (top) and archaeological (bottom; sample COP0101 from 16-22 Coppergate) samples of *Pleuronectes platessa*.

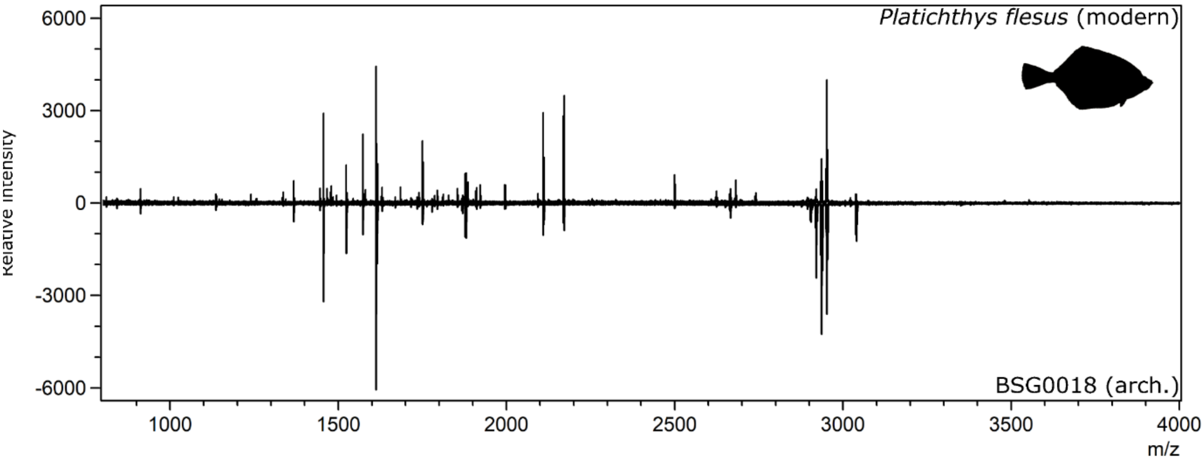

Figure D129. Collagen fingerprints of modern (top) and archaeological (bottom; sample BSG0018 from Barreau Saint-George) samples of *Platichthys flesus*.

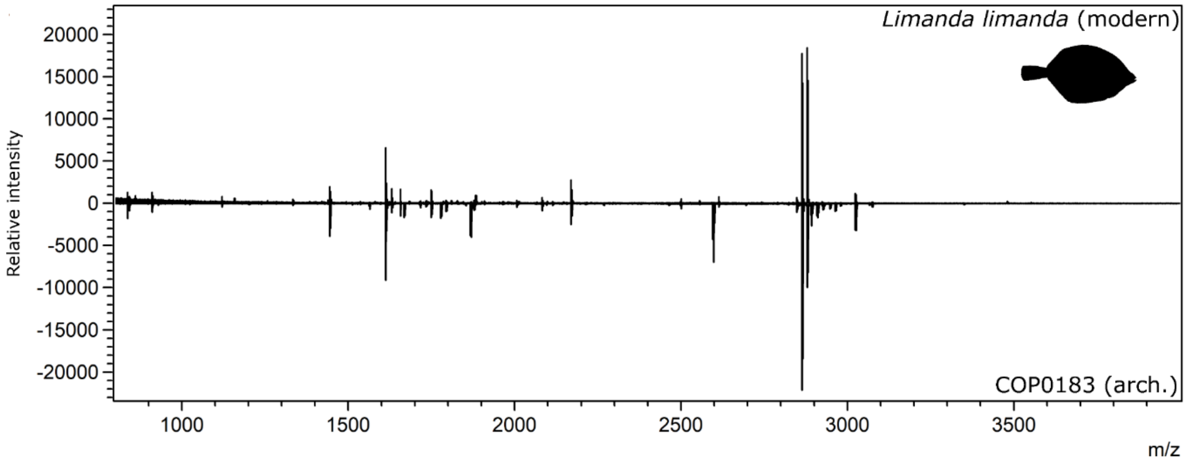

Figure D130. Collagen fingerprints of modern (top) and archaeological (bottom; sample COP0183 from 16-22 Coppergate) samples of *Limanda limanda*.

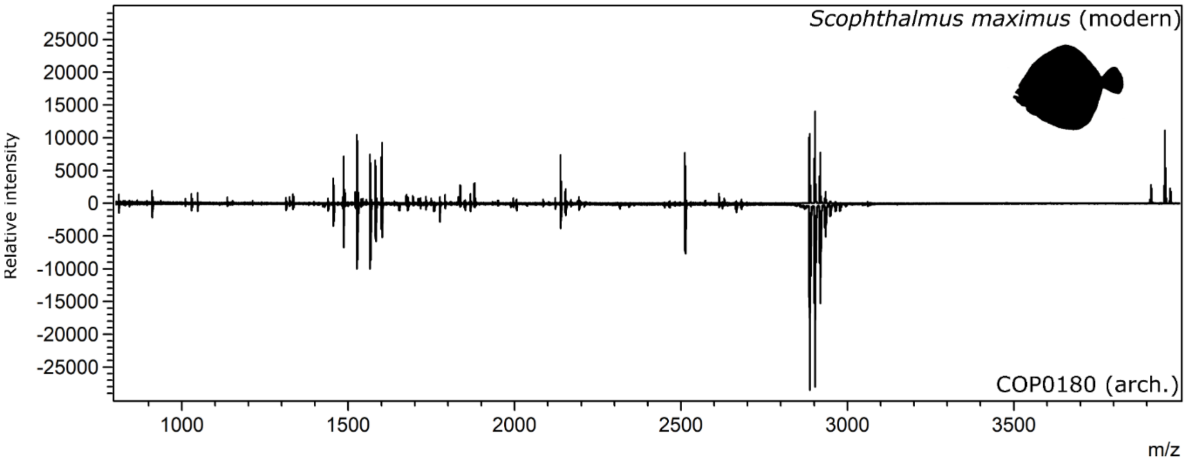

Figure D131. Collagen fingerprints of modern (top) and archaeological (bottom; sample COP0180 from 16-22 Coppergate) samples of *Scophthalmus maximus*.

Table D9. Archaeological fish samples analysed and identified using ZooMS.

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Blue Bridge Lane	BBL0901	*Melanogrammus aeglefinus*	cleithrum	c1442; 2471	7a	early - mid 14th	30-40	collagen	
Blue Bridge Lane	BBL0902	*Platichthys flesus*	caudal vertebra	c1065; 2443	3	7th - 8th	20-30	collagen	
Blue Bridge Lane	BBL0903	*Pleuronectes platessa*	precaudal vertebra	c1341; 2241	3	7th - 8th	40-50	collagen	
Blue Bridge Lane	BBL0904	cf *Esox lucius*	vertebra	c1571; 2341	6	late 12th - mid 14th	70-80	collagen	
Blue Bridge Lane	BBL0905	*Pleuronectes platessa*	precaudal vertebra	c1571; 2341	6	late 12th - mid 14th	40-50	collagen	
Blue Bridge Lane	BBL0906	*Pleuronectes platessa*	quadrate	c1571; 2266	6	late 12th - mid 14th	20-30	collagen	
Blue Bridge Lane	BBL0907	*Pleuronectes platessa*	precaudal vertebra	c1571; 2266	6	late 12th - mid 14th	20-30	collagen	
Blue Bridge Lane	BBL0908	*Pleuronectes platessa*	caudal vertebra	c1571; 2440	6	late 12th - mid 14th	50-60	collagen	
Blue Bridge Lane	BBL0909	*Pleuronectes platessa*	precaudal vertebra	c1571; 2440	6	late 12th - mid 14th	40-50	collagen	
Blue Bridge Lane	BBL0910	*Pleuronectes platessa*	caudal vertebra	c1571; 2440	6	late 12th - mid 14th	40-50	collagen	
Blue Bridge Lane	BBL0911	*Pleuronectes platessa*	caudal vertebra	c1571; 2440	6	late 12th - mid 14th	20-30	collagen	
Blue Bridge Lane	BBL0913	*Pleuronectes platessa*	dentary	c1571; 2440	6	late 12th - mid 14th	40-50	collagen	
Blue Bridge Lane	BBL0914	*Melanogrammus aeglefinus*	quadrate	c1590; 2451	8b	late 14th - early 16th	40-50	collagen	
Blue Bridge Lane	BBL0915	cf *Limanda limanda*	caudal vertebra	c1884; 2323	8b	late 14th - early 16th	20-30	collagen	
Blue Bridge Lane	BBL0916	*Esox lucius*	vertebra	c1904; 2293	3	7-8th	40-50	collagen	
Blue Bridge Lane	BBL0917	*Platichthys flesus*	caudal vertebra	c2114; 2307	3	7th - 8th	20-30	collagen	
Blue Bridge Lane	BBL0918	*Platichthys flesus*	caudal vertebra	c1859; 2469	3	7th - 8th	30-40	collagen	
Blue Bridge Lane	BBL0919	*Pleuronectes platessa*	caudal vertebra	c1528; 4615	8b	late 14th - early 16th	20-30	collagen	
Barreau Saint-George	BSG0001	*Platichthys flesus*	caudal vertebra	st215		11th century	5-15	22.4	
Barreau Saint-George	BSG0002	*Platichthys flesus*	os anale	st47		11th century	20-30	19.9	
Barreau Saint-George	BSG0005	*Platichthys flesus*	quadrate	st215		11th century	20-30	28.6	
Barreau Saint-George	BSG0009	*Pleuronectes platessa*	cleithrum	st215		11th century	25-35 or larger	collagen	
Barreau Saint-George	BSG0010	cf *Platichthys flesus*	cleithrum	st215		11th century	10-20	24.4	
Barreau Saint-George	BSG0013	*Platichthys flesus*	epihyal	st215		11th century	15-25	13.9	
Barreau Saint-George	BSG0014	*Platichthys flesus*	atlas	st215		11th century	15-25	12.6	
Barreau Saint-George	BSG0015	*Pleuronectes platessa*	atlas	st215		11th century	5-15	12.1	
Barreau Saint-George	BSG0016	*Platichthys flesus*	atlas	st215		11th century	5-15	11.2	
Barreau Saint-George	BSG0017	*Pleuronectes platessa*	atlas	st215		11th century	5-15	5.5	
Barreau Saint-George	BSG0018	*Platichthys flesus*	cervical vertebra	st215		11th century	10-20	12.8	
Barreau Saint-George	BSG0019	cf *Pleuronectes platessa*	urohyal	st47		11th century	50-60	collagen	
Barreau Saint-George	BSG0020	*Platichthys flesus*	precaudal vertebra	st215		11th century	10-20	21.4	
Barreau Saint-George	BSG0021	*Platichthys flesus*	caudal vertebra	st215		11th century	5-15	9.5	
Barreau Saint-George	BSG0022	*Pleuronectes platessa*	precaudal vertebra	st215		11th century	5-15	6.8	
Barreau Saint-George	BSG0023	*Platichthys flesus*	precaudal vertebra	st215		11th century	10-20	20.1	
Barreau Saint-George	BSG0024	*Platichthys flesus*	precaudal vertebra	st215		11th century	10-20	17.3	
Barreau Saint-George	BSG0025	*Platichthys flesus*	precaudal vertebra	st215		11th century	10-20	21.2	
Barreau Saint-George	BSG0026	*Platichthys flesus*	precaudal vertebra	st215		11th century	5-15	17.6	
Barreau Saint-George	BSG0027	*Platichthys flesus*	precaudal vertebra	st215		11th century	5-15	24.7	
Barreau Saint-George	BSG0028	*Platichthys flesus*	precaudal vertebra	st215		11th century	5-15	12.8	
Barreau Saint-George	BSG0029	*Pleuronectes platessa*	first caudal vertebra	st215		11th century	15-25	collagen	
Barreau Saint-George	BSG0030	*Platichthys flesus*	first caudal vertebra	st215		11th century	5-15	18.2	
Barreau Saint-George	BSG0031	*Pleuronectes platessa*	caudal vertebra	st215		11th century	25-35	collagen	
Barreau Saint-George	BSG0032	*Pleuronectes platessa*	caudal vertebra	st215		11th century	20-30	14.3	
Barreau Saint-George	BSG0033	*Platichthys flesus*	caudal vertebra	st215		11th century	10-25	12.2	
Barreau Saint-George	BSG0034	*Platichthys flesus*	caudal vertebra	st215		11th century	10-20	27.1	
Barreau Saint-George	BSG0035	*Platichthys flesus*	caudal vertebra	st215		11th century	10-20	25.1	
Barreau Saint-George	BSG0036	*Platichthys flesus*	caudal vertebra	st215		11th century	10-20	21.5	
Barreau Saint-George	BSG0037	*Platichthys flesus*	articular	st215		11th century	10-20	10.1	
Barreau Saint-George	BSG0039	*Platichthys flesus*	atlas	st215		11th century	5-15	13.5	
Barreau Saint-George	BSG0040	*Platichthys flesus*	precaudal vertebra	st215		11th century	15-25	29.9	
Barreau Saint-George	BSG0041	*Platichthys flesus*	caudal vertebra	st215		11th century	10-20	18.4	
Barreau Saint-George	BSG0043	*Pleuronectes platessa*	atlas	st215		11th century	30-40	25.6	
Barreau Saint-George	BSG0044	*Pleuronectes platessa*	cleithrum	st215		11th century	20-30	collagen	
Barreau Saint-George	BSG0046	*Platichthys flesus*	vertebra	st215		11th century	10-20	28.5	
Barreau Saint-George	BSG0048	*Platichthys flesus*	first caudal vertebra	st215		11th century	10-20	25.5	
Barreau Saint-George	BSG0049	*Platichthys flesus*	first caudal vertebra	st215		11th century	10-20	25.3	
Barreau Saint-George	BSG0050	*Pleuronectes platessa*	precaudal vertebra	st215		11th century	10-20	14	
Barreau Saint-George	BSG0051	*Pleuronectes platessa*	precaudal vertebra	st215		11th century	5-15	6.2	
Barreau Saint-George	BSG0052	*Platichthys flesus*	caudal vertebra	st215		11th century	20-30	19	
Barreau Saint-George	BSG0053	*Platichthys flesus*	caudal vertebra	st215		11th century	20-30	24.1	
Barreau Saint-George	BSG0054	*Pleuronectes platessa*	caudal vertebra	st215		11th century	15-25	24.3	
Barreau Saint-George	BSG0055	*Platichthys flesus*	caudal vertebra	st215		11th century	15-25	22.5	
Barreau Saint-George	BSG0056	*Pleuronectes platessa*	caudal vertebra	st215		11th century	15-25	24.4	
Barreau Saint-George	BSG0057	*Pleuronectes platessa*	caudal vertebra	st215		11th century	10-20	22.8	
Barreau Saint-George	BSG0058	*Platichthys flesus*	caudal vertebra	st215		11th century	10-20	21.4	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Barreau Saint-George	BSG0059	*Pleuronectes platessa*	caudal vertebra	st215		11th century	15-25	28.4	
Barreau Saint-George	BSG0060	*Platichthys flesus*	caudal vertebra	st215		11th century	15-25	25.9	
Barreau Saint-George	BSG0061	*Pleuronectes platessa*	cervical vertebra	st215		11th century	30-40	20	
Barreau Saint-George	BSG0062	*Platichthys flesus*	cervical vertebra	st215		11th century	20-30	20.9	
Barreau Saint-George	BSG0063	*Platichthys flesus*	cervical vertebra	st215		11th century	5-15	13.1	
Barreau Saint-George	BSG0064	*Platichthys flesus*	cervical vertebra	st215		11th century	10-20	16.4	
Barreau Saint-George	BSG0065	*Platichthys flesus*	cervical vertebra	st215		11th century	5-15	6.4	
Barreau Saint-George	BSG0066	*Platichthys flesus*	cervical vertebra	st215		11th century	10-20	22.7	
Barreau Saint-George	BSG0067	*Platichthys flesus*	precaudal vertebra	st215		11th century	10-20	25.8	
Barreau Saint-George	BSG0068	*Platichthys flesus*	precaudal vertebra	st215		11th century	10-20	12.4	
Barreau Saint-George	BSG0069	*Platichthys flesus*	precaudal vertebra	st215		11th century	5-15	9.6	
Barreau Saint-George	BSG0070	*Pleuronectes platessa*	precaudal vertebra	st215		11th century	10-20	25.7	
Barreau Saint-George	BSG0071	*Platichthys flesus*	precaudal vertebra	st215		11th century	20-30	21.1	
Barreau Saint-George	BSG0073	*Platichthys flesus*	preoperculum	st215		11th century	10-20	21.6	
Barreau Saint-George	BSG0075	cf *Platichthys flesus*	hyomandibula	st215		11th century	15-25	28.8	
Barreau Saint-George	BSG0078	cf *Platichthys flesus*	frontalia	st215		11th century	5-15	11.3	
Barreau Saint-George	BSG0081	cf *Platichthys flesus*	os anale	st47		11th century	10-20	33.3	
Barreau Saint-George	BSG0082	*Platichthys flesus*	atlas	st47		11th century	10-20	13.3	
Barreau Saint-George	BSG0083	*Platichthys flesus*	precaudal vertebra	st47		11th century	10-20	15.8	
Barreau Saint-George	BSG0084	*Platichthys flesus*	caudal vertebra	st47		11th century	10-20	20.2	
Barreau Saint-George	BSG0085	*Pleuronectes platessa*	precaudal vertebra	st47		11th century	30-40	collagen	
Barreau Saint-George	BSG0086	FAILED	parasphenoid	st47		11th century	30-40	collagen	
Barreau Saint-George	BSG0086_new	FAILED	parasphenoid	st47		11th century	30-40	collagen	
Barreau Saint-George	BSG0086_newnew	*Melanogrammus aeglefinus*	parasphenoid	st47		11th century	30-40	collagen	
Barreau Saint-George	BSG0087	*Pleuronectes platessa*	posttemporal	st47		11th century	50-60	collagen	
Barreau Saint-George	BSG0088	*Pleuronectes platessa*	atlas	st47		11th century	25-35	23.1	
Barreau Saint-George	BSG0089	*Platichthys flesus*	first caudal vertebra	st47		11th century	25-35	14.6	
Barreau Saint-George	BSG0090	*Pleuronectes platessa*	caudal vertebra	st47		11th century	25-35	collagen	
Barreau Saint-George	BSG0091	FAILED	cleithrum	us215		11th century	?	collagen	
Barreau Saint-George	BSG0091_new	FAILED	cleithrum	us215		11th century	?	collagen	
Barreau Saint-George	BSG0091_newnew	*Scophthalmus maximus*	cleithrum	us215		11th century	?	collagen	
Barreau Saint-George	BSG0092	cf *Platichthys flesus*	os anale	us215		11th century	15-25	collagen	
Barreau Saint-George	BSG0093	cf *Platichthys flesus*	os anale	us215		11th century	20-30	collagen	
Barreau Saint-George	BSG0094	*Platichthys flesus*	hyomandibula	st215		11th century	5-15	9.2	
Barreau Saint-George	BSG0095	*Platichthys flesus*	os anale	st215		11th century	20-25	23.3	
Barreau Saint-George	BSG0096	*Gadus morhua*	dentary	st37		11th century	100-110	collagen	
Barreau Saint-George	BSG0097	*Gadus morhua*	operculum	st47		11th century	100-110	collagen	
Barreau Saint-George	BSG0098	*Gadus morhua*	premaxilla	us229		11th century	100-110	collagen	
Barreau Saint-George	BSG0099	*Gadus morhua*	dentary	us208		11th century	90-100	collagen	
Barreau Saint-George	BSG0100	*Gadus morhua*	maxilla	st47		11th century	100-110	collagen	
Barreau Saint-George	BSG0102	*Pleuronectes platessa*	cleithrum	32a		11th century	40-50	collagen	
Barreau Saint-George	BSG0103	*Platichthys flesus*	os anale	st215		11th century	20-25	collagen	
Barreau Saint-George	BSG0104	*Pleuronectes platessa*	os anale	st215		11th century	50-60,>60	collagen	
Barreau Saint-George	BSG0105	*Pleuronectes platessa*	os anale	st215		11th century	45-55	collagen	
Barreau Saint-George	BSG0106	*Pleuronectes platessa*	os anale	us215		11th century	30-34	collagen	
Barreau Saint-George	BSG0107	*Pleuronectes platessa*	cleithrum	us215		11th century	?	collagen	
Barreau Saint-George	BSG0108	*Platichthys flesus*	cleithrum	us215		11th century	15-25	collagen	
Barreau Saint-George	BSG0109	cf *Platichthys flesus*	first caudal vertebra	us215		11th century	15-25	collagen	
Barreau Saint-George	BSG0110	*Pleuronectes platessa*	hyomandibula	us215		11th century	25-35?	collagen	
Barreau Saint-George	BSG0111	*Pleuronectes platessa*	preoperculum	us215		11th century	20-30	collagen	
Barreau Saint-George	BSG0112	*Platichthys flesus*	os anale	us215		11th century	15-25	collagen	
Barreau Saint-George	BSG0113	*Pleuronectes platessa*	cleithrum	st215		11th century	30-40	collagen	
Barreau Saint-George	BSG0114	*Pleuronectes platessa*	hyomandibula	st47		11th century	30-40	collagen	
Barreau Saint-George	BSG0115	*Pleuronectes platessa*	os anale	st47		11th century	>50	collagen	
Barreau Saint-George	BSG0116	*Pleuronectes platessa*	first caudal vertebra	st47		11th century	50-60	collagen	
Barreau Saint-George	BSG0117	*Pleuronectes platessa*	ultimate vertebra	us215		11th century	40-50	collagen	
Tradescent Lane	CAN0401	*Pleuronectes platessa*	os anale	26	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0402	*Pleuronectes platessa*	os anale	26	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0403	*Pleuronectes platessa*	os anale	26	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0404	*Pleuronectes platessa*	precaudal vertebra	119	4	post 1275	30-40	collagen	
Tradescent Lane	CAN0405	*Pleuronectes platessa*	hyomandibula	119	4	post 1275	40-60	collagen	
Tradescent Lane	CAN0406	*Gadus morhua*	epihyal	119	4	post 1275	60-80	collagen	
Tradescent Lane	CAN0407	FAILED	articular	24	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0407_new	*Melanogrammus aeglefinus*	articular	24	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0408	*Pleuronectes platessa*	quadrate	24	3	early 12 - mid 13	40-60	collagen	
Tradescent Lane	CAN0409	*Pleuronectes platessa*	hyomandibula	24	3	early 12 - mid 13	30-40	collagen	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Tradescent Lane	CAN0410	*Pleuronectes platessa*	maxilla	24	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0411	*Solea solea*	urohyal	24	3	early 12 - mid 13	20-40	21.1	
Tradescent Lane	CAN0412	*Pleuronectes platessa*	atlas	19	3	early 12 - mid 13	40-50	collagen	
Tradescent Lane	CAN0413	*Pleuronectes platessa*	cleithrum	19	3	early 12 - mid 13	20-30	collagen	
Tradescent Lane	CAN0414	*Scophthalmus rhombus*	supracleithrum	19	3	early 12 - mid 13	>30	collagen	
Tradescent Lane	CAN0415	*Gadus morhua*	parasphenoid	34	3	early 12 - mid 13	40-60	collagen	
Tradescent Lane	CAN0416	*Pleuronectes platessa*	articular	34	3	early 12 - mid 13	40-60	collagen	
Tradescent Lane	CAN0417	*Pleuronectes platessa*	caudal vertebra	34	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0418	*Pleuronectes platessa*	supracleithrum	12	3	early 12 - mid 13	20-30	20.3	
Tradescent Lane	CAN0419	*Pleuronectes platessa*	os anale	16	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0420	*Gadus morhua*	parasphenoid	16	3	early 12 - mid 13	70-80	collagen	
Tradescent Lane	CAN0421	*Pleuronectes platessa*	os anale	20	3	early 12 - mid 13	20-30	collagen	
Tradescent Lane	CAN0422	*Pleuronectes platessa*	maxilla	42	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0423	*Pleuronectes platessa*	quadrate	42	3	early 12 - mid 13	30-60	collagen	
Tradescent Lane	CAN0424	*Platichthys flesus*	cranial	23	3	early 12 - mid 13	>30	collagen	
Tradescent Lane	CAN0425	*Platichthys flesus*	os anale	13	3	early 12 - mid 13	20-30	collagen	
Tradescent Lane	CAN0426	*Pleuronectes platessa*	dentary	13	3	early 12 - mid 13	20-30	collagen	
Tradescent Lane	CAN0427	*Platichthys flesus*	articular	13	3	early 12 - mid 13	20-30	collagen	
Tradescent Lane	CAN0428	*Pleuronectes platessa*	cleithrum	13	3	early 12 - mid 13	30-60	collagen	
Tradescent Lane	CAN0429	*Solea solea*	cleithrum	13	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0429_new	*Solea solea*	cleithrum	13	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0430	*Scophthalmus rhombus*	dentary	13	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0431	*Gadus morhua*	parasphenoid	13	3	early 12 - mid 13	70-100	collagen	
Tradescent Lane	CAN0432	*Pleuronectes platessa*	quadrate	13	3	early 12 - mid 13	40-50	collagen	
Tradescent Lane	CAN0433	*Pleuronectes platessa*	premaxilla	119	4	post 1275	40-60	collagen	
Tradescent Lane	CAN0434	cf *Platichthys flesus*	caudal vertebra	119	4	post 1275	30-40	collagen	
Tradescent Lane	CAN0435	*Solea solea*	caudal vertebra	16	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0436	*Pleuronectes platessa*	cleithrum	23	3	early 12 - mid 13	40-60	collagen	
Tradescent Lane	CAN0437	*Pleuronectes platessa*	caudal vertebra	27	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0438	*Solea solea*	caudal vertebra	13	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0439	*Pleuronectes platessa*	caudal vertebra	13	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0440	*Pleuronectes platessa*	caudal vertebra	13	3	early 12 - mid 13	30-40	collagen	
Tradescent Lane	CAN0441	*Conger conger*	parasphenoid	26	3	early 12 - mid 13	>70	collagen	
Tradescent Lane	CAN0441_new	*Conger conger*	parasphenoid	26	3	early 12 - mid 13	>70	collagen	
Tradescent Lane	CAN0442	*Solea solea*	caudal vertebra	12	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0443	*Solea solea*	caudal vertebra	16	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0444	*Solea solea*	preoperculum	23	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0445	cf *Platichthys flesus*	caudal vertebra	23	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0445_new	cf *Platichthys flesus*	caudal vertebra	23	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0446	*Solea solea*	caudal vertebra	13	3	early 12 - mid 13	20-40	collagen	
Tradescent Lane	CAN0450	cf Cyprinidae	hyomandibula	st gregory		early 12 - mid 13	>30	collagen	Type B
Tradescent Lane	CAN0451	FAILED	vertebra	st gregory		early 12 - mid 13	NA	collagen	
Tradescent Lane	CAN0451_new	cf *Salmo trutta*	vertebra	st gregory		early 12 - mid 13	NA	collagen	
CAO96	CAO0822	*Gadus morhua*	epihyal	418	7	900-1150	90-110	collagen	
CAO96	CAO0823	*Gadus morhua*	dentary	418	7	900-1150	90-110	collagen	
CAO96	CAO0824	*Pleuronectes platessa*	precaudal vertebra	77	8	1150-1270	20-30	collagen	
CAO96	CAO0825	*Esox lucius*	vertebra	194	8	1150-1270	40-50	collagen	
CAO96	CAO0826	*Pleuronectes platessa*	quadrate	194	8	1150-1270	30-40	collagen	
CAO96	CAO0827	*Pleuronectes platessa*	dentary	77	8	1150-1270	30-40	collagen	
CAO96	CAO0828	*Pleuronectes platessa*	preoperculum	77	8	1150-1270	20-30	collagen	
CAO96	CAO0829	*Pleuronectes platessa*	caudal vertebra	164	8	1150-1270	30-40	collagen	
CAO96	CAO0830	*Pleuronectes platessa*	caudal vertebra	856	7	900-1150	20-30	collagen	
CAO96	CAO0831	*Pleuronectes platessa*	atlas	856	7	900-1150	25-35	collagen	
CAO96	CAO0832	*Pleuronectes platessa*	ectopterygoid	303	9	1240-1380	30-40	collagen	
CAO96	CAO0833	*Pleuronectes platessa*	cleithrum	146	9	1240-1380	30-40	collagen	
CAO96	CAO0834	*Pleuronectes platessa*	precaudal vertebra	146	9	1240-1380	30-40	collagen	
CAO96	CAO0835	*Pleuronectes platessa*	caudal vertebra	78	9	1240-1380	30-40	collagen	
Coppergate	COP0100	*Pleuronectes platessa*	cleithrum	5240	D6d	1250 - 1275	20-30	collagen	
Coppergate	COP0101	*Pleuronectes platessa*	vertebra	5240	D6d	1250 - 1275	25-35	16.3	
Coppergate	COP0103	*Pleuronectes platessa*	premaxilla	5241	D6d	1250 - 1275	25-35	13.8	
Coppergate	COP0104	*Limanda limanda*	preoperculum	5241	D6d	1250 - 1275	15-25	14.8	
Coppergate	COP0109	*Pleuronectes platessa*	vertebra	5241	D6d	1250 - 1275	30-40	collagen	
Coppergate	COP0113	*Pleuronectes platessa*	precaudal vertebra	5241	D6d	1250 - 1275	30-40	18.3	
Coppergate	COP0114	*Pleuronectes platessa*	caudal vertebra	5241	D6d	1250 - 1275	30-40	21.3	
Coppergate	COP0121	*Pleuronectes platessa*	os anale	5245	D6d	1250 - 1275	30-50	collagen	
Coppergate	COP0122	*Platichthys flesus*	quadrate	5331	D6a	1040 - 1220	10-20	23.7	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Coppergate	COP0126	*Pleuronectes platessa*	cleithrum	5484	C6e/D6a	1040 - 1280	20-40	collagen	
Coppergate	COP0129	*Pleuronectes platessa*	preoperculum	5484	C6e/D6a	1040 - 1280	20-40	collagen	
Coppergate	COP0131	*Pleuronectes platessa*	os anale	15040	B6c	1200 - 1240	40-50	collagen	
Coppergate	COP0132	*Scophthalmus maximus*	preoperculum	5586	C6e	1200 - 1280	30-50	collagen	
Coppergate	COP0133	unknown; cf flatfish	vertebra	5510	C6e	1200 - 1280	10-20	16.5	
Coppergate	COP0137	*Platichthys flesus*	cleithrum	5981	C6c/D6a	1040 - 1220	5-15	13.2	
Coppergate	COP0139	*Pleuronectes platessa*	caudal vertebra	9224	C6e	1200 - 1280	30-50	collagen	
Coppergate	COP0140	*Scophthalmus maximus*	cleithrum	9224	C6e	1200 - 1280	30-50	collagen	
Coppergate	COP0141	*Pleuronectes platessa*	os anale	9224	C6e	1200 - 1280	40-60	collagen	
Coppergate	COP0142	*Pleuronectes platessa*	caudal vertebra	9224	C6e	1200 - 1280	10-20	18.9	
Coppergate	COP0143	perciform?	precaudal vertebra	9224	C6e	1200 - 1280	5-15	28.2	
Coppergate	COP0147	*Pleuronectes platessa*	os anale	16465	D6a	1040 - 1220	40-60	collagen	
Coppergate	COP0148	*Pleuronectes platessa*	cervical vertebra	16465	D6a	1040 - 1220	20-40	collagen	
Coppergate	COP0152	*Scophthalmus maximus*	cleithrum	16512	B6b/C6d	1140 - 1200	30-50	collagen	
Coppergate	COP0153	*Pleuronectes platessa*	os anale	16464	D6a	1040 - 1220	20-40	collagen	
Coppergate	COP0155	*Melanogrammus aeglefinus*	ceratohyal	16464	D6a	1040-1220	50-70	collagen	
Coppergate	COP0156	*Pleuronectes platessa*	preoperculum	16517	D6a	1040 - 1220	20-40	collagen	
Coppergate	COP0157	*Esox lucius*	vertebra	16522	D6a	1040-1220	50-70	collagen	
Coppergate	COP0158	*Pleuronectes platessa*	hyomandibula	16443	B6c	1200 - 1240	20-40	collagen	
Coppergate	COP0160	*Platichthys flesus*	articular	21674	5B	c.955/6 - early/mid 1000s	10-20	16.5	
Coppergate	COP0161	*Platichthys flesus*	caudal vertebra	31973	1	late 1st - late 4th or later	5-15	21.4	
Coppergate	COP0164	*Platichthys flesus*	os anale	24064	4B	c. 930/935 - c. 955/6	10-20	21.7	
Coppergate	COP0166	*Pleuronectes platessa*	caudal vertebra	12274	D6e	1275 - mid 1300s	20-30	16.2	
Coppergate	COP0167	cf *Clupea harengus*	caudal vertebra	6823	unphased	unphased	?	13	
Coppergate	COP0168	*Pleuronectes platessa*	hyomandibula	5510	C6e	1200 - 1280	40-60	collagen	
Coppergate	COP0169	*Platichthys flesus*	cervical vertebra	30801	3	mid - late 800s/early 900s	10-20	23.2	
Coppergate	COP0170	*Pleuronectes platessa*	caudal vertebra	11416	B6c	1200 - 1240	40-50	collagen	
Coppergate	COP0171	*Pleuronectes platessa*	caudal vertebra	11818	B6c	1200 - 1240	15-25	19.3	
Coppergate	COP0172	*Platichthys flesus*	hyomandibula	12412	C6e	1200 - 1280	10-20	18.8	
Coppergate	COP0173	*Platichthys flesus*	hyomandibula	15311	5CR	mid - later 1000s	5-15	7.3	
Coppergate	COP0174	*Pleuronectes platessa*	caudal vertebra	21252	5B	c. 955/6 - early/mid1000s	10-20	16.3	
Coppergate	COP0175	*Platichthys flesus*	caudal vertebra	35560	4B	c. 930/935 - c. 955/6	5-15	12.4	
Coppergate	COP0176	*Platichthys flesus*	caudal vertebra	29885	4B	c. 930/935 - c. 955/6	10-20	20.1	
Coppergate	COP0177	*Platichthys flesus*	caudal vertebra	30704	3	mid - late 800s/early 900s	5-15	19.7	
Coppergate	COP0178	*Limanda limanda*	precaudal vertebra	1118	D6e	1275 - mid 1300s	20-30	17.5	
Coppergate	COP0179	*Pleuronectes platessa*	caudal vertebra	1118	D6e	1275 - mid 1300s	10-20	27.5	
Coppergate	COP0180	*Scophthalmus maximus*	urohyal	10333	unknown	unknown	40-50	collagen	
Coppergate	COP0181	*Melanogrammus aeglefinus*	cleithrum	10333	unknown	unknown	40-50	collagen	
Coppergate	COP0182	*Pleuronectes platessa*	caudal vertebra	18331	B6a/C6c	1040 - 1160	40-50	collagen	
Coppergate	COP0183	*Limanda limanda*	caudal vertebra	16605	B6b	1160 - 1200	10-20	32.8	
Coppergate	COP0184	*Platichthys flesus*	caudal vertebra	22808	4B	c. 930/935 - c. 955/6	15-25	17	
Coppergate	COP0185	*Platichthys flesus*	cervical vertebra	22154	5A	c. 955/6	10-20	29.6	
Coppergate	COP0187	*Platichthys flesus*	precaudal vertebra	7863	5CR	mid - later 1000s	20-30	19.1	
Coppergate	COP0188	*Pleuronectes platessa*	caudal vertebra	13568	B6a	1040 - 1160	20-30	25.6	
Coppergate	COP0189	*Pleuronectes platessa*	precaudal vertebra	11458	B6c	1200 - 1240	20-30	19.1	
Coppergate	COP0190	*Platichthys flesus*	caudal vertebra	11458	B6c	1200 - 1240	10-20	25.2	
Coppergate	COP0195	*Pleuronectes platessa*	os anale	11458	B6c	1200 - 1240	20-40	collagen	
Coppergate	COP0196	perciform?	caudal vertebra	19212	5CR	mid - later 1000s	20-30	19.4	
Coppergate	COP0198	*Pleuronectes platessa*	vomer	18256	B6a	1040 - 1160	50-60	collagen	
Coppergate	COP0202	*Platichthys flesus*	first caudal vertebra	20982	4B	c. 930/935 - c. 955/6	40-50	collagen	
Coppergate	COP0203	perciform?	caudal vertebra	15608	5B	c. 955/6 - early/mid1000s	5-15	17.3	
Coppergate	COP0204	*Pleuronectes platessa*	os anale	1119	D6e	1275 - mid 1300s	30-50	collagen	
Coppergate	COP0205	*Pleuronectes platessa*	vertebra	1502	C6e/D6e	1200 - mid 1300s	50-60	collagen	
Coppergate	COP0206	*Pleuronectes platessa*	os anale	1585	C6v	1040 - 1100	50-60	collagen	
Coppergate	COP0207	*Limanda limanda*	os anale	2231	A6z	1040 - 1300 and 1440 - 1480	30-40	collagen	
Coppergate	COP0208	*Pleuronectes platessa*	caudal vertebra	4620	C6e	1200 - 1280	30-40	18.5	
Coppergate	COP0209	*Pleuronectes platessa*	os anale	4597	C6e	1200 - 1280	50-60	collagen	
Coppergate	COP0210	*Pleuronectes platessa*	preoperculum	4620	C6e	1200 - 1280	50-60	collagen	
Coppergate	COP0213	*Pleuronectes platessa*	cleithrum	4620	C6e	1200 - 1280	40-50	collagen	
Coppergate	COP0214	*Pleuronectes platessa*	os anale	4620	C6e	1200 - 1280	50-60	collagen	
Coppergate	COP0215	*Platichthys flesus*	urohyal	4620	C6e	1200 - 1280	20-30	collagen	
Coppergate	COP0216	*Limanda limanda*	caudal vertebra	4620	C6e	1200 - 1280	10-20	14.9	
Coppergate	COP0217	*Pleuronectes platessa*	precaudal vertebra	4620	C6e	1200 - 1280	40-50	collagen	
Coppergate	COP0218	*Pleuronectes platessa*	caudal vertebra	4620	C6e	1200 - 1280	25-35	20.6	
Coppergate	COP0220	*Platichthys flesus*	os anale	26630	3	mid - late 800s/early 900s	20-30	collagen	
Coppergate	COP0221	*Platichthys flesus*	precaudal vertebra	27234	4A	late 800s/early 900s - c. 930/5	20-30	12.9	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Coppergate	COP0222	*Pleuronectes platessa*	precaudal vertebra	16653	B6a	1040 - 1160	40-50	collagen	
Coppergate	COP0223	*Platichthys flesus*	caudal vertebra	13568	B6a	1040 - 1160	20-30	27.1	
Coppergate	COP0224	*Pleuronectes platessa*	os anale	13554	B6a	1040 - 1160	50-60	collagen	
Coppergate	COP0226	cf Cyprinidae	precaudal vertebra	30352	4a	late 800s/early 900s-c930/5	30-40	collagen	Type A
Coppergate	COP0229	*Melanogrammus aeglefinus*	cleithrum	16605	B6b	1160-1200	50-60	collagen	
Coppergate	COP0233	*Melanogrammus aeglefinus*	cleithrum	18331	B6a/C6c	1040-1160	40-60	collagen	
Coppergate	COP0234	*Melanogrammus aeglefinus*	hyomandibula	5241	D6d	1250-1275	40-50	collagen	
Coppergate	COP0237	*Platichthys flesus*	caudal vertebra	8304	A6z	1040 - 1300 and 1440 - 1480	5-15	17.5	
Coppergate	COP0238	*Esox lucius*	dentary	8304	A6z	1040-1300 and 1440-1480	40-60	collagen	
Coppergate	COP0242	*Melanogrammus aeglefinus*	cleithrum	1605	D6e	1275-mid1300s	40-60	collagen	
Coppergate	COP0247	*Gadus morhua*	ceratohyal	2191	A6z	1040-1300 and 1440-1480	70-80	collagen	
Coppergate	COP0251	*Pleuronectes platessa*	quadrate	1506	D6e	1275 - mid 1300s	70-80	collagen	
Coppergate	COP0260	*Gadus morhua*	vertebra	24560	4B	c930/935-c955/6	60-80	collagen	
Coppergate	COP0261	*Esox lucius*	vertebra	24560	4B	c930/935-c955/6	50-60	collagen	
Coppergate	COP0270	*Platichthys flesus*	cervical vertebra	25380	4B	c. 930/935 - c. 955/6	10-20	27.3	
Coppergate	COP0279	*Platichthys flesus*	caudal vertebra	19269	5CR	mid - later 1000s	10-20	24.1	
Coppergate	COP0280	*Gadus morhua*	quadrate	19269	5CR	mid-later 1000s	40-60	collagen	
Coppergate	COP0282	*Platichthys flesus*	first caudal vertebra	35679	4B	c. 930/935 - c. 955/6	5-15	14.5	
Coppergate	COP0284	*Melanogrammus aeglefinus*	articular	13568	B6a	1040-1160	40-60	collagen	
Coppergate	COP0291	*Esox lucius*	quadrate	20105	5A	c955/6	50-60	collagen	
Coppergate	COP0307	*Pleuronectes platessa*	urohyal	5464	C6e	1200 - 1280	40-50	collagen	
Coppergate	COP0308	*Gadus morhua*	articular	5415	C6c/D6a	1040-1220	80-100	collagen	
Coppergate	COP0310	*Pleuronectes platessa*	vertebra	5484	C6e/D6a	1040 - 1280	25-35	32.4	
Coppergate	COP0313	*Pleuronectes platessa*	quadrate	13785	B6a	1040 - 1160	30-40	collagen	
Coppergate	COP0318	*Gadus morhua*	dentary	5588	5B	c955/6-early/mid1000s	60-80	collagen	
Coppergate	COP0320	*Pleuronectes platessa*	caudal vertebra	7405	5B	c. 955/6 - early/mid 1000s	40-60	collagen	
Coppergate	COP0323	*Esox lucius*	vertebra	22107	5B	c955/6-early/mid1000s	50-70	collagen	
Coppergate	COP0328	*Pleuronectes platessa*	os anale	2238	5A	c. 955/6	40-50	collagen	
Coppergate	COP0329	*Pleuronectes platessa*	os anale	5245	D6d	1250 - 1275	40-50	collagen	
Coppergate	COP0330	*Pleuronectes platessa*	vertebra	5245	D6d	1250 - 1275	30-50	collagen	
Coppergate	COP0331	*Pleuronectes platessa*	hyomandibula	5241	D6d	1250 - 1275	40-50	collagen	
Coppergate	COP0332	*Pleuronectes platessa*	caudal vertebra	5241	D6d	1250 - 1275	40-60	collagen	
Coppergate	COP0333	*Pleuronectes platessa*	maxilla	5241	D6d	1250 - 1275	35-45	18.3	
Coppergate	COP0334	FAILED	atlas	5241	D6d	1250 - 1275	30-40	25.9	
Coppergate	COP0335	*Pleuronectes platessa*	os anale	5348	C6e/D6a	1040 - 1280	30-50	collagen	
Coppergate	COP0336	*Pleuronectes platessa*	os anale	5238	C6e/D6a	1040 - 1280	50-60	collagen	
Coppergate	COP0337	*Pleuronectes platessa*	ceratohyal	18256	B6a	1040 - 1160	40-50	collagen	
Coppergate	COP0338	*Pleuronectes platessa*	os anale	16465	D6a	1040 - 1220	20-30	collagen	
Coppergate	COP0339	*Pleuronectes platessa*	caudal vertebra	11416	B6c	1200 - 1240	50-60	20.7	
Coppergate	COP0347	*Esox lucius*	parasphenoid	18344	5A	c955/6	50-70	collagen	
Coppergate	COP0349	*Esox lucius*	vertebra	20894	3	mid-late 800s/early 900s	40-60	collagen	
Coppergate	COP0350	*Esox lucius*	vertebra	21257	5B	c955/6-early/mid1000s	50-70	collagen	
Zwarte Laag	GEN0600	cf Cyprinidae	pharyngeal	7		1000-1025	20-30	collagen	Type B
Zwarte Laag	GEN0601	*Pleuronectes platessa*	ectopterygoid	7		1000-1025	20-30	collagen	
Zwarte Laag	GEN0602	*Pleuronectes platessa*	quadrate	10		950-975	30-40	collagen	
Zwarte Laag	GEN0603	*Platichthys flesus*	vertebra	9		975-1000	20-30	collagen	
Zwarte Laag	GEN0604	*Platichthys flesus*	vertebra	9		975-1000	30-40	collagen	
Zwarte Laag	GEN0605	cf Cyprinidae	articular	8		987-1012	>30	collagen	Type B
Zwarte Laag	GEN0606	*Platichthys flesus*	posttemporal	11		937-962	20-30	collagen	
Zwarte Laag	GEN0607	*Pleuronectes platessa*	caudal vertebra	11		937-962	20-30	collagen	
Zwarte Laag	GEN0608	*Pleuronectes platessa*	lower hypohyal	1		1175-1200	30-40	collagen	
Zwarte Laag	GEN0609	cf Cyprinidae	pharyngeal	1		1175-1200	20-30	collagen	Type B
Zwarte Laag	GEN0611	*Platichthys flesus*	posttemporal	3		1125-1150	30-40	collagen	
Zwarte Laag	GEN0612	*Platichthys flesus*	palatine	3		1125-1150	20-30	collagen	
Zwarte Laag	GEN0613	*Pleuronectes platessa*	caudal vertebra	5		1025-1050	20-30	collagen	
Zwarte Laag	GEN0614	*Pleuronectes platessa*	os anale	4		1100-1125	40-50	collagen	
Zwarte Laag	GEN0615	*Melanogrammus aeglefinus*	cleithrum			10th-first half 11th	60-70	collagen	
Zwarte Laag	GEN0616	*Pleuronectes platessa*	quadrate			10th-first half 11th	50-60	collagen	
Zwarte Laag	GEN0617	*Pleuronectes platessa*	os anale			10th-first half 11th	30-40	collagen	
Zwarte Laag	GEN0618	*Pleuronectes platessa*	os anale			10th-first half 11th	30-40	collagen	
Zwarte Laag	GEN0619	*Pleuronectes platessa*	dentary			10th-first half 11th	40-50	collagen	
Zwarte Laag	GEN0620	FAILED	os anale			10th - first half 11th	40-50	collagen	
Zwarte Laag	GEN0620_new	*Platichthys flesus*	os anale			10th - first half 11th	40-50	collagen	
Zwarte Laag	GEN0621	FAILED	cleithrum			10th-first half 11th	50-60	collagen	
Zwarte Laag	GEN0621_new	*Melanogrammus aeglefinus*	cleithrum			10th-first half 11th	50-60	collagen	
Zwarte Laag	GEN0622	*Scophthalmus rhombus*	os anale			12th C	50-60	collagen	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Zwarte Laag	GEN0623	*Scophthalmus maximus*	preoperculum			12th C	30-40	collagen	
Zwarte Laag	GEN0624	*Scophthalmus maximus*	os anale			12th C	40-50	collagen	
Zwarte Laag	GEN0625	*Pleuronectes platessa*	basioccipital	10		950-975	50-60	collagen	
Zwarte Laag	GEN0626	cf Cyprinidae	precaudal vertebra	9		975-1000	>30	collagen	Type B?
Zwarte Laag	GEN0627	*Platichthys flesus*	caudal vertebra	9		975-1000	20-30	collagen	
Zwarte Laag	GEN0628	*Pleuronectes platessa*	cleithrum	7		1000-1025	30-40	collagen	
Zwarte Laag	GEN0629	*Pleuronectes platessa*	caudal vertebra	7		1000-1025	40-50	collagen	
Zwarte Laag	GEN0630	*Pleuronectes platessa*	caudal vertebra	7		1000-1025	40-50	collagen	
Zwarte Laag	GEN0631	cf *Pleuronectes platessa*	caudal vertebra	5		1025-1050	20-30	collagen	
Zwarte Laag	GEN0632	cf Cyprinidae	first spine	4		1100-1125	>40	collagen	Type E
Zwarte Laag	GEN0633	*Pleuronectes platessa*	os anale	4		1100-1125	50-60	collagen	
Zwarte Laag	GEN0634	*Pleuronectes platessa*	urohyal	4		1100-1125	40-50	collagen	
Zwarte Laag	GEN0635	*Pleuronectes platessa*	hyomandibula	4		1100-1125	40-50	collagen	
Zwarte Laag	GEN0636	*Pleuronectes platessa*	caudal vertebra	4		1100-1125	30-40	collagen	
Zwarte Laag	GEN0637	*Pleuronectes platessa*	caudal vertebra	4		1100-1125	30-40	collagen	
Zwarte Laag	GEN0638	*Melanogrammus aeglefinus*	posttemporal	2		1150-1175	50-60	collagen	
Zwarte Laag	GEN0639	*Platichthys flesus*	caudal vertebra	2		1150-1175	20-30	collagen	
Zwarte Laag	GEN0640	*Platichthys flesus*	os anale	2		1150-1175	20-30	collagen	
Zwarte Laag	GEN0641	cf Cyprinidae	cleithrum	2		1150-1175	20-30	collagen	Type C
Zwarte Laag	GEN0642	*Melanogrammus aeglefinus*	supracleithrum	1		1175-1200	50-60	collagen	
Zwarte Laag	GEN0643	*Melanogrammus aeglefinus*	posttemporal	1		1175-1200	50-60	collagen	
Zwarte Laag	GEN0644	cf *Esox lucius*	dentary	1		1175-1200	40-50	collagen	
Zwarte Laag	GEN0645	*Pleuronectes platessa*	quadrate	1		1175-1200	50-60	collagen	
Zwarte Laag	GEN0646	*Platichthys flesus*	urohyal	1		1175-1200	30-40	collagen	
Zwarte Laag	GEN0647	*Pleuronectes platessa*	preoperculum	1		1175-1200	40-50	collagen	
Zwarte Laag	GEN0648	*Platichthys flesus*	quadrate	1		1175-1200	30-40	collagen	
Zwarte Laag	GEN0649	*Pleuronectes platessa*	premaxilla	1		1175-1200	40-50	collagen	
Zwarte Laag	GEN0650	*Pleuronectes platessa*	caudal vertebra	1		1175-1200	40-50	collagen	
Zwarte Laag	GEN0651	*Pleuronectes platessa*	atlas	6		1012-1037	20-30	collagen	
Zwarte Laag	GEN0652	*Pleuronectes platessa*	precaudal vertebra	10		950-975	20-30	collagen	
Zwarte Laag	GEN0653	cf Cyprinidae	caudal vertebra	1		1175-1200	20-30	collagen	Type B?
Zwarte Laag	GEN0654	cf Cyprinidae	caudal vertebra	2		1150-1175	20-30	collagen	Type B
Zwarte Laag	GEN0655	*Platichthys flesus*	caudal vertebra	2		1150-1175	20-30	collagen	
Zwarte Laag	GEN0656	*Platichthys flesus*	caudal vertebra	2		1150-1175	20-30	collagen	
Zwarte Laag	GEN0657	*Pleuronectes platessa*	caudal vertebra	5		1025-1050	20-30	collagen	
Zwarte Laag	GEN0658	*Platichthys flesus*	caudal vertebra	1		1175-1200	20-30	collagen	
Zwarte Laag	GEN0659	FAILED	vomer	3		1125-1150	40-50	collagen	
Zwarte Laag	GEN0659_new	*Melanogrammus aeglefinus*	vomer	3		1125-1150	40-50	collagen	
Zwarte Laag	GEN0660	*Pleuronectes platessa*	vertebra	3		1125-1150	50-60	collagen	
Zwarte Laag	GEN0661	cf Cyprinidae	precaudal vertebra	3		1125-1150	30-40	collagen	Type F
Zwarte Laag	GEN0662	*Platichthys flesus*	caudal vertebra	4		1100-1125	40-50	collagen	
Zwarte Laag	GEN0663	*Pleuronectes platessa*	caudal vertebra	4		1100-1125	40-50	collagen	
Zwarte Laag	GEN0664	*Platichthys flesus*	basipterygium	4		1100-1125	40-50	collagen	
Zwarte Laag	GEN0665	*Melanogrammus aeglefinus*	precaudal vertebra	4		1100-1125	50-60	collagen	
Zwarte Laag	GEN0666	*Melanogrammus aeglefinus*	premaxilla	5		1025-1050	40-50	collagen	
Zwarte Laag	GEN0667	FAILED	operculum	5		1025-1050	40-50	collagen	
Zwarte Laag	GEN0667_new	*Melanogrammus aeglefinus*	operculum	5		1025-1050	40-50	collagen	
Zwarte Laag	GEN0668	cf *Platichthys flesus*	caudal vertebra	7		1000-1025	20-30	collagen	
Zwarte Laag	GEN0669	*Pleuronectes platessa*	os anale			10th-first half 11th	40-50	collagen	
Zwarte Laag	GEN0670	*Pleuronectes platessa*	caudal vertebra			10th-first half 11th	40-50	collagen	
Zwarte Laag	GEN0671	*Pleuronectes platessa*	ectopterygoid			10th-first half 11th	40-50	collagen	
Zwarte Laag	GEN0672	*Pleuronectes platessa*	caudal vertebra			10th-first half 11th	50-60	collagen	
GSJ06	GSJ0800	*Melanogrammus aeglefinus*	dentary	27	7	10-12th century	35-45	collagen	
GSJ06	GSJ0801	cf Cyprinidae	pharyngeal	27	7	10-12th century	10-20	collagen	Type G?
GSJ06	GSJ0802	*Pleuronectes platessa*	ectopterygoid	27	7	10-12th century	30-40	collagen	
GSJ06	GSJ0803	*Pleuronectes platessa*	precaudal vertebra	27	7	10-12th century	30-40	collagen	
GSJ06	GSJ0804	*Pleuronectes platessa*	caudal vertebra	27	7	10-12th century	30-40	collagen	
GSJ06	GSJ0805	*Platichthys flesus*	precaudal vertebra	27	7	10-12th century	20-30	collagen	
GSJ06	GSJ0806	*Pleuronectes platessa*	quadrate	22	7	10-12th century	30-40	collagen	
GSJ06	GSJ0807	*Pleuronectes platessa*	caudal vertebra	27	7	10-12th century	20-30	collagen	
GSJ06	GSJ0808	*Platichthys flesus*	precaudal vertebra	27	7	10-12th century	20-30	collagen	
GSJ06	GSJ0809	*Platichthys flesus*	caudal vertebra	27	7	10-12th century	20-30	collagen	
GSJ06	GSJ0810	*Platichthys flesus*	caudal vertebra	27	7	10-12th century	20-30	collagen	
GSJ06	GSJ0811	*Gadus morhua*	supracleithrum	23	7	10-12th century	60-70	collagen	
GSJ06	GSJ0811	*Gadus morhua*	supracleithrum	23	7	10-12th century	60-70	collagen	
GSJ06	GSJ0811_OLD	*Gadus morhua*	supracleithrum	23	7	10-12th century	60-70	collagen	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
GSJ06	GSJ0812	*Pleuronectes platessa*	basioccipital	23	7	10-12th century	30-40	collagen	
GSJ06	GSJ0813	*Pleuronectes platessa*	caudal vertebra	13	7	10-12th century	20-30	collagen	
GSJ06	GSJ0814	*Pleuronectes platessa*	premaxilla	23	7	10-12th century	50-60	collagen	
GSJ06	GSJ0815	*Merlangius merlangius*	caudal vertebra	17	7	10-12th century	30-40	collagen	
GSJ06	GSJ0817	*Platichthys flesus*	caudal vertebra	17	7	10-12th century	20-30	collagen	
GSJ06	GSJ0818	*Pleuronectes platessa*	articular	18	7	10-12th century	30-40	collagen	
GSJ06	GSJ0819	cf *Platichthys flesus*	caudal vertebra	18	7	10-12th century	30-40	collagen	
GSJ06	GSJ0820	*Pleuronectes platessa*	caudal vertebra	18	7	10-12th century	20-30	collagen	
GSJ06	GSJ0821	*Platichthys flesus*	precaudal vertebra	22	7	10-12th century	20-30	collagen	
GSJ06	GSJ0836	*Platichthys flesus*	caudal vertebra	5	7	10-12th century	20-30	collagen	
GSJ06	GSJ0837	*Conger conger*	vertebra	9	7	10-12th century	?	collagen	
GSJ06	GSJ0837_new	*Conger conger*	vertebra	9	7	10-12th century	?	collagen	
GSJ06	GSJ0838	cf Cyprinidae	pharyngeal	1	7	10-12th century	15-25	collagen	Type B?
GSJ06	GSJ0839	*Pleuronectes platessa*	precaudal vertebra	1	7	10-12th century	30-40	collagen	
Kastanjelaan	KAS0700	cf *Platichthys flesus*	pharyngeal	229		8th -10th	10-30	collagen	
Kastanjelaan	KAS0701	FAILED	os anale	229		8th -10th	20-30	collagen	
Kastanjelaan	KAS0701_NEW	*Platichthys flesus*	os anale	229		8th -10th	20-30	collagen	
Kastanjelaan	KAS0702	cf *Pleuronectes platessa*	urohyal	229		8th -10th	30-40	collagen	
Kastanjelaan	KAS0703	cf Cyprinidae	hyomandibula	229		8th -10th	15-25	collagen	Type E
Kastanjelaan	KAS0703	FAILED	hyomandibula	229		8th -10th	15-25	collagen	
Kastanjelaan	KAS0704	*Pleuronectes platessa*	posttemporal	229		8th -10th	30-40	collagen	
Hof ter Hille	KOK0500	*Pleuronectes platessa*	precaudal vertebra	176		1020-1150	30-40	collagen	
Hof ter Hille	KOK0501	*Pleuronectes platessa*	precaudal vertebra	176		1020-1150	20-30	collagen	
Hof ter Hille	KOK0502	*Pleuronectes platessa*	caudal vertebra	155		770-1000	20-30	collagen	
Hof ter Hille	KOK0503	*Pleuronectes platessa*	os anale	211		890-1150	20-30	collagen	
Hof ter Hille	KOK0504	*Pleuronectes platessa*	posttemporal	155		770-1000	30-40	collagen	
Hof ter Hille	KOK0505	*Pleuronectes platessa*	os anale	211		890-1150	20-30	collagen	
Hof ter Hille	KOK0506	*Pleuronectes platessa*	caudal vertebra	211		890-1150	30-40	collagen	
Hof ter Hille	KOK0507	*Pleuronectes platessa*	os anale	211		890-1150	30-40	collagen	
Hof ter Hille	KOK0508	*Pleuronectes platessa*	caudal vertebra	155		770-1000	20-30	collagen	
Hof ter Hille	KOK0509	*Pleuronectes platessa*	cleithrum	176		1020-1150	50-60	collagen	
Hof ter Hille	KOK0510	*Pleuronectes platessa*	os anale	211		890-1150	30-40	collagen	
Hof ter Hille	KOK0511	*Pleuronectes platessa*	caudal vertebra	176-153		1020-1150	30-40	collagen	
Hof ter Hille	KOK0512	*Pleuronectes platessa*	urohyal	155		770-1000	30-40	collagen	
Hof ter Hille	KOK0513	*Pleuronectes platessa*	posttemporal	155		770-1000	30-40	collagen	
Hof ter Hille	KOK0514	cf *Platichthys flesus*	os anale	570		880-1030	20-30	collagen	
Hof ter Hille	KOK0515	*Pleuronectes platessa*	os anale	176-153		1020-1150	20-30	collagen	
Hof ter Hille	KOK0516	*Pleuronectes platessa*	urohyal	570		880-1030	40-50	collagen	
Hof ter Hille	KOK0517	cf *Platichthys flesus*	os anale	570		880-1030	30-40	collagen	
Hof ter Hille	KOK0518	*Scophthalmus maximus*	maxilla	477		880-1030	40-50	collagen	
Hof ter Hille	KOK0519	cf *Esox lucius*	dentary	155		770-1000	20-40	collagen	
Hof ter Hille	KOK0520	*Pleuronectes platessa*	os anale	211		890-1150	30-40	collagen	
Hof ter Hille	KOK0522	*Melanogrammus aeglefinus*	precaudal vertebra	155		770-1000	40-50	collagen	
Hof ter Hille	KOK0524	*Pleuronectes platessa*	os anale	472		890-1150	30-40	collagen	
Hof ter Hille	KOK0525	FAILED	precaudal vertebra	211		770-1000	50-60	collagen	
Hof ter Hille	KOK0525_new	*Melanogrammus aeglefinus*	precaudal vertebra	211		770-1000	50-60	collagen	
Hof ter Hille	KOK0526	*Pleuronectes platessa*	caudal vertebra	155		770-1000	30-40	collagen	
Hof ter Hille	KOK0527	*Platichthys flesus*	cleithrum	155		770-1000	20-30	collagen	
Hof ter Hille	KOK0528	*Pleuronectes platessa*	cervical vertebra	211		890-1150	30-40	collagen	
Hof ter Hille	KOK0529	*Pleuronectes platessa*	os anale	211		890-1150	40-50	collagen	
Hof ter Hille	KOK0530	*Esox lucius*	caudal vertebra	155		770-1000	30-40	collagen	
Hof ter Hille	KOK0531	*Scophthalmus maximus*	os anale	212		890-1150	30-40	collagen	
Hof ter Hille	KOK0532	*Pleuronectes platessa*	os anale	212		890-1150	30-40	collagen	
Hof ter Hille	KOK0535	*Pleuronectes platessa*	caudal vertebra	212		890-1150	30-40	collagen	
Hof ter Hille	KOK0536	*Pleuronectes platessa*	cleithrum	477		880-1030	40-50	collagen	
Hof ter Hille	KOK0537	*Pleuronectes platessa*	os anale	212		890-1150	30-40	collagen	
Hof ter Hille	KOK0538	*Scophthalmus maximus*	precaudal vertebra	212		890-1150	20-30	collagen	
Hof ter Hille	KOK0539	cf *Esox lucius*	dentary	155		770-1000	?	collagen	
Hof ter Hille	KOK0540	*Pleuronectes platessa*	caudal vertebra	153		1020-1150	30-40	collagen	
Hof ter Hille	KOK0541	*Platichthys flesus*	cleithrum	212		890-1150	30-40	collagen	
Hof ter Hille	KOK0542	*Platichthys flesus*	caudal vertebra	176-153		1020-1150	30-40	collagen	
Hof ter Hille	KOK0543	*Pleuronectes platessa*	caudal vertebra	176-153		1020-1150	30-40	collagen	
Hof ter Hille	KOK0544	*Pleuronectes platessa*	os anale	153		1020-1150	30-40	collagen	
Hof ter Hille	KOK0545	*Pleuronectes platessa*	os anale	176-153		1020-1150	40-50	collagen	
Hof ter Hille	KOK0546	*Platichthys flesus*	cleithrum	472		880-1030	30-40	collagen	
Hof ter Hille	KOK0547	*Melanogrammus aeglefinus*	maxilla	472		880-1030	50-60	collagen	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Hof ter Hille	KOK0548	*Platichthys flesus*	articular	472		880-1030	30-40	collagen	
Hof ter Hille	KOK0549	*Melanogrammus aeglefinus*	cleithrum	472		880-1030	50-60	collagen	
Hof ter Hille	KOK0550	*Gadus morhua*	dentary	565		890-1150	70-80	collagen	
Hof ter Hille	KOK0551	*Scophthalmus maximus*	urohyal	570		880-1030	40-50	collagen	
Hof ter Hille	KOK0552	*Scophthalmus maximus*	articular	570		880-1030	30-40	collagen	
Hof ter Hille	KOK0553	*Pleuronectes platessa*	cleithrum	570		880-1030	40-50	collagen	
Hof ter Hille	KOK0554	*Pleuronectes platessa*	ceratohyal	570		880-1030	30-40	collagen	
Hof ter Hille	KOK0555	*Pleuronectes platessa*	os anale	155		770-1000	40-50	collagen	
Hof ter Hille	KOK0556	*Gadus morhua*	precaudal vertebra	155		770-1000	90-110	collagen	
Hof ter Hille	KOK0557	*Gadus morhua*	caudal vertebra	176		1020-1150	60-70	collagen	
Hof ter Hille	KOK0558	*Gadus morhua*	precaudal vertebra	153		1020-1150	100-110	collagen	
Hof ter Hille	KOK0559	*Pleuronectes platessa*	urohyal	155		770-1000	40-50	collagen	
Hof ter Hille	KOK0560	*Pleuronectes platessa*	caudal vertebra	155		770-1000	30-40	collagen	
Hof ter Hille	KOK0561	*Pleuronectes platessa*	caudal vertebra	177		770-1000	30-40	collagen	
Hof ter Hille	KOK0562	*Pleuronectes platessa*	precaudal vertebra	153		1020-1150	30-40	collagen	
Hof ter Hille	KOK0563	*Platichthys flesus*	cranial	570		880-1030	large	collagen	
Plantage	PLA0705	*Platichthys flesus*	os anale	3356		800-850	30-40	collagen	
Plantage	PLA0706	*Platichthys flesus*	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0707	*Pleuronectes platessa*	os anale	3061		807-840	40-50	collagen	
Plantage	PLA0708	*Pleuronectes platessa*	os anale	3061		807-840	40-50	collagen	
Plantage	PLA0713	cf Cyprinidae	cleithrum	1332		675-750	30-40	collagen	Type B
Plantage	PLA0714	cf *Platichthys flesus*	caudal vertebra	1332		675-750	30-40	collagen	
Plantage	PLA0716	*Platichthys flesus*	os anale	3356		800-850	30-40	collagen	
Plantage	PLA0720	cf *Platichthys flesus*	os anale	5174		807-840	30-40	collagen	
Plantage	PLA0721	*Pleuronectes platessa*	os anale	5174		807-840	40-50	collagen	
Plantage	PLA0722	*Platichthys flesus*	os anale	5174		807-840	20-30	collagen	
Plantage	PLA0723	*Pleuronectes platessa*	os anale	5174		807-840	20-30	collagen	
Plantage	PLA0724	cf Cyprinidae	hyomandibula	5174		807-840	30-40	collagen	Type F
Plantage	PLA0725	*Platichthys flesus*	os anale	5174		807-840	40-50	collagen	
Plantage	PLA0726	*Platichthys flesus*	os anale	3699		675-750	40-50	collagen	
Plantage	PLA0727	*Esox lucius*	dentary	3061		807-840	>50	collagen	
Plantage	PLA0728	cf Cyprinidae	cleithrum	3061		807-840	30-40	collagen	Type C
Plantage	PLA0729	*Platichthys flesus*	cleithrum	1040		650-760	30-40	collagen	
Plantage	PLA0730	cf *Platichthys flesus*	caudal vertebra	1040		650-760	20-30	collagen	
Plantage	PLA0731	cf *Platichthys flesus*	os anale	3061		807-840	10-20	collagen	
Plantage	PLA0732	*Pleuronectes platessa*	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0733	*Platichthys flesus*	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0734	FAILED	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0734_new	*Pleuronectes platessa*	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0735	*Pleuronectes platessa*	preoperculum	3061		807-840	50-60	collagen	
Plantage	PLA0737	*Pleuronectes platessa*	os anale	3061		807-840	30-40	collagen	
Plantage	PLA0738	*Pleuronectes platessa*	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0739	*Platichthys flesus*	os anale	3061		807-840	30-40	collagen	
Plantage	PLA0740	*Platichthys flesus*	os anale	1040		650-760	30-40	collagen	
Plantage	PLA0741	cf *Platichthys flesus*	caudal vertebra	1040		650-760	30-40	collagen	
Plantage	PLA0742	cf *Esox lucius*	dentary	1040		650-760	>50	collagen	
Plantage	PLA0743	cf *Platichthys flesus*	os anale	1040		650-760	20-30	collagen	
Plantage	PLA0744	*Pleuronectes platessa*	dentary	5174		807-840	30-40	collagen	
Plantage	PLA0746	FAILED	cleithrum	3061		807-840	>60	collagen	
Plantage	PLA0746_new	*Melanogrammus aeglefinus*	cleithrum	3061		807-840	>60	collagen	
Plantage	PLA0747	*Gadus morhua*	dentary	3061		807-840	>70	collagen	
Plantage	PLA0748	*Pleuronectes platessa*	os anale	3061		807-840	20-30	collagen	
Plantage	PLA0749	*Pleuronectes platessa*	os anale	3061		807-840	30-40	collagen	
Plantage	PLA0750	*Gadus morhua*	dentary	3061		807-840	60-70	collagen	
Plantage	PLA0751	*Gadus morhua*	ceratohyal	3061		807-840	80-90	collagen	
Plantage	PLA0752	*Esox lucius*	dentary	1332		675-750	>50	collagen	
Plantage	PLA0753	*Esox lucius*	dentary	1332		675-750	>50	collagen	
Plantage	PLA0756	*Melanogrammus aeglefinus*	ceratohyal	5174		807-840	40-50	collagen	
Plantage	PLA0757	*Pleuronectes platessa*	os anale	3061		807-840	30-40	collagen	
Plantage	PLA0759	cf Cyprinidae	cleithrum	3061		807-840	40-50	collagen	Type C
Plantage	PLA0760	cf Cyprinidae	hyomandibula	1040		650-760	30-40	collagen	Type E
Plantage	PLA0761	cf *Platichthys flesus*	preoperculum	1332		675-750	30-40	collagen	
Plantage	PLA0764	*Platichthys flesus*	os anale	3061		807-840	50-60	collagen	
Plantage	PLA0765	*Platichthys flesus*	cleithrum	5174		807-840	40-50	collagen	
Plantage	PLA0766	cf *Platichthys flesus*	articular	1332		675-750	20-30	collagen	
SGA89	SGA0841	*Platichthys flesus*	caudal vertebra	1632; 443		7-9th	20-30	collagen	

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
SGA89	SGA0842	*Pleuronectes platessa*	caudal vertebra	361; 94		7-9th	20-30	collagen	
SGA89	SGA0843	*Pleuronectes platessa*	caudal vertebra	361; 94		7-9th	20-30	collagen	
SGA89	SGA0844	*Pleuronectes platessa*	caudal vertebra	361; 94		7-9th	30-40	collagen	
SGA89	SGA0845	cf *Platichthys flesus*	caudal vertebra	416; 105		7-9th	20-30	collagen	
SGA89	SGA0846	*Melanogrammus aeglefinus*	vertebra	1603; 393		7-9th	30-50	collagen	
SGA89	SGA0847	*Platichthys flesus*	caudal vertebra	1603; 393		7-9th	10-20	collagen	
SGA89	SGA0848	*Pleuronectes platessa*	precaudal vertebra	1590; 375		7-9th	30-40	collagen	
SGA89	SGA0849	*Platichthys flesus*	caudal vertebra	472; 121		7-9th	20-30	collagen	
SGA89	SGA0850	cf Cyprinidae	pharyngeal	37; 2		7-9th	20-30	collagen	Type E
SGA89	SGA0851	cf Cyprinidae	vertebra	250; 61		7-9th	10-20	collagen	Type B
SGA89	SGA0852	cf *Pleuronectes platessa*	caudal vertebra	250; 61		7-9th	50-60	collagen	
SGA89	SGA0853	*Pleuronectes platessa*	caudal vertebra	250; 61		7-9th	10-20	collagen	
SGA89	SGA0854	*Pleuronectes platessa*	caudal vertebra	250; 61		7-9th	20-30	collagen	
SGA89	SGA0855	*Pleuronectes platessa*	caudal vertebra	119; 34		7-9th	30-40	collagen	
SGA89	SGA0856	cf *Pleuronectes platessa*	caudal vertebra	119; 34		7-9th	40-50	collagen	
SGA89	SGA0857	*Platichthys flesus*	os anale	99; 24		7-9th	30-40	collagen	
SGA89	SGA0858	*Pleuronectes platessa*	ceratohyal	1609; 403		7-9th	30-40	collagen	
SGA89	SGA0859	cf Cyprinidae	pharyngeal	1089; 385		7-9th	20-30	collagen	Type B
SOT89	SOT0860	*Platichthys flesus*	caudal vertebra	25; 8		7-9th	20-30	collagen	
SOT89	SOT0861	*Pleuronectes platessa*	caudal vertebra	25; 8		7-9th	40-50	collagen	
SOT89	SOT0862	*Pleuronectes platessa*	vertebra	26; 9		7-9th	20-30	collagen	
SOT89	SOT0863	*Platichthys flesus*	caudal vertebra	26; 9		7-9th	10-20	collagen	
SOT89	SOT0864	*Platichthys flesus*	cervical vertebra	172; 19		7-9th	20-30	collagen	
SOT89	SOT0865	*Pleuronectes platessa*	vertebra	172; 19		7-9th	20-30	collagen	
SOT89	SOT0866	cf Cyprinidae	pharyngeal	184; 21		7-9th	20-30	collagen	Type B
SOT89	SOT0867	*Platichthys flesus*	cleithrum	26		7-9th	20-30	collagen	
Gat in de Markt	VLA0301	*Pleuronectes platessa*	quadrate	1117	3b	1000-1050	30-40	collagen	
Gat in de Markt	VLA0302	cf Cyprinidae	caudal vertebra	1714	3b	1000-1050	20-30	collagen	Type B
Gat in de Markt	VLA0303	cf Cyprinidae	caudal vertebra	784.2	3b	1000-1050	20-30	collagen	Type B
Gat in de Markt	VLA0304	*Gadus morhua*	articular	701	3a	1000-1050	100-110	collagen	
Gat in de Markt	VLA0305	*Gadus morhua*	maxilla	701	3a	1000-1050	70-80	collagen	
Gat in de Markt	VLA0306	*Pleuronectes platessa*	preoperculum	701	3a	1000-1050	40-50	collagen	
Gat in de Markt	VLA0307	*Pleuronectes platessa*	preoperculum	843	3b	1000-1050	30-40	collagen	
Gat in de Markt	VLA0308	*Pleuronectes platessa*	preoperculum	282	2d	891-933	40-50	collagen	
Gat in de Markt	VLA0309	cf Cyprinidae	preoperculum	166	4	1050-1170	>45	collagen	Type D
Gat in de Markt	VLA0310	cf Cyprinidae	operculum	188	4	1050-1170	30-50	collagen	Type D
Gat in de Markt	VLA0311	*Melanogrammus aeglefinus*	cleithrum	188	4	1050-1170	>50	collagen	
Gat in de Markt	VLA0313	*Pleuronectes platessa*	os anale	188	4	1050-1170	30-40	collagen	
Gat in de Markt	VLA0313	*Pleuronectes platessa*	os anale	188	4	1050-1170	30-40	collagen	
Gat in de Markt	VLA0313_NEW	FAILED	os anale	188	4	1050-1170	30-40	collagen	
Gat in de Markt	VLA0313_OLD	*Gadus morhua*	os anale	188	4	1050-1170	30-40	collagen	
Gat in de Markt	VLA0314	*Pleuronectes platessa*	os anale	180	4	1050-1170	40-60	collagen	
Gat in de Markt	VLA0315	*Pleuronectes platessa*	os anale	189	4	1050-1170	40-50	collagen	
Gat in de Markt	VLA0316	*Pleuronectes platessa*	os anale	189	4	1050-1170	40-50	collagen	
Gat in de Markt	VLA0317	*Pleuronectes platessa*	os anale	165	5b	1180-1217	50-60	collagen	
Gat in de Markt	VLA0318	*Gadus morhua*	articular	171	5b	1180-1217	60-70	collagen	
Gat in de Markt	VLA0319	*Gadus morhua*	articular	171	5b	1180-1217	60-70	collagen	
Gat in de Markt	VLA0320	*Pleuronectes platessa*	cleithrum	503	5c	1217-1250	50-60	collagen	
Gat in de Markt	VLA0321	*Platichthys flesus*	caudal vertebra	407	5c	1217-1250	20-30	collagen	
Gat in de Markt	VLA0322	*Platichthys flesus*	os anale	339	5c	1217-1250	20-30	collagen	
Gat in de Markt	VLA0323	*Platichthys flesus*	first caudal vertebra	339	5c	1217-1250	10-20	13.3	
Gat in de Markt	VLA0324	*Platichthys flesus*	atlas	339	5c	1217-1250	20-30	24	
Gat in de Markt	VLA0325	*Pleuronectes platessa*	preoperculum	487	5c	1217-1250	20-30	collagen	
Gat in de Markt	VLA0326	*Gadus morhua*	dentary	408	5c	1217-1250	100-120	collagen	
Gat in de Markt	VLA0327	*Gadus morhua*	dentary	76	5c	1217-1250	100-120	collagen	
Gat in de Markt	VLA0328	*Pleuronectes platessa*	os anale	76	5c	1217-1250	40-60	collagen	
Gat in de Markt	VLA0329	*Pleuronectes platessa*	os anale	66	5d	1250-1299	30-50	collagen	
Gat in de Markt	VLA0330	*Pleuronectes platessa*	hyomandibula	172	5d	1250-1299	30-40	collagen	
Gat in de Markt	VLA0331	*Platichthys flesus*	caudal vertebra	172	5d	1250-1299	20-30	collagen	
Gat in de Markt	VLA0332	*Pleuronectes platessa*	os anale	67	5d	1250-1299	40-50	collagen	
Gat in de Markt	VLA0333	*Pleuronectes platessa*	caudal vertebra	175	5d	1250-1299	40-60	collagen	
Gat in de Markt	VLA0334	*Pleuronectes platessa*	os anale	174	5d	1250-1299	30-40	collagen	
Gat in de Markt	VLA0335	*Platichthys flesus*	os anale	174	5d	1250-1299	30-40	collagen	
Gat in de Markt	VLA0336	*Pleuronectes platessa*	os anale	174	5d	1250-1299	30-40	collagen	
Gat in de Markt	VLA0337	cf Cyprinidae	pharyngeal	174	5d	1250-1299	30-40	collagen	Type B
Gat in de Markt	VLA0338	cf Cyprinidae	pharyngeal	172	5d	1250-1299	20-40	collagen	Type B

Table D9 continued

Site	ID number	Species	Element	Context	Phase	Period	Size	Weight	Comment
Gat in de Markt	VLA0339	*Melanogrammus aeglefinus*	parasphenoid	174	5d	1250-1299	30-50	collagen	
Gat in de Markt	VLA0340	*Melanogrammus aeglefinus*	parasphenoid	1095	5d	1250-1299	10-40	collagen	
Gat in de Markt	VLA0341	*Platichthys flesus*	parasphenoid	1095	5d	1250-1299	20-30	collagen	
Gat in de Markt	VLA0342	*Gadus morhua*	quadrate	1083	5e	1250-1300	>70	collagen	
Gat in de Markt	VLA0343	*Platichthys flesus*	caudal vertebra	1083	5e	1250-1300	20-30	collagen	
Gat in de Markt	VLA0344	*Platichthys flesus*	os anale	57	5f	1300-1350	10-20	collagen	
Gat in de Markt	VLA0345	*Pleuronectes platessa*	os anale	1080	5f	1300-1350	10-20	collagen	
Gat in de Markt	VLA0346	*Melanogrammus aeglefinus*	quadrate	61	5f	1300-1350	40-50	collagen	
Gat in de Markt	VLA0347	*Pleuronectes platessa*	cleithrum	1091	5f	1300-1350	20-30	collagen	
Gat in de Markt	VLA0348	*Platichthys flesus*	pharyngeal	1091	5f	1300-1350	20-30	collagen	
Gat in de Markt	VLA0349	*Scophthalmus maximus*	caudal vertebra	63	5f	1300-1350	50-60	collagen	
Gat in de Markt	VLA0350	*Platichthys flesus*	caudal vertebra	1091	5f	1300-1350	30-40	collagen	
Gat in de Markt	VLA0351	*Platichthys flesus*	caudal vertebra	61	5f	1300-1350	40-50	collagen	
Gat in de Markt	VLA0352	*Melanogrammus aeglefinus*	cleithrum	50	5f	1300-1350	40-70	collagen	
Gat in de Markt	VLA0353	*Gadus morhua*	quadrate	97	5f	1300-1350	100-120	collagen	
Gat in de Markt	VLA0354	*Pleuronectes platessa*	os anale	282	2d	891-933	40-50	collagen	
Gat in de Markt	VLA0355	*Pleuronectes platessa*	preoperculum	701	3a	1000-1050	40-50	collagen	
Gat in de Markt	VLA0356	*Pleuronectes platessa*	cleithrum	162	4	1050-1170	40-60	collagen	
Gat in de Markt	VLA0357	*Pleuronectes platessa*	preoperculum		4	1050-1170	50-60	collagen	

Table D10. Ratios of identified *P. platessa* and *P. flesus* in Barreau Saint-George, Coppergate, and Blue Bridge Lane.

Site	**Barreau Saint-George (FR)**		**Coppergate, York (UK)**		**Blue Bridge Lane, York (UK)**	
Method	Report	ZooMS	Report	ZooMS	Report	ZooMS
P. platessa	35	34	12	57	15	10
P. flesus	56	58	4	24	1	3
Ratio *P. flesus* to *P. platessa*	1.6	1.71	0.33	0.42	0.07	0.3

Table D11. Success rate of morphological identification verified by ZooMS.

	Count		**Percentage**	
Morphological ID level	correct	incorrect	correct	incorrect
Species	16	3	18.2%	3.4%
Species group (i.e. plaice/flounder)	2		2.3%	
Family	61	2	69.3%	2.3%
Order	2	2	2.3%	2.3%
Total	81	7	92.0%	8.0%

Appendix E – Chapter 6. Finding the right plaice at the right time: Multi-isotope analysis and collagen peptide mass fingerprinting of flatfish remains reveal historical catch habitats

Part E1. Additional tables and figures

Table E1. Overview of published isotope values of flatfish from various studied areas and periods in Europe (Müldner & Richards, 2005; Fischer, 2007; Müldner & Richards, 2007; Antanaitis-Jacobs *et al.*, 2009; Fuller *et al.*, 2012; Göhring *et al.*, 2016; Robson *et al.*, 2016; Ervynck *et al.*, 2018; Dahliwal *et al.*, 2019).

Taxon	**Locality**	**Period**	**Size est. (cm)**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C:N**	**%C**	**%N**	**Reference**
Platichthys flesus	Nivågård DK	mesolithic		-13.1	6.5	3.3	40.3	14.4	Fischer *et al.* (2007)
Pleuronectidae	Šventoji 4 LT	Early Subboreal (5000-4000)		-16.6	11.6	3.3			Antanaitis-Jacobs *et al.* (2009)
Pleuronectidae	Asnæs Havnemark DK	ca. 4300-4100 cal. B.C.		-15.5	8.5		27.4		Robson *et al.* (2016)
Pleuronectidae	Dragsholm DK	ca. 5000-3500 cal. B.C.		-11.8	7.1				Robson *et al.* (2016)
Pleuronectidae	Dragsholm DK	ca. 5000-3500 cal. B.C.		-16.6	7.2				Robson *et al.* (2016)
Pleuronectidae	Nederst DK	ca. 5400-3950 cal. B.C.		-8.1	6.5		44.3		Robson *et al.* (2016)
Pleuronectidae	Nederst DK	ca. 5400-3950 cal. B.C.		-10.4	7.5		42.3		Robson *et al.* (2016)
Pleuronectidae	Tournai BE	3rd-4th	30-40	-14.3	11.1	3.2			Fuller *et al.* (2012)
Pleuronectidae	Ghent BE	10th-12th	ca. 40	-15.3	10.4	3.3			Fuller *et al.* (2012)
Pleuronectes platessa	Schleswig DE	1070–1350		-14.9	10.7				Göhring *et al.* (2016)
Pleuronectidae	Beverley UK	14-15th		-13.2	11.7	3.3	5.4		Müldner & Richards (2005)
Pleuronectidae	Beverley UK	14-15th		-12.4	13.7	3.2	6.1		Müldner & Richards (2005)
Pleuronectes platessa	Raversijde BE	15th	ca. 40	-13.4	12.4	3.1			Fuller *et al.* (2012)
Pleuronectidae	York UK	Late Medieval		-13.1	13	3.2	44	15.7	Müldner & Richards (2007)
Platichthys flesus	Dendermonde BE	16th	10-20	-26.1	13.9	3.3	40.7	14.5	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	10-20	-24.1	14.9	3.2	37.6	13.7	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	20-30	-15.7	12.4	3.3	39.2	14	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	20-30	-23.6	15	3.3	27.1	9.5	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	20-30	-23	14.6	3.2	42.8	15.6	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-23.9	13.9	4.2	20.2	5.7	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-14.6	11.7	3.4	39.4	13.6	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-16.2	11.3	3.4	39.5	13.7	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-11.2	11.9	3.2	35.5	13	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-12	11.5	3.2	48.8	18	Ervynck *et al.* (2018)
Platichthys flesus	Dendermonde BE	16th	30-40	-14	11.9	3.1	40.4	15	Ervynck *et al.* (2018)
Pleuronectidae	Chichester UK	medieval/postmedieval		-12.8	12.7				Dahliwal *et al.* (2019)
Pleuronectes platessa	Antwerpen BE	17th	ca. 30	-14.7	11.2	3.3			Fuller *et al.* (2012)
Platichthys flesus	Antwerpen BE	17th	25-30	-15.4	14.3	3.4			Fuller *et al.* (2012)
Hippoglossus hippoglossus	Antwerpen BE	17th	80-90	-13.6	14.4	3.4			Fuller *et al.* (2012)

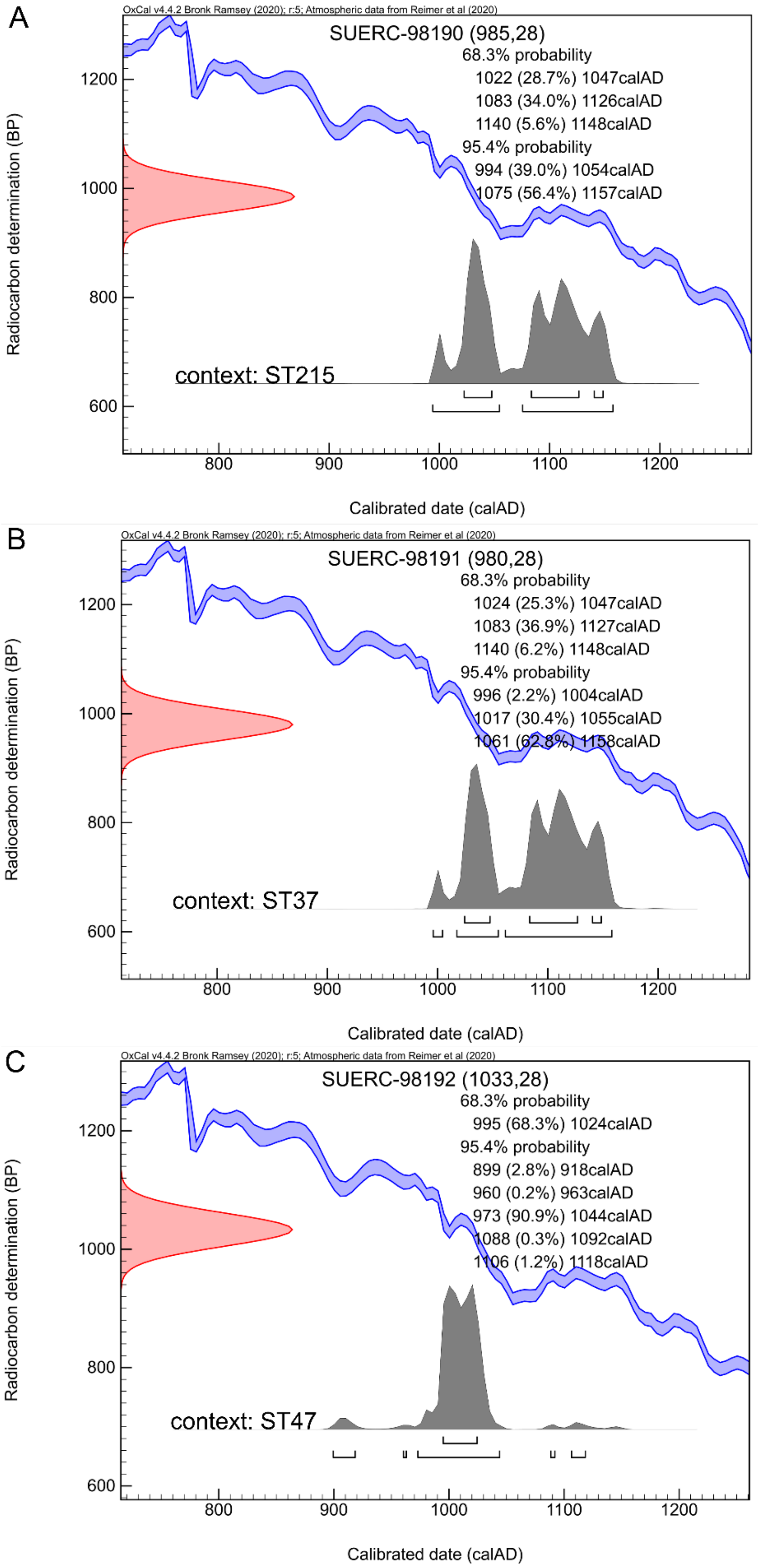

Figure E1. Radiocarbon date plots of three bovine samples from the same pits/contexts as the fish remains. A: ST215; B: ST37; C: ST47 (data provided by SUERC).

Table E2. $\delta^{13}C$ and $\delta^{15}N$ of samples treated with DCM and NaOH.

Sample	**Species**	**Element**	**Treatment**	**Weight bone (mg)**	**Yield (%)**	**NaOH wash**	**%C**	**%N**	**C:N**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**
COP140	*Scophthalmus maximus*	cleithrum	DCM	259.88	6.95		41.94	15.02	3.26	-13.19	16.48
			NaOH	?		2 washes	49.32	17.60	3.27	-13.26	17.04
			NaOH + DCM	381.08	6.86	4 washes	43.17	15.22	3.31	-13.13	17.09
			nothing	450.49	7.79		43.67	15.68	3.25	-13.14	17.16
COP141	*Pleuronectes platessa*	os anale	DCM	379.58	11.19		44.57	16.73	3.11	-13.36	11.34
			NaOH	?		1-3 washes	41.72	15.64	3.11	-13.37	11.51
			NaOH + DCM	490.72	11.53	3 washes	45.03	16.63	3.16	-13.60	12.06
			nothing	288.3	9.60		43.24	16.25	3.10	-12.69	12.05
COP147	*Pleuronectes platessa*	os anale	DCM	301.16	8.14		42.14	15.54	3.16	-13.43	11.47
			NaOH	?		1-3 washes	40.30	14.93	3.15	-13.65	12.09
			NaOH + DCM	461.18	9.35	3 washes	44.11	16.22	3.17	-13.54	11.84
			nothing	256.89	6.98		40.09	14.62	3.20	-14.22	11.49
COP152	*Scophthalmus maximus*	cleithrum	DCM	327.09	7.14		43.15	15.75	3.20	-13.21	16.50
			NaOH	?		2 washes	38.87	14.09	3.22	-13.10	17.13
			NaOH + DCM	490.33	7.24	4 washes	44.66	15.77	3.30	-13.36	17.53
			nothing	490.41	3.64		42.22	15.27	3.22	-13.42	17.21
COP335	*Pleuronectes platessa*	os anale	DCM	345.81	7.04		42.51	15.82	3.14	-14.59	11.88
			NaOH	?		1-3 washes	42.98	16.30	3.08	-14.07	12.30
			NaOH + DCM	387.92	5.98	3 washes	44.38	16.78	3.09	-14.05	12.31
			nothing	276.57	8.46		42.00	15.27	3.21	-14.63	12.02

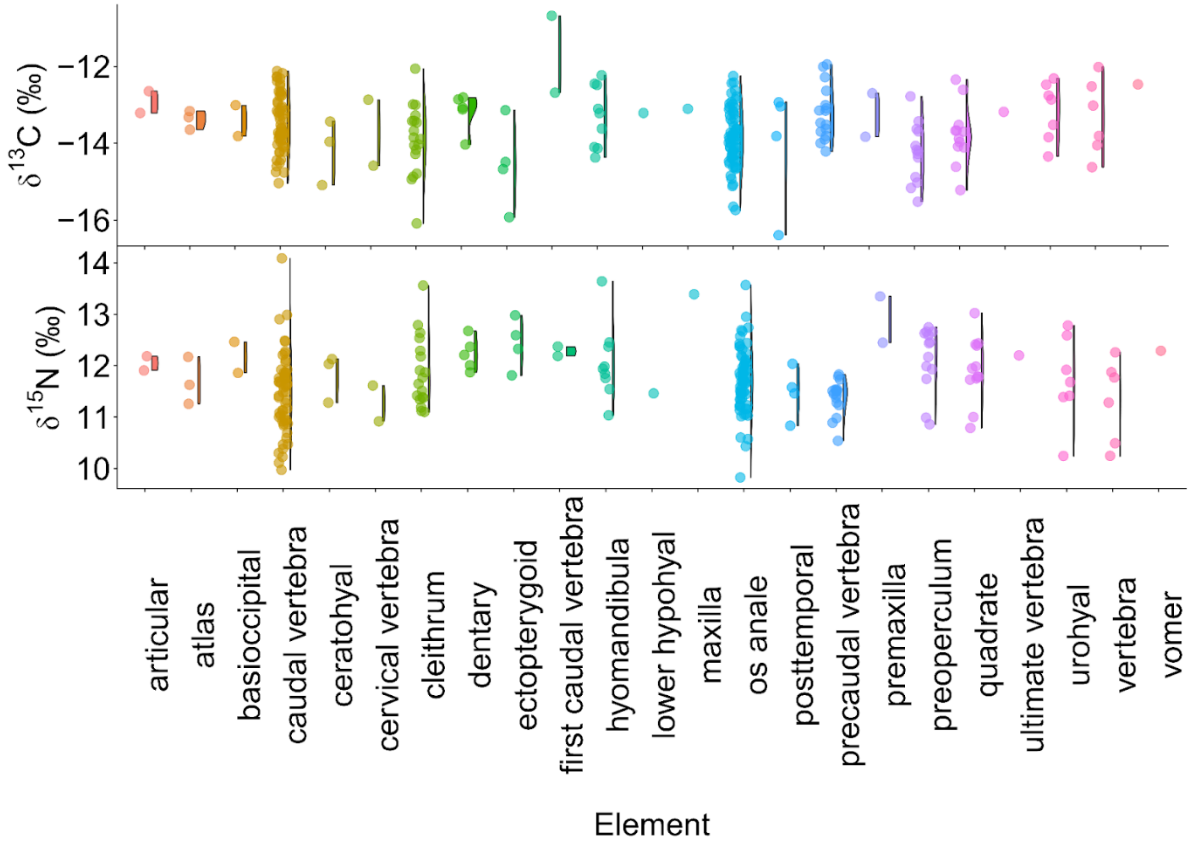

Figure E2. $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) per skeletal element of *P. platessa*. As different skeletal elements were used in this study to compare different variables, it is important to verify if these different elements don't influence the isotope values within a species. Therefore, the isotope values were plotted per skeletal element to demonstrate this is not the case. No clear trend showing differences between certain elements for either of the isotope values could be found for *P. platessa*. No trends were observed for *P. flesus* either. Therefore, it can be assumed that comparisons of isotope data for flatfish using different skeletal elements will result in minimal differences in interpretation. No further analyses were performed to test for isotopic differences between the different elements due to the small sample size and the limited knowledge of fish bone remodelling.

Table E3. Descriptive statistics for each freshwater and marine species.

	Esox lucius	**Cypriniformes**	***Cf. Salmo trutta trutta***	***Gadus morhua***	***Melanogrammus aeglefinus***	***Conger conger***	~~***Merlangius. merlangus***~~
N	18	27	1	27	29	2	~~1~~
$\delta^{13}C$							
min	-26.80	-29.29	-27.25	-15.03	-15.29	-11.88	~~14.01~~
max	-22.47	-16.33		-10.22	-12.65	-11.34	
mean	-24.28	-23.96		-13.03	-14.01	-11.61	
median	-24.16	-23.74		-13.28	-13.91	-11.61	
sd	1.22	2.54		1.14	0.73	0.38	
variance	1.48	6.46		1.30	0.54	0.15	
$\delta^{15}N$							
min	8.71	6.23	13.26	14.60	13.48	14.42	~~15.32~~
max	16.16	14.54		18.42	16.30	15.73	
mean	12.17	11.26		15.97	14.69	15.07	
median	12.16	11.57		15.62	14.63	15.07	
sd	2.11	2.26		0.96	0.68	0.93	
variance	4.43	5.12		0.92	0.46	0.86	
C:N							
min	3.14	3.15	3.15	3.04	3.06	3.18	~~3.55~~
max	3.47	3.40		3.44	3.48	3.19	
mean	3.27	3.24		3.24	3.26	3.19	
median	3.29	3.23		3.20	3.26	3.19	
sd	0.1038	0.0609		0.13	0.11	0.007	
variance	0.0108	0.0037		0.02	0.01	0.00	

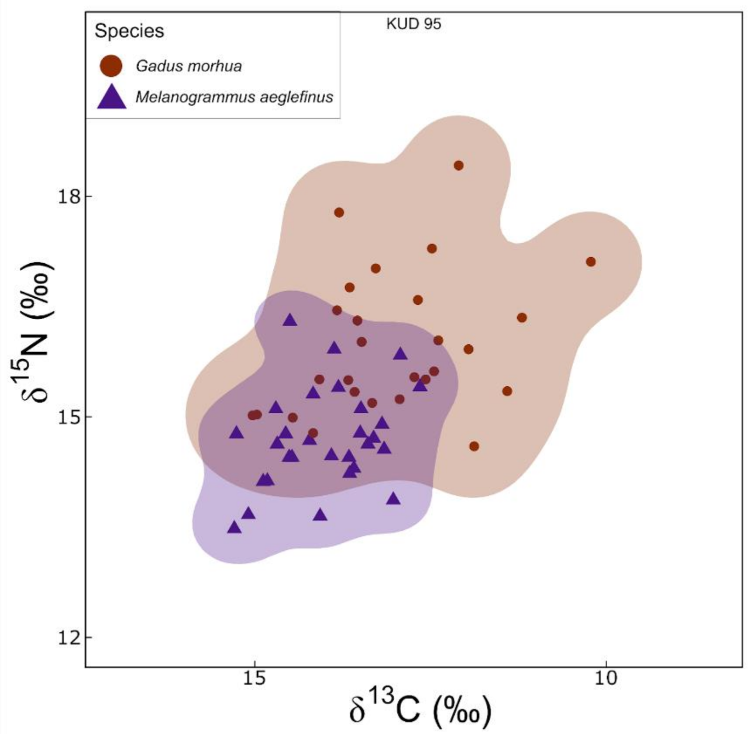

Figure E3. rKIN plot using KUD at 95% for *G. morhua* and *M. aeglefinus*. *Gadus morhua* and *M. aeglefinus* are the main marine habitat species in the dataset. *Gadus morhua* generally has a slightly higher trophic level than *M. aeglefinus*. There is a large overlap between the two species, showing that these have similar isotope niches.

Table E4. Shape area of the isotope niche space and overlap of polygons of the isotope niche space of each marine species at 95% KUD.

	Shape area	**Overlap of polygons**	
Species		*G. morhua*	*M. aeglefinus*
G. morhua	21.50991	1	0.343
M. aeglefinus	10.04657	0.735	1

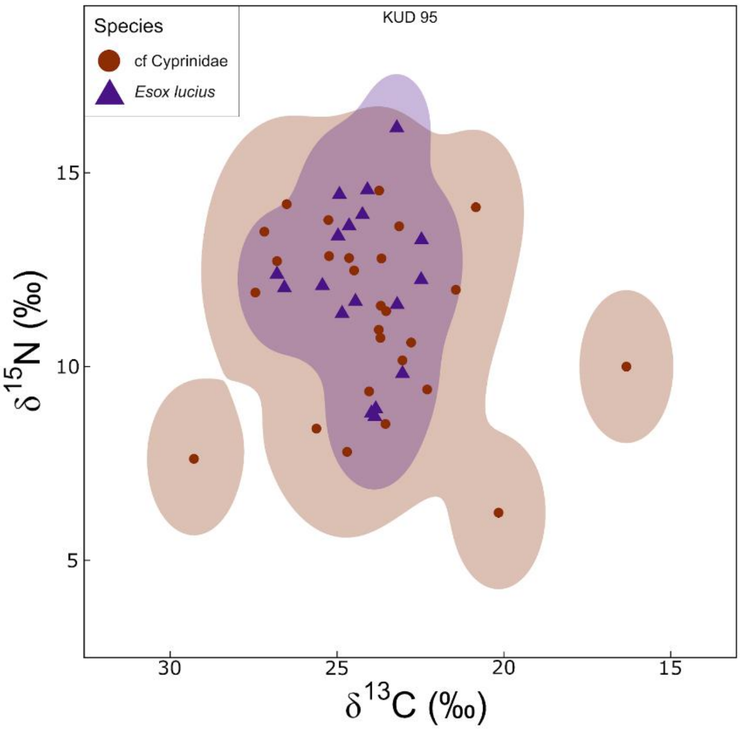

Figure E4. rKIN plot using KUD at 95% for *E. lucius* and Cypriniformes. *Esox lucius* and Cypriniformes are the main freshwater habitat taxa in the dataset. Although *E. lucius* is generally a predatory piscivorous species, while Cyprinids eat invertebrates, this is not reflected in the isotopic niche space, with the two taxa showing similar trophic levels. As the Cypriniformes group comprises multiple species (see chapter 5), this could explain the large isotopic niche space shown here, which almost completely encompasses that of *E. lucius*. Individual species of Cypriniformes could have more restricted isotopic niches.

Table E5. Shape area of the isotope niche space and overlap of polygons of the isotope niche space of each freshwater species at 95% KUD.

	Shape area	**Overlap of polygons**	
Species		*Esox lucius*	Cf Cyprinidae
Esox lucius	44.38133	1	0.965
cf. Cyprinidae	108.22087	0.396	1

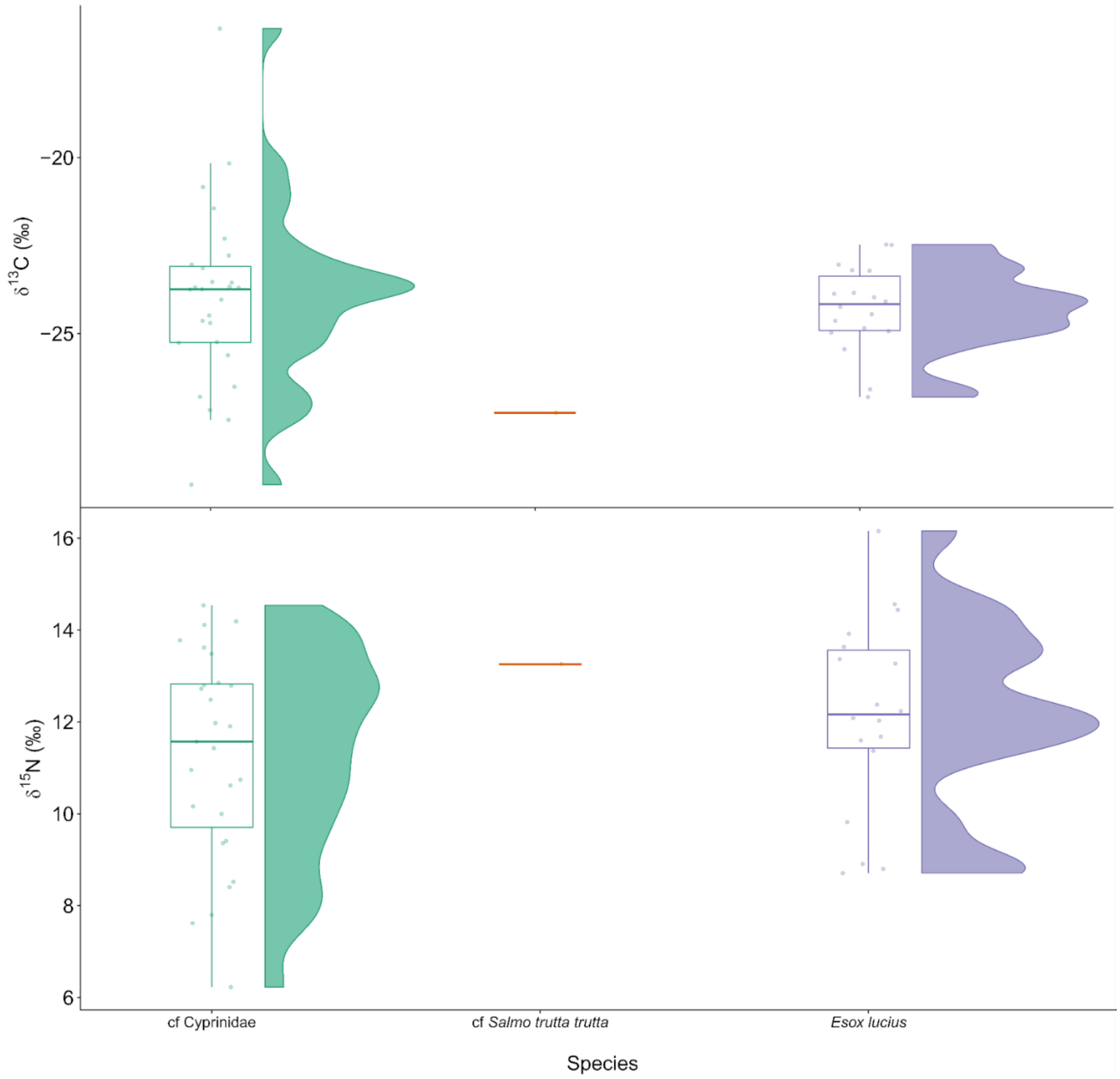

Figure E5. Boxplots and density plots of $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) of each freshwater taxon.

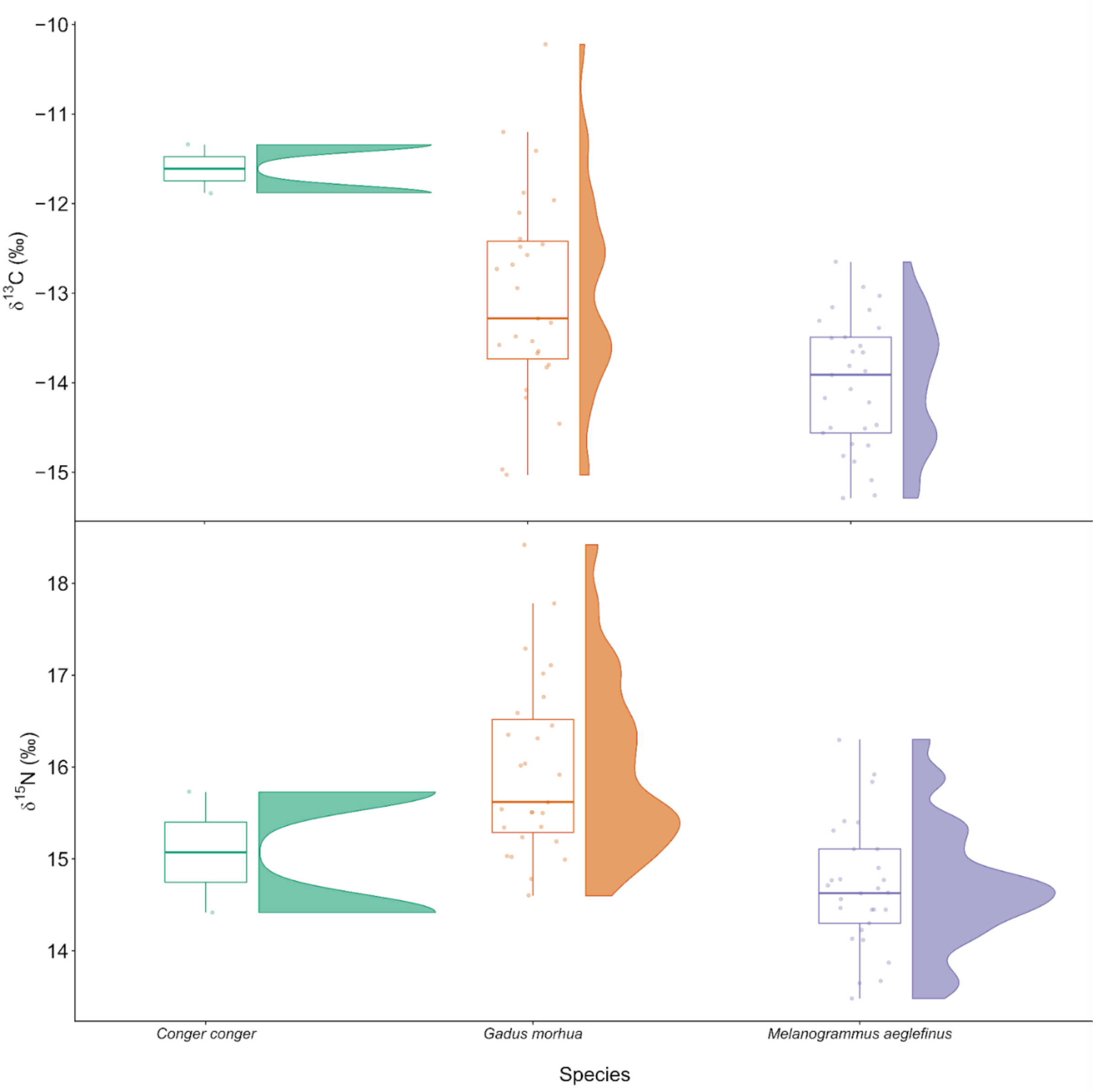

Figure E6. Boxplots and density plots of δ^{13}C (top) and δ^{15}N (bottom) of each marine taxon.

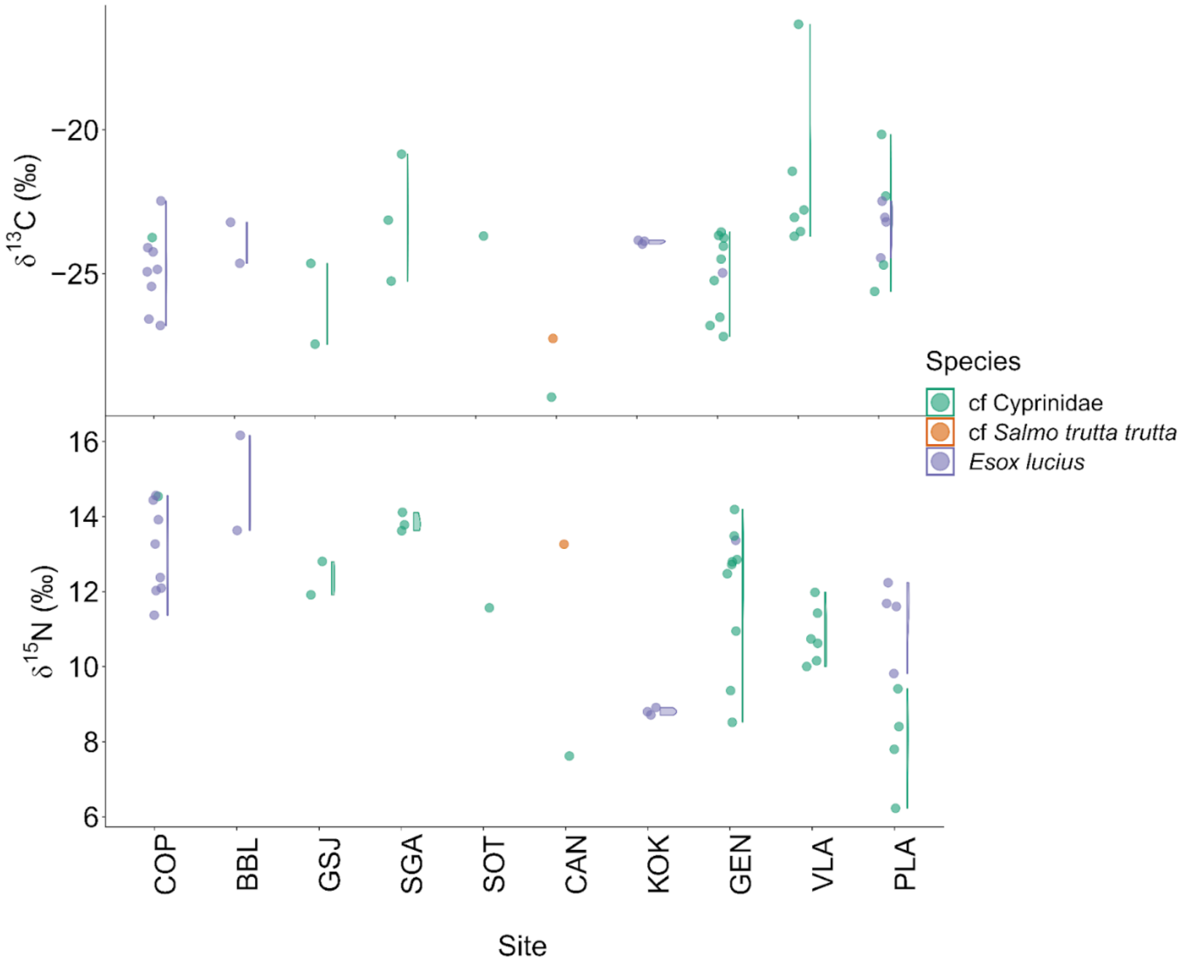

Figure E7. δ^{13}C (top) and δ^{15}N (bottom) of freshwater species per site.

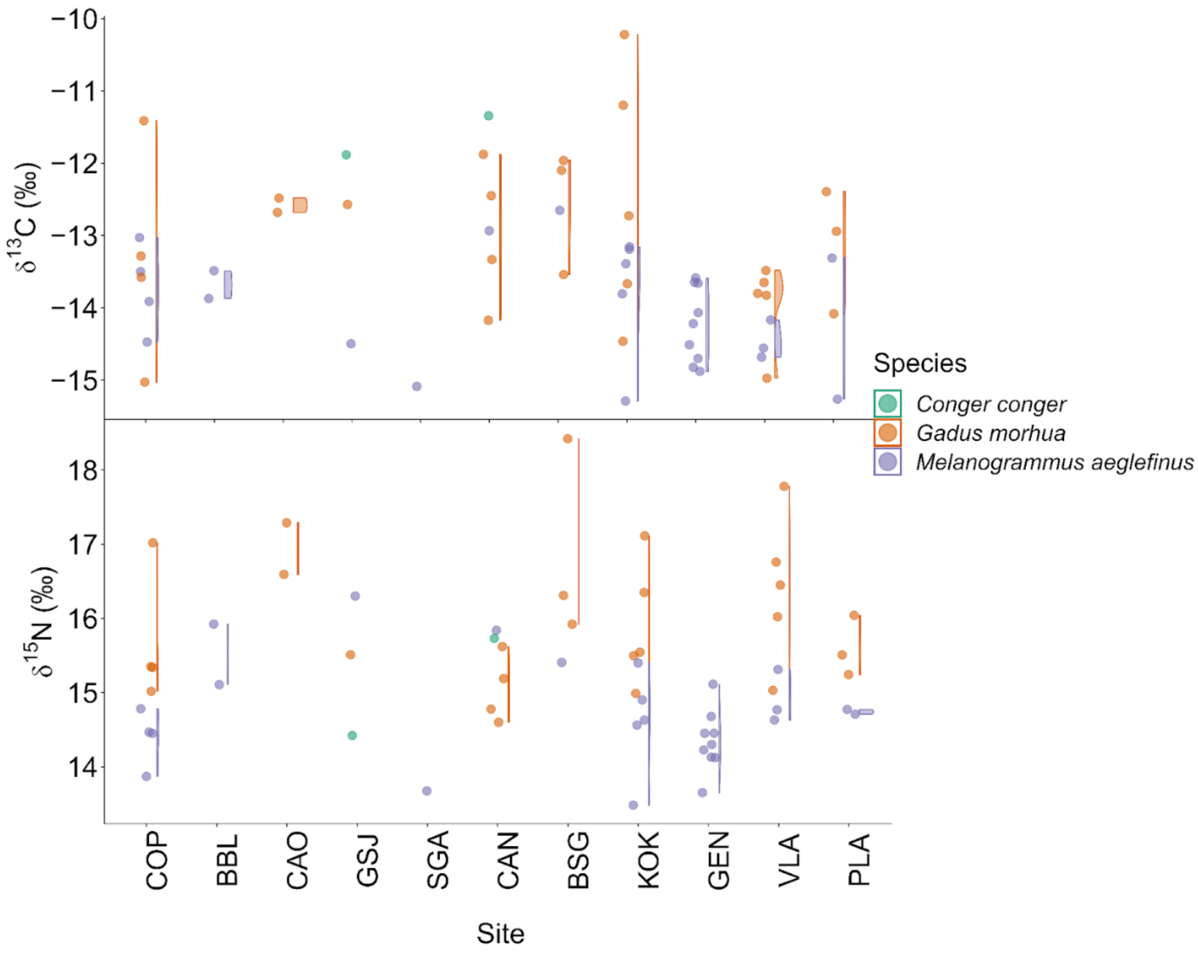

Figure E8. δ^{13}C (top) and δ^{15}N (bottom) of marine species per site.

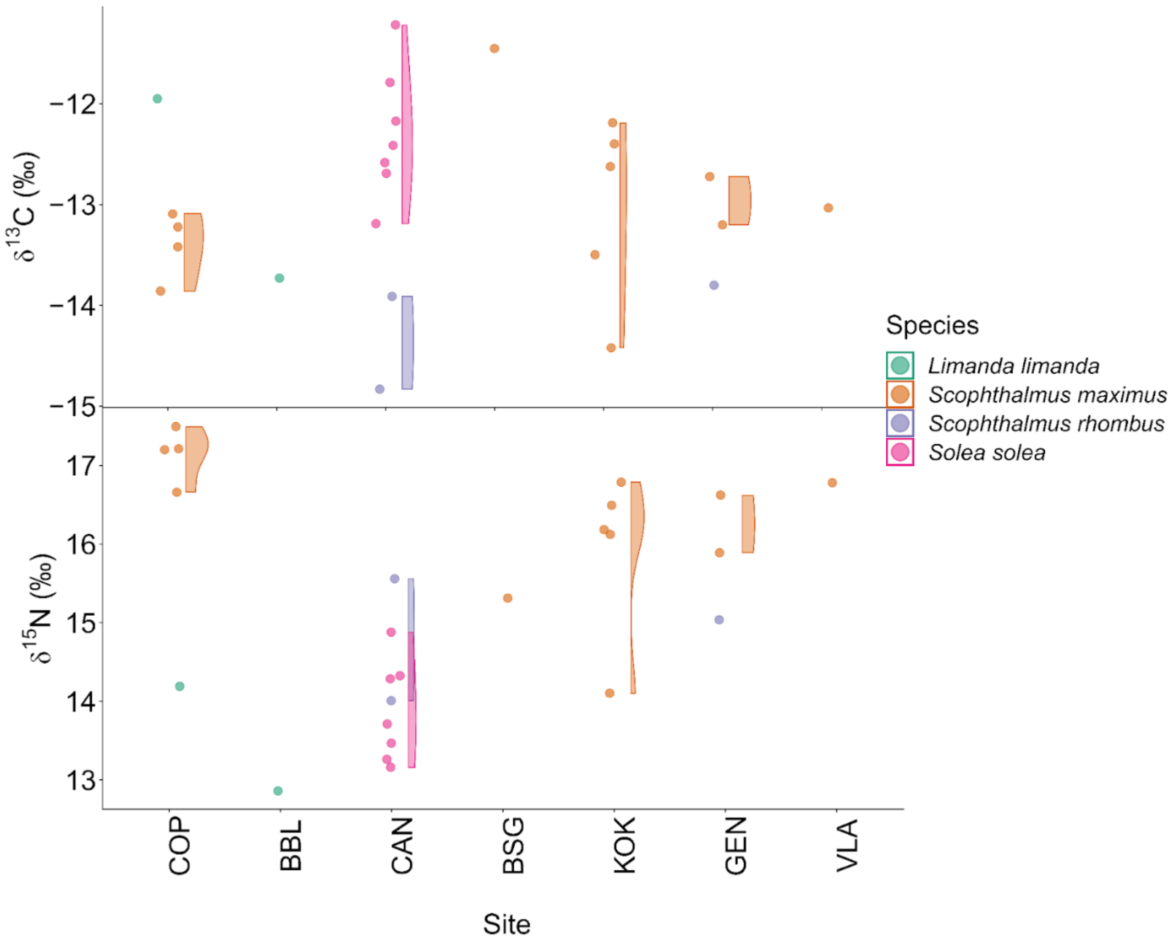

Figure E9. $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) of other flatfish species per site.

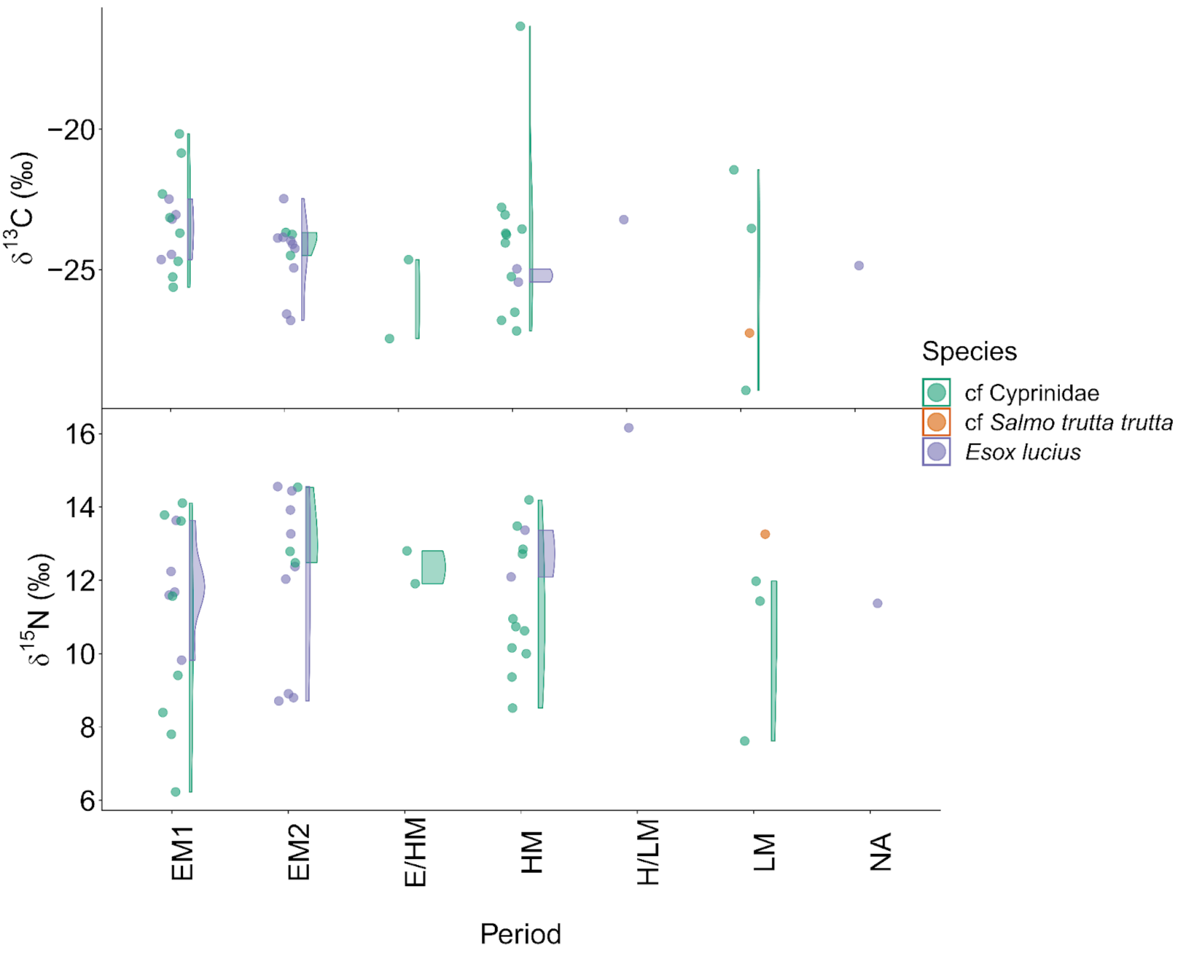

Figure E10. $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) of freshwater species per chronological period.

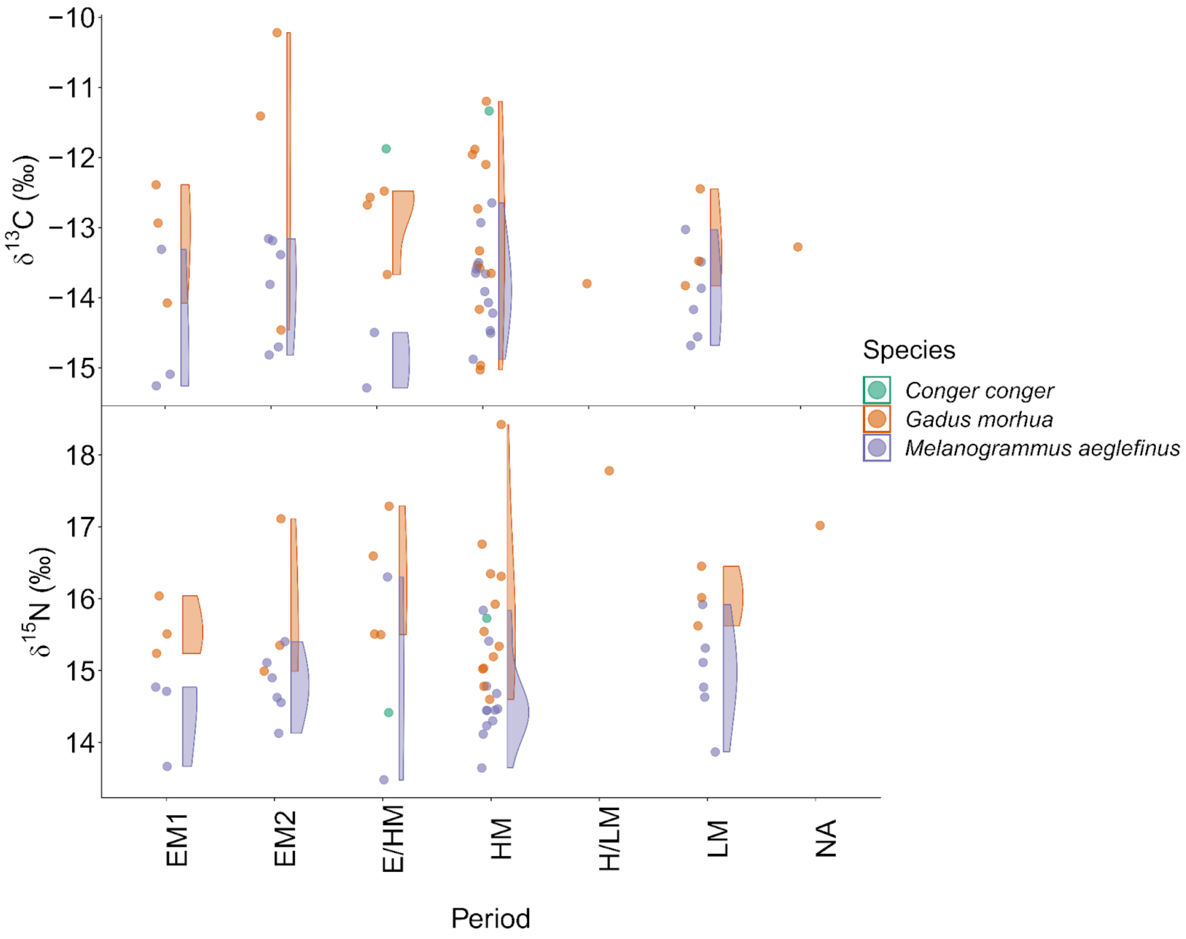

Figure E11. $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) of marine species per chronological period.

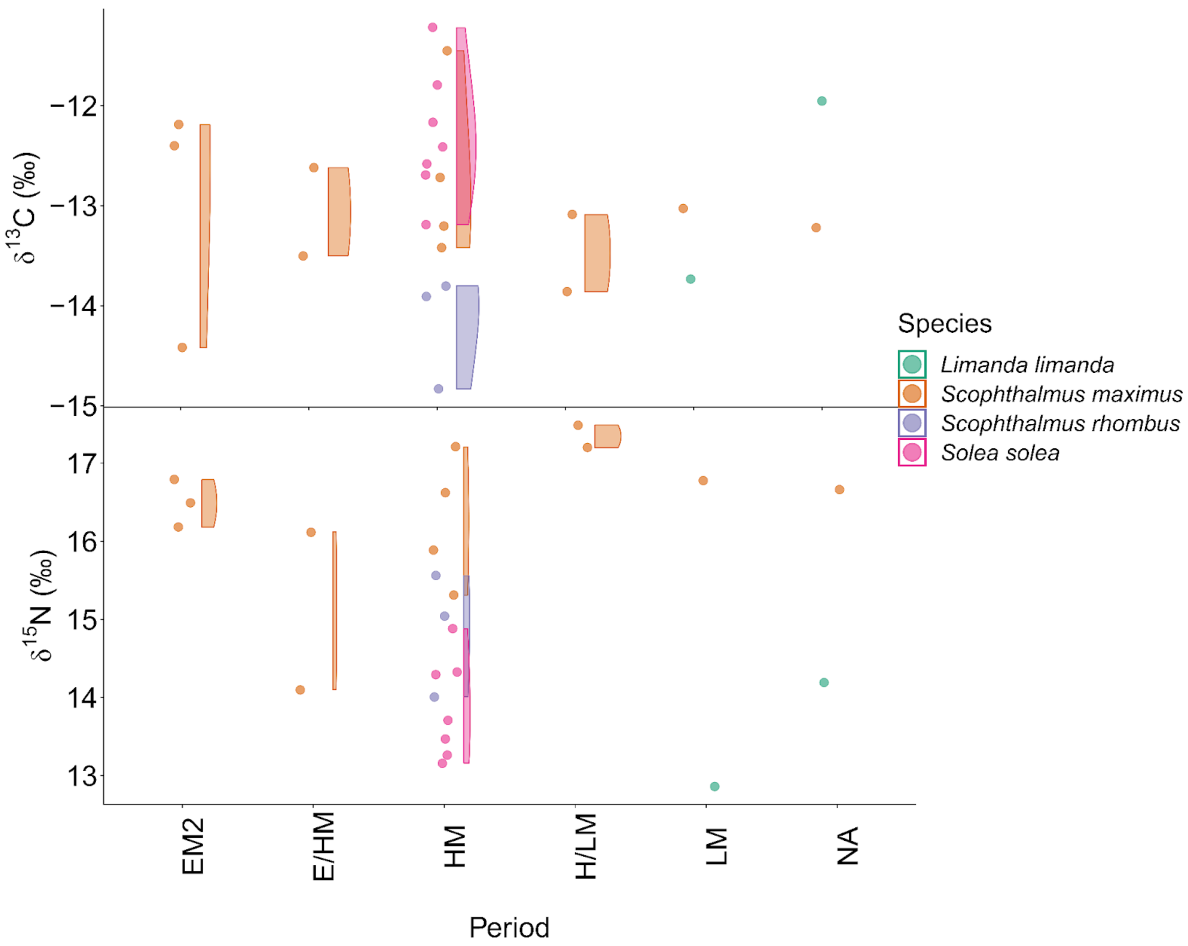

Figure E12. δ^{13}C (top) and δ^{15}N (bottom) of other flatfish species per chronological period.

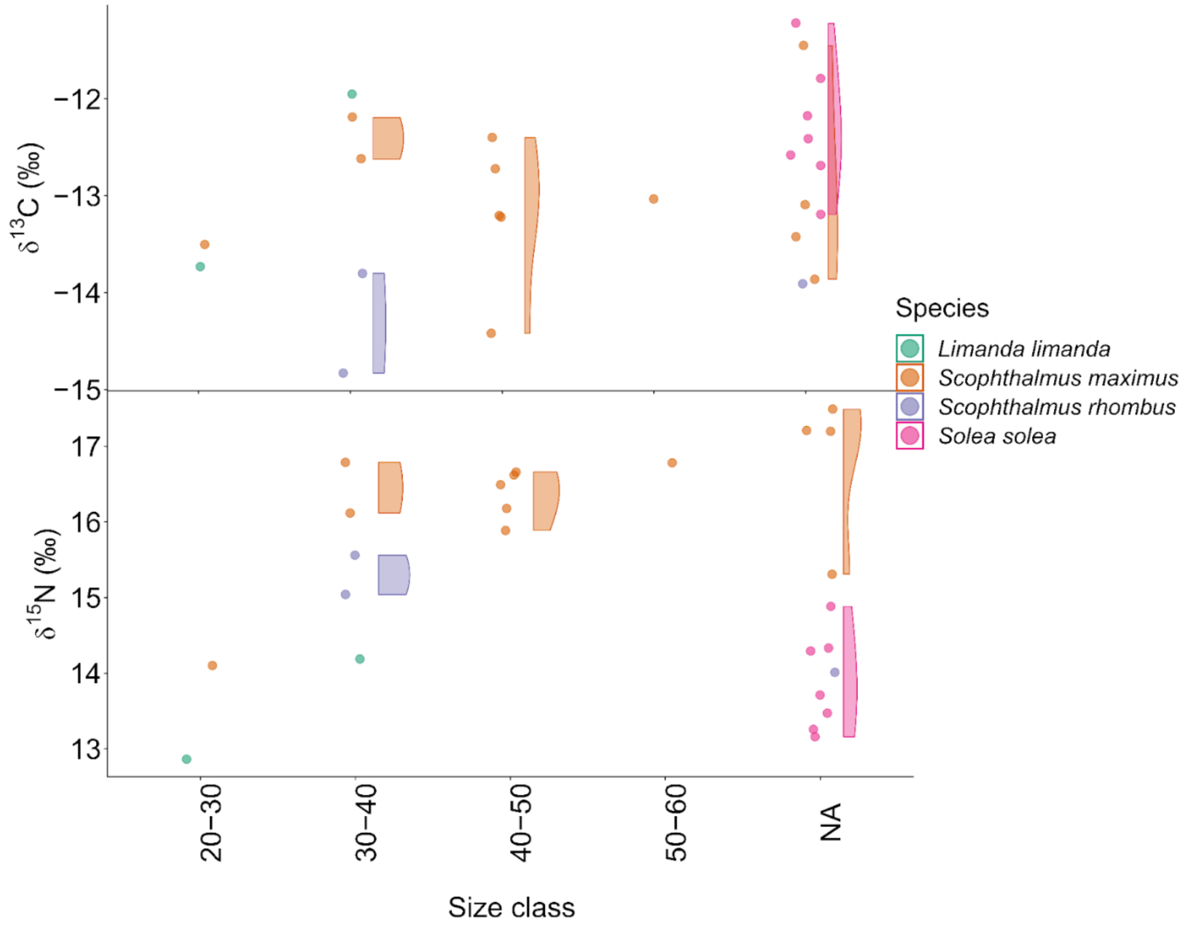

Figure E13. δ^{13}C (top) and δ^{15}N (bottom) of other flatfish species per size class.

Table E6. Shapiro-Wilk test for isotope values of each freshwater and marine species.

	δ^{13}C		δ^{15}N	
Species	**W-statistic**	**p-value**	**W-statistic**	**p-value**
Esox lucius	0.95394	0.4902	0.95355	0.4834
Cypriniformes	0.94547	0.1661	0.95603	0.299
Cf. *Salmo trutta*	/	/	/	/
Gadus morhus	0.97944	0.8496	0.93973	0.12
Melanogrammus aeglefinus	0.97047	0.5724	0.97168	0.606
Conger conger	/	/	/	/
Merlangius merlangus	/	/	/	/

Table E7. W-statistics and p-values of the Shapiro-Wilk normality test per site for both *P. platessa* and *P. flesus* for δ^{13}C and δ^{15}N. Bold results indicate significant differences.

P. platessa					***P. flesus***				
	δ^{13}C		**δ^{15}N**			**δ^{13}C**		**δ^{15}N**	
Site (n)	W-stat	p-value	W-stat	p-value	**Site (n)**	W-stat	p-value	W-stat	p-value
COP (41)	0.96999	0.3446	0.97137	0.3816	COP (3)	0.77111	**0.04725**	0.97087	0.6725
BBL (9)	0.93297	0.5101	0.95269	0.7196	BBL (3)	0.75902	**0.02002**	0.92347	0.4647
CAO (11)	0.9666	0.8503	0.96761	0.8614	CAO (0)	NA	NA	NA	NA
GSJ (11)	0.91598	0.2866	0.97481	0.9305	GSJ (8)	0.91284	0.3745	0.86026	0.1208
SGA (10)	0.90058	0.2223	0.97657	0.9442	SGA (4)	0.93031	0.5962	0.96162	0.7891
SOT (3)	0.95201	0.5782	0.98646	0.7773	SOT (3)	0.97558	0.7003	0.97476	0.6953
CAN (23)	0.93131	0.1168	0.93712	0.1558	CAN (5)	0.96655	0.8527	0.89895	0.4041
BSG (19)	0.9353	0.2167	0.90878	0.07031	BSG (7)	0.95503	0.7751	0.89584	0.3065
KOK (36)	0.95291	0.1291	0.96662	0.3406	KOK (8)	0.87312	0.1617	0.94527	0.6636
GEN (33)	0.98927	0.9816	0.95822	0.2301	GEN (17)	0.97087	0.8334	0.92241	0.1622
VLA (23)	0.96451	0.5601	0.96109	0.4856	VLA (10)	0.94235	0.5794	0.94316	0.5887
PLA (12)	0.89604	0.141	0.89047	0.1195	PLA (17)	0.9762	0.9148	0.97579	0.9094
KAS (2)	NA	NA	NA	NA	KAS (0)	NA	NA	NA	NA

Table E8. W-statistics and p-values of the Shapiro-Wilk normality test per site for both *P. platessa* and *P. flesus* for δ^{34}S. Bold results indicate significant differences.

P. platessa			***P. flesus***		
Site (n)	W-stat	p-value	**Site (n)**	W-stat	p-value
COP (12)	0.98997	0.9997	COP (3)	0.97772	0.7139
BBL (4)	0.8762	0.3227	BBL (3)	0.76363	**0.03035**
CAO (7)	0.94749	0.7068	CAO (0)	/	/
GSJ (4)	0.81228	0.1261	GSJ (5)	0.6526	**0.002857**
SGA (4)	0.84682	0.216	SGA (2)	/	/
SOT (2)	/	/	SOT (2)	/	/
CAN (8)	0.96946	0.8937	CAN (4)	0.90121	0.4371
BSG (9)	0.91619	0.3616	BSG (5)	0.92055	0.5335
KOK (12)	0.95767	0.7501	KOK (6)	0.90054	0.3771
GEN (11)	0.74386	**0.001729**	GEN (8)	0.96094	0.819
VLA (9)	0.87366	0.1345	VLA (1)	/	/

Table E9. p-values of the Shapiro-Wilk normality test per chronological period for both *P. platessa* and *P. flesus* for δ^{13}C and δ^{15}N. Bold results indicate significant differences.

P. platessa					***P. flesus***				
	δ^{13}C		**δ^{15}N**			**δ^{13}C**		**δ^{15}N**	
Period	W-stat	p-value	W-stat	p-value	**Period**	W-stat	p-value	W-stat	p-value
EM1 (28)	0.97285	0.6588	0.96909	0.5564	EM1 (27)	0.9435	0.1486	0.96832	0.5582
EM2 (30)	0.96062	0.3213	0.96792	0.4839	EM2 (13)	0.75841	**0.002278**	0.95056	0.6068
E/HM (25)	0.95704	0.3586	0.96357	0.49	E/HM (9)	0.88702	0.1859	0.88884	0.1941
HM (102)	0.98622	0.3732	0.99143	0.7678	HM (24)	0.94392	0.1994	0.95062	0.2794
H/LM (23)	0.96947	0.6764	0.95938	0.4509	H/LM (3)	0.86871	0.2919	0.90506	0.4018
LM (25)	0.95148	0.2707	0.90814	0.02771	LM (9)	0.95719	0.7685	0.96108	0.8096

Table E10. W-statistics and p-values of the Shapiro-Wilk normality test per chronological period for both *P. platessa* and *P. flesus* for δ^{34}S. Bold results indicate significant differences.

P. platessa			***P. flesus***		
Site (n)	W-stat	p-value	**Site (n)**	W-stat	p-value
EM1 (7)	0.92082	0.4758	EM1 (7)	0.83314	0.08567
EM2 (12)	0.95255	0.6745	EM2 (9)	0.87385	**0.01352**
E/HM (9)	0.83636	0.05261	E/HM (6)	0.61793	**0.0007507**
HM (39)	0.92746	**0.01491**	HM (14)	0.87097	**0.0433**
H/LM (7)	0.97121	0.907	H/LM (1)	/	/
LM (8)	0.85695	0.1119	LM (2)	/	/

Table E11. p-values of the Shapiro-Wilk normality test per size class for both *P. platessa* and *P. flesus* for both δ^{13}C and δ^{15}N. Bold results indicate significant differences.

P. platessa					***P. flesus***				
	δ^{13}C		**δ^{15}N**			**δ^{13}C**		**δ^{15}N**	
Size (cm SL)	W-stat	p-value	W-stat	p-value	**Size (cm SL)**	W-stat	p-value	W-stat	p-value
10-20 (3)	0.9905	0.8136	0.81723	0.1563	10-20 (8)	0.96784	0.8806	0.92389	0.4622
20-30 (43)	0.95251	0.07363	0.97228	0.3779	20-30 (41)	0.95043	0.07248	0.97441	0.4745
30-40 (76)	0.97296	0.104	0.98601	0.5718	30-40 (24)	0.98095	0.9127	0.97216	0.7203
40-50 (52)	0.96926	0.2503	0.97713	0.3316	40-50 (8)	0.89564	0.2638	0.90717	0.3346
50-60 (25)	0.97815	0.8461	0.97934	0.8718	50-60 (1)	NA	NA	NA	NA

Table E12. W-statistics and p-values of the Shapiro-Wilk normality test per size class for both *P. platessa* and *P. flesus* for δ^{34}S. Bold results indicate significant differences.

P. platessa			***P. flesus***		
Size (cm SL)	W-stat	p-value	**Size (cm SL)**	W-stat	p-value
10-20 (2)	/	/	10-20 (4)	0.71335	**0.01643**
20-30 (19)	0.8993	**0.04726**	20-30 (19)	0.72207	**0.0001031**
30-40 (19)	0.89849	**0.0457**	30-40 (11)	0.97049	0.8914
40-50 (28)	0.96416	0.4354	40-50 (3)	0.89692	0.3758
50-60 (9)	0.86312	0.1037	50-60 (0)	/	/

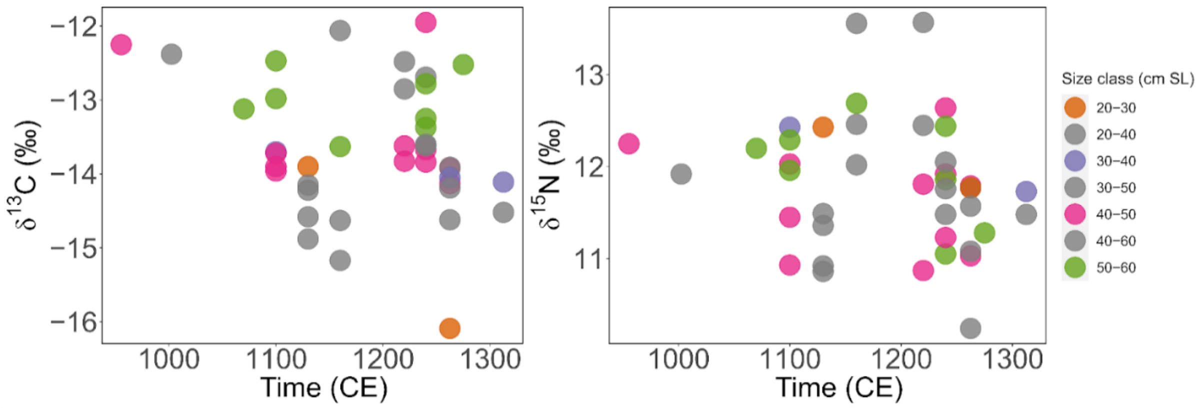

Figure E14. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in Coppergate.

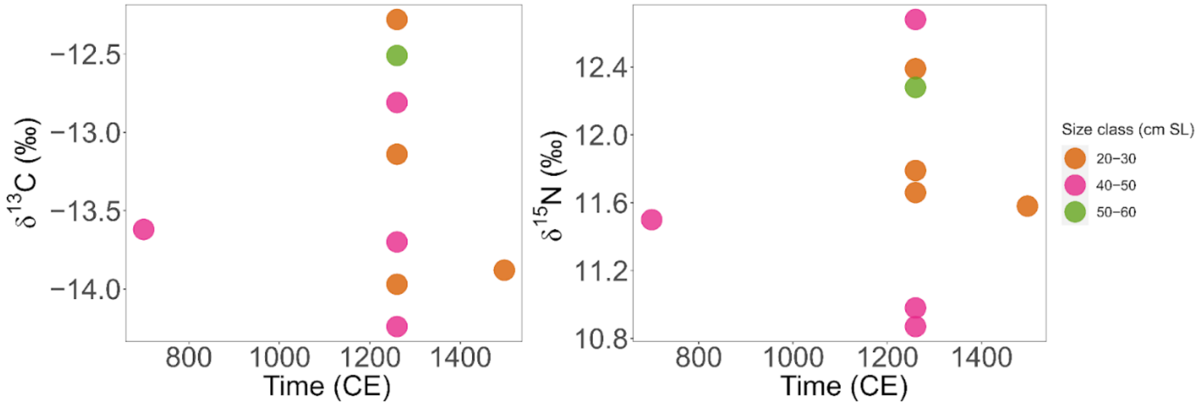

Figure E15. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in Blue Bridge Lane.

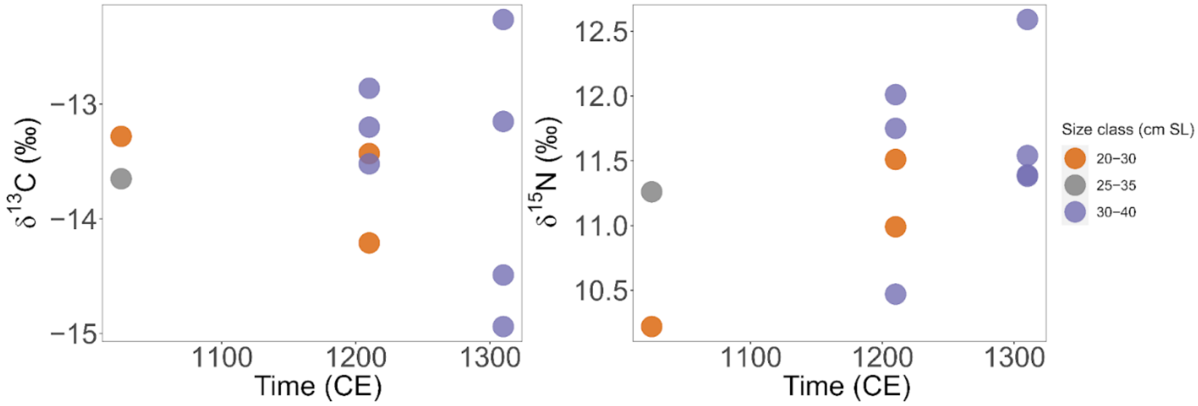

Figure E16. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in CAO96.

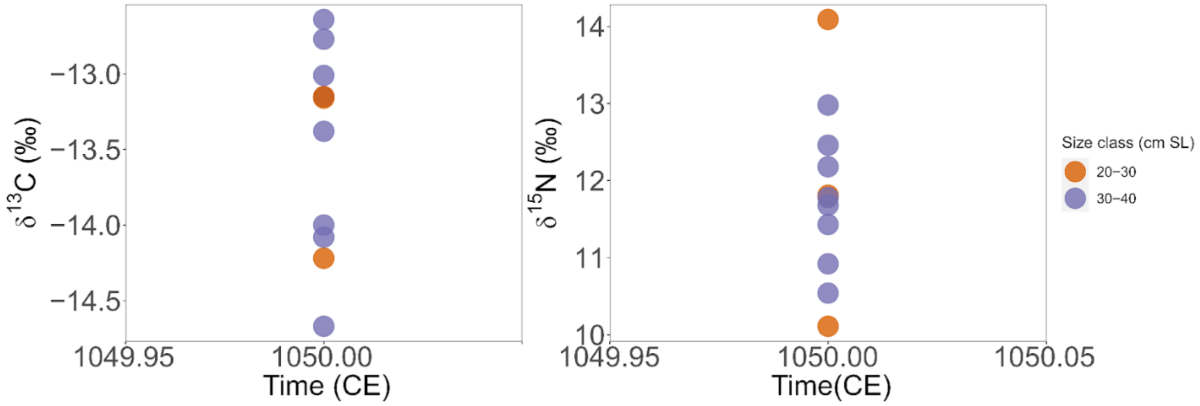

Figure E17. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in GSJ06.

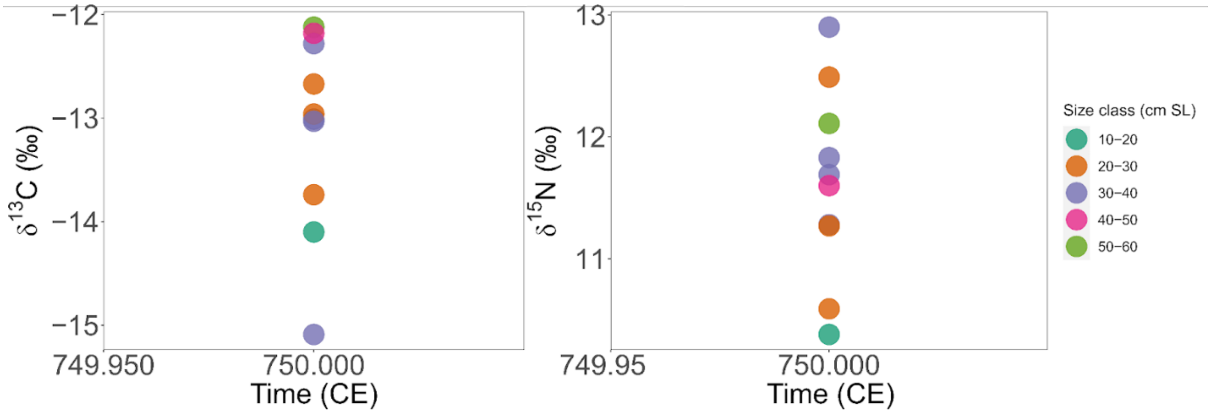

Figure E18. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in SGA89.

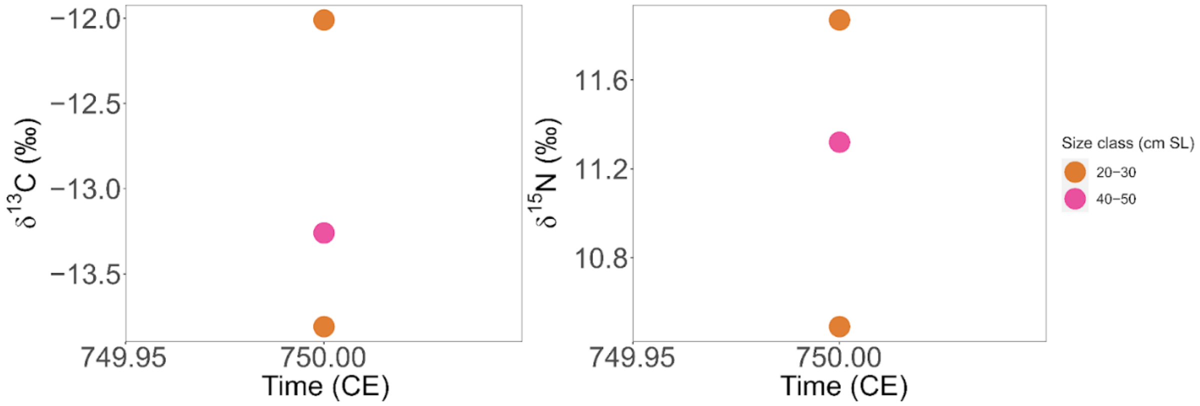

Figure E19. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in SOT89.

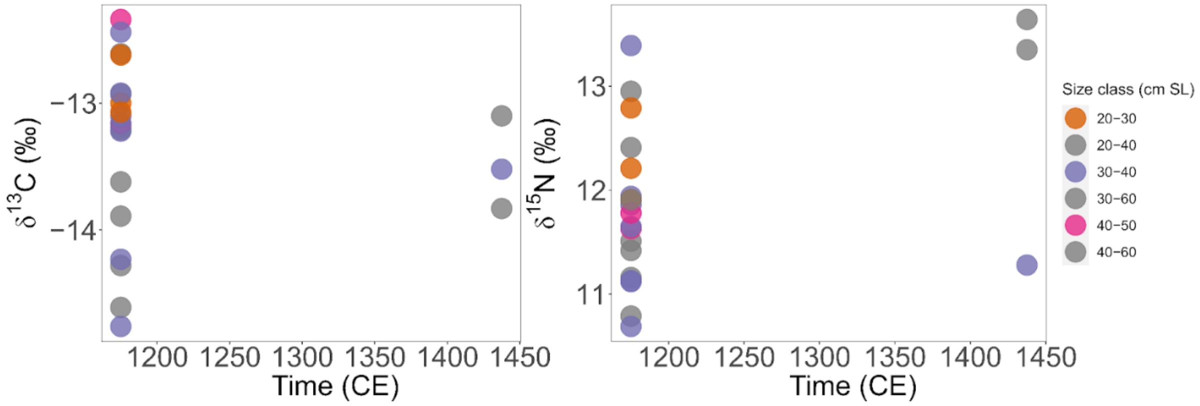

Figure E20. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in Tradescent Lane.

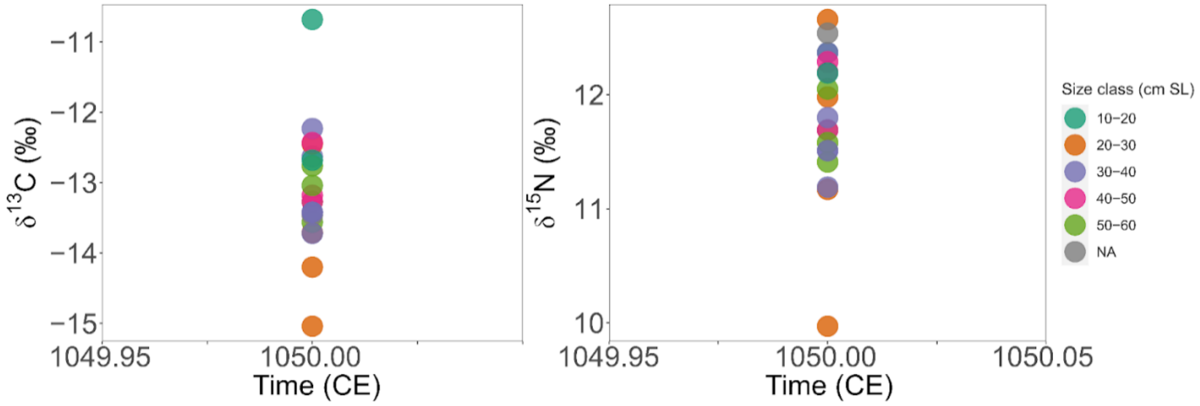

Figure E21. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in Barreau Saint-George.

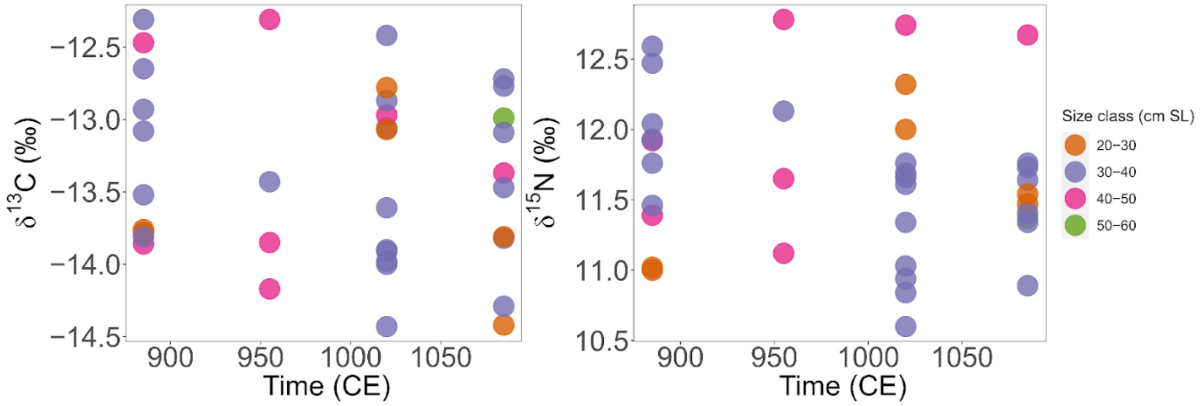

Figure E22. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in Koksijde.

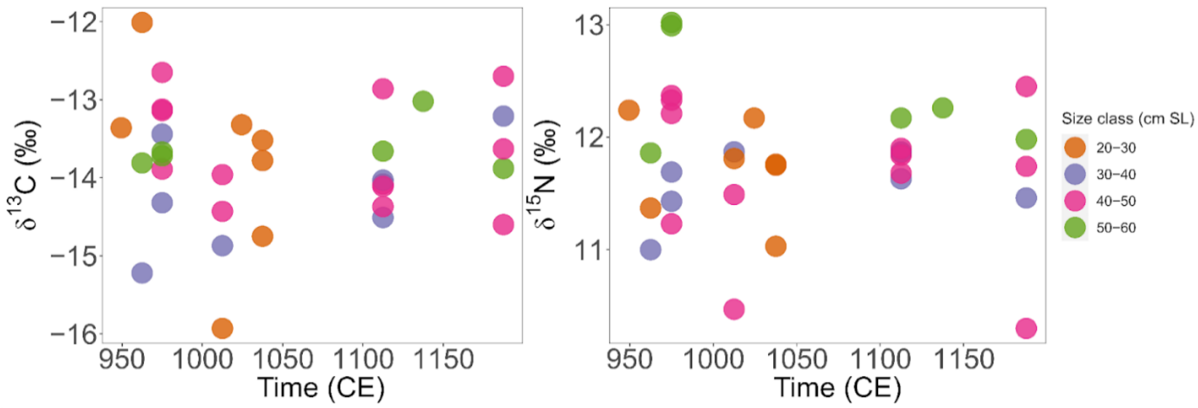

Figure E23. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. platessa* chronologically in Gent.

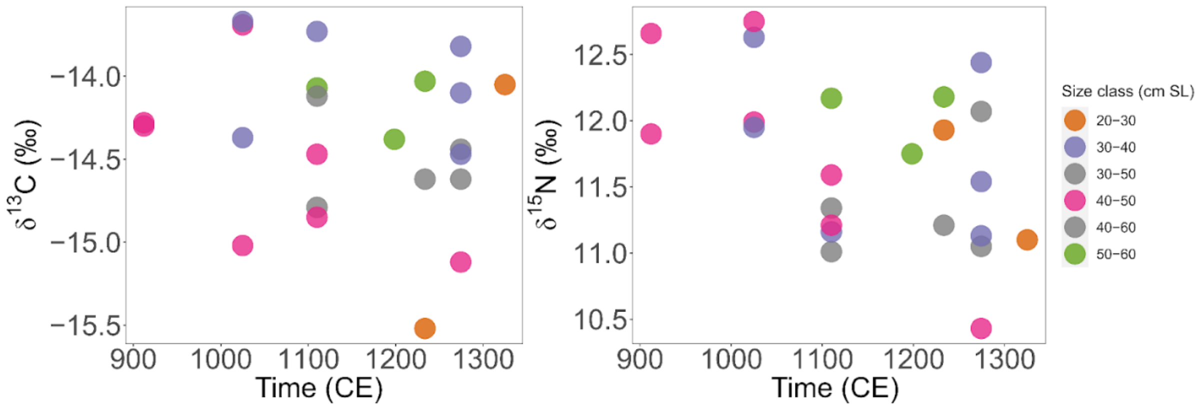

Figure E24. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. platessa* chronologically in Vlaardingen.

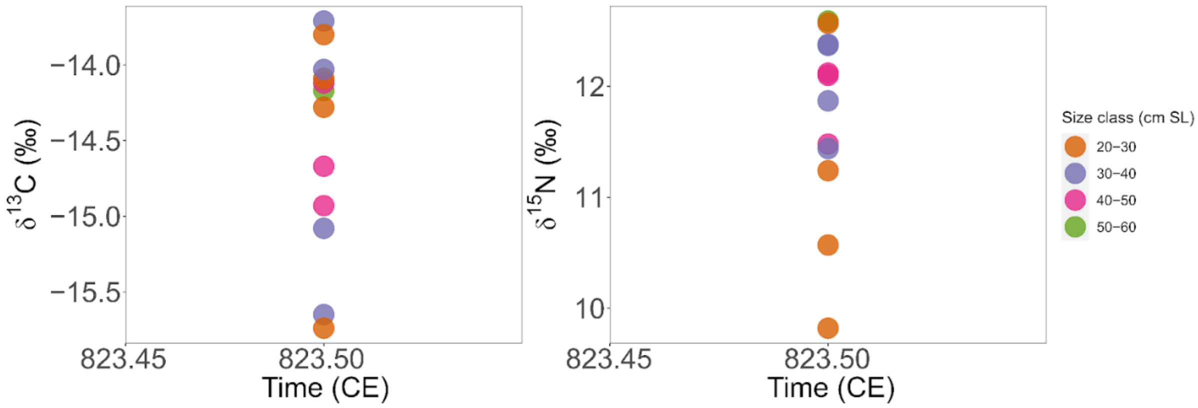

Figure E25. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. platessa* chronologically in Plantage.

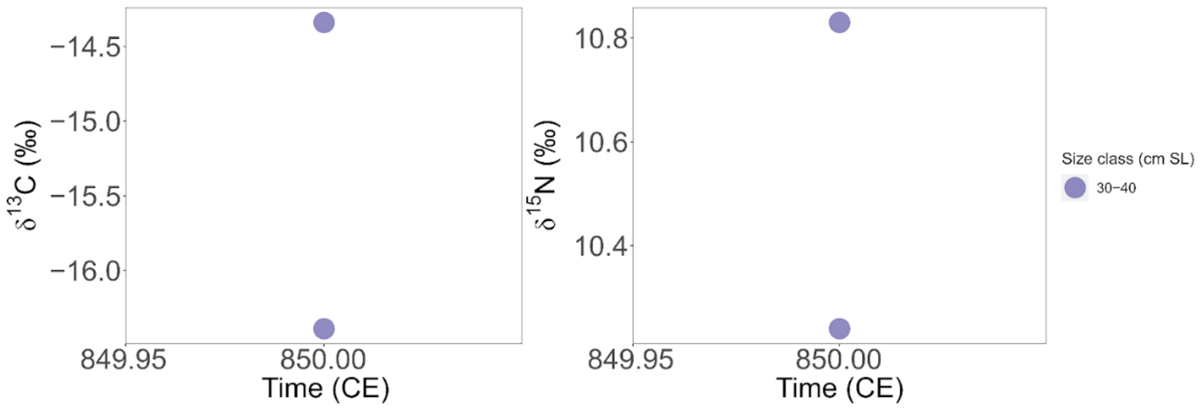

Figure E26. δ^{13}C (left) and δ^{15}N (right) of *P. platessa* chronologically in Kastanjelaan.

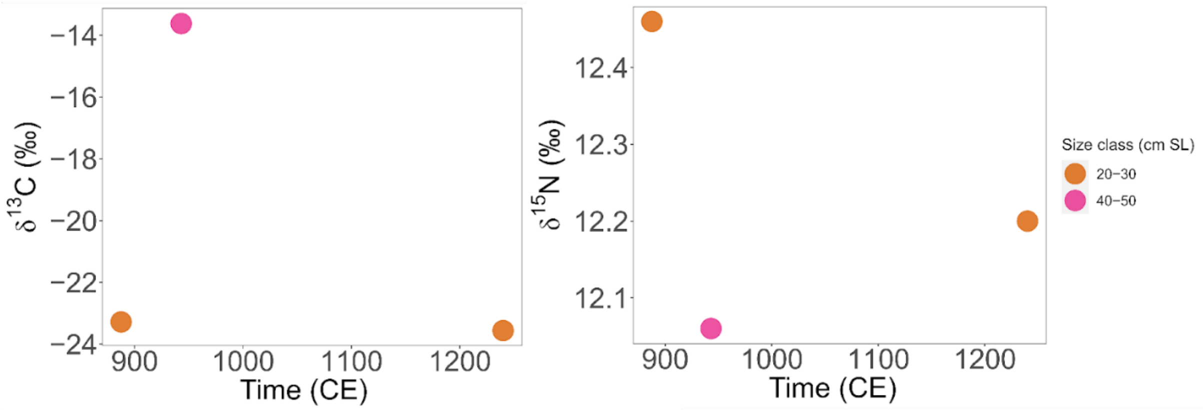

Figure E27. δ^{13}C (left) and δ^{15}N (right) of *P. flesus* chronologically in Coppergate.

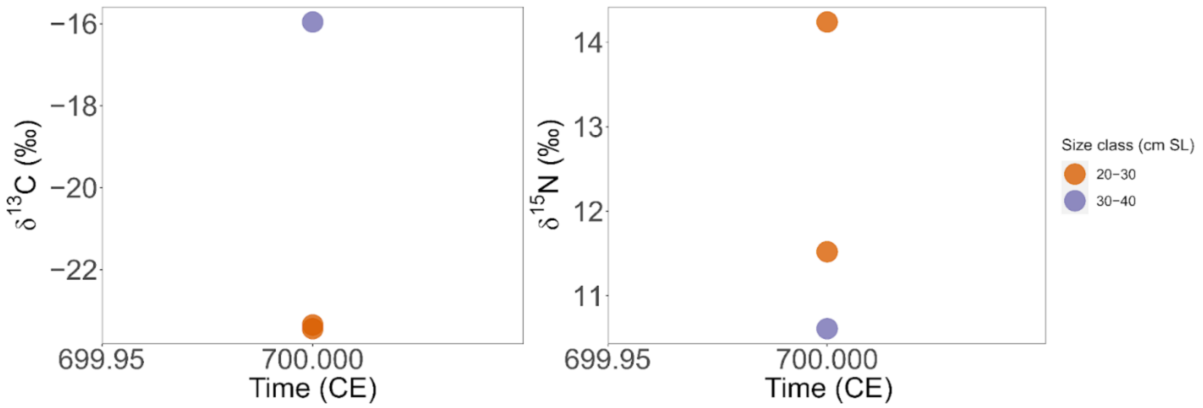

Figure E28. δ^{13}C (left) and δ^{15}N (right) of *P. flesus* chronologically in Blue Bridge Lane.

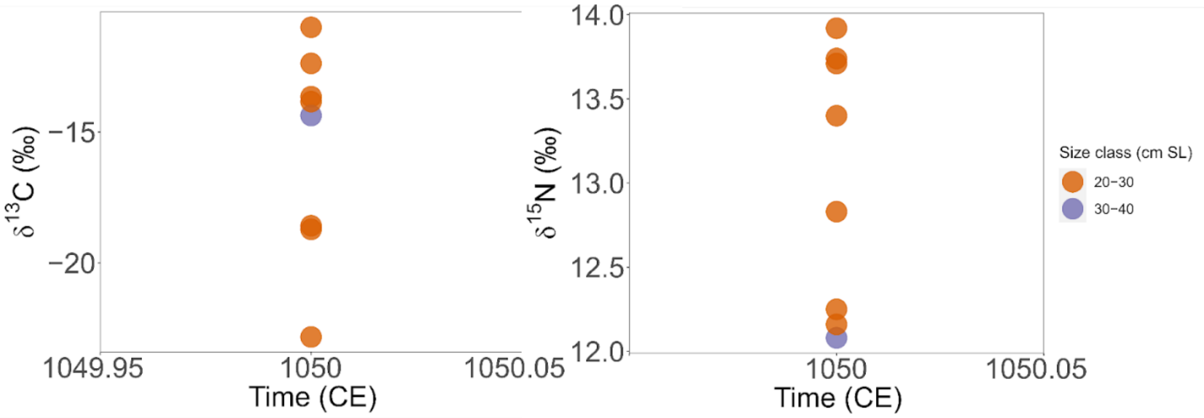

Figure E29. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. flesus* chronologically in GSJ06.

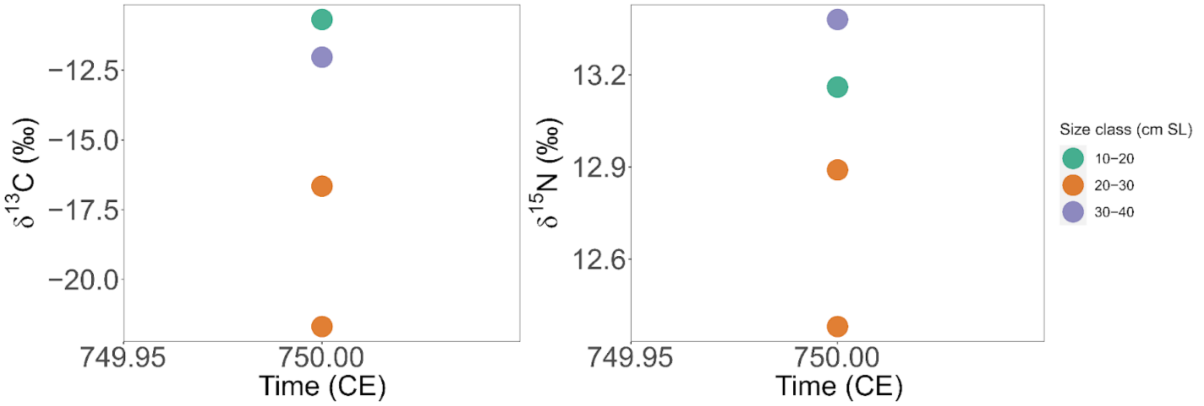

Figure E30. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. flesus* chronologically in SGA89.

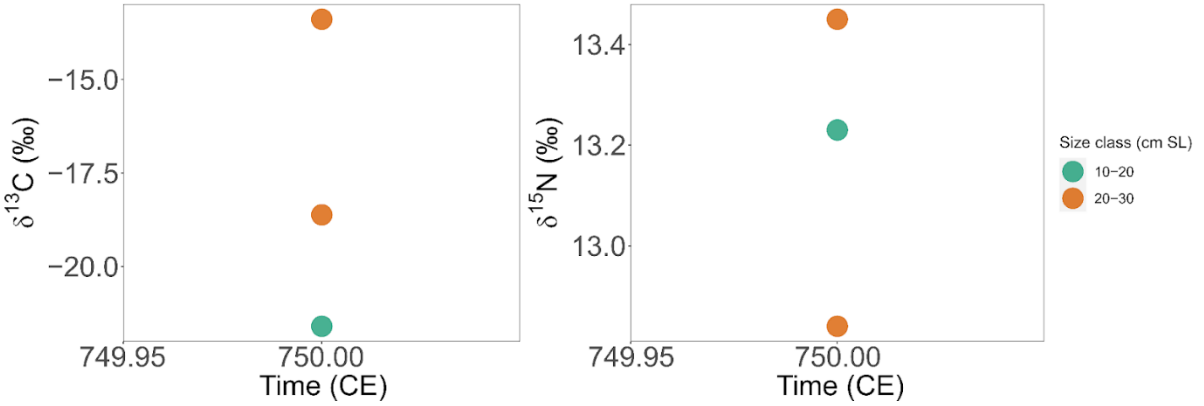

Figure E31. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. flesus* chronologically in SOT89.

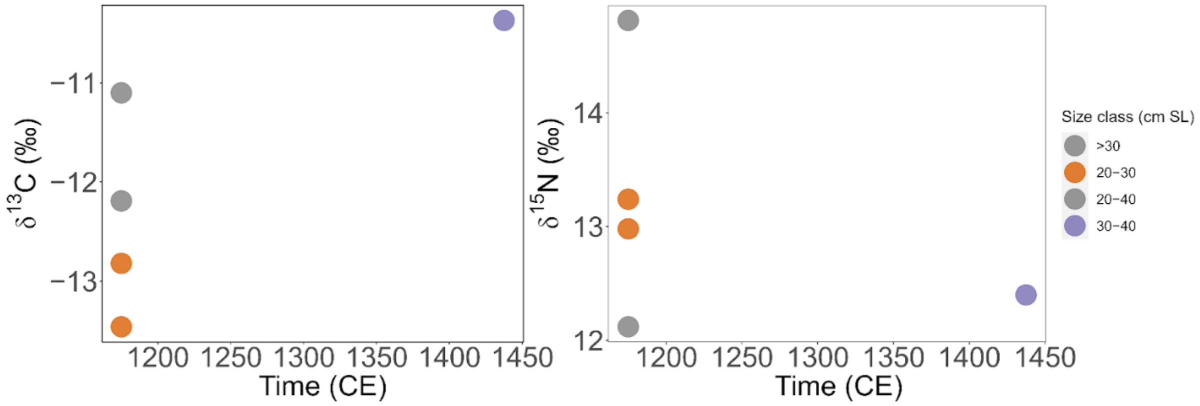

Figure E32. δ^{13}C (left) and δ^{15}N (right) of *P. flesus* chronologically in Tradescent Lane.

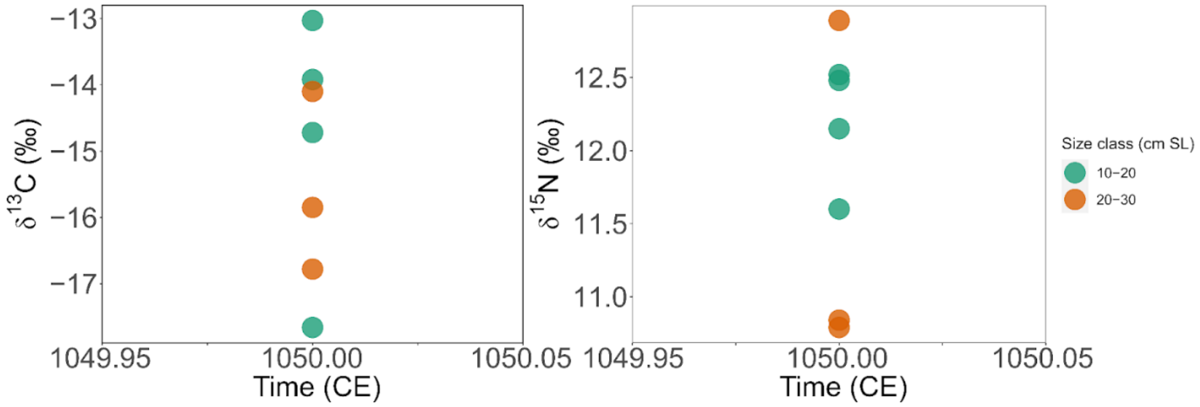

Figure E33. δ^{13}C (left) and δ^{15}N (right) of *P. flesus* chronologically in Barreau Saint-George.

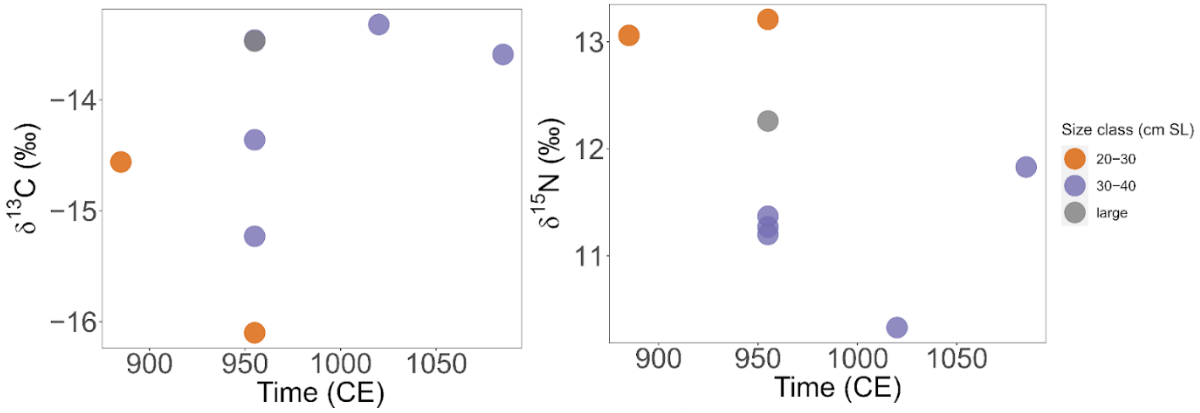

Figure E34. δ^{13}C (left) and δ^{15}N (right) of *P. flesus* chronologically in Koksijde.

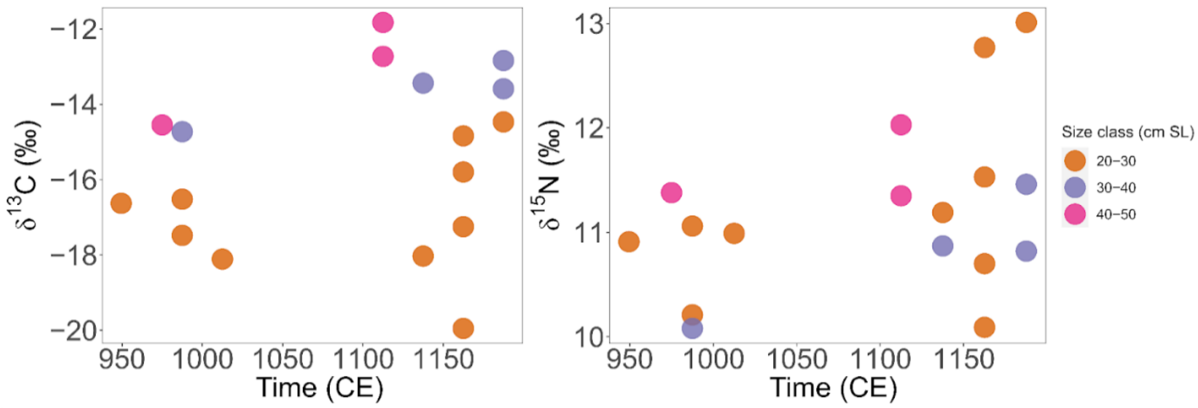

Figure E35. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. flesus* chronologically in Gent.

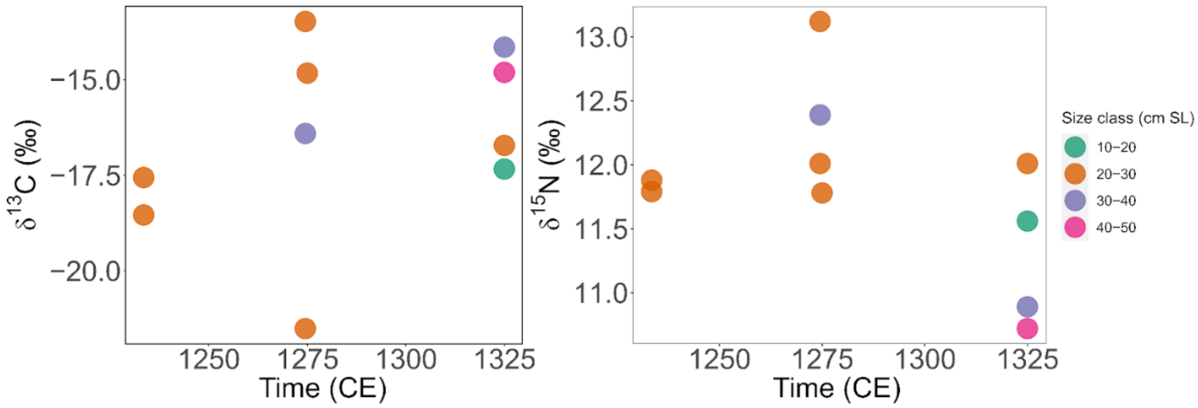

Figure E36. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. flesus* chronologically in Vlaardingen.

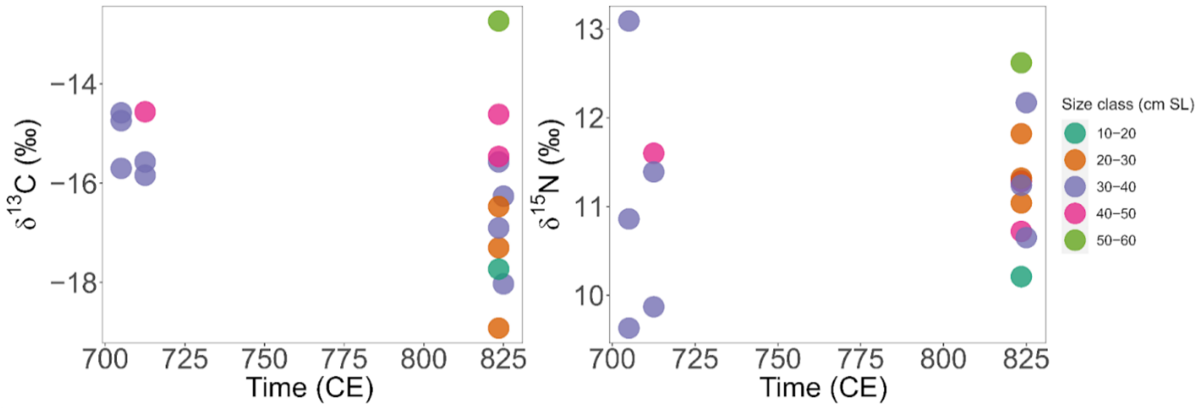

Figure E37. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of *P. flesus* chronologically in Plantage.

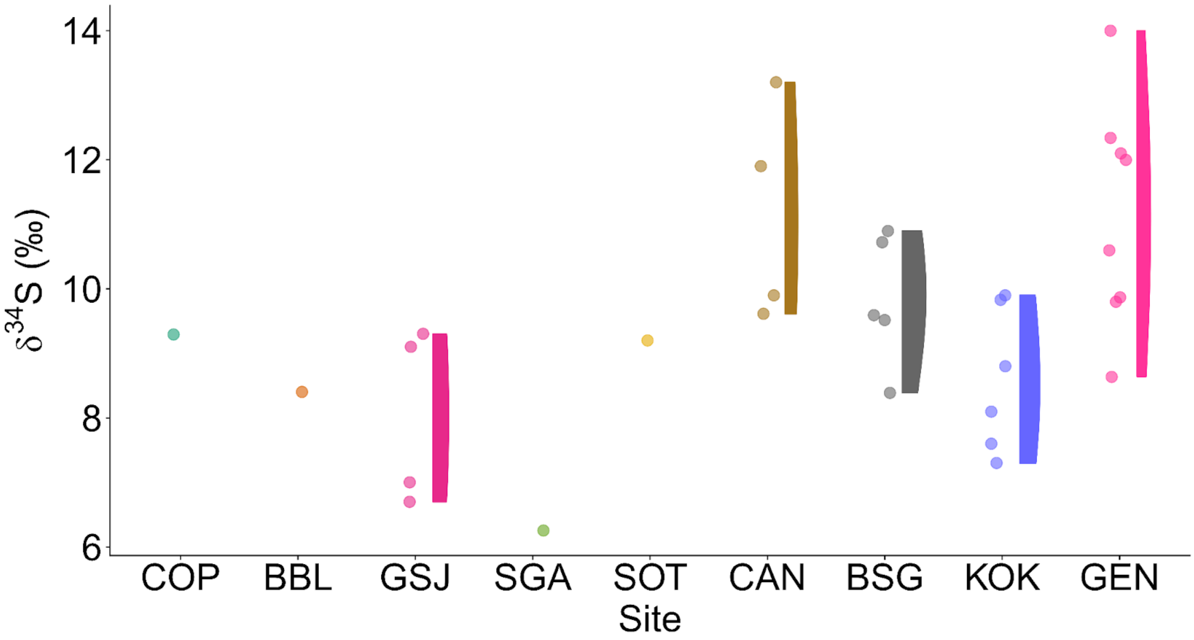

Figure E38. δ^{34}S per site of marine *P. flesus.*

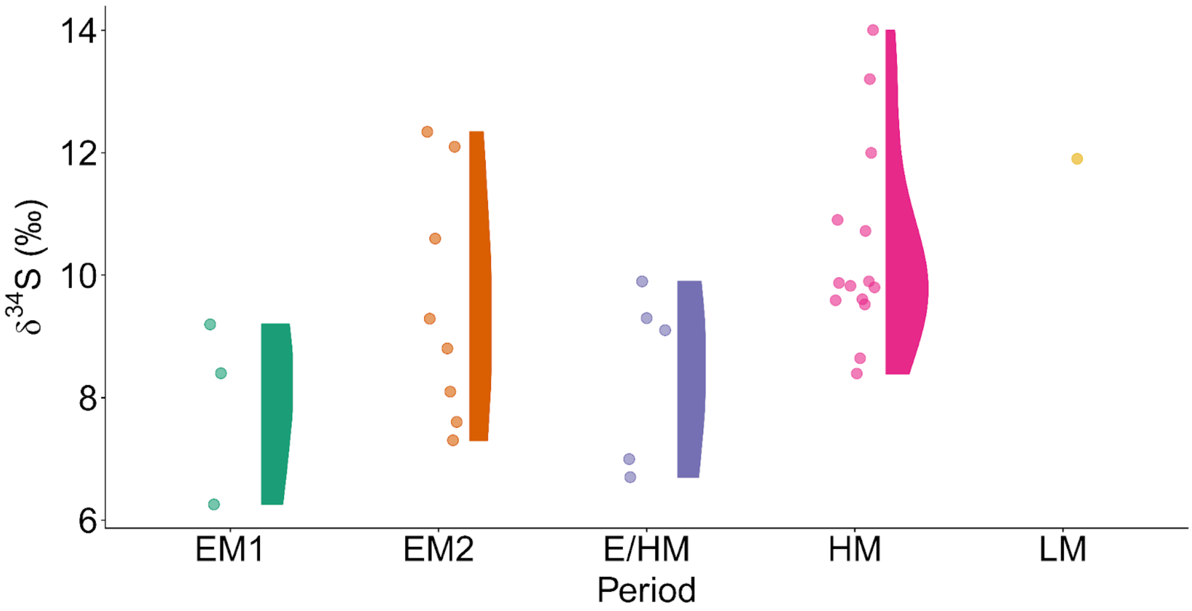

Figure E39. δ^{34}S per time period of marine *P. flesus.*

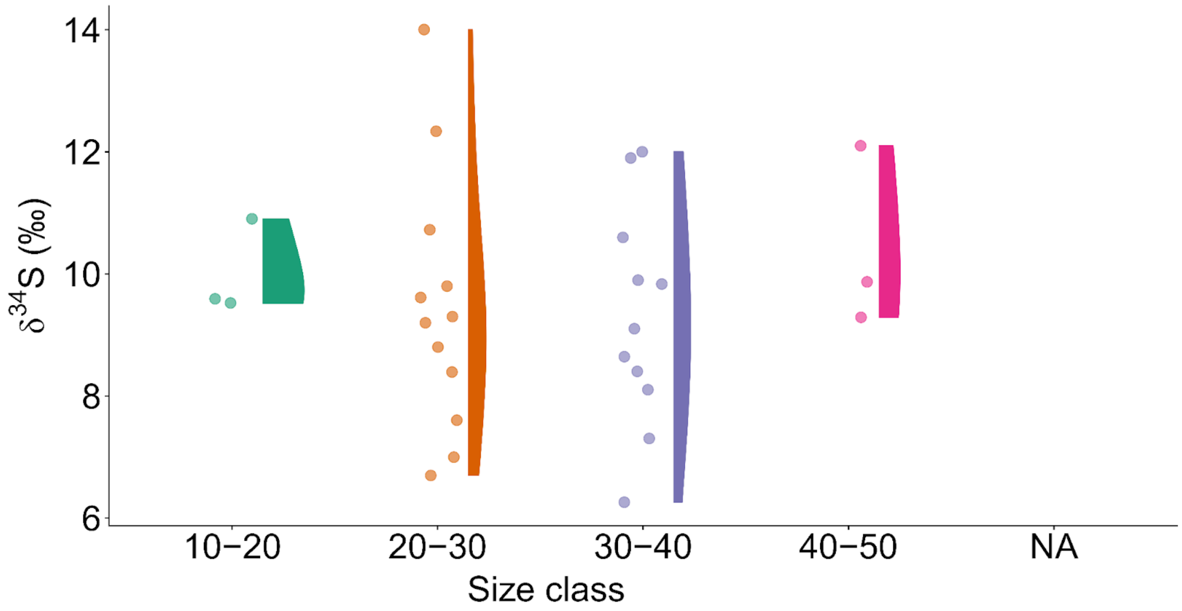

Figure E40. δ^{34}S per size class of marine *P. flesus.*

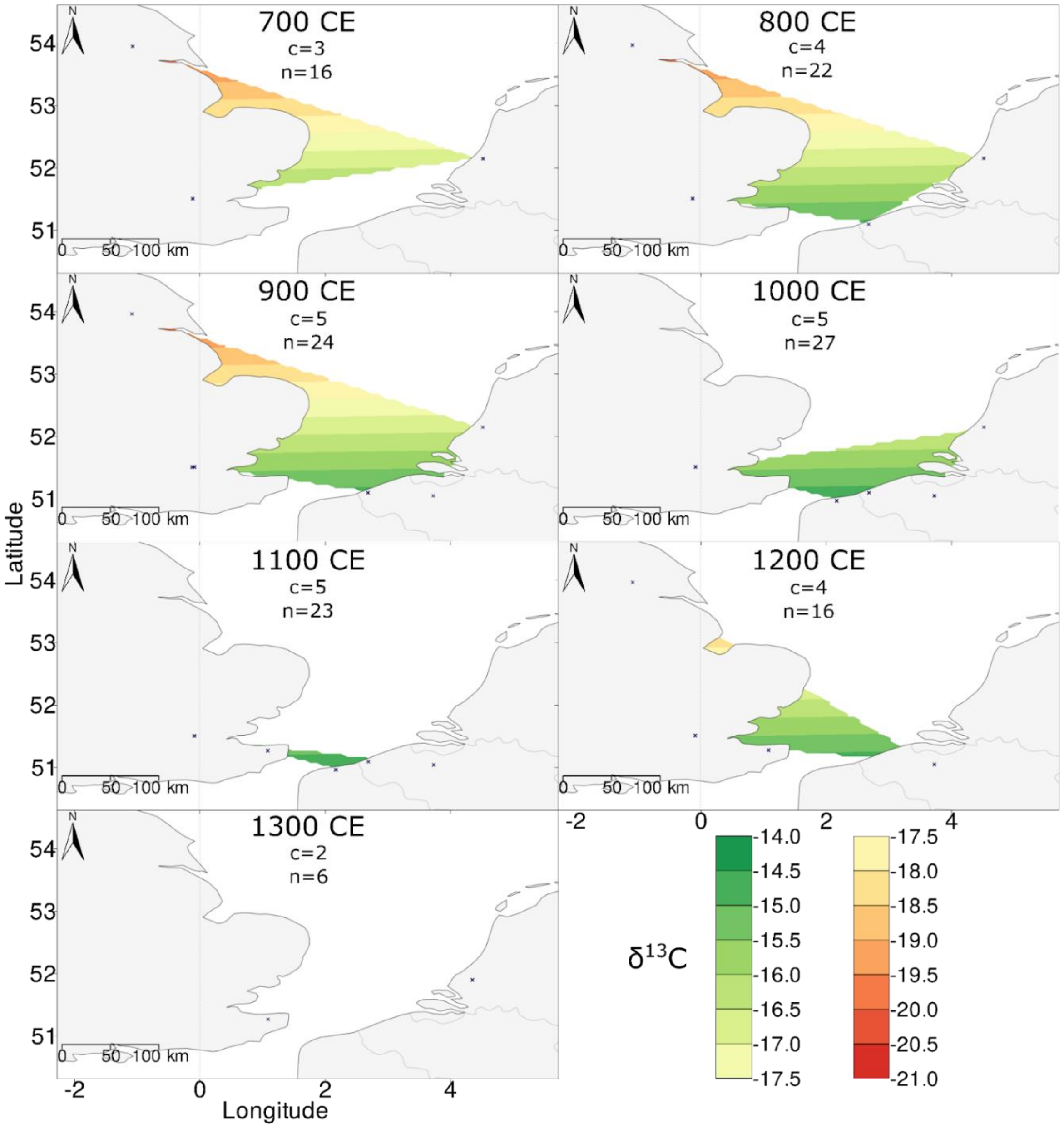

Figure E41. TimeR map of δ^{13}C for *P. flesus* per 100 year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

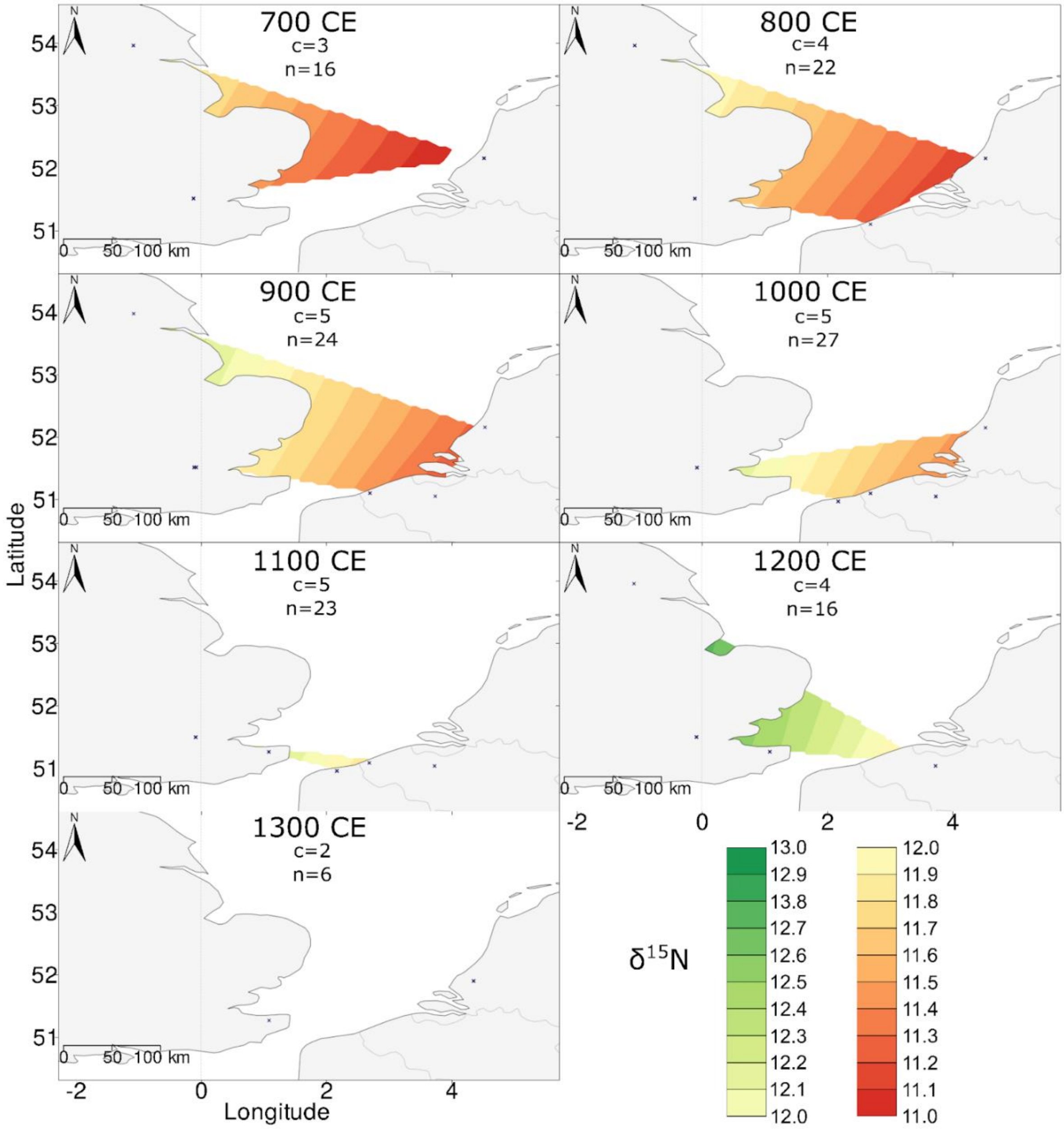

Figure E42. TimeR map of δ^{15}N for *P. flesus* per 100 year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

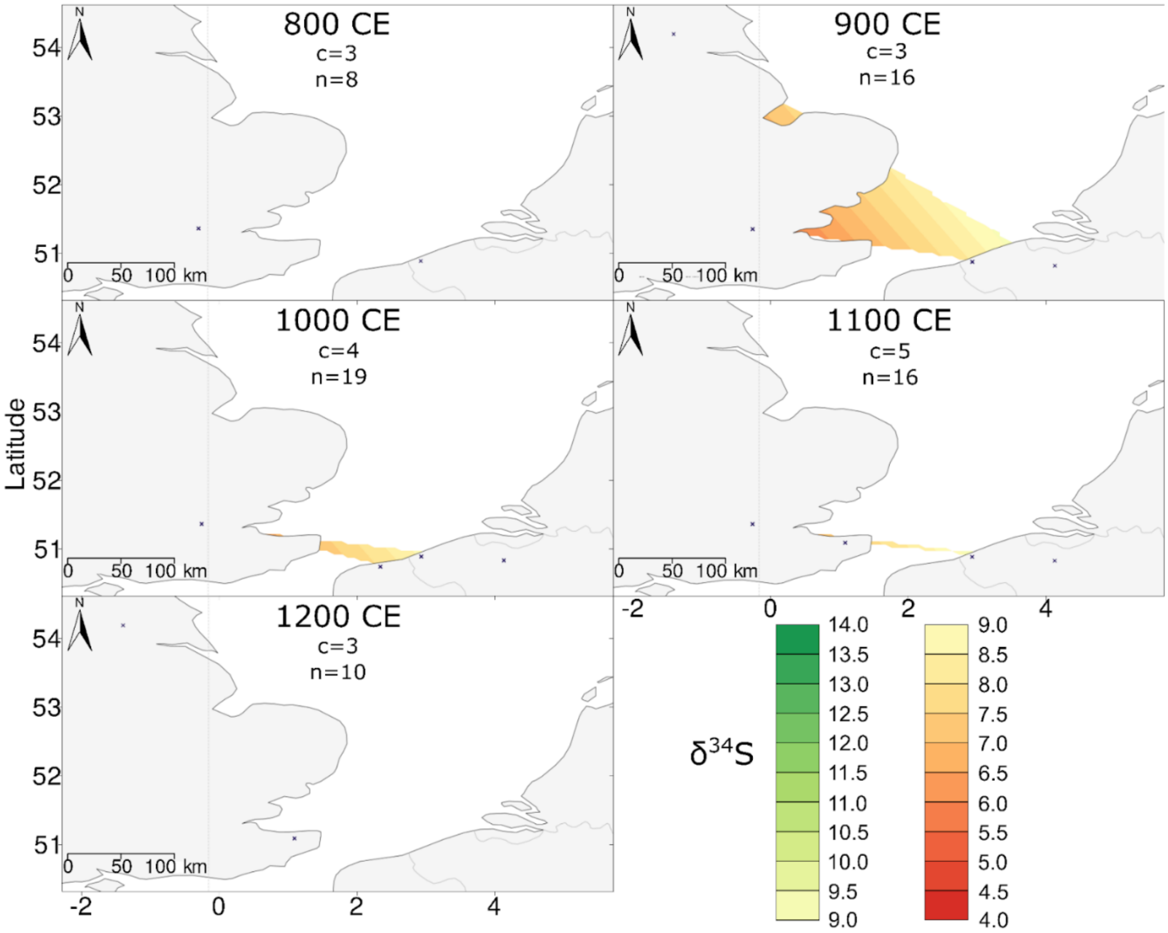

Figure E43. TimeR map of δ^{34}S for *P. flesus* per 100 year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

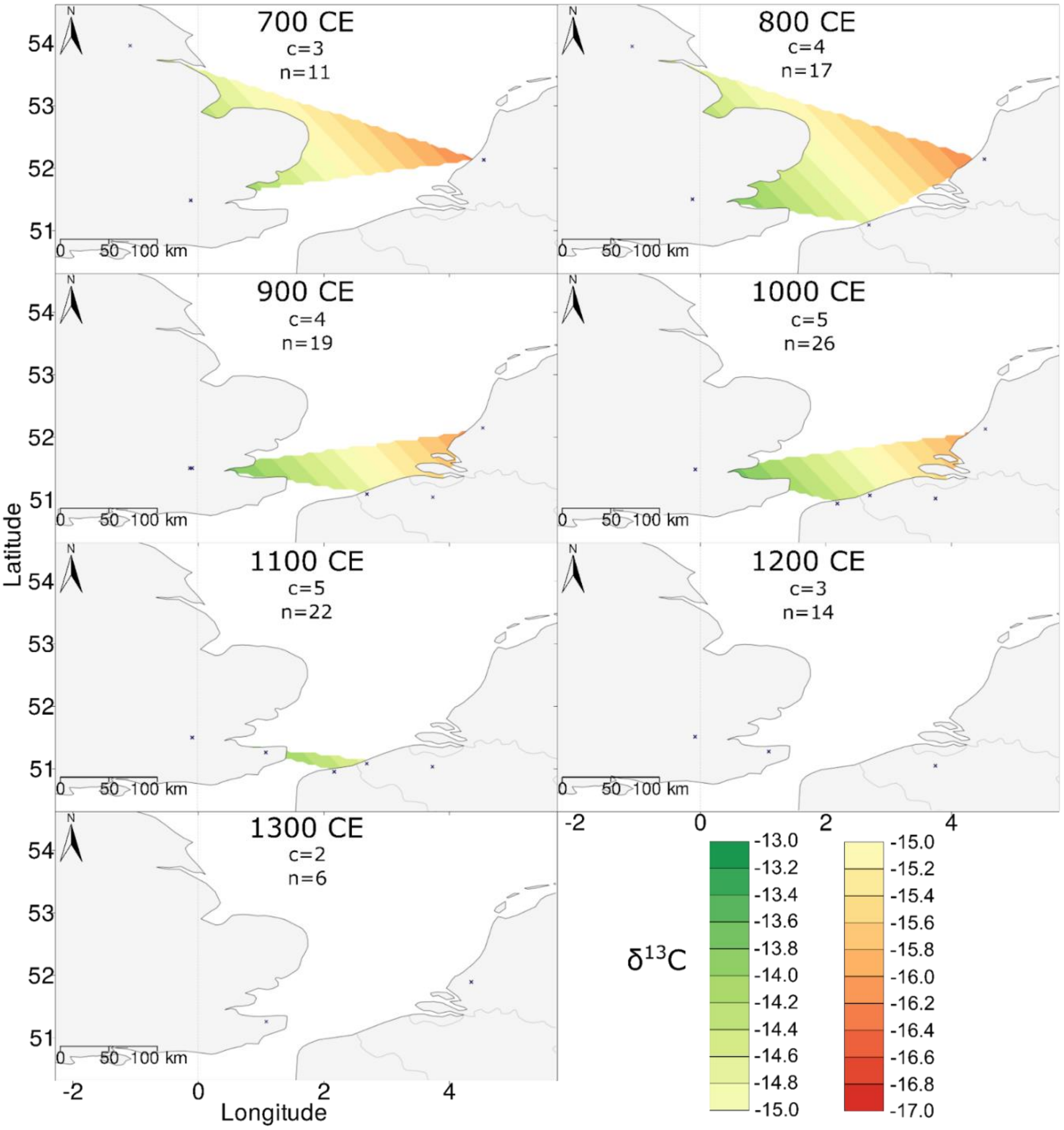

Figure E44. TimeR map of δ^{13}C for marine *P. flesus* per 100 year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

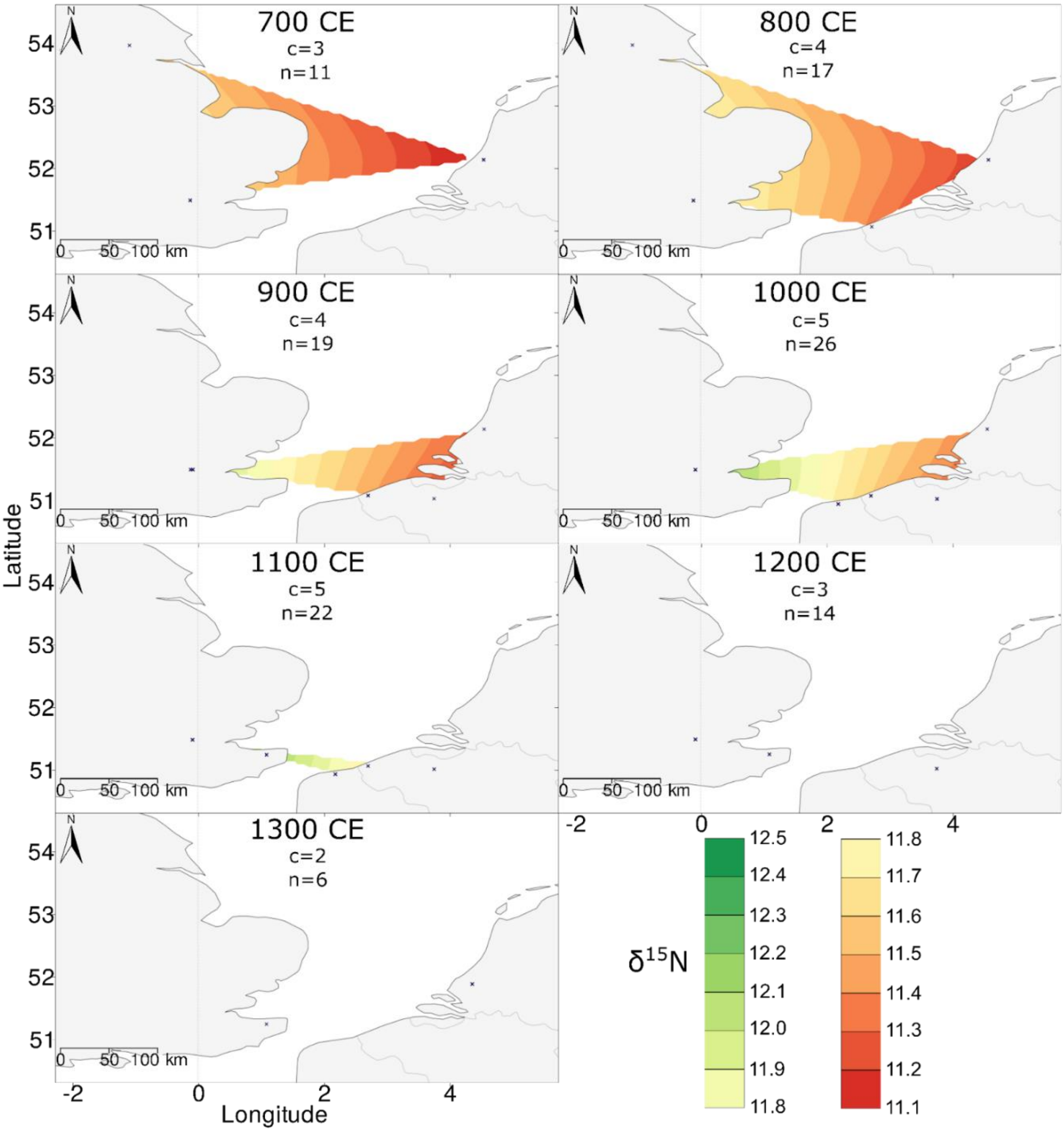

Figure E45. TimeR map of δ^{15}N for marine *P. flesus* per 100 year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

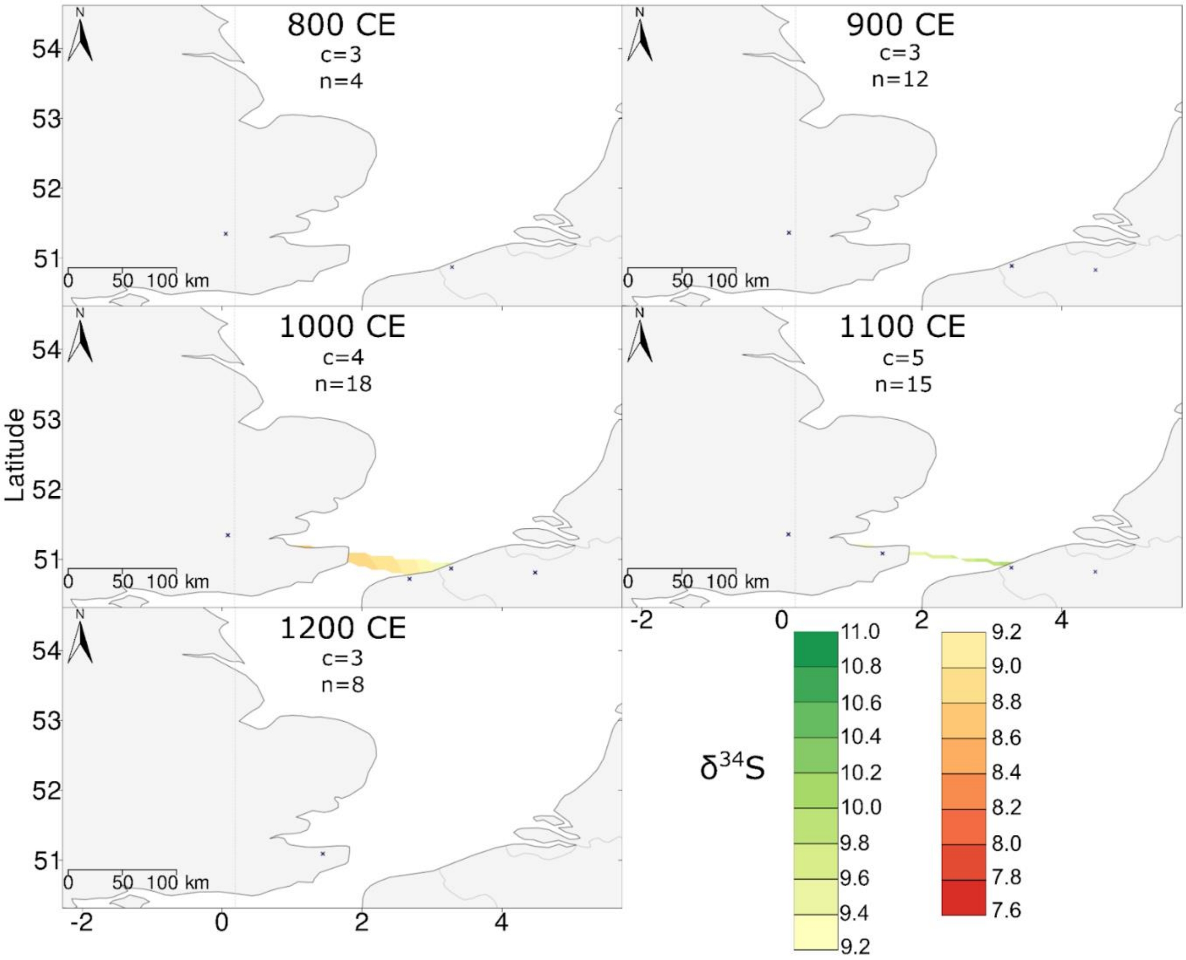

Figure E46. TimeR map of δ^{34}S for marine *P. flesus* per 100 year time periods (c: number of cities/settlements; and n: number of samples included in the model for each time period).

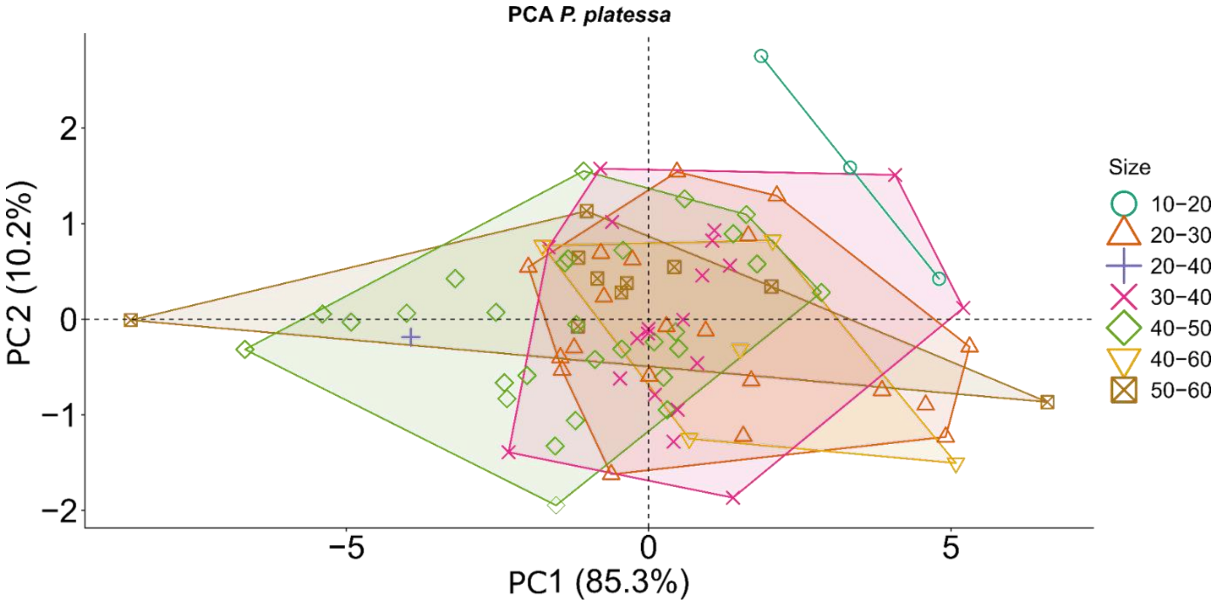

Figure E47. Principal component analysis of *P. platessa*, coloured and grouped by size class.

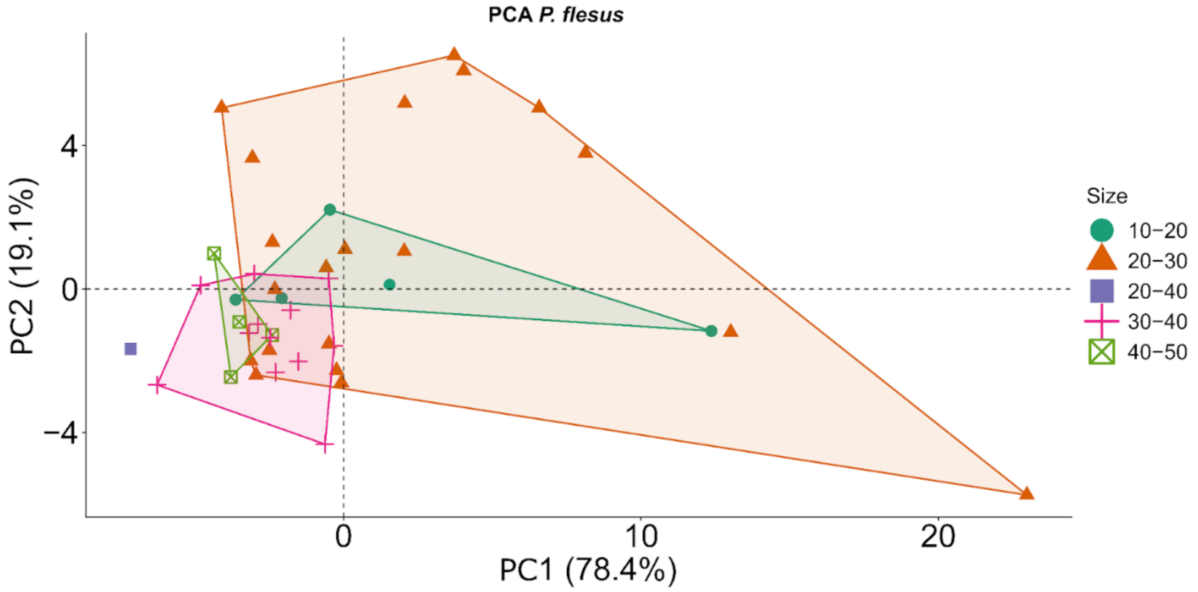

Figure E48. Principal component analysis of *P. flesus*, coloured and grouped by size class.

Part E2. Data tables

Table E13. Stable isotope data for carbon and nitrogen analysis of all 501 samples. Species names highlighted in yellow could not be identified to species (Cypriniformes). Samples highlighted in red were not included in the analysis as there was no collagen available for analysis or the data did not match the quality criteria. Samples highlighted in orange have low yield.

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Remarks
COP0100	Coppergate	1250 - 1275	Late Medieval	1262.5	20-30	*Pleuronectes platessa*	cleithrum	80.9	5.78	7.14	39.55	13.96	3.31	-16.09	11.77	
COP0109	Coppergate	1250 - 1275	Late Medieval	1262.5	30-40	*Pleuronectes platessa*	vertebra	182.2	17.48	9.59	40.13	14.63	3.20	-14.05	11.77	
COP0121	Coppergate	1250 - 1275	Late Medieval	1262.5	30-50	*Pleuronectes platessa*	os anale	415.8	30.48	7.33	43.62	15.89	3.20	-14.19	11.57	
COP0126	Coppergate	1040 - 1280	High Medieval	1160	20-40	*Pleuronectes platessa*	cleithrum	213.7	17.48	8.18	41.85	15.45	3.16	-12.06	13.56	
COP0129	Coppergate	1040 - 1280	High Medieval	1160	20-40	*Pleuronectes platessa*	preoperculum	210.0	18.88	8.99	42.21	15.07	3.27	-15.17	12.46	
COP0131	Coppergate	1200 - 1240	High/Late Medieval	1220	40-50	*Pleuronectes platessa*	os anale	405.9	23.50	5.79	44.24	16.12	3.20	-13.83	11.81	
COP0132	Coppergate	1200 - 1280	High/Late Medieval	1240	30-50	*Scophthalmus maximus*	preoperculum	415.3	29.44	7.09	32.59	11.37	3.34	-13.86	17.49	
COP0139	Coppergate	1200 - 1280	High/Late Medieval	1240	30-50	*Pleuronectes platessa*	caudal vertebra	215.5	25.43	11.80	42.91	15.88	3.15	-13.60	11.48	
COP0140	Coppergate	1200 - 1280	High/Late Medieval	1240	30-50	*Scophthalmus maximus*	cleithrum	450.5	21.46	7.79	42.59	15.23	3.26	-13.09	17.20	
COP0141	Coppergate	1200 - 1280	High/Late Medieval	1240	40-60	*Pleuronectes platessa*	os anale	288.3	17.43	9.60	43.24	16.25	3.10	-12.69	12.05	
COP0147	Coppergate	1040 - 1220	High Medieval	1130	40-60	*Pleuronectes platessa*	os anale	256.9	10.23	6.98	40.09	14.62	3.20	-14.22	11.49	
COP0148	Coppergate	1040 - 1220	High Medieval	1130	20-40	*Pleuronectes platessa*	cervical vertebra	206.0	17.41	8.45	41.17	15.20	3.16	-14.58	10.92	
COP0152	Coppergate	1140 - 1200	High Medieval	1170	30-50	*Scophthalmus maximus*	cleithrum	490.4	12.41	3.64	42.22	15.27	3.22	-13.42	17.21	
COP0153	Coppergate	1040 - 1220	High Medieval	1130	20-40	*Pleuronectes platessa*	os anale	428.5	42.39	9.89	43.40	15.96	3.17	-14.15	11.36	
COP0155	Coppergate	1040 - 1220	High Medieval	1130	50-70	*Melanogrammus aeglefinus*	ceratohyal	280.7	13.88	4.95	37.53	13.92	3.15	-13.50	14.78	
COP0156	Coppergate	1040 - 1220	High Medieval	1130	20-40	*Pleuronectes platessa*	preoperculum	361.1	29.17	8.08	41.67	15.06	3.23	-14.88	10.86	
COP0157	Coppergate	1040 - 1220	High Medieval	1130	50-70	*Esox lucius*	vertebra	298.1	27.47	9.21	44.58	15.69	3.32	-25.44	12.09	
COP0158	Coppergate	1200 - 1240	High/Late Medieval	1220	20-40	*Pleuronectes platessa*	hyomandibula	251.7	24.99	9.93	40.04	14.56	3.21	-12.48	12.45	
COP0168	Coppergate	1200 - 1280	High/Late Medieval	1240	40-60	*Pleuronectes platessa*	hyomandibula	201.9	23.33	11.56	42.92	16.03	3.12	-13.62	11.76	
COP0170	Coppergate	1200 - 1240	High/Late Medieval	1220	40-50	*Pleuronectes platessa*	caudal vertebra	341.5	36.57	10.71	40.97	15.08	3.17	-13.62	10.87	
COP0180	Coppergate	unknown	unknown	NA	40-50	*Scophthalmus maximus*	urohyal	344.6	15.78	4.58	42.39	15.57	3.18	-13.22	16.66	
COP0181	Coppergate	unknown	unknown	NA	40-50	*Melanogrammus aeglefinus*	cleithrum	507.5	10.30	2.03	32.18	10.15	3.70	-16.07	13.13	
COP0182	Coppergate	1040 - 1160	High Medieval	1100	40-50	*Pleuronectes platessa*	caudal vertebra	173.1	15.34	8.86	39.18	14.26	3.21	-13.72	10.93	
COP0195	Coppergate	1200 - 1240	High/Late Medieval	1220	20-40	*Pleuronectes platessa*	os anale	200.0	13.90	6.95	41.86	14.99	3.26	-12.85	13.57	
COP0198	Coppergate	1040 - 1160	High Medieval	1100	50-60	*Pleuronectes platessa*	vomer	234.4	18.40	7.85	37.05	14.03	3.08	-12.47	12.29	
COP0202	Coppergate	c930/935 - c955/6	Early Medieval 2	943	40-50	*Platichthys flesus*	first caudal vertebra	334.3	37.50	11.22	44.13	16.07	3.21	-13.62	12.06	
COP0204	Coppergate	1275 - mid1300s	Late Medieval	1312.5	30-50	*Pleuronectes platessa*	os anale	337.4	17.22	5.10	37.94	13.96	3.17	-14.52	11.48	
COP0205	Coppergate	1200 - mid 1300s	Late Medieval	1275	50-60	*Pleuronectes platessa*	vertebra	447.2	44.45	9.94	42.97	15.76	3.18	-12.52	11.28	
COP0206	Coppergate	1040 - 1100	High Medieval	1070	50-60	*Pleuronectes platessa*	os anale	342.3	30.17	8.81	43.39	16.33	3.10	-13.12	12.20	
COP0207	Coppergate	1040 - 1300 and 1440 - 1480	unknown	1260	30-40	*Limanda limanda*	os anale	510.8	46.46	9.10	44.34	16.44	3.15	-11.95	14.19	
COP0209	Coppergate	1200 - 1280	High/Late Medieval	1240	50-60	*Pleuronectes platessa*	os anale	273.2	12.98	8.23	41.07	14.99	3.20	-13.25	11.86	
COP0210	Coppergate	1200 - 1280	High/Late Medieval	1240	50-60	*Pleuronectes platessa*	preoperculum	483.4	46.05	9.53	42.21	15.88	3.10	-12.78	12.44	
COP0213	Coppergate	1200 - 1280	High/Late Medieval	1240	40-50	*Pleuronectes platessa*	cleithrum	351.8	24.23	6.89	43.16	16.09	3.13	-13.67	12.64	
COP0214	Coppergate	1200 - 1280	High/Late Medieval	1240	50-60	*Pleuronectes platessa*	os anale	330.5	18.45	5.58	41.23	15.21	3.16	-13.37	11.05	
COP0215	Coppergate	1200 - 1280	High/Late Medieval	1240	20-30	*Platichthys flesus*	urohyal	66.4	6.61	9.96	43.03	15.61	3.22	-23.56	12.20	
COP0217	Coppergate	1200 - 1280	High/Late Medieval	1240	40-50	*Pleuronectes platessa*	precaudal vertebra	301.1	32.92	10.93	39.54	14.91	3.09	-11.95	11.23	
COP0220	Coppergate	mid - late 800s/early 900s	Early Medieval 2	887.5	20-30	*Platichthys flesus*	os anale	261.8	15.25	5.83	43.23	15.62	3.23	-23.28	12.46	
COP0222	Coppergate	1040 - 1160	High Medieval	1100	40-50	*Pleuronectes platessa*	precaudal vertebra	229.1	16.50	7.20	38.79	14.01	3.23	-13.90	11.45	
COP0224	Coppergate	1040 - 1160	High Medieval	1100	50-60	*Pleuronectes platessa*	os anale	449.0	32.57	7.25	42.92	15.91	3.15	-12.98	11.96	
COP0226	Coppergate	late 800s/early 900s - c930/5	Early Medieval 2	905	30-40	cf Cyprinidae	precaudal vertebra	178.8	23.42	13.10	43.36	15.39	3.29	-23.74	14.54	
COP0229	Coppergate	1160 - 1200	High Medieval	1180	50-60	*Melanogrammus aeglefinus*	cleithrum	246.2	19.52	7.93	42.91	14.86	3.37	-14.47	14.45	
COP0233	Coppergate	1040 - 1160	High Medieval	1100	40-60	*Melanogrammus aeglefinus*	cleithrum	502.8	12.49	2.48	18.30	5.44	3.93	-16.54	13.79	
COP0234	Coppergate	1250 - 1275	Late Medieval	1262.5	40-50	*Melanogrammus aeglefinus*	hyomandibula	188.9	9.38	4.97	38.98	13.95	3.26	-13.03	13.87	
COP0238	Coppergate	1040 - 1300 and 1440 - 1480	unknown	NA	40-60	*Esox lucius*	dentary	460.1	28.81	6.26	30.69	10.80	3.32	-24.85	11.37	
COP0242	Coppergate	1275 - mid1300s	Late Medieval	1312.5	40-60	*Melanogrammus aeglefinus*	cleithrum	461.2	2.47	0.54	27.81	9.17	3.54	-15.32	14.36	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
COP0247	Coppergate	1040 - 1300 and 1440 - 1480	unknown	NA	70-80	*Gadus morhua*	ceratohyal	525.7	28.99	5.51	39.55	14.45	3.19	-13.28	17.02	
COP0251	Coppergate	1275 - mid1300s	Late Medieval	1312.5	30-40	*Pleuronectes platessa*	quadrate	196.3	13.74	7.00	43.23	15.85	3.18	-14.11	11.73	
COP0260	Coppergate	c930/935 - c955/6	Early Medieval 2	943	60-80	*Gadus morhua*	vertebra	421.7	31.56	7.48	34.99	12.76	3.20	-11.41	15.35	
COP0261	Coppergate	c930/935 - c955/6	Early Medieval 2	943	50-60	*Esox lucius*	vertebra	151.3	10.31	6.81	38.17	13.25	3.36	-22.47	13.27	
COP0280	Coppergate	mid - later 1000s	High Medieval	1062.5	40-60	*Gadus morhua*	quadrate	300.7	12.15	4.04	34.98	12.28	3.32	-13.58	15.34	
COP0284	Coppergate	1040 - 1160	High Medieval	1100	40-60	*Melanogrammus aeglefinus*	articular	177.0	13.09	7.40	40.40	14.67	3.21	-13.91	14.47	
COP0291	Coppergate	c955/6	Early Medieval 2	955.5	50-60	*Esox lucius*	quadrate	206.8	15.07	7.29	37.73	13.45	3.27	-24.24	13.92	
COP0307	Coppergate	1200 - 1280	High/Late Medieval	1240	40-50	*Pleuronectes platessa*	urohyal	373.9	38.88	10.40	45.30	16.95	3.12	-13.84	11.92	
COP0308	Coppergate	1040 - 1220	High Medieval	1130	80-100	*Gadus morhua*	articular	425.9	4.85	1.14	22.48	7.68	3.41	-15.03	15.02	
COP0313	Coppergate	1040 - 1160	High Medieval	1100	30-40	*Pleuronectes platessa*	quadrate	485.1	24.09	4.97	41.22	14.90	3.23	-13.70	12.43	
COP0318	Coppergate	c955/6 - early/mid 1000s	Early Medieval 2	1002.5	60-80	*Gadus morhua*	dentary	509.0	8.52	1.67	17.49	3.85	5.30	-20.54	15.01	single run
COP0320	Coppergate	c955/6 - early/mid 1000s	Early Medieval 2	1002.5	40-60	*Pleuronectes platessa*	caudal vertebra	356.9	46.66	13.07	44.45	16.53	3.14	-12.38	11.92	
COP0323	Coppergate	c955/6 - early/mid 1000s	Early Medieval 2	1002.5	50-70	*Esox lucius*	vertebra	304.0	20.78	6.84	41.20	13.86	3.47	-24.09	14.56	
COP0328	Coppergate	c955/6	Early Medieval 2	955.5	40-50	*Pleuronectes platessa*	os anale	310.8	30.00	9.65	44.50	16.64	3.12	-12.25	12.25	
COP0329	Coppergate	1250 - 1275	Late Medieval	1262.5	40-50	*Pleuronectes platessa*	os anale	295.9	31.03	10.49	44.33	16.80	3.08	-13.92	11.79	
COP0330	Coppergate	1250 - 1275	Late Medieval	1262.5	30-50	*Pleuronectes platessa*	vertebra	298.8	34.81	11.65	41.96	15.73	3.11	-14.62	10.24	
COP0331	Coppergate	1250 - 1275	Late Medieval	1262.5	40-50	*Pleuronectes platessa*	hyomandibula	257.5	26.39	10.25	44.38	16.70	3.10	-14.13	11.03	
COP0332	Coppergate	1250 - 1275	Late Medieval	1262.5	40-60	*Pleuronectes platessa*	caudal vertebra	283.8	25.37	8.94	39.82	14.68	3.17	-13.91	11.08	
COP0335	Coppergate	1040 - 1280	High Medieval	1160	30-50	*Pleuronectes platessa*	os anale	276.6	11.53	8.46	42.00	15.27	3.21	-14.63	12.02	
COP0336	Coppergate	1040 - 1280	High Medieval	1160	50-60	*Pleuronectes platessa*	os anale	327.8	15.07	4.60	41.87	15.18	3.22	-13.63	12.69	
COP0337	Coppergate	1040 - 1160	High Medieval	1100	40-50	*Pleuronectes platessa*	ceratohyal	232.0	18.75	8.08	43.39	16.15	3.14	-13.96	12.03	
COP0338	Coppergate	1040 - 1220	High Medieval	1130	20-30	*Pleuronectes platessa*	os anale	268.0	12.58	7.66	43.12	15.76	3.19	-13.90	12.43	
COP0347	Coppergate	c955/6	Early Medieval 2	955.5	50-70	*Esox lucius*	parasphenoid	498.1	28.44	5.71	40.14	14.07	3.33	-24.93	14.44	
COP0349	Coppergate	mid - late 800s/early 900s	Early Medieval 2	887.5	40-60	*Esox lucius*	vertebra	140.4	9.59	6.83	42.14	14.68	3.35	-26.58	12.03	
COP0350	Coppergate	c955/6 - early/mid 1000s	Early Medieval 2	1002.5	50-70	*Esox lucius*	vertebra	254.5	24.34	9.56	43.16	14.49	3.47	-26.80	12.38	
BBL0901	Blue Bridge Lane	early - mid 14th	Late Medieval	1260	30-40	*Melanogrammus aeglefinus*	cleithrum	396.9	26.51	6.68	43.84	15.52	3.29	-13.87	15.92	
BBL0902	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	20-30	*Platichthys flesus*	caudal vertebra	97.1	8.56	8.82	37.12	13.72	3.16	-23.35	11.52	
BBL0903	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	40-50	*Pleuronectes platessa*	precaudal vertebra	134.3	11.28	8.40	40.02	14.63	3.19	-13.62	11.50	
BBL0904	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	70-80	*Esox lucius*	vertebra	208.4	8.03	3.85	35.13	12.76	3.21	-23.21	16.16	
BBL0905	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	40-50	*Pleuronectes platessa*	precaudal vertebra	179.6	7.04	3.92	33.63	12.21	3.21	-13.70	10.98	
BBL0906	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	20-30	*Pleuronectes platessa*	quadrate	116.0	6.62	5.71	35.80	12.77	3.27	-13.97	12.39	
BBL0907	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	20-30	*Pleuronectes platessa*	precaudal vertebra	49.3	3.07	6.23	33.75	12.28	3.21	-12.28	11.79	
BBL0908	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	50-60	*Pleuronectes platessa*	caudal vertebra	223.5	12.81	5.73	39.32	14.18	3.23	-12.51	12.28	
BBL0909	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	40-50	*Pleuronectes platessa*	precaudal vertebra	152.6	7.62	4.99	17.36	6.57	1.59	15.13	3.34	
BBL0910	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	40-50	*Pleuronectes platessa*	caudal vertebra	218.4	11.86	5.43	41.13	14.92	3.22	-14.24	10.87	
BBL0911	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	20-30	*Pleuronectes platessa*	caudal vertebra	65.4	2.97	4.54	35.06	12.67	3.23	-13.14	11.66	
BBL0912	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	20-30	[Not enough collagen]	articular	52.1	2.38	4.57	NA	NA	NA	NA	NA	
BBL0913	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	40-50	*Pleuronectes platessa*	dentary	167.0	7.59	4.54	37.81	13.83	3.19	-12.81	12.68	
BBL0914	Blue Bridge Lane	late 14th - early 16th	Late Medieval	1497.5	40-50	*Melanogrammus aeglefinus*	quadrate	122.2	8.64	7.07	40.74	14.60	3.26	-13.49	15.11	
BBL0915	Blue Bridge Lane	late 14th - early 16th	Late Medieval	1497.5	20-30	cf *Limanda limanda*	caudal vertebra	68.3	8.36	12.23	41.37	15.16	3.18	-13.73	12.86	
BBL0916	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	40-50	*Esox lucius*	vertebra	118.3	10.35	8.75	38.24	14.06	3.17	-24.64	13.63	
BBL0917	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	20-30	*Platichthys flesus*	caudal vertebra	127.1	7.12	5.60	38.64	14.24	3.17	-23.44	14.24	
BBL0918	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	30-40	*Platichthys flesus*	caudal vertebra	157.5	11.65	7.40	40.43	14.86	3.17	-15.96	10.61	
BBL0919	Blue Bridge Lane	late 14th - early 16th	Late Medieval	1497.5	20-30	*Pleuronectes platessa*	caudal vertebra	93.0	13.15	14.14	41.12	15.11	3.18	-13.88	11.58	
CAO0822	CAO96	900 - 1150	Early/High Medieval	1025	90-110	*Gadus morhua*	epihyal	322.4	31.67	9.82	41.31	15.56	3.10	-12.48	17.29	
CAO0823	CAO96	900 - 1150	Early/High Medieval	1025	90-110	*Gadus morhua*	dentary	785.5	66.01	8.40	44.06	16.31	3.15	-12.68	16.59	
CAO0824	CAO96	1150 - 1270	High Medieval	1210	20-30	*Pleuronectes platessa*	precaudal vertebra	173.1	13.48	7.79	40.83	15.19	3.14	-14.21	11.51	
CAO0825	CAO96	1150 - 1270	High Medieval	1210	40-50	*Esox lucius*	vertebra	124.4	6.15	4.94	40.84	13.55	3.52	-24.65	15.39	
CAO0826	CAO96	1150 - 1270	High Medieval	1210	30-40	*Pleuronectes platessa*	quadrate	233.3	11.21	4.81	35.10	12.84	3.19	-13.52	11.75	
CAO0827	CAO96	1150 - 1270	High Medieval	1210	30-40	*Pleuronectes platessa*	dentary	280.6	21.23	7.57	38.47	14.31	3.14	-12.86	12.01	
CAO0828	CAO96	1150 - 1270	High Medieval	1210	20-30	*Pleuronectes platessa*	preoperculum	215.7	13.68	6.34	41.31	15.38	3.13	-13.43	10.99	
CAO0829	CAO96	1150 - 1270	High Medieval	1210	30-40	*Pleuronectes platessa*	caudal vertebra	145.2	10.63	7.32	40.61	15.37	3.08	-13.20	10.47	
CAO0830	CAO96	900 - 1150	Early/High Medieval	1025	20-30	*Pleuronectes platessa*	caudal vertebra	107.6	9.70	9.01	41.67	15.22	3.19	-13.28	10.22	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
CAO0831	CAO96	900 - 1150	Early/High Medieval	1025	25-35	*Pleuronectes platessa*	atlas	122.8	6.58	5.36	38.87	13.89	3.26	-13.65	11.26	
CAO0832	CAO96	1240 - 1380	Late Medieval	1310	30-40	*Pleuronectes platessa*	ectopterygoid	164.8	6.43	3.90	37.16	12.48	3.47	-14.49	12.59	
CAO0833	CAO96	1240 - 1380	Late Medieval	1310	30-40	*Pleuronectes platessa*	cleithrum	266.4	17.38	6.52	40.64	14.65	3.24	-14.94	11.39	
CAO0834	CAO96	1240 - 1380	Late Medieval	1310	30-40	*Pleuronectes platessa*	precaudal vertebra	205.4	14.83	7.22	41.34	15.37	3.14	-13.15	11.54	
CAO0835	CAO96	1240 - 1380	Late Medieval	1310	30-40	*Pleuronectes platessa*	caudal vertebra	174.6	16.87	9.66	42.37	15.74	3.14	-12.26	11.38	
GSJ0800	GSJ06	10th - 12th	Early/High Medieval	1050	35-45	*Melanogrammus aeglefinus*	dentary	198.3	12.04	6.07	34.90	11.69	3.48	-14.50	16.30	
GSJ0801	GSJ06	10th - 12th	Early/High Medieval	1050	10-20	cf Cyprinidae	pharyngeal	58.1	9.10	15.68	42.07	14.52	3.38	-27.45	11.91	
GSJ0802	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	ectopterygoid	92.4	6.21	6.72	37.71	13.10	3.36	-14.67	12.98	
GSJ0803	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	precaudal vertebra	129.7	7.57	5.84	38.84	13.85	3.27	-14.00	10.54	
GSJ0804	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	caudal vertebra	123.3	11.01	8.93	40.88	14.84	3.21	-12.77	11.68	
GSJ0805	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	precaudal vertebra	99.8	8.54	8.56	40.76	14.44	3.29	-13.65	13.71	
GSJ0806	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	quadrate	156.9	17.05	10.87	42.80	15.30	3.26	-14.08	11.78	
GSJ0807	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	113.9	13.61	11.95	41.36	15.06	3.20	-13.16	10.11	
GSJ0808	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	precaudal vertebra	42.5	7.14	16.79	37.23	12.74	3.41	-18.72	12.83	single run
GSJ0809	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	caudal vertebra	48.5	5.72	11.80	40.37	14.75	3.19	-11.00	13.74	
GSJ0810	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	caudal vertebra	59.6	9.13	15.33	38.50	13.30	3.38	-18.58	12.16	
GSJ0811	GSJ06	10th - 12th	Early/High Medieval	1050	60-70	*Gadus morhua*	supracleithrum	301.1	32.18	10.69	42.40	15.84	3.12	-12.57	15.51	
GSJ0812	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	caudal vertebra	145.9	9.75	6.68	39.54	14.12	3.27	-13.38	10.92	
GSJ0813	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	basioccipital	137.5	14.06	10.22	41.08	15.38	3.12	-13.01	12.46	
GSJ0814	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	146.8	9.35	6.37	40.22	14.49	3.24	-13.15	11.81	
GSJ0815	GSJ06	10th - 12th	Early/High Medieval	1050	50-60	*Merlangius merlangius*	premaxilla	226.4	7.34	3.24	22.19	7.29	3.55	-14.01	15.32	
GSJ0816	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	[Not enough collagen]	caudal vertebra	126.6	8.94	7.06	NA	NA	NA	NA	NA	
GSJ0817	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	caudal vertebra	86.2	8.82	10.23	41.00	14.72	3.25	-13.84	13.40	
GSJ0818	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	articular	248.0	27.66	11.16	39.91	15.00	3.10	-12.64	12.18	
GSJ0819	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	cf *Platichthys flesus*	caudal vertebra	133.4	9.59	7.19	41.19	14.62	3.29	-14.37	12.08	
GSJ0820	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	81.4	6.63	8.15	39.72	13.35	3.47	-14.22	14.09	single run
GSJ0821	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	precaudal vertebra	141.8	15.15	10.69	40.48	14.72	3.21	-12.38	13.92	
GSJ0836	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	caudal vertebra	107.7	10.85	10.08	40.24	14.76	3.18	-22.83	12.25	
GSJ0837	GSJ06	10th - 12th	Early/High Medieval	1050	NA	*Conger conger*	vertebra	171.3	21.02	12.27	42.21	15.49	3.18	-11.88	14.42	
GSJ0838	GSJ06	10th - 12th	Early/High Medieval	1050	15-25	cf Cyprinidae	pharyngeal	80.9	11.36	14.04	42.12	15.05	3.26	-24.64	12.8	
GSJ0839	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	precaudal vertebra	133.4	9.94	7.45	39.13	14.16	3.23	-13.15	11.43	
SGA0840	SGA89	7th - 9th	Early Medieval 1	750	10-20	[Not enough collagen]	pharyngeal	71.8	?	?	NA	NA	NA	NA	NA	
SGA0841	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	caudal vertebra	102.1	2.00	1.96	17.65	6.39	1.65	-3.79	4.08	
SGA0842	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	caudal vertebra	47.6	1.81	3.80	38.37	13.73	3.26	-12.67	12.49	
SGA0843	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	caudal vertebra	89.3	4.05	4.54	39.38	14.51	3.15	-12.96	11.27	
SGA0844	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Pleuronectes platessa*	caudal vertebra	104.5	3.45	3.30	36.53	13.16	3.24	-13.03	11.69	
SGA0845	SGA89	7th - 9th	Early Medieval 1	750	20-30	cf *Platichthys flesus*	caudal vertebra	56.1	?	?	38.65	14.01	3.22	-16.66	12.38	
SGA0846	SGA89	7th - 9th	Early Medieval 1	750	30-50	*Melanogrammus aeglefinus*	vertebra	96.5	2.16	2.24	36.95	12.60	3.42	-15.09	13.67	
SGA0847	SGA89	7th - 9th	Early Medieval 1	750	10-20	*Platichthys flesus*	caudal vertebra	43.0	0.58	1.35	39.21	14.07	3.25	-10.69	13.16	
SGA0848	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Pleuronectes platessa*	precaudal vertebra	145.1	5.77	3.98	38.74	14.15	3.20	-13.01	11.83	
SGA0849	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	caudal vertebra	118.9	8.04	6.76	39.07	14.31	3.16	-21.69	12.89	
SGA0850	SGA89	7th - 9th	Early Medieval 1	750	20-30	cf Cyprinidae	pharyngeal	61.6	4.96	8.05	37.30	13.41	3.25	-23.14	13.62	
SGA0851	SGA89	7th - 9th	Early Medieval 1	750	10-20	cf Cyprinidae	vertebra	37.7	1.43	3.79	37.00	13.26	3.25	-25.26	13.78	
SGA0852	SGA89	7th - 9th	Early Medieval 1	750	50-60	cf *Pleuronectes platessa*	caudal vertebra	268.8	15.00	5.58	37.42	14.04	3.12	-12.12	12.11	
SGA0853	SGA89	7th - 9th	Early Medieval 1	750	10-20	*Pleuronectes platessa*	caudal vertebra	38.3	0.94	2.45	37.17	13.04	3.33	-14.10	10.38	
SGA0854	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	caudal vertebra	117.2	7.61	6.49	40.10	14.87	3.15	-13.74	10.59	
SGA0855	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Pleuronectes platessa*	caudal vertebra	176.0	12.84	7.29	40.87	15.20	3.14	-12.28	12.90	
SGA0856	SGA89	7th - 9th	Early Medieval 1	750	40-50	cf *Pleuronectes platessa*	caudal vertebra	142.9	12.96	9.07	41.60	15.65	3.11	-12.18	11.60	
SGA0857	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Platichthys flesus*	os anale	261.9	13.59	5.19	37.41	13.84	3.14	-12.04	13.38	
SGA0858	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Pleuronectes platessa*	ceratohyal	93.4	3.86	4.13	39.49	14.70	3.13	-15.09	11.28	
SGA0859	SGA89	7th - 9th	Early Medieval 1	750	20-30	cf Cyprinidae	pharyngeal	223.3	11.61	5.20	38.02	13.74	3.25	-20.84	14.11	
SOT0860	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	caudal vertebra	84.8	8.27	9.75	19.64	7.30	1.62	-26.73	3.97	
SOT0861	SOT89	7th - 9th	Early Medieval 1	750	40-50	*Pleuronectes platessa*	caudal vertebra	215.8	18.50	8.57	40.54	15.16	3.12	-13.26	11.32	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
SOT0862	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	vertebra	74.9	3.01	4.02	33.67	12.07	3.26	-13.81	10.49	
SOT0863	SOT89	7th - 9th	Early Medieval 1	750	10-20	*Platichthys flesus*	caudal vertebra	76.7	7.77	10.14	40.31	14.91	3.15	-21.60	13.23	
SOT0864	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	cervical vertebra	47.0	1.63	3.47	38.78	14.31	3.16	-18.62	13.45	
SOT0865	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	vertebra	98.8	5.33	5.40	38.10	13.90	3.20	-12.01	11.87	
SOT0866	SOT89	7th - 9th	Early Medieval 1	750	20-30	cf Cyprinidae	pharyngeal	100.2	5.65	5.64	36.17	12.71	3.32	-23.69	11.57	
SOT0867	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	cleithrum	142.3	10.93	7.68	39.95	14.93	3.11	-13.39	12.84	
CAN0401	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Pleuronectes platessa*	os anale	419.3	21.37	5.10	40.37	14.75	3.19	-13.62	11.16	
CAN0402	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Pleuronectes platessa*	os anale	242.9	9.17	3.78	36.22	13.52	3.13	-12.93	11.51	
CAN0403	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Pleuronectes platessa*	os anale	252.0	13.41	5.32	36.64	13.93	3.07	-13.19	12.95	
CAN0404	Tradescent Lane	post 1275	Late Medieval	1437.5	30-40	*Pleuronectes platessa*	precaudal vertebra	126.7	12.21	9.64	40.04	14.75	3.17	-13.52	11.28	
CAN0405	Tradescent Lane	post 1275	Late Medieval	1437.5	40-60	*Pleuronectes platessa*	hyomandibula	124.0	9.58	7.73	40.30	15.03	3.13	-13.10	13.64	
CAN0406	Tradescent Lane	post 1275	Late Medieval	1437.5	60-80	*Gadus morhua*	epihyal	347.5	11.25	3.24	40.93	15.07	3.17	-12.45	15.62	
CAN0407	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Melanogrammus aeglefinus*	articular	131.3	12.75	9.71	38.06	14.53	3.06	-12.93	15.84	
CAN0408	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-60	*Pleuronectes platessa*	quadrate	126.1	6.34	5.03	36.43	13.64	3.12	-12.61	12.41	
CAN0409	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	hyomandibula	100.6	8.14	8.10	37.37	14.22	3.06	-13.22	11.94	
CAN0410	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	maxilla	192.7	6.04	3.13	30.15	9.67	3.64	-15.91	12.51	
CAN0412	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-50	*Pleuronectes platessa*	atlas	168.4	12.04	7.15	36.04	13.65	3.08	-13.16	11.63	
CAN0413	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Pleuronectes platessa*	cleithrum	264.2	15.78	5.97	37.94	14.06	3.15	-13.00	12.79	
CAN0414	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	>30	*Scophthalmus rhombus*	supracleithrum	155.1	18.51	11.93	39.76	14.82	3.13	-13.91	14.01	
CAN0415	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-60	*Gadus morhua*	parasphenoid	445.7	12.16	2.73	39.41	13.38	3.44	-14.17	14.78	
CAN0416	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-60	*Pleuronectes platessa*	articular	214.2	8.73	4.08	38.54	14.18	3.17	-13.21	11.91	
CAN0417	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	caudal vertebra	203.5	13.94	6.85	40.42	15.19	3.11	-12.92	11.86	
CAN0419	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	os anale	435.4	27.26	6.26	42.17	15.50	3.17	-13.16	11.65	
CAN0420	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	70-80	*Gadus morhua*	parasphenoid	460.1	16.29	3.54	41.04	14.80	3.23	-13.33	15.19	
CAN0421	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Pleuronectes platessa*	os anale	150.6	8.54	5.67	35.07	12.43	3.29	-12.62	11.91	
CAN0422	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	maxilla	183.2	11.60	6.33	38.67	14.31	3.15	-13.10	13.39	
CAN0423	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-60	*Pleuronectes platessa*	quadrate	199.3	8.52	4.27	38.31	14.22	3.14	-14.61	10.79	
CAN0424	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	>30	*Platichthys flesus*	cranial	99.9	7.94	7.95	37.22	13.71	3.17	-12.19	14.81	
CAN0425	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Platichthys flesus*	os anale	272.1	7.42	2.73	34.90	12.79	3.18	-13.46	13.24	
CAN0426	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Pleuronectes platessa*	dentary	111.8	8.50	7.61	37.17	13.88	3.12	-13.07	12.21	
CAN0427	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Platichthys flesus*	articular	92.6	8.36	9.03	39.82	14.64	3.17	-12.82	12.98	
CAN0428	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-60	*Pleuronectes platessa*	cleithrum	137.3	14.50	10.56	39.12	14.72	3.10	-14.28	11.42	
CAN0429	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	cleithrum	215.0	16.69	7.76	41.42	15.43	3.13	-13.19	14.88	
CAN0430	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Scophthalmus rhombus*	dentary	185.2	13.36	7.21	39.26	14.19	3.23	-14.83	15.56	
CAN0431	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	70-100	*Gadus morhua*	parasphenoid	579.2	30.60	5.28	40.10	15.12	3.09	-11.88	14.60	
CAN0432	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-50	*Pleuronectes platessa*	quadrate	312.3	14.87	4.76	39.69	14.65	3.16	-12.34	11.78	
CAN0433	Tradescent Lane	post 1275	Late Medieval	1437.5	40-60	*Pleuronectes platessa*	premaxilla	141.6	11.25	7.95	40.10	14.79	3.16	-13.83	13.35	
CAN0434	Tradescent Lane	post 1275	Late Medieval	1437.5	30-40	cf *Platichthys flesus*	caudal vertebra	164.3	19.18	11.67	40.79	15.22	3.13	-10.37	12.40	
CAN0435	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	caudal vertebra	111.7	13.26	11.87	40.65	15.13	3.14	-11.22	13.47	
CAN0436	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-60	*Pleuronectes platessa*	cleithrum	175.9	10.57	6.01	37.52	13.65	3.21	-13.89	11.91	
CAN0437	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	caudal vertebra	185.5	16.25	8.76	38.93	14.41	3.15	-14.76	10.69	
CAN0438	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	caudal vertebra	145.3	14.80	10.19	40.50	15.07	3.14	-12.17	13.26	
CAN0439	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	caudal vertebra	221.1	10.72	4.85	35.37	12.87	3.21	-14.23	11.13	
CAN0440	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	caudal vertebra	223.0	26.37	11.83	35.70	13.47	3.09	-12.44	11.12	
CAN0441	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	>70	*Conger conger*	parasphenoid	407.0	21.03	5.17	39.03	14.26	3.19	-11.34	15.73	
CAN0442	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	caudal vertebra	147.0	14.83	10.09	37.79	14.00	3.15	-11.79	14.29	
CAN0443	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	caudal vertebra	106.0	11.49	10.84	40.14	14.70	3.18	-12.69	14.33	
CAN0444	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	preoperculum	92.3	11.30	12.24	39.72	14.84	3.12	-12.41	13.16	
CAN0445	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	cf *Platichthys flesus*	caudal vertebra	94.2	10.35	10.99	38.94	14.45	3.14	-11.10	12.12	
CAN0446	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	*Solea solea*	caudal vertebra	113.3	11.93	10.53	38.81	14.54	3.12	-12.58	13.71	
CAN0450	Tradescent Lane	late 14th - 15th	Late Medieval	1435	>30	cf Cyprinidae	hyomandibula	180.9	21.89	12.10	43.90	16.09	3.18	-29.29	7.62	
CAN0451	Tradescent Lane	late 14th - 15th	Late Medieval	1435	NA	cf *Salmo trutta*	vertebra	114.9	17.05	14.84	42.62	15.78	3.15	-27.25	13.26	
BGS0116	Barreau Saint-George	11th	High Medieval	1050	10-20	*Pleuronectes platessa*	first caudal vertebra	403.0	15.31	3.80	41.00	14.98	3.18	-12.68	12.19	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
BSG0009	Barreau Saint-George	11th	High Medieval	1050	30-40	*Pleuronectes platessa*	cleithrum	172.7	17.92	10.38	41.48	15.54	3.13	-13.42	11.51	
BSG0019	Barreau Saint-George	11th	High Medieval	1050	50-60	*Pleuronectes platessa*	urohyal	306.7	19.09	6.22	40.38	15.16	3.10	-12.76	11.41	
BSG0029	Barreau Saint-George	11th	High Medieval	1050	10-20	*Pleuronectes platessa*	first caudal vertebra	142.6	13.76	9.65	42.24	15.70	3.15	-10.68	12.37	
BSG0031	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	151.7	10.60	6.99	41.34	15.16	3.17	-13.71	11.17	
BSG0044	Barreau Saint-George	11th	High Medieval	1050	20-30	*Platichthys flesus*	cleithrum	52.3	10.51	20.09	41.38	15.33	3.15	-14.10	10.79	
BSG0085	Barreau Saint-George	11th	High Medieval	1050	30-40	*Pleuronectes platessa*	precaudal vertebra	112.7	6.55	5.81	39.47	14.33	3.20	-12.63	11.51	
BSG0086	Barreau Saint-George	11th	High Medieval	1050	30-40	*Melanogrammus aeglefinus*	parasphenoid	231.4	12.06	5.21	39.35	14.36	3.20	-12.65	15.41	
BSG0087	Barreau Saint-George	11th	High Medieval	1050	50-60	*Pleuronectes platessa*	posttemporal	194.2	14.79	7.62	38.93	14.48	3.16	-13.04	11.58	
BSG0090	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	121.1	9.94	8.21	40.96	14.81	3.24	-15.04	9.97	
BSG0091	Barreau Saint-George	11th	High Medieval	1050	NA	*Scophthalmus maximus*	cleithrum	340.1	27.59	8.11	42.58	15.37	3.25	-11.45	15.31	
BSG0092	Barreau Saint-George	11th	High Medieval	1050	10-20	cf *Platichthys flesus*	os anale	129.2	10.51	8.14	40.41	14.83	3.18	-13.03	11.60	
BSG0093	Barreau Saint-George	11th	High Medieval	1050	20-30	cf *Platichthys flesus*	os anale	159.8	12.22	7.65	41.27	14.86	3.27	-16.78	10.84	
BSG0096	Barreau Saint-George	11th	High Medieval	1050	100-110	*Gadus morhua*	dentary	423.3	11.71	2.77	41.01	12.23	3.89	-16.45	15.37	
BSG0097	Barreau Saint-George	11th	High Medieval	1050	100-110	*Gadus morhua*	operculum	409.4	22.74	5.56	42.08	15.54	3.14	-11.96	15.92	
BSG0098	Barreau Saint-George	11th	High Medieval	1050	100-110	*Gadus morhua*	premaxilla	380.8	14.21	3.73	39.12	14.57	3.13	-12.10	18.42	
BSG0099	Barreau Saint-George	11th	High Medieval	1050	90-100	*Gadus morhua*	dentary	346.1	4.91	1.42	39.68	13.89	3.29	-13.54	16.31	
BSG0100	Barreau Saint-George	11th	High Medieval	1050	100-110	*Gadus morhua*	maxilla	557.4	15.62	2.80	43.01	14.02	3.58	-15.49	15.67	
BSG0102	Barreau Saint-George	11th	High Medieval	1050	40-50	*Pleuronectes platessa*	cleithrum	408.3	39.79	9.75	40.07	14.80	3.14	-13.27	12.29	
BSG0103	Barreau Saint-George	11th	High Medieval	1050	20-30	*Platichthys flesus*	os anale	127.9	5.70	4.46	40.35	14.54	3.25	-15.85	12.89	
BSG0104	Barreau Saint-George	11th	High Medieval	1050	50-60	*Pleuronectes platessa*	os anale	318.7	24.24	7.61	42.13	15.66	3.14	-13.27	12.05	
BSG0105	Barreau Saint-George	11th	High Medieval	1050	40-50	*Pleuronectes platessa*	os anale	373.4	24.75	6.63	41.39	15.10	3.21	-12.43	11.69	
BSG0106	Barreau Saint-George	11th	High Medieval	1050	30-40	*Pleuronectes platessa*	os anale	406.5	20.11	4.95	41.76	15.28	3.17	-13.72	11.80	
BSG0107	Barreau Saint-George	11th	High Medieval	1050	NA	*Pleuronectes platessa*	cleithrum	231.4	25.74	11.13	41.82	15.54	3.14	-13.46	12.54	
BSG0108	Barreau Saint-George	11th	High Medieval	1050	10-20	*Platichthys flesus*	cleithrum	143.8	15.78	10.97	42.45	15.40	3.22	-13.92	12.48	
BSG0109	Barreau Saint-George	11th	High Medieval	1050	10-20	cf *Platichthys flesus*	first caudal vertebra	139.6	9.89	7.09	42.88	15.92	3.14	-14.72	12.15	
BSG0110	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	hyomandibula	149.9	9.68	6.46	41.97	15.41	3.16	-12.45	11.98	
BSG0111	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	preoperculum	199.6	12.79	6.41	42.91	15.68	3.19	-14.20	12.66	
BSG0112	Barreau Saint-George	11th	High Medieval	1050	10-20	*Platichthys flesus*	os anale	210.5	9.22	4.38	41.91	15.37	3.20	-17.66	12.52	
BSG0113	Barreau Saint-George	11th	High Medieval	1050	30-40	*Pleuronectes platessa*	cleithrum	211.9	18.54	8.75	42.43	15.54	3.17	-13.42	11.19	
BSG0114	Barreau Saint-George	11th	High Medieval	1050	30-40	*Pleuronectes platessa*	hyomandibula	167.8	13.90	8.28	40.19	15.18	3.07	-12.23	12.37	
BSG0115	Barreau Saint-George	11th	High Medieval	1050	50-60	*Pleuronectes platessa*	os anale	261.1	5.65	2.16	35.52	12.87	3.17	-13.56	11.69	
BSG0117	Barreau Saint-George	11th	High Medieval	1050	40-50	*Pleuronectes platessa*	ultimate vertebra	167.4	15.64	9.34	42.22	15.74	3.12	-13.18	12.20	
KOK0500	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	precaudal vertebra	239.9	24.39	10.17	40.60	15.44	3.07	-13.09	11.73	
KOK0501	Hof ter Hille	1020 - 1150	High Medieval	1085	20-30	*Pleuronectes platessa*	precaudal vertebra	121.2	10.47	8.64	38.61	14.46	3.12	-13.81	11.54	
KOK0502	Hof ter Hille	770 - 1000	Early Medieval 2	885	20-30	*Pleuronectes platessa*	caudal vertebra	124.6	10.65	8.54	38.68	14.32	3.15	-13.76	11.02	
KOK0503	Hof ter Hille	890 - 1150	Early/High Medieval	1020	20-30	*Pleuronectes platessa*	os anale	323.6	18.72	5.78	40.33	15.06	3.13	-13.07	12.00	
KOK0504	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	posttemporal	86.3	7.77	9.01	39.83	14.72	3.16	-13.81	11.46	
KOK0505	Hof ter Hille	890 - 1150	Early/High Medieval	1020	20-30	*Pleuronectes platessa*	os anale	430.4	18.23	4.24	37.05	13.88	3.11	-12.78	12.32	
KOK0506	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	caudal vertebra	174.0	9.96	5.72	40.46	14.99	3.15	-13.90	10.84	
KOK0507	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	132.3	8.21	6.20	39.52	14.59	3.16	-13.91	11.03	
KOK0508	Hof ter Hille	770 - 1000	Early Medieval 2	885	20-30	*Pleuronectes platessa*	caudal vertebra	130.6	10.08	7.72	40.90	14.96	3.19	-13.78	11.00	
KOK0509	Hof ter Hille	1020 - 1150	High Medieval	1085	50-60	*Pleuronectes platessa*	cleithrum	268.3	21.26	7.92	40.31	15.19	3.10	-12.99	11.37	
KOK0510	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	307.6	13.76	4.47	37.53	13.58	3.22	-13.98	11.69	
KOK0511	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	caudal vertebra	105.3	10.62	10.09	41.78	15.49	3.15	-13.82	11.64	
KOK0512	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	urohyal	127.8	11.68	9.14	36.89	13.53	3.18	-13.52	12.59	
KOK0513	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	posttemporal	132.2	8.83	6.68	36.95	13.63	3.16	-12.93	12.04	
KOK0514	Hof ter Hille	880 - 1030	Early Medieval 2	955	20-30	cf *Platichthys flesus*	os anale	398.9	32.70	8.20	42.02	15.41	3.18	-16.10	13.21	
KOK0515	Hof ter Hille	1020 - 1150	High Medieval	1085	20-30	*Pleuronectes platessa*	os anale	356.5	15.07	4.23	34.23	12.72	3.14	-14.42	11.47	
KOK0516	Hof ter Hille	880 - 1030	Early Medieval 2	955	40-50	*Pleuronectes platessa*	urohyal	303.4	21.46	7.07	38.66	14.56	3.10	-12.31	12.78	
KOK0517	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	cf *Platichthys flesus*	os anale	259.9	17.39	6.69	40.56	14.82	3.19	-14.36	11.20	
KOK0518	Hof ter Hille	880 - 1030	Early Medieval 2	955	40-50	*Scophthalmus maximus*	maxilla	325.8	22.35	6.86	41.91	15.32	3.19	-14.42	16.18	
KOK0519	Hof ter Hille	770 - 1000	Early Medieval 2	885	20-40	*Esox lucius*	dentary	261.3	19.43	7.44	40.80	14.90	3.19	-23.97	8.80	
KOK0520	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	390.4	15.81	4.05	42.12	15.41	3.19	-14.43	11.34	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
KOK0522	Hof ter Hille	770 - 1000	Early Medieval 2	885	40-50	*Melanogrammus aeglefinus*	precaudal vertebra	267.2	17.95	6.72	39.06	14.49	3.15	-13.81	15.40	
KOK0523	Hof ter Hille	880 - 1030	Early Medieval 2	955	60-70	*Gadus morhua*	articular	490.2	3.88	0.79	39.22	13.46	3.40	-14.46	14.99	
KOK0524	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	196.2	9.54	4.86	37.66	13.97	3.14	-13.06	11.76	
KOK0525	Hof ter Hille	770 - 1000	Early Medieval 2	885	50-60	*Melanogrammus aeglefinus*	precaudal vertebra	352.6	26.93	7.64	41.57	15.12	3.21	-13.19	14.90	
KOK0526	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	caudal vertebra	296.0	26.88	9.08	38.85	14.65	3.09	-12.65	11.93	
KOK0527	Hof ter Hille	770 - 1000	Early Medieval 2	885	20-30	*Platichthys flesus*	cleithrum	145.9	13.80	9.46	40.60	14.92	3.17	-14.56	13.06	
KOK0528	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	cervical vertebra	262.3	15.15	5.78	37.89	14.35	3.08	-12.87	11.61	
KOK0529	Hof ter Hille	890 - 1150	Early/High Medieval	1020	40-50	*Pleuronectes platessa*	os anale	237.8	12.34	5.19	38.83	14.51	3.12	-12.97	12.74	
KOK0530	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Esox lucius*	caudal vertebra	218.7	27.09	12.39	41.37	15.29	3.16	-23.87	8.71	
KOK0531	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Scophthalmus maximus*	os anale	316.4	22.31	7.05	41.22	14.93	3.22	-12.62	16.12	
KOK0532	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	172.6	10.62	6.15	40.29	15.11	3.11	-14.00	10.60	
KOK0534	Hof ter Hille	890 - 1150	Early/High Medieval	1020	40-50	*Melanogrammus aeglefinus*	cleithrum	456.4	12.29	2.69	32.54	10.97	3.46	-15.29	13.48	
KOK0535	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	caudal vertebra	174.2	12.12	6.96	37.88	13.96	3.16	-13.61	10.94	
KOK0536	Hof ter Hille	880 - 1030	Early Medieval 2	955	40-50	*Pleuronectes platessa*	cleithrum	311.5	21.14	6.79	41.18	15.29	3.14	-14.17	11.65	
KOK0537	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	355.5	24.59	6.92	39.60	14.82	3.12	-12.42	11.66	
KOK0538	Hof ter Hille	890 - 1150	Early/High Medieval	1020	20-30	*Scophthalmus maximus*	precaudal vertebra	158.7	17.06	10.75	41.97	15.45	3.17	-13.50	14.10	
KOK0539	Hof ter Hille	770 - 1000	Early Medieval 2	885	NA	*Esox lucius*	dentary	160.5	14.05	8.75	39.98	14.66	3.18	-23.84	8.91	
KOK0540	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	caudal vertebra	211.4	20.48	9.69	41.97	15.75	3.11	-12.72	11.41	
KOK0541	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Platichthys flesus*	cleithrum	174.8	14.32	8.19	40.87	15.14	3.15	-13.32	10.33	
KOK0542	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Platichthys flesus*	caudal vertebra	171.1	19.47	11.38	41.82	15.56	3.14	-13.59	11.83	
KOK0543	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	caudal vertebra	227.5	20.73	9.11	42.20	15.75	3.13	-12.77	11.76	
KOK0544	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	os anale	258.5	17.84	6.90	40.28	14.75	3.19	-14.29	11.34	
KOK0545	Hof ter Hille	1020 - 1150	High Medieval	1085	40-50	*Pleuronectes platessa*	os anale	372.5	17.29	4.64	41.84	15.75	3.10	-13.37	12.67	
KOK0546	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	*Platichthys flesus*	cleithrum	242.3	17.61	7.27	38.21	14.26	3.13	-13.46	11.27	
KOK0547	Hof ter Hille	880 - 1030	Early Medieval 2	955	50-60	*Melanogrammus aeglefinus*	maxilla	120.2	12.26	10.20	43.84	16.43	3.11	-13.39	14.63	
KOK0548	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	*Platichthys flesus*	articular	171.4	19.05	11.11	42.46	15.78	3.14	-15.23	11.37	
KOK0549	Hof ter Hille	880 - 1030	Early Medieval 2	955	50-60	*Melanogrammus aeglefinus*	cleithrum	229.9	9.94	4.32	35.88	12.94	3.24	-13.16	14.56	
KOK0550	Hof ter Hille	890 - 1150	Early/High Medieval	1020	70-80	*Gadus morhua*	dentary	284.4	24.39	8.58	38.76	14.39	3.14	-13.67	15.50	
KOK0551	Hof ter Hille	880 - 1030	Early Medieval 2	955	40-50	*Scophthalmus maximus*	urohyal	147.3	15.35	10.42	39.90	15.02	3.10	-12.40	16.49	
KOK0552	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	*Scophthalmus maximus*	articular	374.6	18.21	4.86	38.47	14.33	3.13	-12.19	16.79	
KOK0553	Hof ter Hille	880 - 1030	Early Medieval 2	955	40-50	*Pleuronectes platessa*	cleithrum	144.4	10.25	7.10	39.74	14.73	3.15	-13.85	11.12	
KOK0554	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	*Pleuronectes platessa*	ceratohyal	247.7	16.86	6.81	37.24	13.82	3.14	-13.43	12.13	
KOK0555	Hof ter Hille	770 - 1000	Early Medieval 2	885	40-50	*Pleuronectes platessa*	os anale	361.5	22.62	6.26	40.30	14.87	3.16	-13.86	11.92	
KOK0556	Hof ter Hille	770 - 1000	Early Medieval 2	885	90-110	*Gadus morhua*	precaudal vertebra	289.1	16.94	5.86	39.08	14.99	3.04	-10.22	17.11	
KOK0557	Hof ter Hille	1020 - 1150	High Medieval	1085	60-70	*Gadus morhua*	caudal vertebra	518.0	20.01	3.86	39.52	14.80	3.11	-12.73	15.54	
KOK0558	Hof ter Hille	1020 - 1150	High Medieval	1085	100-110	*Gadus morhua*	precaudal vertebra	337.7	15.81	4.68	38.45	14.45	3.11	-11.20	16.35	
KOK0559	Hof ter Hille	770 - 1000	Early Medieval 2	885	40-50	*Pleuronectes platessa*	urohyal	192.7	15.26	7.92	40.84	15.42	3.09	-12.47	11.39	
KOK0560	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	caudal vertebra	277.6	30.97	11.16	41.10	15.53	3.09	-13.08	11.76	
KOK0561	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	caudal vertebra	187.9	18.96	10.09	40.76	15.30	3.11	-12.31	12.47	
KOK0562	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	precaudal vertebra	300.8	24.88	8.27	41.20	15.33	3.14	-13.47	10.89	
KOK0563	Hof ter Hille	880 - 1030	Early Medieval 2	955	large	*Platichthys flesus*	cranial	194.8	21.05	10.81	39.66	14.87	3.11	-13.47	12.26	
GEN0600	Zwarte Laag	1000 - 1025	High Medieval	1012.5	20-30	cf Cyprinidae	pharyngeal	126.5	18.74	14.81	40.47	14.73	3.20	-25.24	12.85	
GEN0601	Zwarte Laag	1000 - 1025	High Medieval	1012.5	20-30	*Pleuronectes platessa*	ectopterygoid	36.8	7.84	21.32	41.26	15.04	3.20	-15.93	11.81	
GEN0602	Zwarte Laag	950 - 975	Early Medieval 2	962.5	30-40	*Pleuronectes platessa*	quadrate	94.6	10.65	11.26	42.31	15.36	3.21	-15.22	11.00	
GEN0603	Zwarte Laag	975 - 1000	Early Medieval 2	987.5	20-30	*Platichthys flesus*	vertebra	61.1	11.39	18.63	41.54	15.21	3.19	-16.52	11.06	
GEN0604	Zwarte Laag	975 - 1000	Early Medieval 2	987.5	30-40	*Platichthys flesus*	vertebra	95.8	15.15	15.81	40.54	14.71	3.22	-14.73	10.08	
GEN0605	Zwarte Laag	987 - 1012	Early Medieval 2	999.5	>30	cf Cyprinidae	articular	113.8	23.89	20.99	42.84	15.82	3.16	-24.49	12.48	
GEN0606	Zwarte Laag	937 - 962	Early Medieval 2	949.5	20-30	*Platichthys flesus*	posttemporal	39.9	7.46	18.71	39.69	14.52	3.19	-16.63	10.91	
GEN0607	Zwarte Laag	937 - 962	Early Medieval 2	949.5	20-30	*Pleuronectes platessa*	caudal vertebra	60.7	7.89	13.00	41.07	14.90	3.21	-13.36	12.24	
GEN0608	Zwarte Laag	1175 - 1200	High Medieval	1187.5	30-40	*Pleuronectes platessa*	lower hypohyal	50.4	8.82	17.50	39.89	15.44	3.01	-13.21	11.46	
GEN0609	Zwarte Laag	1175 - 1200	High Medieval	1187.5	20-30	cf Cyprinidae	pharyngeal	141.4	14.49	10.25	42.08	15.48	3.17	-26.51	14.19	
GEN0611	Zwarte Laag	1125 - 1150	High Medieval	1137.5	30-40	*Platichthys flesus*	posttemporal	67.6	13.71	20.30	42.01	15.20	3.23	-13.44	10.87	
GEN0612	Zwarte Laag	1125 - 1150	High Medieval	1137.5	20-30	*Platichthys flesus*	palatine	64.6	8.44	13.06	42.28	14.81	3.33	-18.03	11.19	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ¹³C (‰)	δ¹⁵N (‰)	Remarks
GEN0613	Zwarte Laag	1025 - 1050	High Medieval	1037.5	20-30	*Pleuronectes platessa*	caudal vertebra	73.4	16.98	23.12	40.71	14.51	3.27	-14.75	11.75	
GEN0614	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Pleuronectes platessa*	os anale	168.2	13.34	7.93	37.10	13.94	3.11	-14.11	11.90	
GEN0615	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	60-70	*Melanogrammus aeglefinus*	cleithrum	607.4	10.80	1.78	32.03	11.10	3.37	-14.70	15.11	
GEN0616	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	50-60	*Pleuronectes platessa*	quadrate	208.4	23.27	11.17	42.74	15.78	3.16	-13.67	13.02	
GEN0617	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	30-40	*Pleuronectes platessa*	os anale	141.5	12.01	8.49	41.63	15.14	3.21	-14.32	11.43	
GEN0618	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	30-40	*Pleuronectes platessa*	os anale	274.1	22.35	8.15	40.78	15.12	3.15	-13.44	11.69	
GEN0619	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Pleuronectes platessa*	dentary	306.3	19.88	6.49	39.24	14.85	3.08	-13.12	12.37	
GEN0620	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Platichthys flesus*	os anale	364.9	29.32	8.04	43.64	16.01	3.18	-14.55	11.38	
GEN0621	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	50-60	*Melanogrammus aeglefinus*	cleithrum	675.9	22.78	3.37	41.89	14.97	3.26	-14.82	14.13	
GEN0622	Zwarte Laag	12th	High Medieval	1150	30-40	*Scophthalmus rhombus*	os anale	183.3	19.05	10.39	43.62	16.14	3.15	-13.80	15.04	
GEN0623	Zwarte Laag	12th	High Medieval	1150	40-50	*Scophthalmus maximus*	preoperculum	171.9	16.92	9.84	40.38	14.65	3.22	-13.20	15.89	
GEN0624	Zwarte Laag	12th	High Medieval	1150	40-50	*Scophthalmus maximus*	os anale	311.2	27.02	8.68	39.64	14.69	3.15	-12.72	16.62	
GEN0625	Zwarte Laag	950 - 975	Early Medieval 2	962.5	50-60	*Pleuronectes platessa*	basioccipital	276.6	34.34	12.41	43.25	16.15	3.12	-13.81	11.86	
GEN0626	Zwarte Laag	975 - 1000	Early Medieval 2	987.5	>30	cf Cyprinidae	precaudal vertebra	99.6	17.74	17.81	43.17	15.80	3.19	-23.67	12.79	
GEN0627	Zwarte Laag	975 - 1000	Early Medieval 2	987.5	20-30	*Platichthys flesus*	caudal vertebra	108.4	13.25	12.23	42.09	15.38	3.19	-17.48	10.21	
GEN0628	Zwarte Laag	1000 - 1025	High Medieval	1012.5	30-40	*Pleuronectes platessa*	cleithrum	421.6	41.33	9.80	43.86	16.16	3.17	-14.87	11.87	
GEN0629	Zwarte Laag	1000 - 1025	High Medieval	1012.5	40-50	*Pleuronectes platessa*	caudal vertebra	356.0	38.91	10.93	41.24	15.52	3.10	-14.43	11.49	
GEN0630	Zwarte Laag	1000 - 1025	High Medieval	1012.5	40-50	*Pleuronectes platessa*	caudal vertebra	154.1	20.23	13.13	42.20	15.78	3.12	-13.96	10.47	
GEN0631	Zwarte Laag	1025 - 1050	High Medieval	1037.5	20-30	cf *Pleuronectes platessa*	caudal vertebra	117.1	10.47	8.94	42.76	15.69	3.18	-13.78	11.03	
GEN0632	Zwarte Laag	1100 - 1125	High Medieval	1112.5	>40	cf Cyprinidae	first spine	376.5	22.58	6.00	42.38	15.33	3.23	-26.80	12.72	
GEN0633	Zwarte Laag	1100 - 1125	High Medieval	1112.5	50-60	*Pleuronectes platessa*	os anale	159.7	13.73	8.60	42.58	15.75	3.15	-13.66	12.17	
GEN0634	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Pleuronectes platessa*	urohyal	282.0	35.19	12.48	43.01	16.45	3.05	-12.86	11.68	
GEN0635	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Pleuronectes platessa*	hyomandibula	196.7	26.06	13.25	42.52	16.04	3.09	-14.37	11.84	
GEN0636	Zwarte Laag	1100 - 1125	High Medieval	1112.5	30-40	*Pleuronectes platessa*	caudal vertebra	162.2	18.26	11.26	41.95	15.53	3.15	-14.03	11.63	
GEN0637	Zwarte Laag	1100 - 1125	High Medieval	1112.5	30-40	*Pleuronectes platessa*	caudal vertebra	99.4	10.20	10.26	41.37	14.72	3.28	-14.51	11.87	
GEN0638	Zwarte Laag	1150 - 1175	High Medieval	1162.5	50-60	*Melanogrammus aeglefinus*	posttemporal	431.5	19.44	4.51	42.27	15.14	3.26	-13.66	14.45	
GEN0639	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	*Platichthys flesus*	caudal vertebra	86.0	11.55	13.43	43.33	16.06	3.15	-17.25	11.53	
GEN0640	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	*Platichthys flesus*	os anale	264.1	21.81	8.26	41.90	15.35	3.19	-15.80	12.77	
GEN0641	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	cf Cyprinidae	cleithrum	97.4	16.66	17.11	41.95	15.28	3.20	-27.18	13.48	
GEN0642	Zwarte Laag	1175 - 1200	High Medieval	1187.5	50-60	*Melanogrammus aeglefinus*	supracleithrum	241.5	6.39	2.65	32.72	11.49	3.32	-14.51	14.45	
GEN0643	Zwarte Laag	1175 - 1200	High Medieval	1187.5	50-60	*Melanogrammus aeglefinus*	posttemporal	174.3	6.09	3.49	32.47	11.49	3.29	-14.07	13.65	
GEN0644	Zwarte Laag	1175 - 1200	High Medieval	1187.5	40-50	*Esox lucius*	dentary	266.4	17.76	6.67	40.55	14.29	3.31	-24.97	13.37	
GEN0645	Zwarte Laag	1175 - 1200	High Medieval	1187.5	50-60	*Pleuronectes platessa*	quadrate	114.7	15.35	13.39	42.06	15.68	3.13	-13.88	11.98	
GEN0646	Zwarte Laag	1175 - 1200	High Medieval	1187.5	30-40	*Platichthys flesus*	urohyal	190.9	19.47	10.20	42.53	15.59	3.18	-12.84	11.46	
GEN0647	Zwarte Laag	1175 - 1200	High Medieval	1187.5	40-50	*Pleuronectes platessa*	preoperculum	328.3	26.51	8.08	40.00	15.00	3.11	-13.63	11.74	
GEN0648	Zwarte Laag	1175 - 1200	High Medieval	1187.5	30-40	*Platichthys flesus*	quadrate	167.5	19.51	11.65	43.48	16.03	3.16	-13.59	10.82	
GEN0649	Zwarte Laag	1175 - 1200	High Medieval	1187.5	40-50	*Pleuronectes platessa*	premaxilla	252.7	22.93	9.08	42.95	15.54	3.22	-12.70	12.45	
GEN0650	Zwarte Laag	1175 - 1200	High Medieval	1187.5	40-50	*Pleuronectes platessa*	caudal vertebra	140.0	11.85	8.46	40.97	15.28	3.13	-14.60	10.30	
GEN0651	Zwarte Laag	1012 - 1037	High Medieval	1024.5	20-30	*Pleuronectes platessa*	atlas	60.4	10.19	16.87	39.27	14.46	3.17	-13.32	12.17	
GEN0652	Zwarte Laag	950 - 975	Early Medieval 2	962.5	20-30	*Pleuronectes platessa*	precaudal vertebra	49.4	15.00	30.38	42.68	15.65	3.18	-12.01	11.37	
GEN0653	Zwarte Laag	1175 - 1200	High Medieval	1187.5	20-30	cf Cyprinidae	caudal vertebra	58.5	16.68	28.53	44.32	16.04	3.22	-23.75	10.95	
GEN0654	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	cf Cyprinidae	caudal vertebra	89.1	15.58	17.49	42.47	15.22	3.25	-23.55	8.52	
GEN0655	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	*Platichthys flesus*	caudal vertebra	60.3	12.69	21.03	43.90	16.12	3.18	-14.84	10.70	
GEN0656	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	*Platichthys flesus*	caudal vertebra	56.3	11.25	19.98	41.80	15.33	3.18	-19.95	10.09	
GEN0657	Zwarte Laag	1025 - 1050	High Medieval	1037.5	20-30	*Pleuronectes platessa*	caudal vertebra	59.9	13.34	22.27	41.23	14.95	3.22	-13.52	11.76	
GEN0658	Zwarte Laag	1175 - 1200	High Medieval	1187.5	20-30	*Platichthys flesus*	caudal vertebra	77.5	14.71	18.98	41.21	15.28	3.15	-14.47	13.01	
GEN0659	Zwarte Laag	1125 - 1150	High Medieval	1137.5	40-50	*Melanogrammus aeglefinus*	vomer	304.3	19.72	6.48	44.04	16.03	3.21	-13.65	14.23	
GEN0660	Zwarte Laag	1125 - 1150	High Medieval	1137.5	50-60	*Pleuronectes platessa*	vertebra	251.6	28.12	11.17	40.21	15.12	3.10	-13.02	12.26	
GEN0661	Zwarte Laag	1125 - 1150	High Medieval	1137.5	30-40	cf Cyprinidae	precaudal vertebra	107.3	18.69	17.42	42.89	15.50	3.23	-24.04	9.36	
GEN0662	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Platichthys flesus*	caudal vertebra	281.8	23.62	8.38	40.92	15.19	3.14	-11.83	12.03	
GEN0663	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Pleuronectes platessa*	caudal vertebra	184.5	14.19	7.69	40.64	15.06	3.15	-14.08	11.86	
GEN0664	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Platichthys flesus*	basipterygium	112.5	18.59	16.53	41.40	15.26	3.17	-12.73	11.35	
GEN0665	Zwarte Laag	1100 - 1125	High Medieval	1112.5	50-60	*Melanogrammus aeglefinus*	precaudal vertebra	277.2	25.34	9.14	40.23	15.22	3.08	-13.59	14.30	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
GEN0666	Zwarte Laag	1025 - 1050	High Medieval	1037.5	40-50	*Melanogrammus aeglefinus*	premaxilla	193.2	14.29	7.40	39.21	14.13	3.24	-14.22	14.68	
GEN0667	Zwarte Laag	1025 - 1050	High Medieval	1037.5	40-50	*Melanogrammus aeglefinus*	operculum	194.1	12.03	6.20	40.23	14.67	3.20	-14.88	14.12	
GEN0668	Zwarte Laag	1000 - 1025	High Medieval	1012.5	20-30	cf *Platichthys flesus*	caudal vertebra	77.0	7.14	9.28	40.76	15.05	3.16	-18.11	10.99	
GEN0669	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Pleuronectes platessa*	os anale	185.0	13.36	7.22	41.87	15.40	3.17	-13.89	11.23	
GEN0670	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Pleuronectes platessa*	caudal vertebra	194.5	30.35	15.60	43.56	16.46	3.09	-12.65	12.21	
GEN0671	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Pleuronectes platessa*	ectopterygoid	303.0	27.44	9.06	41.44	15.61	3.10	-13.14	12.33	
GEN0672	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	50-60	*Pleuronectes platessa*	caudal vertebra	206.4	34.62	16.78	46.41	17.34	3.12	-13.72	12.99	
VLA0301	Gat in de Markt	1000 - 1050	High Medieval	1025	30-40	*Pleuronectes platessa*	quadrate	77.9	10.59	13.60	41.51	15.66	3.09	-13.67	11.95	
VLA0302	Gat in de Markt	1000 - 1050	High Medieval	1025	20-30	cf Cyprinidae	caudal vertebra	92.2	14.28	15.49	43.63	16.01	3.18	-16.33	10.00	
VLA0303	Gat in de Markt	1000 - 1050	High Medieval	1025	20-30	cf Cyprinidae	caudal vertebra	90.0	16.25	18.06	43.38	16.06	3.15	-22.78	10.62	
VLA0304	Gat in de Markt	1000 - 1050	High Medieval	1025	100-110	*Gadus morhua*	articular	727.2	19.71	2.71	39.16	13.60	3.36	-13.65	16.76	
VLA0305	Gat in de Markt	1000 - 1050	High Medieval	1025	70-80	*Gadus morhua*	maxilla	511.0	4.51	0.88	19.96	6.61	3.52	-13.90	12.59	
VLA0306	Gat in de Markt	1000 - 1050	High Medieval	1025	40-50	*Pleuronectes platessa*	preoperculum	198.3	20.53	10.35	40.84	15.22	3.13	-13.69	11.99	
VLA0307	Gat in de Markt	1000 - 1050	High Medieval	1025	30-40	*Pleuronectes platessa*	preoperculum	123.3	18.55	15.04	43.83	15.86	3.23	-14.37	12.63	
VLA0308	Gat in de Markt	891 - 933	Early Medieval 2	912	40-50	*Pleuronectes platessa*	preoperculum	297.8	34.95	11.74	44.11	16.59	3.10	-14.28	12.66	
VLA0309	Gat in de Markt	1050 - 1170	High Medieval	1110	>45	cf Cyprinidae	preoperculum	220.0	26.01	11.82	43.95	16.02	3.20	-23.04	10.16	
VLA0310	Gat in de Markt	1050 - 1170	High Medieval	1110	30-50	cf Cyprinidae	operculum	414.1	40.69	9.83	43.77	15.90	3.21	-23.70	10.74	
VLA0311	Gat in de Markt	1050 - 1170	High Medieval	1110	>50	*Melanogrammus aeglefinus*	cleithrum	549.2	11.06	2.01	28.51	8.44	3.94	-17.17	14.16	
VLA0313	Gat in de Markt	1050 - 1170	High Medieval	1110	30-40	*Pleuronectes platessa*	os anale	421.4	32.37	7.68	42.62	15.90	3.13	-13.73	11.16	
VLA0314	Gat in de Markt	1050 - 1170	High Medieval	1110	40-60	*Pleuronectes platessa*	os anale	389.8	34.20	8.77	43.11	15.91	3.16	-14.12	11.01	
VLA0315	Gat in de Markt	1050 - 1170	High Medieval	1110	40-50	*Pleuronectes platessa*	os anale	238.3	21.06	8.84	40.56	14.85	3.19	-14.85	11.21	
VLA0316	Gat in de Markt	1050 - 1170	High Medieval	1110	40-50	*Pleuronectes platessa*	os anale	198.1	25.33	12.78	40.05	15.11	3.09	-14.47	11.59	
VLA0317	Gat in de Markt	1180 - 1217	High Medieval	1198.5	50-60	*Pleuronectes platessa*	os anale	260.7	26.95	10.34	43.87	16.23	3.15	-14.38	11.75	
VLA0318	Gat in de Markt	1180 - 1217	High Medieval	1198.5	60-70	*Gadus morhua*	articular	385.4	10.79	2.80	39.80	13.56	3.42	-14.97	15.03	
VLA0319	Gat in de Markt	1180 - 1217	High Medieval	1198.5	60-70	*Gadus morhua*	articular	610.0	14.27	2.34	33.74	10.57	3.72	-16.74	15.09	
VLA0320	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	50-60	*Pleuronectes platessa*	cleithrum	467.3	39.78	8.51	44.52	16.34	3.18	-14.03	12.18	
VLA0321	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	20-30	*Platichthys flesus*	caudal vertebra	67.3	8.99	13.35	40.28	14.64	3.21	-18.54	11.79	
VLA0322	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	20-30	*Platichthys flesus*	os anale	186.2	19.75	10.61	41.12	15.18	3.16	-17.56	11.88	
VLA0325	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	20-30	*Pleuronectes platessa*	preoperculum	166.4	16.40	9.86	44.25	16.35	3.16	-15.52	11.93	
VLA0326	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	100-120	*Gadus morhua*	dentary	681.5	13.89	2.04	40.94	14.38	3.32	-13.80	17.78	
VLA0327	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	100-120	*Gadus morhua*	dentary	542.9	4.67	0.86	35.38	10.32	4.00	-17.15	17.09	
VLA0328	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	40-60	*Pleuronectes platessa*	os anale	234.8	23.02	9.81	43.51	16.10	3.15	-14.62	11.21	
VLA0329	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-50	*Pleuronectes platessa*	os anale	216.7	16.39	7.56	42.58	15.43	3.22	-14.62	11.05	
VLA0330	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Pleuronectes platessa*	hyomandibula	101.0	13.73	13.59	41.02	15.19	3.15	-14.10	11.54	
VLA0331	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	20-30	*Platichthys flesus*	caudal vertebra	134.5	10.86	8.07	41.46	15.18	3.19	-13.48	13.12	
VLA0332	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	40-50	*Pleuronectes platessa*	os anale	236.2	24.45	10.35	42.40	15.99	3.09	-15.12	10.43	
VLA0333	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	40-60	*Pleuronectes platessa*	caudal vertebra	206.4	19.37	9.38	38.46	14.33	3.13	-14.44	12.07	
VLA0334	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Pleuronectes platessa*	os anale	329.6	16.37	4.97	37.81	13.52	3.26	-14.47	11.13	
VLA0335	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Platichthys flesus*	os anale	229.0	19.71	8.61	41.59	15.22	3.19	-16.41	12.39	
VLA0336	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Pleuronectes platessa*	os anale	430.7	32.16	7.47	39.50	14.64	3.15	-13.82	12.44	
VLA0337	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	cf Cyprinidae	pharyngeal	218.9	28.37	12.96	43.90	15.88	3.22	-21.44	11.98	
VLA0338	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	20-40	cf Cyprinidae	pharyngeal	331.5	40.40	12.19	43.50	15.41	3.29	-23.53	11.43	
VLA0339	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-50	*Melanogrammus aeglefinus*	parasphenoid	539.7	15.38	2.85	36.46	12.81	3.32	-14.56	14.77	
VLA0340	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	10-40	*Melanogrammus aeglefinus*	parasphenoid	172.2	9.76	5.67	37.12	13.46	3.22	-14.17	15.31	
VLA0341	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	20-30	*Platichthys flesus*	parasphenoid	97.0	16.88	17.41	42.19	15.89	3.10	-21.51	12.01	
VLA0342	Gat in de Markt	1250 - 1300	Late Medieval	1275	>70	*Gadus morhua*	quadrate	456.7	24.87	5.45	37.94	13.26	3.34	-13.48	16.02	
VLA0343	Gat in de Markt	1250 - 1300	Late Medieval	1275	20-30	*Platichthys flesus*	caudal vertebra	142.5	15.74	11.05	43.32	15.91	3.18	-14.83	11.78	
VLA0344	Gat in de Markt	1300 - 1350	Late Medieval	1325	10-20	*Platichthys flesus*	os anale	150.8	15.93	10.56	41.91	15.29	3.20	-17.34	11.56	
VLA0345	Gat in de Markt	1300 - 1350	Late Medieval	1325	10-20	*Pleuronectes platessa*	os anale	146.1	8.76	6.00	32.70	10.67	3.58	-15.61	11.10	
VLA0346	Gat in de Markt	1300 - 1350	Late Medieval	1325	40-50	*Melanogrammus aeglefinus*	quadrate	184.9	8.40	4.54	34.36	11.90	3.37	-14.68	14.63	
VLA0347	Gat in de Markt	1300 - 1350	Late Medieval	1325	20-30	*Pleuronectes platessa*	cleithrum	129.2	10.61	8.21	39.59	14.10	3.27	-14.05	11.10	
VLA0348	Gat in de Markt	1300 - 1350	Late Medieval	1325	20-30	*Platichthys flesus*	pharyngeal	105.1	10.44	9.94	41.56	15.00	3.23	-16.72	12.01	
VLA0349	Gat in de Markt	1300 - 1350	Late Medieval	1325	50-60	*Scophthalmus maximus*	caudal vertebra	495.8	21.20	4.28	38.32	14.17	3.15	-13.03	16.78	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	δ^{13}C (‰)	δ^{15}N (‰)	Remarks
VLA0350	Gat in de Markt	1300 - 1350	Late Medieval	1325	30-40	*Platichthys flesus*	caudal vertebra	249.2	19.31	7.75	37.45	13.84	3.16	-14.15	10.89	
VLA0351	Gat in de Markt	1300 - 1350	Late Medieval	1325	40-50	*Platichthys flesus*	caudal vertebra	211.5	20.21	9.56	42.12	15.47	3.18	-14.81	10.72	
VLA0352	Gat in de Markt	1300 - 1350	Late Medieval	1325	40-70	*Melanogrammus aeglefinus*	cleithrum	413.1	8.21	1.99	29.50	9.64	3.57	-14.99	13.88	
VLA0353	Gat in de Markt	1300 - 1350	Late Medieval	1325	100-120	*Gadus morhua*	quadrate	671.4	12.34	1.84	34.20	11.72	3.40	-13.83	16.45	
VLA0354	Gat in de Markt	891 - 933	Early Medieval 2	912	40-50	*Pleuronectes platessa*	os anale	325.5	32.12	9.87	42.21	15.85	3.11	-14.30	11.90	
VLA0355	Gat in de Markt	1000 - 1050	High Medieval	1025	40-50	*Pleuronectes platessa*	preoperculum	309.4	21.10	6.82	40.30	14.86	3.17	-15.02	12.75	
VLA0356	Gat in de Markt	1050 - 1170	High Medieval	1110	40-60	*Pleuronectes platessa*	cleithrum	319.5	38.60	12.08	39.80	14.86	3.12	-14.79	11.34	
VLA0357	Gat in de Markt	1050 - 1170	High Medieval	1110	50-60	*Pleuronectes platessa*	preoperculum	345.5	38.67	11.19	44.28	16.57	3.12	-14.07	12.17	
PLA0705	Plantage	800 - 850	Early Medieval 1	825	30-40	*Platichthys flesus*	os anale	132.7	6.77	5.10	36.27	12.90	3.28	-18.03	12.17	
PLA0706	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Platichthys flesus*	os anale	232.3	19.53	8.41	38.73	14.19	3.18	-16.47	11.82	
PLA0707	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Pleuronectes platessa*	os anale	225.0	16.61	7.38	38.59	14.59	3.09	-14.67	11.48	
PLA0708	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Pleuronectes platessa*	os anale	209.0	10.01	4.79	34.51	13.01	3.09	-14.12	12.10	
PLA0713	Plantage	675 - 750	Early Medieval 1	712.5	30-40	cf Cyprinidae	cleithrum	135.9	14.36	10.57	41.56	14.92	3.25	-22.30	9.41	
PLA0714	Plantage	675 - 750	Early Medieval 1	712.5	30-40	cf *Platichthys flesus*	caudal vertebra	209.2	15.99	7.64	40.88	15.01	3.18	-15.57	9.87	
PLA0716	Plantage	800 - 850	Early Medieval 1	825	30-40	*Platichthys flesus*	os anale	163.4	9.66	5.91	34.36	12.18	3.29	-16.26	10.65	
PLA0720	Plantage	807 - 840	Early Medieval 1	823.5	30-40	cf *Platichthys flesus*	os anale	245.1	16.18	6.60	38.74	13.47	3.36	-16.90	11.24	
PLA0721	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Pleuronectes platessa*	os anale	150.4	9.65	6.42	39.40	13.98	3.29	-14.93	12.12	
PLA0722	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Platichthys flesus*	os anale	144.5	11.16	7.72	38.73	14.06	3.21	-17.30	11.04	
PLA0723	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	144.0	15.00	10.41	36.47	13.40	3.18	-15.74	10.57	
PLA0724	Plantage	807 - 840	Early Medieval 1	823.5	30-40	cf Cyprinidae	hyomandibula	306.8	29.76	9.70	41.64	15.28	3.18	-20.16	6.23	
PLA0725	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Platichthys flesus*	os anale	228.3	12.78	5.60	38.07	13.74	3.23	-15.46	11.28	
PLA0726	Plantage	675 - 750	Early Medieval 1	712.5	40-50	*Platichthys flesus*	os anale	182.2	13.67	7.50	39.92	14.38	3.24	-14.56	11.60	
PLA0727	Plantage	807 - 840	Early Medieval 1	823.5	>50	*Esox lucius*	dentary	154.9	9.98	6.44	41.49	14.52	3.33	-23.04	9.82	
PLA0728	Plantage	807 - 840	Early Medieval 1	823.5	30-40	cf Cyprinidae	cleithrum	151.3	12.15	8.03	39.92	14.40	3.23	-24.70	7.80	
PLA0729	Plantage	650 - 760	Early Medieval 1	705	30-40	*Platichthys flesus*	cleithrum	133.1	9.90	7.44	40.57	14.72	3.21	-14.74	10.86	
PLA0730	Plantage	650 - 760	Early Medieval 1	705	20-30	cf *Platichthys flesus*	caudal vertebra	112.8	6.98	6.19	40.75	13.44	3.54	-16.92	9.65	
PLA0731	Plantage	807 - 840	Early Medieval 1	823.5	10-20	cf *Platichthys flesus*	os anale	134.4	9.21	6.85	42.11	14.91	3.29	-17.73	10.21	
PLA0732	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	150.7	4.97	3.30	36.70	12.00	3.57	-15.91	11.13	
PLA0733	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Platichthys flesus*	os anale	108.0	8.80	8.15	41.34	14.52	3.32	-18.92	11.32	
PLA0734	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	168.2	19.39	11.53	38.31	13.85	3.23	-13.80	9.82	
PLA0735	Plantage	807 - 840	Early Medieval 1	823.5	50-60	*Pleuronectes platessa*	preoperculum	169.6	15.21	8.97	40.38	14.91	3.16	-14.17	12.59	
PLA0737	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Pleuronectes platessa*	os anale	197.9	12.63	6.38	39.54	14.66	3.15	-13.71	12.38	
PLA0738	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	177.3	6.17	3.48	33.41	11.38	3.42	-14.09	12.57	
PLA0739	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Platichthys flesus*	os anale	276.4	17.21	6.23	38.27	13.79	3.24	-15.57	11.29	
PLA0740	Plantage	650 - 760	Early Medieval 1	705	30-40	*Platichthys flesus*	os anale	112.5	6.49	5.77	36.71	12.81	3.34	-14.58	13.09	
PLA0741	Plantage	650 - 760	Early Medieval 1	705	30-40	cf *Platichthys flesus*	caudal vertebra	133.7	9.68	7.24	40.53	14.14	3.34	-15.70	9.63	
PLA0742	Plantage	650 - 760	Early Medieval 1	705	>50	*Esox lucius*	dentary	387.9	25.19	6.49	39.66	14.76	3.14	-24.45	11.68	
PLA0743	Plantage	650 - 760	Early Medieval 1	705	20-30	cf *Platichthys flesus*	os anale	85.6	3.80	4.44	34.39	10.58	3.79	-19.33	11.33	
PLA0744	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Pleuronectes platessa*	dentary	119.5	11.88	9.94	40.40	15.06	3.13	-14.03	11.87	
PLA0746	Plantage	807 - 840	Early Medieval 1	823.5	>60	*Melanogrammus aeglefinus*	cleithrum	376.1	7.56	2.01	25.27	8.71	3.39	-15.26	14.77	
PLA0747	Plantage	807 - 840	Early Medieval 1	823.5	>70	*Gadus morhua*	dentary	289.2	8.52	2.95	23.78	8.22	3.38	-12.94	15.24	
PLA0748	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	220.7	8.60	3.90	35.67	12.61	3.30	-14.28	11.24	
PLA0749	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Pleuronectes platessa*	os anale	163.7	13.29	8.12	38.84	14.44	3.14	-15.08	12.37	
PLA0750	Plantage	807 - 840	Early Medieval 1	823.5	60-70	*Gadus morhua*	dentary	307.6	17.91	5.82	36.52	13.65	3.12	-12.39	16.04	
PLA0751	Plantage	807 - 840	Early Medieval 1	823.5	80-90	*Gadus morhua*	ceratohyal	373.2	13.40	3.59	31.41	10.67	3.43	-14.08	15.51	
PLA0752	Plantage	675 - 750	Early Medieval 1	712.5	>50	*Esox lucius*	dentary	260.7	20.79	7.98	41.79	15.34	3.18	-22.48	12.24	
PLA0753	Plantage	675 - 750	Early Medieval 1	712.5	>50	*Esox lucius*	dentary	275.2	25.58	9.30	41.37	15.20	3.17	-23.20	11.60	
PLA0756	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Melanogrammus aeglefinus*	ceratohyal	462.0	35.47	7.68	38.19	14.48	3.08	-13.31	14.71	
PLA0757	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Pleuronectes platessa*	os anale	224.4	7.89	3.52	37.23	13.18	3.30	-15.65	11.44	
PLA0759	Plantage	807 - 840	Early Medieval 1	823.5	40-50	cf Cyprinidae	cleithrum	183.0	15.46	8.45	41.38	14.20	3.40	-25.62	8.40	
PLA0760	Plantage	650 - 760	Early Medieval 1	705	30-40	cf Cyprinidae	hyomandibula	176.2	8.24	4.68	28.74	8.64	3.88	-22.64	8.70	
PLA0761	Plantage	675 - 750	Early Medieval 1	712.5	30-40	cf *Platichthys flesus*	preoperculum	200.7	14.65	7.30	40.36	14.86	3.17	-15.84	11.39	
PLA0764	Plantage	807 - 840	Early Medieval 1	823.5	50-60	*Platichthys flesus*	os anale	211.2	10.44	4.94	38.33	13.70	3.26	-12.73	12.62	

Table E13 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	Weight (mg)	Collagen weight (mg)	Collagen Yield (%)	%C	%N	C:N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Remarks
PLA0765	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Platichthys flesus*	cleithrum	132.3	12.46	9.42	41.66	15.00	3.24	-14.61	10.72	
PLA0766	Plantage	675 - 750	Early Medieval 1	712.5	20-30	cf *Platichthys flesus*	articular	66.3	5.06	7.64	39.62	12.96	3.57	-13.80	13.12	
KAS0700	Kastanjelaan	8th - 10th	Early Medieval 1	850	10-30	[Not enough collagen]	pharyngeal	45.8	5.16	11.27	NA	NA	NA	NA	NA	
KAS0701	Kastanjelaan	8th - 10th	Early Medieval 1	850	20-30	*Platichthys flesus*	os anale	203.0	8.17	4.02	28.33	8.99	3.68	-18.94	10.09	
KAS0702	Kastanjelaan	8th - 10th	Early Medieval 1	850	30-40	cf *Pleuronectes platessa*	urohyal	123.6	5.09	4.12	29.95	10.20	3.43	-14.34	10.24	
KAS0703	Kastanjelaan	8th - 10th	Early Medieval 1	850	15-25	cf Cyprinidae	hyomandibula	69.2	3.44	4.97	32.14	10.59	3.54	-22.34	8.45	
KAS0704	Kastanjelaan	8th - 10th	Early Medieval 1	850	30-40	*Pleuronectes platessa*	posttemporal	62.4	3.13	5.02	33.87	11.80	3.35	-16.39	10.83	
1966	North Sea	modern	Modern	2020	20-30	*Pleuronectes platessa*	caudal vertebra	72.8	16.84	23.14	41.66	15.31	3.17	-15.47	11.90	
1967	North Sea	modern	Modern	2020	20-30	*Pleuronectes platessa*	caudal vertebra	144.9	25.98	17.93	41.54	15.46	3.13	-14.43	11.93	
1968	North Sea	modern	Modern	2020	20-30	*Pleuronectes platessa*	caudal vertebra	153.2	30.88	20.15	42.04	14.35	3.42	-16.08	12.45	
1973	North Sea	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	131.7	22.20	16.86	42.61	14.70	3.38	-18.29	10.65	
1974	North Sea	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	123.5	23.91	19.36	41.66	15.15	3.21	-17.95	9.99	
1979	North Sea	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	174.5	35.08	20.11	41.64	15.16	3.20	-13.04	14.15	
1984	Norwegian coast	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	75.5	17.18	22.75	41.51	15.46	3.13	-10.18	16.68	
BBL_C1	NA	modern	NA	2020	NA	bovid	bone powder	100.5	20.37	20.27	42.93	15.77	3.18	-22.93	6.12	
MOD_C1	NA	modern	NA	2020	NA	bovid	bone powder	100.1	18.65	18.63	44.25	16.28	3.17	-23.11	6.02	
BSG_C2	NA	modern	NA	2020	NA	bovid	bone powder	123.9	31.65	25.56	45.06	16.36	3.21	-23.37	5.44	
CAO_C1	NA	modern	NA	2020	NA	bovid	bone powder	104.8	18.46	17.61	45.62	16.91	3.15	-23.26	5.81	
PLA_C1	NA	modern	NA	2020	NA	bovid	bone powder	101.5	18.55	18.28	43.36	16.00	3.16	-23.01	6.07	
CAN_C2	NA	modern	NA	2020	NA	bovid	bone powder	101.2	22.14	21.87	44.42	16.36	3.17	-23.12	6.07	
PLA_C2	NA	modern	NA	2020	NA	bovid	bone powder	121.1	21.45	17.71	45.36	16.55	3.20	-23.20	5.69	
VLA_C2	NA	modern	NA	2020	NA	bovid	bone powder	100.0	19.93	19.93	45.69	16.68	3.20	-23.20	6.32	
COP_C1	NA	modern	NA	2020	NA	bovid	bone powder	101.8	14.85	14.59	44.26	16.22	3.18	-23.19	5.44	
COP_C2	NA	modern	NA	2020	NA	bovid	bone powder	101.1	20.08	19.87	46.12	16.79	3.21	-23.22	6.01	
KOK_C1	NA	modern	NA	2020	NA	bovid	bone powder	104.7	19.92	19.02	43.98	16.25	3.16	-23.06	6.01	
COP_C3	NA	modern	NA	2020	NA	bovid	bone powder	101.0	21.04	20.83	45.23	16.58	3.18	-23.33	6.13	
COP_C4	NA	modern	NA	2020	NA	bovid	bone powder	100.0	18.38	18.39	44.01	16.07	3.20	-23.12	6.39	
GEN_C2	NA	modern	NA	2020	NA	bovid	bone powder	101.3	22.41	22.12	44.94	16.60	3.16	-23.21	6.02	
GSJ_C1	NA	modern	NA	2020	NA	bovid	bone powder	100.3	20.83	20.77	43.14	15.83	3.18	-23.15	6.50	
KOK_C2	NA	modern	NA	2020	NA	bovid	bone powder	100.4	24.62	24.53	45.62	16.71	3.18	-23.20	6.20	
SGA_C1	NA	modern	NA	2020	NA	bovid	bone powder	100.0	19.08	19.07	44.14	16.23	3.18	-22.96	6.11	
VLA_C1	NA	modern	NA	2020	NA	bovid	bone powder	113.5	23.64	20.83	44.80	16.39	3.19	-23.12	6.27	

Table E14. Stable isotope data for sulfur analysis of 173 samples. Samples highlighted in red were not included in the analysis as the data did not match the quality criteria.

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	%C	%N	%S	C:N	C:S	N:S	δ¹³C (‰)	δ¹⁵N (‰)	δ³⁴S (‰)	Remarks
COP0109	Coppergate	1250 - 1275	Late Medieval	1262.5	30-40	*Pleuronectes platessa*	vertebra	37.4	14	1.08	3.1	92	30	-14.07	11.83	14.15	duplicate
COP0131	Coppergate	1200 - 1240	High/Late Medieval	1220	40-50	*Pleuronectes platessa*	os anale	41.1	15.5	0.64	3.1	172	56	-13.97	12.14	14.58	duplicate
COP0148	Coppergate	1040 - 1220	High Medieval	1130	20-40	*Pleuronectes platessa*	cervical vertebra	39.2	14.8	0.87	3.1	120	39	-14.78	10.88	11.72	duplicate
COP0153	Coppergate	1040 - 1220	High Medieval	1130	20-40	*Pleuronectes platessa*	os anale	41.1	15.4	0.69	3.1	159	51	-14.24	11.86	15.97	duplicate
COP0156	Coppergate	1040 - 1220	High Medieval	1130	20-40	*Pleuronectes platessa*	preoperculum	40.7	14.7	1.05	3.2	103	32	-15.03	11.44	10.57	duplicate
COP0158	Coppergate	1200 - 1240	High/Late Medieval	1220	20-40	*Pleuronectes platessa*	hyomandibula	39.1	14.6	0.89	3.1	118	38	-12.67	12.77	13.88	duplicate
COP0202	Coppergate	c930/935 - c955/6	Early Medieval 2	943	40-50	*Platichthys flesus*	first caudal vertebra	41.1	15.5	0.65	3.1	169	55	-13.79	12.14	9.29	duplicate
COP0206	Coppergate	1040 - 1100	High Medieval	1070	50-60	*Pleuronectes platessa*	os anale	41.3	15.7	0.68	3.1	163	53	-13.49	12.29	12.94	duplicate
COP0207	Coppergate	1040 - 1300 and 1440 - 1480	unknown	1260	30-40	*Limanda limanda*	os anale	41.4	15.3	0.7	3.2	159	50	-12.25	14.57	14.73	duplicate
COP0209	Coppergate	1200 - 1280	High/Late Medieval	1240	50-60	*Pleuronectes platessa*	os anale	38.6	14.5	0.85	3.1	121	39	-13.24	12.52	17.69	duplicate
COP0213	Coppergate	1200 - 1280	High/Late Medieval	1240	40-50	*Pleuronectes platessa*	cleithrum	39.9	15.3	0.75	3	142	47	-13.98	12.75	15.25	duplicate
COP0214	Coppergate	1200 - 1280	High/Late Medieval	1240	50-60	*Pleuronectes platessa*	os anale	39.5	14.9	1.04	3.1	101	33	-13.57	11.19	21.62	duplicate
COP0215	Coppergate	1200 - 1280	High/Late Medieval	1240	20-30	*Platichthys flesus*	urohyal	39.8	15.3	0.72	3	147	48	-23.88	12.22	4.93	duplicate
COP0220	Coppergate	mid - late 800s/early 900s	Early Medieval 2	887.5	20-30	*Platichthys flesus*	os anale	40.5	14.8	0.65	3.2	167	52	-23.46	12.79	7.68	duplicate
COP0224	Coppergate	1040 - 1160	High Medieval	1100	50-60	*Pleuronectes platessa*	os anale	40	15	0.85	3.1	126	41	-13.24	12.29	6.51	duplicate
COP0251	Coppergate	1275 - mid1300s	Late Medieval	1312.5	30-40	*Pleuronectes platessa*	quadrate	39.8	14.9	1.02	3.1	105	34	-14.29	11.93	16.57	duplicate
COP0307	Coppergate	1200 - 1280	High/Late Medieval	1240	40-50	*Pleuronectes platessa*	urohyal	40.5	15.7	0.58	3	186	62	-14.11	12.12	16.05	duplicate
COP0313	Coppergate	1040 - 1160	High Medieval	1100	30-40	*Pleuronectes platessa*	quadrate	38.2	14.4	0.77	3.1	133	43	-14.17	12.46	12.03	duplicate
COP0320	Coppergate	c955/6 - early/mid 1000s	Early Medieval 2	1002.5	40-60	*Pleuronectes platessa*	caudal vertebra	40.7	15	0.82	3.2	133	42	-12.51	11.87	10.13	duplicate
COP0328	Coppergate	c955/6	Early Medieval 2	955.5	40-50	*Pleuronectes platessa*	os anale	41.7	15.8	0.59	3.1	190	62	-12.46	12.71	13.27	duplicate
COP0329	Coppergate	1250 - 1275	Late Medieval	1262.5	40-50	*Pleuronectes platessa*	os anale	41.2	15.9	0.63	3	174	58	-14.13	11.91	17.45	duplicate
COP0331	Coppergate	1250 - 1275	Late Medieval	1262.5	40-50	*Pleuronectes platessa*	hyomandibula	40.9	15.6	0.67	3.1	164	53	-14.29	11.24	18.73	duplicate
COP0336	Coppergate	1040 - 1280	High Medieval	1160	50-60	*Pleuronectes platessa*	os anale	39.4	15	1.53	3.1	69	22	-13.97	12.68	14.05	duplicate
COP0337	Coppergate	1040 - 1160	High Medieval	1100	40-50	*Pleuronectes platessa*	ceratohyal	39.3	15.2	0.82	3	128	42	-14.24	12.01	16.96	duplicate
COP0338	Coppergate	1040 - 1220	High Medieval	1130	20-30	*Pleuronectes platessa*	os anale	40.8	15	0.57	3.2	193	61	-13.97	13.17	14.03	duplicate
BBL0902	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	20-30	*Platichthys flesus*	caudal vertebra	36.7	14.2	0.56	3	174	58	-23.6	11.6	2.9	
BBL0903	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	40-50	*Pleuronectes platessa*	precaudal vertebra	37.2	14.3	0.5	3	198	65	-13.9	11.6	12.5	
BBL0908	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	50-60	*Pleuronectes platessa*	caudal vertebra	38.4	13.9	0.49	3.2	209	65	-12.7	12.3	13.2	
BBL0910	Blue Bridge Lane	late 12th - mid 14th	High/Late Medieval	1260	40-50	*Pleuronectes platessa*	caudal vertebra	39.8	14.2	0.48	3.3	220	67	-14.47	10.97	13.22	duplicate
BBL0917	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	20-30	*Platichthys flesus*	caudal vertebra	38	13.8	0.51	3.2	200	62	-23.7	14.8	8.3	
BBL0918	Blue Bridge Lane	7th - 8th	Early Medieval 1	700	30-40	*Platichthys flesus*	caudal vertebra	40.2	14.7	0.55	3.2	195	61	-16.1	10.8	8.4	
BBL0919	Blue Bridge Lane	late 14th - early 16th	Late Medieval	1497.5	20-30	*Pleuronectes platessa*	caudal vertebra	39.5	14.7	0.61	3.1	174	56	-14.1	11.6	13.5	
CAO0824	CAO96	1150 - 1270	High Medieval	1210	20-30	*Pleuronectes platessa*	precaudal vertebra	39.4	14.6	0.53	3.1	199	63	-14.3	11.8	12	
CAO0827	CAO96	1150 - 1270	High Medieval	1210	30-40	*Pleuronectes platessa*	dentary	39.1	14.5	0.53	3.2	199	63	-13.04	12.03	13.8	duplicate
CAO0828	CAO96	1150 - 1270	High Medieval	1210	20-30	*Pleuronectes platessa*	preoperculum	41.1	14.7	0.54	3.2	203	63	-13.5	11.5	11.8	
CAO0829	CAO96	1150 - 1270	High Medieval	1210	30-40	*Pleuronectes platessa*	caudal vertebra	40	14.8	0.58	3.1	183	58	-13.4	11	12.3	
CAO0830	CAO96	900 - 1150	Early/High Medieval	1025	20-30	*Pleuronectes platessa*	caudal vertebra	40	14.2	0.61	3.3	176	53	-13.5	10.6	10.4	
CAO0833	CAO96	1240 - 1380	Late Medieval	1310	30-40	*Pleuronectes platessa*	cleithrum	38.9	13.9	0.68	3.3	153	47	-14.97	11.66	11.53	duplicate
CAO0835	CAO96	1240 - 1380	Late Medieval	1310	30-40	*Pleuronectes platessa*	caudal vertebra	41.3	15.5	0.63	3.1	174	56	-12.6	11.1	11.3	
GSJ0805	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	precaudal vertebra	38.6	14	0.63	3.2	162	50	-13.9	13.6	6.7	
GSJ0806	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	quadrate	40.1	14.7	0.6	3.2	178	56	-14.3	12.2	11.2	
GSJ0807	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	40.1	14.4	0.62	3.3	172	53	-13.33	10.28	7.52	duplicate
GSJ0814	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	38.4	13.8	0.64	3.2	160	49	-13.46	11.83	6.76	duplicate
GSJ0817	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	caudal vertebra	39.4	14.2	0.61	3.2	172	53	-14.1	13.4	7	
GSJ0818	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	*Pleuronectes platessa*	articular	38.4	14.1	0.56	3.2	182	57	-12.8	12.2	11.1	
GSJ0819	GSJ06	10th - 12th	Early/High Medieval	1050	30-40	cf *Platichthys flesus*	caudal vertebra	39.5	14	0.6	3.3	177	54	-14.7	11.8	9.1	
GSJ0821	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	precaudal vertebra	38.8	14.2	0.56	3.2	186	58	-12.6	14.2	9.3	
GSJ0836	GSJ06	10th - 12th	Early/High Medieval	1050	20-30	*Platichthys flesus*	caudal vertebra	38.2	14	0.47	3.2	219	69	-23.2	12.8	-14.7	
SGA0848	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Pleuronectes platessa*	precaudal vertebra	37.1	13.6	0.52	3.2	192	61	-13.1	12	6.9	
SGA0849	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	caudal vertebra	38.6	14.3	0.57	3.2	182	58	-21.9	13	-3.8	
SGA0854	SGA89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	caudal vertebra	37.7	14.1	0.57	3.1	175	56	-14.1	11	7.1	
SGA0855	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Pleuronectes platessa*	caudal vertebra	40.2	14.5	0.53	3.2	203	63	-12.3	13.2	8.1	

Table E14 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	%C	%N	%S	C:N	C:S	N:S	δ^{13}C (‰)	δ^{15}N (‰)	δ^{34}S (‰)	Remarks
SGA0856	SGA89	7th - 9th	Early Medieval 1	750	40-50	cf *Pleuronectes platessa*	caudal vertebra	39.6	14.5	0.52	3.2	205	64	-12.2	11.8	10.6	
SGA0857	SGA89	7th - 9th	Early Medieval 1	750	30-40	*Platichthys flesus*	os anale	37.3	13.4	0.55	3.3	181	56	-12.14	13.41	6.26	duplicate
SOT0861	SOT89	7th - 9th	Early Medieval 1	750	40-50	*Pleuronectes platessa*	caudal vertebra	39.4	14.7	0.52	3.1	201	64	-13.59	11.23	11.59	duplicate
SOT0863	SOT89	7th - 9th	Early Medieval 1	750	10-20	*Platichthys flesus*	caudal vertebra	38.9	14.5	0.57	3.1	183	58	-21.6	13.4	-3.2	
SOT0865	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Pleuronectes platessa*	vertebra	36.5	13.4	0.55	3.2	178	56	-12.1	12.1	10.1	
SOT0867	SOT89	7th - 9th	Early Medieval 1	750	20-30	*Platichthys flesus*	cleithrum	38.3	14.1	0.53	3.2	193	61	-13.4	12.9	9.2	
CAN0404	Tradescent Lane	post 1275	Late Medieval	1437.5	30-40	*Pleuronectes platessa*	precaudal vertebra	39.7	14.6	0.53	3.2	200	63	-13.5	11.4	12.1	
CAN0412	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-50	*Pleuronectes platessa*	atlas	35.1	13.4	0.45	3.1	208	68	-13.3	12.2	13.5	
CAN0421	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Pleuronectes platessa*	os anale	34.8	12.5	0.47	3.2	198	61	-12.8	12.4	10.5	
CAN0424	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	>30	*Platichthys flesus*	cranial	36.6	13.6	0.47	3.1	209	67	-12.3	15	9.9	
CAN0426	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Pleuronectes platessa*	dentary	38	14	0.51	3.2	198	62	-13.3	12.5	12.9	
CAN0427	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-30	*Platichthys flesus*	articular	39	14.3	0.5	3.2	209	66	-12.83	13.31	9.61	duplicate
CAN0432	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	40-50	*Pleuronectes platessa*	quadrate	37.7	14	0.49	3.1	206	65	-12.4	12.3	11.6	
CAN0433	Tradescent Lane	post 1275	Late Medieval	1437.5	40-60	*Pleuronectes platessa*	premaxilla	37.5	14	0.53	3.1	189	60	-13.95	13.62	13.79	duplicate
CAN0434	Tradescent Lane	post 1275	Late Medieval	1437.5	30-40	cf *Platichthys flesus*	caudal vertebra	39	14.7	0.53	3.1	197	64	-10.6	12.6	11.9	
CAN0437	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	caudal vertebra	37.9	14.1	0.47	3.1	217	69	-14.8	10.7	14.3	
CAN0440	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	30-40	*Pleuronectes platessa*	caudal vertebra	34.2	13	0.45	3.1	202	65	-12.5	11.8	12.8	
CAN0445	Tradescent Lane	early 12th - mid 13th	High Medieval	1175	20-40	cf *Platichthys flesus*	caudal vertebra	37.9	14.3	0.47	3.1	214	69	-11	12.8	13.2	
BGS0116	Barreau Saint-George	11th	High Medieval	1050	10-20	*Pleuronectes platessa*	first caudal vertebra	40	15.1	0.6	3.1	178	58	-13.07	12.49	7.3	duplicate
BSG0019	Barreau Saint-George	11th	High Medieval	1050	50-60	*Pleuronectes platessa*	urohyal	39.3	14.7	0.46	3.1	227	73	-13.08	11.89	10.09	duplicate
BSG0029	Barreau Saint-George	11th	High Medieval	1050	10-20	*Pleuronectes platessa*	first caudal vertebra	39	15	0.47	3	219	72	-10.94	12.96	10.47	duplicate
BSG0031	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	caudal vertebra	40.2	15	0.53	3.1	203	65	-14.02	11.7	13.28	duplicate
BSG0093	Barreau Saint-George	11th	High Medieval	1050	20-30	cf Platichthys flesus	os anale	39.2	15	0.55	3	189	62	-17.09	11.28	8.39	duplicate
BSG0102	Barreau Saint-George	11th	High Medieval	1050	40-50	*Pleuronectes platessa*	cleithrum	36.8	14.3	0.47	3	210	70	-13.58	12.78	13.41	duplicate
BSG0103	Barreau Saint-George	11th	High Medieval	1050	20-30	*Platichthys flesus*	os anale	37.4	14.4	0.5	3	201	67	-16.04	13.45	10.72	duplicate
BSG0104	Barreau Saint-George	11th	High Medieval	1050	50-60	*Pleuronectes platessa*	os anale	37	14.3	0.47	3	212	70	-13.38	12.55	11.67	duplicate
BSG0105	Barreau Saint-George	11th	High Medieval	1050	40-50	*Pleuronectes platessa*	os anale	38.7	15	0.49	3	210	70	-12.73	12.28	10.76	duplicate
BSG0108	Barreau Saint-George	11th	High Medieval	1050	10-20	*Platichthys flesus*	cleithrum	39.5	15.2	0.55	3	192	63	-14.01	12.83	10.9	duplicate
BSG0109	Barreau Saint-George	11th	High Medieval	1050	10-20	cf Platichthys flesus	first caudal vertebra	40.7	15.3	0.5	3.1	219	71	-14.85	12.7	9.59	duplicate
BSG0110	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	hyomandibula	39.3	14.7	0.47	3.1	222	71	-12.59	13.17	11.7	duplicate
BSG0111	Barreau Saint-George	11th	High Medieval	1050	20-30	*Pleuronectes platessa*	preoperculum	41.3	15.1	0.5	3.2	221	69	-14.28	13.29	12.74	duplicate
BSG0112	Barreau Saint-George	11th	High Medieval	1050	10-20	*Platichthys flesus*	os anale	39.8	14.9	0.53	3.1	201	65	-17.81	13.17	9.52	duplicate
KOK0500	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	precaudal vertebra	39.5	15.4	0.46	3	230	77	-13.2	11.9	11.6	
KOK0503	Hof ter Hille	890 - 1150	Early/High Medieval	1020	20-30	*Pleuronectes platessa*	os anale	37.5	14.3	0.5	3	200	66	-13.1	12.1	12.4	
KOK0508	Hof ter Hille	770 - 1000	Early Medieval 2	885	20-30	*Pleuronectes platessa*	caudal vertebra	37.4	13.9	0.58	3.1	173	55	-13.7	11.1	8.2	
KOK0509	Hof ter Hille	1020 - 1150	High Medieval	1085	50-60	*Pleuronectes platessa*	cleithrum	40.1	15.1	0.49	3.1	221	71	-13.1	11.6	12.5	
KOK0514	Hof ter Hille	880 - 1030	Early Medieval 2	955	20-30	cf *Platichthys flesus*	os anale	38.4	14.4	0.51	3.1	203	65	-16.37	13.42	8.8	duplicate
KOK0515	Hof ter Hille	1020 - 1150	High Medieval	1085	20-30	*Pleuronectes platessa*	os anale	34.4	13.1	0.45	3.1	203	66	-14.7	11.5	10.4	
KOK0516	Hof ter Hille	880 - 1030	Early Medieval 2	955	40-50	*Pleuronectes platessa*	urohyal	37.9	14.2	0.45	3.1	226	72	-12.6	12.7	12	
KOK0517	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	cf *Platichthys flesus*	os anale	37.5	14	0.57	3.1	175	56	-14.6	11.3	7.3	
KOK0520	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	37.5	14.1	0.47	3.1	211	68	-14.6	11.7	11.5	
KOK0526	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	caudal vertebra	37.5	14.4	0.47	3	215	71	-12.9	11.9	10.8	
KOK0527	Hof ter Hille	770 - 1000	Early Medieval 2	885	20-30	*Platichthys flesus*	cleithrum	37.8	14.4	0.55	3.1	184	60	-14.6	13.2	7.6	
KOK0529	Hof ter Hille	890 - 1150	Early/High Medieval	1020	40-50	*Pleuronectes platessa*	os anale	37.6	13.9	0.49	3.1	204	65	-13.3	12.7	10.3	
KOK0537	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Pleuronectes platessa*	os anale	38.7	14.5	0.47	3.1	218	70	-12.5	11.9	11.1	
KOK0541	Hof ter Hille	890 - 1150	Early/High Medieval	1020	30-40	*Platichthys flesus*	cleithrum	38.7	14.3	0.51	3.2	202	64	-13.4	10.8	9.9	
KOK0542	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Platichthys flesus*	caudal vertebra	39.4	15	0.5	3.1	210	69	-13.8	11.76	9.83	duplicate
KOK0544	Hof ter Hille	1020 - 1150	High Medieval	1085	30-40	*Pleuronectes platessa*	os anale	39.1	14.5	0.57	3.1	184	58	-14.4	11.6	11.9	
KOK0545	Hof ter Hille	1020 - 1150	High Medieval	1085	40-50	*Pleuronectes platessa*	os anale	40.7	15.1	0.51	3.1	214	68	-13.6	12.8	9.2	
KOK0546	Hof ter Hille	880 - 1030	Early Medieval 2	955	30-40	*Platichthys flesus*	cleithrum	37	13.8	0.5	3.1	197	63	-13.6	11.3	8.1	
KOK0555	Hof ter Hille	770 - 1000	Early Medieval 2	885	40-50	*Pleuronectes platessa*	os anale	39.2	14.6	0.47	3.1	223	71	-13.9	12.1	11.6	
KOK0560	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	caudal vertebra	38.4	14.6	0.45	3.1	230	75	-13.29	11.59	11.26	duplicate
KOK0561	Hof ter Hille	770 - 1000	Early Medieval 2	885	30-40	*Pleuronectes platessa*	caudal vertebra	38.7	14.8	0.5	3	207	68	-12.4	12.7	13	
GEN0602	Zwarte Laag	950 - 975	Early Medieval 2	962.5	30-40	*Pleuronectes platessa*	quadrate	38.5	14.2	0.75	3.2	137	43	-15.4	11.4	10.5	

Table E14 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	%C	%N	%S	C:N	C:S	N:S	δ^{13}C (‰)	δ^{15}N (‰)	δ^{34}S (‰)	Remarks
GEN0604	Zwarte Laag	975 - 1000	Early Medieval 2	987.5	30-40	*Platichthys flesus*	vertebra	38.9	14.2	0.73	3.2	142	44	-14.9	10.6	10.6	
GEN0611	Zwarte Laag	1125 - 1150	High Medieval	1137.5	30-40	*Platichthys flesus*	posttemporal	39.9	14.6	0.65	3.2	163	51	-13.7	11	12	
GEN0614	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Pleuronectes platessa*	os anale	36.1	13.4	0.61	3.1	158	50	-14.3	12	12.9	
GEN0618	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	30-40	*Pleuronectes platessa*	os anale	39.4	14.6	0.88	3.1	119	38	-13.62	11.92	7.24	duplicate
GEN0620	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Platichthys flesus*	os anale	40.3	14.6	0.6	3.2	179	56	-14.7	11.4	12.1	
GEN0625	Zwarte Laag	950 - 975	Early Medieval 2	962.5	50-60	*Pleuronectes platessa*	basioccipital	40.5	15.2	0.56	3.1	191	62	-14.1	12.3	13.2	
GEN0627	Zwarte Laag	975 - 1000	Early Medieval 2	987.5	20-30	*Platichthys flesus*	caudal vertebra	39.2	14.6	0.61	3.1	172	55	-17.63	10.56	12.34	duplicate
GEN0629	Zwarte Laag	1000 - 1025	High Medieval	1012.5	40-50	*Pleuronectes platessa*	caudal vertebra	39.6	14.8	0.53	3.1	198	63	-14.59	11.77	14.38	duplicate
GEN0630	Zwarte Laag	1000 - 1025	High Medieval	1012.5	40-50	*Pleuronectes platessa*	caudal vertebra	41.1	15.1	0.57	3.2	192	60	-14.1	10.6	14.4	
GEN0631	Zwarte Laag	1025 - 1050	High Medieval	1037.5	20-30	cf *Pleuronectes platessa*	caudal vertebra	39.9	14.5	0.68	3.2	157	49	-13.9	11	13.5	
GEN0636	Zwarte Laag	1100 - 1125	High Medieval	1112.5	30-40	*Pleuronectes platessa*	caudal vertebra	39.3	14.4	0.61	3.2	172	54	-14.2	11.5	12.5	
GEN0639	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	*Platichthys flesus*	caudal vertebra	39.6	15	0.86	3.1	123	40	-17.4	11.7	9.8	
GEN0645	Zwarte Laag	1175 - 1200	High Medieval	1187.5	50-60	*Pleuronectes platessa*	quadrate	41.6	15.4	0.73	3.2	152	48	-14.1	12	5.4	
GEN0646	Zwarte Laag	1175 - 1200	High Medieval	1187.5	30-40	*Platichthys flesus*	urohyal	40.3	14.9	0.78	3.2	137	44	-12.96	11.99	8.64	duplicate
GEN0649	Zwarte Laag	1175 - 1200	High Medieval	1187.5	40-50	*Pleuronectes platessa*	premaxilla	39.7	14.4	1.02	3.2	104	33	-12.9	12.5	10.2	
GEN0650	Zwarte Laag	1175 - 1200	High Medieval	1187.5	40-50	*Pleuronectes platessa*	caudal vertebra	39.9	14.7	0.89	3.2	120	38	-14.9	10.1	12.8	
GEN0655	Zwarte Laag	1150 - 1175	High Medieval	1162.5	20-30	*Platichthys flesus*	caudal vertebra	40.2	15.1	0.57	3.1	189	61	-14.9	10.9	9.8	
GEN0660	Zwarte Laag	1125 - 1150	High Medieval	1137.5	50-60	*Pleuronectes platessa*	vertebra	39.7	14.6	0.59	3.2	181	57	-13.1	12	13.3	
GEN0662	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Platichthys flesus*	caudal vertebra	39.4	14.7	0.53	3.1	199	64	-12.07	12.24	9.87	duplicate
GEN0663	Zwarte Laag	1100 - 1125	High Medieval	1112.5	40-50	*Pleuronectes platessa*	caudal vertebra	40.6	15.2	0.9	3.1	120	38	-14.3	12.1	5.6	
GEN0668	Zwarte Laag	1000 - 1025	High Medieval	1012.5	20-30	cf *Platichthys flesus*	caudal vertebra	38.2	14.1	0.58	3.2	176	56	-18.3	11.3	14	
GEN0669	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Pleuronectes platessa*	os anale	40.6	15	0.56	3.2	195	61	-14	11.3	11.8	
GEN0671	Zwarte Laag	10th - first half 11th	Early Medieval 2	975	40-50	*Pleuronectes platessa*	ectopterygoid	39.4	15	0.54	3.1	195	64	-13.23	12.5	12.54	duplicate
VLA0308	Gat in de Markt	891 - 933	Early Medieval 2	912	40-50	*Pleuronectes platessa*	preoperculum	40.5	15.3	0.51	3.1	213	69	-14.4	12.7	11.9	
VLA0314	Gat in de Markt	1050 - 1170	High Medieval	1110	40-60	*Pleuronectes platessa*	os anale	40.6	15.1	0.75	3.1	144	46	-14.4	11	6.9	
VLA0315	Gat in de Markt	1050 - 1170	High Medieval	1110	40-50	*Pleuronectes platessa*	os anale	35.8	13.2	0.65	3.2	147	47	-15	11.3	13.5	
VLA0317	Gat in de Markt	1180 - 1217	High Medieval	1198.5	50-60	*Pleuronectes platessa*	os anale	40.4	14.7	0.81	3.2	133	41	-14.5	11.9	20.6	
VLA0322	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	20-30	*Platichthys flesus*	os anale	38.6	14.6	1.03	3.1	100	33	-17.6	12.27	8.81	duplicate
VLA0325	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	20-30	*Pleuronectes platessa*	preoperculum	40.3	14.7	0.56	3.2	193	61	-15.6	11.9	12.5	
VLA0328	Gat in de Markt	1217 - 1250	High/Late Medieval	1233.5	40-60	*Pleuronectes platessa*	os anale	39	14.7	0.81	3.1	129	42	-14.7	11.3	11.3	
VLA0332	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	40-50	*Pleuronectes platessa*	os anale	39.7	14.6	0.62	3.2	172	54	-15.22	10.45	13.47	duplicate
VLA0334	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Pleuronectes platessa*	os anale	35.7	12.9	1.8	3.2	53	16	-14.7	11.1	0.3	
VLA0335	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Platichthys flesus*	os anale	39.8	14.6	1.12	3.2	95	30	-16.4	12.7	2.9	
VLA0336	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	30-40	*Pleuronectes platessa*	os anale	38.1	14	1.58	3.2	64	20	-14	12.6	8.3	
VLA0341	Gat in de Markt	1250 - 1299	Late Medieval	1274.5	20-30	*Platichthys flesus*	parasphenoid	39.5	15.2	0.69	3	154	51	-21.63	11.86	8.84	duplicate
VLA0343	Gat in de Markt	1250 - 1300	Late Medieval	1275	20-30	*Platichthys flesus*	caudal vertebra	41.5	15	0.92	3.2	120	37	-14.7	11.7	4	
VLA0344	Gat in de Markt	1300 - 1350	Late Medieval	1325	10-20	*Platichthys flesus*	os anale	39.3	14.6	0.97	3.1	108	34	-17.4	11.7	9.5	
VLA0348	Gat in de Markt	1300 - 1350	Late Medieval	1325	20-30	*Platichthys flesus*	pharyngeal	39.1	13.9	0.84	3.3	124	38	-16.8	11.9	10.9	
VLA0350	Gat in de Markt	1300 - 1350	Late Medieval	1325	30-40	*Platichthys flesus*	caudal vertebra	35.2	12.9	0.86	3.2	110	35	-14.2	11	12	
VLA0351	Gat in de Markt	1300 - 1350	Late Medieval	1325	40-50	*Platichthys flesus*	caudal vertebra	38.6	14.5	1.04	3.1	99	32	-14.99	10.85	18.12	duplicate
VLA0354	Gat in de Markt	891 - 933	Early Medieval 2	912	40-50	*Pleuronectes platessa*	os anale	40.7	15.3	0.52	3.1	207	67	-14.6	12	14	
VLA0355	Gat in de Markt	1000 - 1050	High Medieval	1025	40-50	*Pleuronectes platessa*	preoperculum	39.6	14.5	0.58	3.2	183	58	-15.28	12.84	11.59	duplicate
PLA0705	Plantage	800 - 850	Early Medieval 1	825	30-40	*Platichthys flesus*	os anale	35.5	12.7	1.24	3.3	77	23	-18.2	12.1	5.9	
PLA0706	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Platichthys flesus*	os anale	36.7	13.3	2.01	3.2	49	15	-16.6	12	1.8	
PLA0707	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Pleuronectes platessa*	os anale	37.5	13.6	1.23	3.2	81	25	-15.1	11.6	8	
PLA0708	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Pleuronectes platessa*	os anale	33.8	12.6	2.14	3.1	42	13	-14.5	11.8	13.5	
PLA0714	Plantage	675 - 750	Early Medieval 1	712.5	30-40	cf *Platichthys flesus*	caudal vertebra	39.3	14.4	0.88	3.2	119	37	-15.6	10.6	7.5	
PLA0716	Plantage	800 - 850	Early Medieval 1	825	30-40	*Platichthys flesus*	os anale	34.1	12	1.86	3.3	49	15	-16.5	10.8	10.1	
PLA0720	Plantage	807 - 840	Early Medieval 1	823.5	30-40	cf *Platichthys flesus*	os anale	35.6	12.6	0.97	3.3	98	30	-16.9	11.5	7.9	
PLA0722	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Platichthys flesus*	os anale	38.5	13.4	1.43	3.3	72	21	-17.6	11.2	-2.1	
PLA0723	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	37	13.3	0.95	3.2	103	32	-16.2	10.9	5.4	
PLA0725	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Platichthys flesus*	os anale	35.5	12.6	1.01	3.3	94	29	-15.7	11	7.9	
PLA0726	Plantage	675 - 750	Early Medieval 1	712.5	40-50	*Platichthys flesus*	os anale	37.8	13.5	1.37	3.3	74	23	-14.8	11.5	4	
PLA0733	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Platichthys flesus*	os anale	38.1	13.5	1.22	3.3	83	25	-18.9	11.3	4.8	

Table E14 continued

Sample	Site	Period published	Period category	Mid	Size class	Species (ZooMS)	Element	%C	%N	%S	C:N	C:S	N:S	δ^{13}C (‰)	δ^{15}N (‰)	δ^{34}S (‰)	Remarks
PLA0734	Plantage	807 - 840	Early Medieval 1	823.5	20-30	*Pleuronectes platessa*	os anale	37.9	13.7	1.4	3.2	72	22	-14	10.2	2.4	
PLA0737	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Pleuronectes platessa*	os anale	36.2	13.4	1.48	3.2	65	21	-13.97	12.34	3.01	duplicate
PLA0749	Plantage	807 - 840	Early Medieval 1	823.5	30-40	*Pleuronectes platessa*	os anale	37.2	13.9	1.18	3.1	84	27	-15.4	12.2	13.8	
PLA0761	Plantage	675 - 750	Early Medieval 1	712.5	30-40	cf *Platichthys flesus*	preoperculum	37.9	13.8	0.84	3.2	121	38	-16.01	11.49	8.4	duplicate
PLA0764	Plantage	807 - 840	Early Medieval 1	823.5	50-60	*Platichthys flesus*	os anale	38.4	13.4	1.56	3.3	66	20	-13.09	12.47	5.4	duplicate
PLA0765	Plantage	807 - 840	Early Medieval 1	823.5	40-50	*Platichthys flesus*	cleithrum	39.8	13.9	1.04	3.3	102	31	-14.9	10.7	12	
1966	North Sea	modern	Modern	2020	20-30	*Pleuronectes platessa*	caudal vertebra	41.60	15.10	0.53	3.20	210.00	65.00	-15.60	12.40	13.7	
1967	North Sea	modern	Modern	2020	20-30	*Pleuronectes platessa*	caudal vertebra	40.40	15.00	0.52	3.10	208.00	66.00	-14.60	12.30	12.5	
1968	North Sea	modern	Modern	2020	20-30	*Pleuronectes platessa*	caudal vertebra	40.90	14.10	0.5	3.40	219.00	65.00	-16.22	12.86	13.74	duplicate
1973	North Sea	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	41.80	14.60	0.52	3.30	215.00	64.00	-18.40	11.10	12.4	
1974	North Sea	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	41.40	14.70	0.58	3.30	191.00	58.00	-17.99	10.28	14.89	duplicate
1979	North Sea	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	41.60	14.80	0.55	3.30	201.00	61.00	-13.10	14.50	11.3	
1984	Norwegian coast	modern	Modern	2020	20-30	*Platichthys flesus*	caudal vertebra	40.60	15.10	0.56	3.10	192.00	61.00	-10.40	17.10	8.9	

Abbreviations

2D: 2 dimensional
3D: 3 dimensional
AIC: Akaike Information Criterion
Ambic: Ammonium bicarbonate buffer
ANCOVA: Analysis of covariance
ANOVA: Analysis of variance
BBL: Blue Bridge Lane, York
BSG: Barreau Saint-George, Saint-George-sur-l'Aa
CAN: Tradescent Lane, Canterbury
CAO: CAO96, London
CE: Common Era
cm: centimeter
COL: collagen
COP: 16-22 Coppergate, York
Da: dalton
DCM: Dichloromethane
df: degrees of freedom
DGLA: Department of Greater London Archaeology
DNA: Desoxyribonucleic acid
E/HM: Early/High Medieval
EM: Early Medieval
EM1: Early Medieval 1
EM2: Early Medieval 2
GEN: Zwarte Laag, Gent
GLM: generalised linear model
Gly: glycine
GMM: Geometric morphometrics
GPA: General Procrustes Analysis
GSJ: GSJ06, London
H/LM: High/Late Medieval
HCl: hydrochloric acid
HL: head length
HM: High Medieval
KAS: Kastanjelaan, Leiderdorp
KOK: Hof ter Hille, Koksijde
LC-MS/MS: liquid chromatography tandem mass spectrometry system
LDA: Linear Discriminant Analysis
LM: Landmark (only used in chapter 4)
LM: Late Medieval (used in all chapters, except chapter 4)
m/z: mass over charge of a peptide
m: meter
MALDI-TOF MS: matrix-assisted laser desorption/ionisation - time of flight mass spectrometry
mm: millimeter
MOLA: Museum of London Archaeology

MoLAS: Museum of London Archaeology Service
n: number
NaOH: sodium hydroxide
PC: Principal Component
PCA: Principal Component Analysis
PLA: Plantage, Leiderdorp
PM: Post-Medieval
Pr. a.: processus articularis
Pro: proline
R: Roman
RBINS: Royal Belgian Institute of Natural Sciences
sd: standard deviation
SGA: SGA89, London
SL: standard length
SOT: SOT89, London
TFA: trifluoroacetic acid
TL: total length
TOT: total
UHQ: Ultra High Quality water
VLA: Gat in de Markt, Vlaardingen
YZL: York Zooarchaeology Laboratory
ZooMS: Zooarchaeology by Mass Spectrometry

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