Global Trends in Marine Biodiversity from Unstructured Data

Alun Henry Jones

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Department of Animal and Plant Sciences

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Declaration

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Abstract

Marine biodiversity is changing in response to numerous, mounting anthropogenic impacts, and effective conservation and management in the face of these threats requires a robust understanding of spatial and temporal patterns and trends in marine biodiversity. Achieving such an understanding is possible with the vast amounts of data present in aggregated online repositories, such as the Ocean Biogeographic Information System (OBIS), however overcoming incomparability between constituent datasets, and issues of variable methodology, detectability, and effort, requires that we employ statistical methods that ensure derived trends are robust to bias from "unstructured data". In this thesis, I explore how one of these methods, occupancy modelling, can be used to overcome issues of detectability and variable surveyor effort in OBIS data, while employing data management and analysis techniques to minimise the effects of variable methodologies. I use this combination of methods and aggregated data to assess temporal trends in the lesser-studied molluscs, expanding our understanding of molluscs in the Celtic Sea, and assessing the utility of multispecies models on a global scale for the genus *Conus*. I then go on to address more fundamental macroecological questions by deriving inter- and intraspecific abundance-occupancy relationships in European cetaceans, to then demonstrate how occupancy modelled unstructured data can be used to robustly estimate relative abundance of species within this group. Finally, I apply occupancy modelling to an Atlantic wide dataset of marine fauna, to attempt to address recent debate surrounding the marine latitudinal diversity gradient. I find throughout this thesis that occupancy modelling and unstructured data are useful in determining robust but coarse scale trends when sufficient data are available, and end by suggesting future avenues of research to both further test the methodology, and improve our knowledge of changes in marine biodiversity.

1: Introduction

1.1 Background

The marine biome is the largest on the planet, covering 71% of the surface of the Earth and representing c. 99.8% of its habitable volume (Jaume and Duarte 2006, Dawson 2012). Despite this, knowledge of exactly what lives in the oceans has historically been lacking (Alexander et al. 2011). Though increasing research effort in recent decades, with notable examples including the decade long Census of Marine Life (www.coml.org, hereafter the COML) and the United Nations World Ocean Assessment (Inniss et al. 2016), has greatly improved our understanding of marine ecology, increasing negative anthropogenic impact on marine systems means much of what we are beginning to understand, or even have no knowledge of, may disappear before we can fully comprehend it (Holt 2010).

Concurrent with these increases in research effort have been improvements in information technology, which have given rise in the past two decades to the concept of "ocean biodiversity informatics" (Costello and Vanden Berghe 2006), the publication of large marine ecology datasets for low cost online. The largest of these databases, OBIS (the Ocean Biogeographic Information System, www.iobis.org), currently holds over 50 million geo-referenced observations of species occurrence. These observations however are taken from more than 2,400 separate datasets, each with the numerous potential biases inherent in presence-only data, such as variations in sampling effort, species detection probabilities of less than 1, and spatial and temporal variations in recording (e.g. Bates et al. 2014; Isaac et al. 2014). As such, analysing these observations at face value will generate information about apparent biodiversity given data biases, as opposed to the true nature of biodiversity (Royle and Kéry 2007, Kéry et al. 2010). In order to accurately discern patterns of biodiversity in space and time, an essential step towards effective conservation and ecosystem management, methods to deal with biases in datasets must be employed. Various methods exist, however their application to marine data has so far been inconsistent. This issue is compounded in large databases such as OBIS, where numerous constituent datasets, likely in themselves to contain biases, are aggregated to form a database. Effectively analysing such databases requires the use and further development of methods to deal with such aggregated, “unstructured data.”

In this introduction, I will briefly outline the current state of knowledge of marine biodiversity, where knowledge is lacking, the threats facing marine ecosystems, and why the effective conservation and management of these systems is important. I will then discuss the rise of “ocean biodiversity informatics”, using OBIS as a primary case study, detailing the data available, their previous use, the inherent problems associated with such ecological datasets, and the statistical solutions available for dealing with these problems. Finally, I will discuss some of the ecological questions that can be answered using aggregated marine biodiversity data, and how these are addressed in the following chapters.

1.2 What do we know about marine biodiversity?

1.2.1 The state of marine biodiversity

Despite harbouring only c. 16% of global species (Costello et al. 2012), the oceans may be considered much more phylogenetically diverse than the terrestrial biome (Jaume and Duarte 2006, Costello et al. 2012). Life originated in the oceans, and 15 phyla are exclusively marine, compared to one exclusively terrestrial phylum (Jaume and Duarte 2006). Additionally, whereas 91% of terrestrial animal species fall into one phylum (the arthropods), 90% of marine animal species fall into 8 phyla, therefore representing a much greater diversity of body plans (Jaume and Duarte 2006), phyla, and classes (Costello et al. 2012). In terms of species richness, one estimate suggests that there may be as many as 0.7-1.0 million eukaryotic species in the oceans, of which approximately 226,000 have been described (Appeltans et al. 2012). Other estimates however put this figure at between 0.5 and 10 million species (Appeltans et al. 2012), demonstrating how the marine biome still remains largely unknown. Indicative of this lack of knowledge is the discovery in recent decades of surprisingly large species that were previously unknown, for example the Megamouth shark *Megachasma pelagios* (discovered as late as 1976; Maisey 1985, Jaume and Duarte 2006) and the spade-toothed beaked whale *Mesoplodon traversii* (formally identified in 2012; Thompson et al. 2012), and the reclassification of a well-studied skate into two separate species in 2010 (Iglésias et al. 2010).

Our knowledge of fundamental ecogeographic gradients in marine biodiversity is also lacking. For instance, some argue that marine biodiversity in the northern hemisphere broadly follows the latitudinal gradient seen in the terrestrial realm, with diversity increasing from the arctic to the tropics (Gray 1997, Kaschner et al. 2011), but that the pattern breaks down in the southern hemisphere, where diversity is high towards the pole (Gray 1997). Others argue that the marine latitudinal biodiversity gradient is bimodal, with peaks at mid latitudes and lows at the poles and equator (Chaudhary et al. 2016, Saeedi et al. 2017), however debate continues as to the validity of these findings (Chaudhary et al. 2017, Fernandez and Marques 2017, Menegotto and Rangel 2018). In addition to a latitudinal pattern in biodiversity, hotspots of diversity and endemism exist, for example the "Coral Triangle" of Indonesia, areas of the Pacific and Indian Oceans, the polar oceans, and semi-enclosed seas (Roberts et al. 2002, Selig et al. 2014). Other trends in distribution are harder to infer because of a lack of detailed knowledge. For example, biodiversity in the open pelagic is largely unknown due to relatively poor sampling effort, despite the fact that this habitat is the largest on Earth by volume (Webb et al. 2010). Likewise, areas previously thought uninhabitable have, in recent decades, been found to host diverse and specialised ecosystems. Notable examples are the ecosystems that exist around deep-sea hydrothermal vents, as well as deep-sea coral reefs and microbial mats (Ausubel et al. 2010, Alexander et al. 2011).

In terms of biodiversity change, all indications point towards large declines in marine biodiversity over recent time. At least 20 cases of global marine species extinction exist (Dulvy et al. 2009), with many regional and local extinctions likely, as well as ecological extinctions and community homogenizations (Sala and Knowlton

2006). Additionally, there is no *a priori* reason to expect extinction risk to be lower in the marine than terrestrial realm, and it is in fact more likely that this reflects a lack of knowledge, rather than a lack of risk (Webb and Mindel 2015). Indicative of this biodiversity decline is the so-called “shifting baseline” of biodiversity knowledge, whereby a person’s idea of baseline biodiversity is ultimately based on the state of biodiversity early in their own life, or at the beginning of their study of the subject (Pauly 1995). Additional suggestions that humanity is increasingly “fishing down marine food webs” (in that the mean trophic level of fisheries catches is decreasing; Pauly et al. 1998) likewise suggest ecosystem declines, though recently both the cause (Essington et al. 2006) of this change and the ability of mean trophic length to effectively monitor marine ecosystems (Branch et al. 2010) have been called into question, again indicating that there is still much we do not know about biodiversity change. The marine Living Planet Index (WWF 2014) similarly suggests large declines in biodiversity, with a 39% decline occurring between 1970 and 2010. However, this index is calculated from only 910 marine species, all of which are either mammals, birds, reptiles or fish. Despite the fact that OBIS represents over 137,000 taxa, and contains historical data waiting for analysis to improve these indices and inform our knowledge of biodiversity change through time, such an analysis is yet to be attempted (with preliminary exceptions, e.g. Dujardin 2014, Appeltans et al. 2015). Were it to be completed, it would provide a detailed indication of global biodiversity change through time, with a much more comprehensive coverage of species and phyla than the Living Planet Index.

There are numerous interacting causes for these declines. Anthropogenically induced climate change is arguably one of the most pressing concerns, with the Intergovernmental Panel on Climate Change (IPCC 2013) stating in its most recent report that atmospheric warming will likely exceed 1.5ºC in all but the most optimistic emission scenario (RCP2.6), with 2ºC changes expected in higher emission scenarios (RCP6.0 and RCP8.5). The oceans have absorbed over 90% of the net energy increase in the climate system between 1971 and 2010, and the addition of approximately 150Gt of carbon has led to a decrease in ocean pH of 0.1 (IPCC

2013). Furthermore, the upper 75m of the oceans warmed approximately 0.44ºC between 1971 and 2010, contributing to sea level rise of 2.0mm y^{-1} since 1971, rising to 3.2mm y^{-1} since 1993 (IPCC 2013). Since the last IPCC assessment, ocean temperatures have continued to rise, with 2017 being named the warmest year on record for the upper 200m of the oceans (Cheng and Zhu 2018). These changes have various subsequent effects on ocean biodiversity. Increasing temperatures cause the bleaching and death of corals (Hoegh-Guldberg et al. 2007), while ocean acidification as a result of CO_2 absorption poses threats to organisms with calcareous skeletal elements and the ecosystems they make up (e.g. Brierley & Kingsford 2009; Hall-Spencer et al. 2008; Hoegh-Guldberg et al. 2007). Ocean temperature changes have been observed to cause range shifts in species as they attempt to remain within suitable temperature ranges (e.g. Perry et al. 2005, Sunday et al. 2012), by keeping pace with so-called climate velocity (Loarie et al. 2009, Burrows et al. 2011, Pinsky et al. 2013), and are predicted to occur in the future under climate change (e.g. Hazen et al. 2013). Such range shifts are not possible for all species however, and those that either already live at the cold extremes and have nowhere colder to go, or are found in areas where range movement may be restricted (e.g. semi-enclosed seas such as the Mediterranean), may be unable to match their range movement to that of climate change, potentially leading to extinction (e.g. Cheung et al. 2009).

There are however numerous other factors affecting marine biodiversity. Excessive fishing of marine ecosystems has caused ecosystem collapse and restructuring (Frank et al. 2011), and in areas such as the North Sea, fishing quota systems have led to a policy of mass discarding of fish that have been caught but cannot be landed, resulting in both positive and negative effects on top predators such as seabirds (Bicknell et al. 2013). Fishing also contributes to the damaging and homogenisation of seabed habitats through the use of destructive methods such as beam trawling and dynamite fishing. Fishing and climate change act as the largest stressors in heavily impacted environments (Selig et al. 2014). Pollution is a further issue, either arising from high profile, major pollution events, for example related to resource extraction (e.g. the Deepwater Horizon or Exxon Valdez oil spills) or through sustained release of pollutants into the ocean. Vast amounts of plastic are currently input into the oceans, with ingestion or entrapment leading to the death of marine animals, and chemical components causing deleterious effects (Moser and Lee 1992, Derraik 2002), while runoff of fertilisers and nutrients from land-based activities lead to phenomena such as dead zones (Diaz and Rosenberg 2008). Invasive species, often a result of movement of water ballast in international shipping or climate change induced range shifts, likewise disrupt ecosystem functioning by competing with or displacing endemic species (Sala and Knowlton 2006, Molnar et al. 2008).

No area of the ocean is excluded from human impact, and over 40% of the ocean is strongly affected by multiple anthropogenic impacts (Halpern et al. 2008), with some of the most threatened areas being semi-enclosed seas, where the effects of different threats accumulate (Costello et al. 2010). Successfully reducing and mitigating these human impacts is therefore challenging but essential for the sustainable management and conservation of marine ecosystems.

1.2.2 The importance of marine biodiversity

In the study of biodiversity and conservation, increasing focus is falling on the importance of biodiversity for human wellbeing. Central to this concept is the idea of ecosystem services, the benefits that humans derive from the environment, with examples including provisioning of resources, regulation of environmental processes, and cultural and supporting services (Millennium Ecosystem Assessment 2005). Ecosystem services form one part of a larger suite of factors affecting how ecosystems are valued and why they should be conserved, including intrinsic and ethical considerations, as well as the services and products to be gained from ecosystems (Roff and Zacharias 2011). Biodiversity itself is important because it underpins the services provided by these ecosystems, with losses of biodiversity reducing ecosystem service functioning (Worm et al. 2006), and possibly leading to ecosystem resilience loss (Scheffer et al. 2009), or collapse and restructuring (Frank et al. 2011). The marine environment provides numerous ecosystem services, not only the provision of protein globally (FAO 2018a), but also the provision of novel chemicals with potential medical or industrial applications (Roff and Zacharias 2011), and half of global annual oxygen production (Inniss et al. 2016). Additionally, the precautionary principal would suggest that marine biodiversity should be conserved because we do not know the full extent of the services ocean ecosystems provide (Roff and Zacharias 2011), particularly in the face of growing anthropogenic threats to the marine environment.

1.3 Global marine ecological data

Ecological data on the global marine environment has become widely available thanks to the advent of low cost Internet based publication (Costello and Vanden Berghe 2006), and such ecological "big-data" has the potential to revolutionise marine conservation science (Edgar et al. 2016). This so-called "Ocean Biodiversity Informatics" represents part of the larger field of biodiversity informatics, which can trace its roots to the 1990s and early 2000s, and couples effective data management and publication with novel analytical methods, at regional and global scales (Canhos et al. 2004). A global scale is important because it is ecologically relevant: local patterns in biodiversity are influenced significantly by regional and global ecological processes, and effective science and conservation can only be achieved at the local scale when access to data at these larger scales is available (Costello and Vanden Berghe 2006).

1.3.1 The Ocean Biogeographic Information System

The COML has possibly provided the largest contribution to ocean biodiversity informatics. This international, multi-disciplinary project ran between 2000 and 2010, and involved 2,700 scientists from 80 nations. By the end of the decade, 30 million new qualitative observations had been made as part of the project, with 6,000 new species discovered, and 1,200 of these formally described (Ausubel et al. 2010). The data legacy of the COML is housed in OBIS, the Ocean Biogeographic Information System (www.iobis.org). This database has continued to grow since the end of the COML, and now contains c. 50.9 million geo-referenced records of observation (Figure 1.1, QGIS Development Team, 2018; shapefiles from naturalearthdata.com) for over 137,000 different taxa, from 2,449 individual datasets. OBIS represents the largest primary provider of geo-referenced marine ecological data (Tittensor et al. 2010, Webb et al. 2010). As well as providing recent data, OBIS also represents a large repository of historical data (Figure 1.2), with an average of 1,800 observations daily since the 1960s, and a peak number of records occurring in the 1990s (Appeltans et al. 2015).

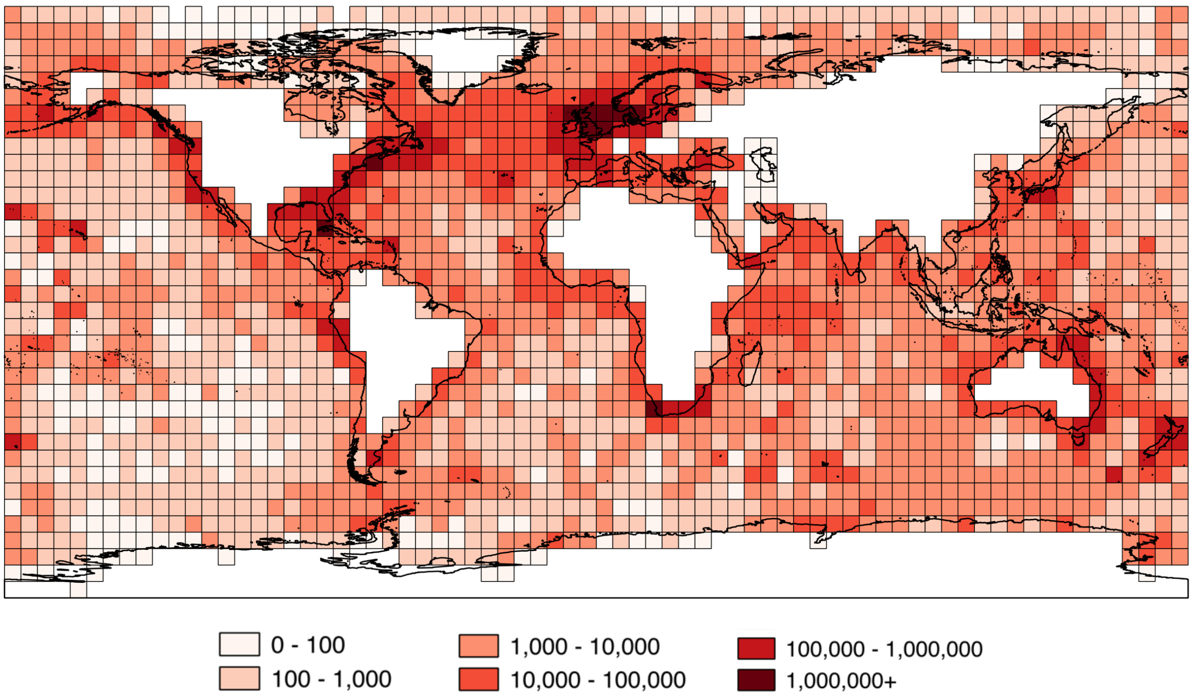

Figure 1.1: *Spatial distribution of the c. 50.9 million records in OBIS, binned into 5° cells.*

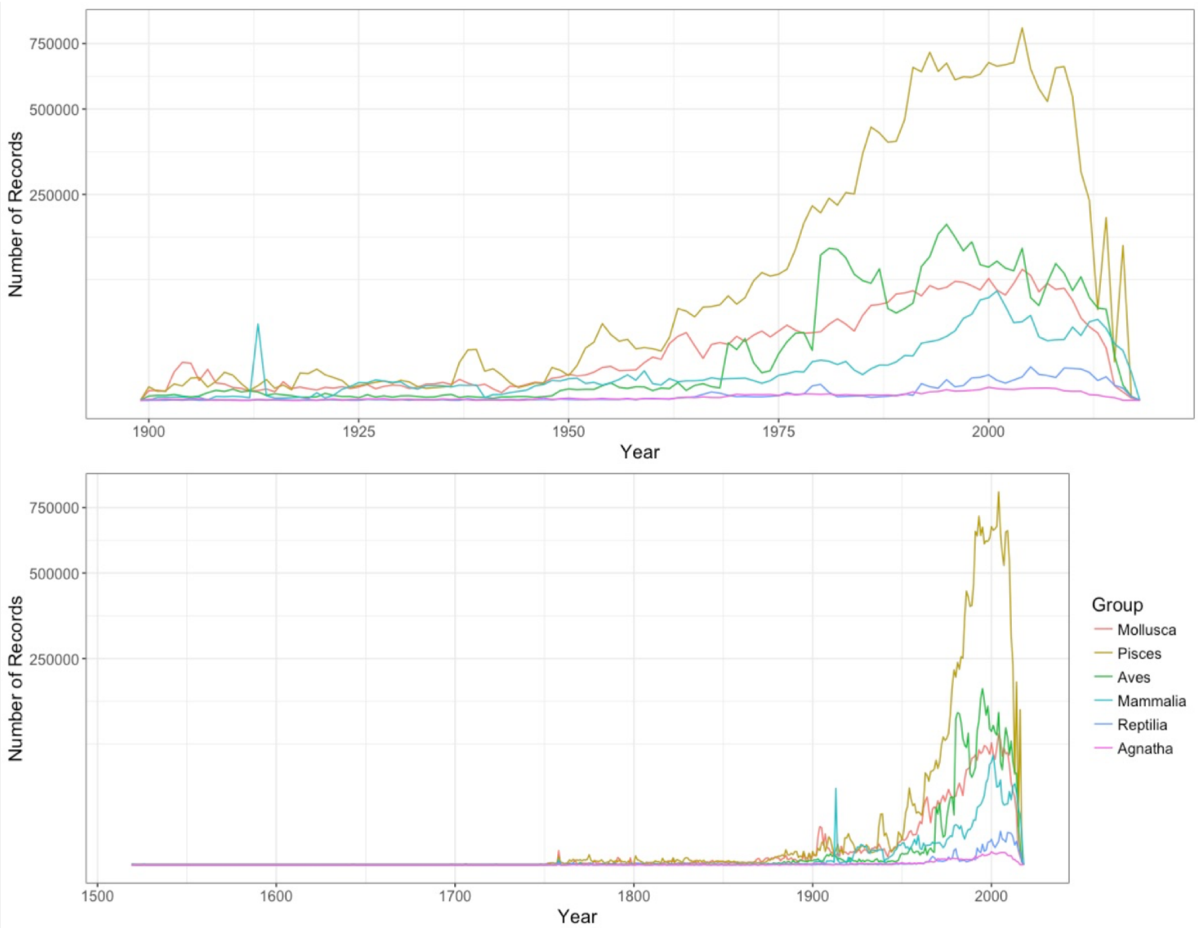

Figure 1.2: *Temporal distribution of records in OBIS for selected groups. Note the varying temporal axes.*

Since its inception, OBIS has been cited over 1,200 times (iobis.org/library). Studies have used the OBIS database for a variety of purposes. For example, Tittensor et al. (2010) used the database to assess the degree to which various environmental factors predict global marine biodiversity, finding sea surface temperature the only predictor to be significant across all species considered, and a significant relationship between the locations of both high biodiversity and high human impacts. Similarly, Ready et al. (2010) used OBIS data to assess the performance for marine mammals of the AquaMaps modelling system.

In addition to its use to model species distribution, OBIS data has also been used to evaluate our knowledge of marine biodiversity. Webb et al. (2010) assessed the number of occurrence records in OBIS with associated depth data, mapping the density of records by depth while accounting for ocean bottom depth. This study revealed chronic under-sampling in the open pelagic ocean, despite the fact the habitat is the largest by volume on Earth. Likewise, Tyler et al. (2012) used OBIS data to help develop an index of biological knowledge for marine species, finding that poorly sampled species also lack detailed trait information. Finally, Jones & Cheung (2014) employed a multi-model ensemble method based on OBIS occurrence data to assess the potential range shifts of exploited fish and invertebrate species, finding shifts of 15.5-25.6 km decade^{-1} under low and high (IPCC 2013) scenarios respectively.

Despite the degree to which OBIS has been utilised as a data source, studies often do not account for the unstructured and biased nature of the data, or do so in a very rudimentary way. For example, both Jones & Cheung (2014) and Ready et al. (2010) employ basic “data clean-up” methods, such as excluding records that fall completely on land, records that fall outside FAO major fishing areas (FAO 2018b), or records falling outside expert defined ranges where the species is known to occur. Tittensor et al. (2010) used more complex methods to directly account for varying sampling efforts, using the Chao-2 estimator to extrapolate species richness from species accumulation curves, in turn independently verified with alternative estimators and independent checklist data. While this method deals with variation in sampling effort, a large source of bias not considered is that of variation in species detectability. In cases such as Webb et al. (2010) and Tyler et al. (2012), no method of correction for bias or structure was used, however given that these studies attempt to analyse state of knowledge rather than true biodiversity, this is not necessarily an issue. Promisingly however, basic data quality tests have recently been developed to automatically quality control marine biogeographic databases such as OBIS (in which they have been implemented), as well as data uploaded by individual users (Vandepitte et al. 2014). While this will not address data bias, it will go some way to ensuring data is adequately structured and complete where required.

1.3.2 Other data sources

Whilst not of the same scale as OBIS, various other global scale marine ecology databases exist. One example is the Reef Life Survey (reeflifesurvey.com), a project consisting of a volunteer network of trained recreational SCUBA divers overseen by a scientific advisory committee based at the University of Tasmania. Quantitative marine biodiversity surveys have been conducted globally as part of this project, with a focus on Australia and the South Pacific, and the output has been utilised to explore both functional hotspots of diversity (Stuart-Smith et al. 2013) and factors contributing to protected area success (Edgar et al. 2014). Additional sources of new marine biodiversity data are citizen science programmes (for example Zooniverse, www.zooniverse.org), which in turn come with their own suite of data problems (Bird et al. 2014, Isaac et al. 2014).

1.3.3 Occupancy modelling

Numerous possible biases can exist in ecological data, particularly in the presence-only data that make up databases such as OBIS. Since presence-only data contains no record of species absences from a location, these must be inferred from where the species is not recorded as present. However, separating true absences from locations where species are present but undetected represents a challenge when using ecological "big data." When using ecological databases, it is often assumed that detection probabilities are 1, in other words that an absence in the data represents a true absence of the species (Kéry et al. 2010). Clearly, this will often not be the case. Detection probabilities are likely to be less than 1 in marine data because of the logistical challenges of surveying (Bates et al. 2015), and this has been demonstrated to be the case in, for example, reef fishes (MacNeil et al. 2008b). Additionally, as well as being less than 1, detection probabilities may change through space and time (Royle et al. 2007).

In increasing recognition of this issue, methods have been developed to account for variations in detection probability in count data, one of the most promising of which is "occupancy modelling" (MacKenzie et al. 2002, 2006, Royle and Kéry 2007, Royle et al. 2007, Kéry et al. 2010). Occupancy modelling considers that there are two stochastic processes at work when ecological data are collected, one defining whether or not a species is present at a site, and one defining whether or not that species is detected by surveyors (Kéry et al. 2010). In order to account for this imperfect detection, the sampling process producing the data in question is modelled, and numerous corrections and covariates may be employed. Temporal replication in survey data at a site may be used to infer the detection probabilities of species under consideration (Kéry et al. 2010), and covariates describing length of species list in opportunistic data, number of visits to a site, number of years of recording at a site, and commonly co-occurring species (van Strien et al. 2013, Isaac et al. 2014) can be used to inform the model.

Occupancy modelling has been widely and successfully employed in the terrestrial realm in which it was developed, to explore detectability bias in atlas and citizen science data, for butterflies and dragonflies (Kéry et al. 2010, van Strien et al. 2013) and birds (Royle and Kéry 2007, Royle et al. 2007), and can be applied to improve other methods such as species distribution modelling (Bird et al. 2014). The technique has also been made more accessible through the release of an occupancy modelling package in the statistical programming language R (August et al. 2015, R Core Team 2017) based on the previous work of Isaac et al. (2014).

As occupancy modelling in the form implemented by Isaac et al. forms a significant part of this thesis's methodology, it is important to describe the conceptual background of the technique. This framework was designed for *sites* typical of terrestrial recording schemes, which observers *visit* multiple times a year, for multiple repeating *years*. On such visits, surveyors list the species they observe, repeating this process on subsequent visits, and in subsequent years. However, because the *detectability* of species varies, possibly because they are rare, cryptic, or difficult to identify, many may not make it to a surveyors list despite being present at a site. Furthermore, the number and identity of species recorded may vary because surveyors expend differing amounts of effort whilst recording. The occupancy models used throughout this thesis attempt to account for these issues in a number of ways.

Firstly, we consider that the length of a list recorded by a surveyor is a reasonable proxy for the effort expended by a surveyor in recording, with short lists likely indicating less surveyor effort than longer lists. This can also give insight into the detectability of a species, in the form of the likelihood that a species will be recorded in a list of length 1. Secondly, we assume that within a *closure period*, whether a particular species is present or absent at a site does not change, i.e. that there is no colonisation or extinction. In terrestrial contexts this closure period is typically a year, such that observation of a species at a site in any one visit during a year indicates that it is likely present there throughout the year, though it may potentially go undetected during other visits. This relationship between detections and non-detections within a closure period provides the model with information about not only the true presence (whether the species was observed at all), but also the detectability of a species (the number of detections compared to the number of non-detections, whilst assuming constant presence). For more information on the modelling technique used here, see Isaac et al. (2014, and references therein).

Despite occupancy modelling's obvious utility, it has seen extremely limited use in marine systems, where it is arguably needed more since marine systems are generally more data poor (though other models to account for abundance related error have been applied, e.g. Bates et al. (2014)). Additionally, the few studies that have applied such a methodology (MacNeil et al. 2008a, Katsanevakis et al. 2011, Issaris et al. 2012, Coggins et al. 2014), have not specifically aimed at generating robust temporal trends, or utilized freely available, representative, and abundant data such as that from OBIS. Occupancy modelling provides an interesting opportunity to account for the often ignored issue of detection bias in marine ecological data (Monk 2014), particularly in the case of OBIS, where the contribution of numerous datasets likely means a large effect of detection bias in the final database, but where it has rarely been considered.

1.3.4 Other data problems and solutions

Bias can also arise from other problems in data collection methodology. If the full geographic extent of individuals is not exposed to sampling, this not only causes bias in the data set but also any inferences that are taken from it. For example species distribution models created from data which does not take into account the full range of individuals may draw incorrect conclusions about the environments in which a species can live, and therefore the potential range it may inhabit (Royle et al. 2007, Costa et al. 2010).

Numerous other statistical methods to account for bias in ecological data exist, as reviewed in Bird et al. (2014). Generalized linear and additive models (GLMs and GAMs respectively) are the most basic method by which to assess species distribution, however this simplicity often limits their usefulness in situations where data are biased. More complex versions of these models taking into account mixed effects (GLMMs and GAMMs) improve on the basic implementations by allowing for a non-normal distribution in response data (Zuur et al. 2007, in Bird et al. 2014), but again are unable to sufficiently deal with the various biases often present in ecological data. Hierarchical models, the category into which occupancy modelling falls, prove more reliable than those previously outlined, dealing with bias and being easily applied using programmes such as R (R Core Team 2017). However, as with all statistical methods, caution needs to be applied, since hierarchical models such as these may produce additive errors. Additional methods include species distribution modelling techniques and machine learning methods (Bird et al. 2014), with their own benefits and drawbacks. One seemingly consistent finding is that more novel or sophisticated methods are more effective in dealing with potentially biased data than simplistic, widely applied methods such as GLMs (Elith et al. 2006, Isaac et al. 2014).

1.4 Future Challenges and Thesis Aims

Our knowledge of marine biodiversity has improved greatly over recent decades, however there is still a great deal we do not know. Even by the end of the COML, authors noted at least one fifth of the ocean by volume still had no records, and many areas and habitats were significantly under-surveyed or had few records (Ausubel et al. 2010). Our knowledge of trends in biodiversity through time is lacking and, though the marine Living Planet Index exists (WWF 2014), only 910 of approximately 226,000 identified marine species are considered. Using the so far underutilised historic data in OBIS, more powerful and representative indicators of marine biodiversity change can be created. Additionally, marine ecological data is often used without consideration of inherent biases (Monk 2014), and the unstructured nature of multiple datasets combined into one database. In order to derive meaningful information from such data, methods need to be employed that can correct for the errors that exists. Despite an expansive history of use in the terrestrial realm, methods such as occupancy modelling have received little attention by marine scientists (Monk 2014), even though they are likely required to a greater extent in marine ecological data (Bates et al. 2015). Development of these methods and their application to databases such as OBIS is required to improve our understanding of marine biodiversity. The following chapters are an exploration of the utility of occupancy modelling with unstructured marine ecological big-data, with the overarching aim to contribute to the statistical toolbox and the state of knowledge concerning marine biodiversity.

I begin in Chapter 2 by applying single species occupancy modelling to a lesser-studied phylum (molluscs) in a well-studied and geographically restricted setting (the Celtic Sea). In doing so, I assess the utility of occupancy modelling for marine data, and explore the particular considerations and procedures required to implement the methodology in aggregated marine data from OBIS, as well as greatly expand on the number of invertebrate species in UK waters assessed for temporal changes in biodiversity.

In Chapter 3, I expand on the work of the previous chapter by assessing *Conus*, a genus of tropical gastropod mollusc with global distribution. *Conus* was the subject of the first comprehensive IUCN assessment of a marine gastropod, and here I use that assessment to consider how well estimated occupancy changes compare to assessed threat status.

Having explored the utility of occupancy modelling and OBIS data in examining trends in species occupancy, I move on in Chapter 4 to assess how aggregated data and occupancy modelling can be used to answer more fundamental macroecological questions, looking specifically at abundance-occupancy relationships for cetaceans (whales, dolphins and porpoises). Here, I use data from effort-based surveys conducted in European waters to derive abundance-occupancy relationships for 20 species of cetaceans, and assess how well occupancy modelled, aggregated data can predict interspecific and intraspecific abundance-occupancy relationships, and abundances of cetacean species.

I continue to explore the applicability of occupancy modelling to macroecological theory in Chapter 5, where I assess marine latitudinal species gradients derived from modelled OBIS data. I aim to determine whether patterns of latitudinal biodiversity for two contrasting groups (elasmobranchs and gastropods) are unimodal or bimodal when sampling effort is accounted for, in response to recent debate over the shape of marine latitudinal diversity gradients.

Finally, the key findings of this thesis, the lessons learned and considerations when implementing occupancy modelling in OBIS data, and potential future directions will be discussed in Chapter 6.

The effective management of marine biodiversity is important for numerous reasons, and it is my hope that the following thesis goes some way to improving our knowledge of marine biodiversity change, and informing successful and sustainable conservation practices.

2: Detecting trends in Celtic Sea marine molluscs from aggregated biodiversity data

2.1 Abstract

Widespread human impacts on marine systems create an urgent need for indices to monitor biodiversity change. However, species trend data for marine ecosystems is limited to the few taxa subject to long-term monitoring, and whether these trends are representative of changes in all marine biodiversity requires more taxonomically comprehensive indices of change. Here, I apply an occupancy modelling methodology to assess the utility of aggregated marine data in biodiversity monitoring, using Ocean Biogeographic Information System data for Celtic Sea marine molluscs. I derive robust trends for 166 species, observing high levels of variation in species occupancy changes on decadal timescales, with 50% of species showing occupancy decreases. I also note that only 6 of these species have previously been formally assessed for conservation status. I conclude that occupancy modelling provides a useful method to assess biodiversity change in marine species, and to identify possible species of concern for further assessment.

2.2 Introduction

Anthropogenic impacts on marine ecosystems are leading to extreme changes in biodiversity unprecedented in recent time, as a result of climate change (Perry et al. 2005, Hoegh-Guldberg et al. 2007, Sunday et al. 2012), pollution (Derraik 2002, Diaz and Rosenberg 2008), and exploitation (Pauly et al. 1998, Frank et al. 2011, McCauley et al. 2015). Such changes have potential far reaching social and economic impacts for human communities (Costanza 1999, Beaumont et al. 2008). However, although a wealth of research exists on the effects of these pressures on marine ecosystems, our understanding of changes in marine biodiversity is still limited by poor taxonomic coverage of large-scale marine biodiversity change studies (Costello et al. 2010, Appeltans et al. 2015), despite our requirement to report on biodiversity change (United Nations 1992). This is not surprising given that some of the best and largest datasets available represent a limited range of taxa, for example commercially valuable or charismatic vertebrate species (e.g. ICES fish assessments, www.ices.dk, or the JNCC Seabird Monitoring Programme, JNCC 2016) or plankton assemblages subject to long-term monitoring (e.g. the Continuous Plankton Recorder, Richardson et al. 2006). Whilst these trends feed into national and international assessments of biodiversity change, which in turn become excellent public engagement tools (e.g. Hayhow et al. 2016; WWF 2016; WWF 2015), the extent to which changes in these relatively few taxa represent changes in marine biodiversity as a whole is unknown, and as such further effort is required to develop trends in a wider range of marine taxa, to then inform conservation and policy.

Given the lack of large-scale, long-term monitoring studies on the lesser-known aspects of marine biodiversity, we must use other available data if we wish to increase taxonomic comprehensiveness in indices of biodiversity change (Edgar et al. 2016). One method to do this is to make use aggregated biodiversity data, which due to issues of bias, lack of structure, or incomparability, has often not been used to its full potential. An example of such a data source is the Ocean Biogeographic Information System (OBIS, www.iobis.org), the data sharing legacy of the Census of

Marine Life, which currently holds more than 50 million records of species occurrence (OBIS 2018), is global in scope, and represents almost 137,000 marine species (www.iobis.org/about/) from all major groups. OBIS has previously been used to assess spatial elements of marine biodiversity (e.g. Byers et al. 2015), including in major assessments (e.g. Miloslavich et al. 2016; Snelgrove et al. 2016; Webb et al. 2010), however less attention has been given to the temporal aspects of the database. While some datasets that make up OBIS are used to assess temporal trends (e.g. Continuous Plankton Recorder data, Richardson et al. 2006), and some studies have compiled multiple individual time series from OBIS in meta-analyses of temporal trends (e.g. Dornelas et al. 2014), the process of combining the numerous OBIS datasets to infer temporal trends across broader taxonomic groups at regional to global scales has yet to be attempted, presumably because the issues of incomparability between datasets lead to it being considered unfit for use. However, for species not subject to long term monitoring programs, and without continuous time-series, the potential information gain from combining numerous temporal records from a source such as OBIS is clear, if steps are taken to deal with potential bias. Indeed, almost 2500 datasets make up the OBIS database, each with their own aims, survey techniques, and biases, meaning great potential for assessing temporal changes in biodiversity, despite being challenging methodologically.

One method developed to account for similar problems of bias in studies of terrestrial biodiversity is hierarchical occupancy modelling (MacKenzie et al. 2006), which is able to address issues of imperfect detection and variable surveyor methodology. Presence-only occurrence records, such as those from OBIS, require users to infer absence in surveyed areas where a species was not recorded. However, due to the inherent difficulty of recording all the species that occur in an area, and the variable (and often unknown) level of effort expended by surveyors, species can be thought of as existing in one of three states: present, absent, or present but unrecorded. Partitioning absence records into true absences and this additional state of “present but unrecorded” improves the accuracy of predictions of species occupancy, and in turn species trends. Methods such as occupancy modelling (MacKenzie et al. 2006) and its additions and modifications (Kéry et al. 2010, van Strien et al. 2013, Isaac et al. 2014) allow us to estimate site level occupancy whilst taking this imperfect detection and surveyor effort into account, by modelling the process through which the input data were collected: at one level modelling the true presence or absence of a species at a site (the state model), and at the other modelling the data collection process that led to the observed presence or absence of a species (the observation model). Occupancy modelling has been used widely in terrestrial systems for taxa including birds (e.g. Boakes et al. 2017; Wan et al. 2009; Zipkin et al. 2009) and insects (e.g. Woodcock et al. 2016; Powney et al. 2015), but has seen extremely limited use in marine systems (MacNeil et al. 2008a, Katsanevakis et al. 2011, Issaris et al. 2012, Coggins et al. 2014), despite having been suggested as a method of improving assessments of marine biodiversity (Bates et al. 2015) – especially considering that the challenges of sampling in the marine environment are rarely considered in assessments of biodiversity in marine systems (MacNeil et al. 2008b, Monk 2014, Bates et al. 2015) outside of the concept of catchability.

Here I show how OBIS data can be combined with a hierarchical Bayesian occupancy model, with observation sub-model for unstructured data (Isaac et al. 2014), to infer trends in mollusc species occupancy over time for the Celtic Sea, basing my modelling strategy around the R package “sparta” (August et al. 2015, R Core Team 2017) and JAGS (Plummer 2003). I assess molluscs as an exemplar of the invertebrate groups rarely included in previous, high profile assessments of marine biodiversity change, for instance the Living Planet Index (WWF 2015, 2016) which only considers vertebrates, and the UK State of Nature Report (Hayhow et al. 2016) which includes only 8 marine invertebrates (copepods and other plankton) compared to 16 plant and 80 vertebrate species. More generally, changes in mollusc biodiversity in recent decades are less well known than those of other groups (e.g. Régnier et al. 2009), with the first comprehensive IUCN Red List assessment (IUCN 2018) of a genus of marine mollusc occurring as recently as 2013 (Peters et al. 2013). At the same time, marine molluscs are incredibly diverse, with approximately

48,000 described species (WoRMS Editorial Board 2018) and as many as 164,000 species in total (Appeltans et al. 2012), and are the second most species rich marine Phylum, behind Arthropoda (Rosenberg 2014, WoRMS Editorial Board 2018). As such, improving our knowledge of marine mollusc biodiversity change presents an excellent opportunity to improve our knowledge of marine biodiversity more generally, as well as to understand a Phylum with significance ecologically (e.g. Gutierrez et al. 2003, Coen et al. 2007), economically (the UK exported approximately £225 million worth of molluscs in 2016, Richardson et al. 2017), as biological indicators (e.g. Bresler et al. 1999) and as food sources vulnerable to climate change (e.g. Cooley et al. 2009, 2012). I chose to assess the Celtic Sea here because northwest Europe is the most densely sampled area in OBIS, and the Celtic and surrounding seas more widely experience significant anthropogenic pressure, but are less well studied than other areas of the North-East Atlantic, such as the North Sea (Rees et al. 1999), while generating ~£1.2 billion annually in fisheries landings (ABPmer 2016). My aims were to (a) assess the utility of occupancy modelling for unstructured marine data, (b) explore recent temporal trends in mollusc species for the Celtic Sea, and (c) identify potential species of concern or further study.

2.3 Methods

2.3.1 Data download and processing

Records for mollusc observations in and around the Celtic Sea, as defined by the International Hydrographic Organisation (www.iho.int), were downloaded from OBIS (OBIS 2018) using the online OBIS interface. Resource IDs (that define the dataset the record originated from) for the downloaded records were retrieved, and these resources were downloaded in their entirety for the area in and around the Celtic Sea (a rectangle of extent -12.5 to -3.5 longitude and 45.5 to 53.5 latitude). This allowed the building of lists of co-occurring species analogous to those of traditional terrestrial recording schemes, for which occupancy modelling was designed. Records from before 1880 were removed, as were records without a date of collection, and those not identified to at least species level. I used the R package “taxizesoap” (Chamberlain 2016, R Core Team 2017, since superceded by the package “taxize”) to query the World Register of Marine Species (WoRMS, WoRMS Editorial Board 2017), to verify taxonomic information provided by OBIS, thus ensuring that taxonomic information from different datasets was standardised by removing synonyms, subspecies information etc., and that records for which species identity could not be verified were removed from analysis. Of the 1.8 million records and 2,031 unique and unverified mollusc taxa in the original OBIS dataset, 1.26 million records and 867 valid mollusc species were retained after data cleaning.

Records were spatially binned to produce cell-level species lists from point-records, based on partitioning the Celtic Sea, with a 0.5° buffer to account for co-ordinate precision, on a 1° square grid of decimal latitude and longitude, such that each 1° square constituted one cell. Thirty-eight cells, with at least 50% of their area representing the Celtic Sea and buffer zone, were retained for analysis (Figure 2.1, QGIS Development Team, 2018; shapefiles from naturalearthdata.com). Records were assigned a cell identifier based on their position in this grid of cells. I chose to use 1° cells as these presented the best compromise between resolution and data availability: smaller cells typically had too little data to be modelled effectively, and larger cells were less useful in drawing conclusions on biodiversity change.

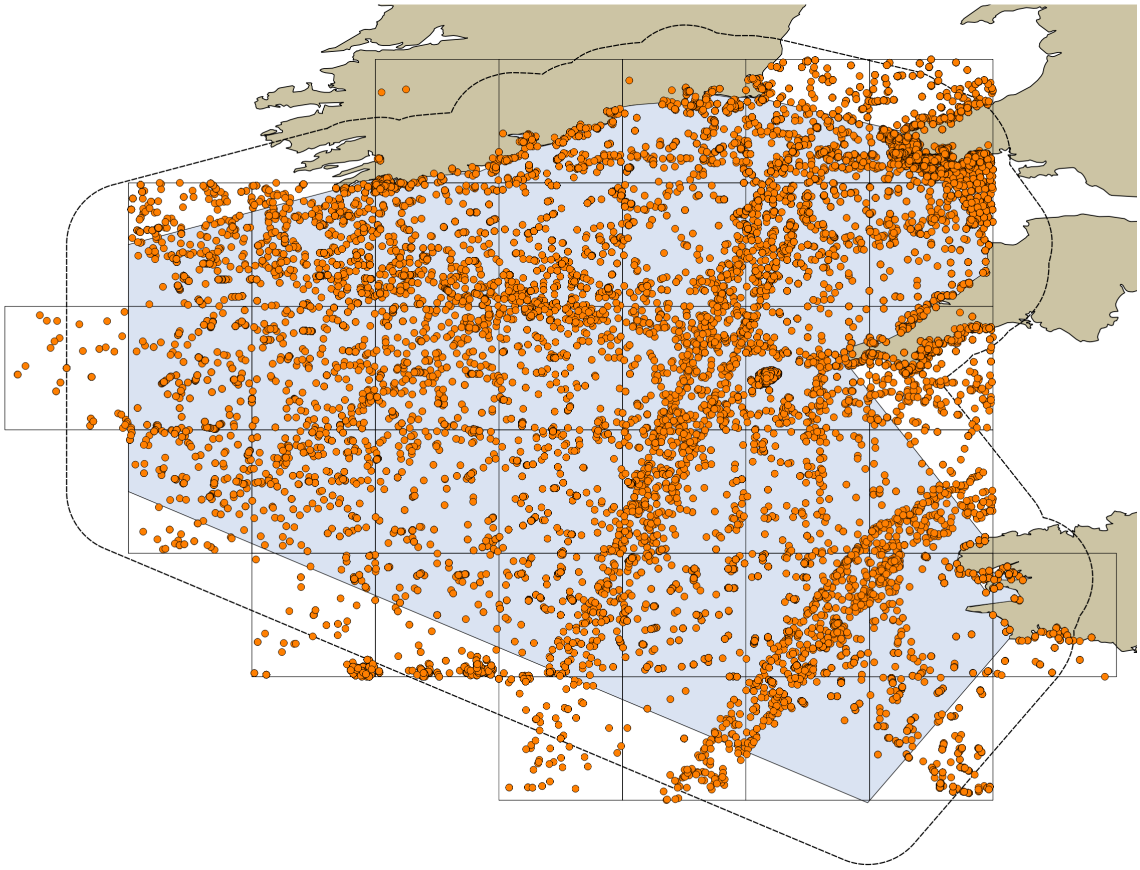

Figure 2.1: *Distribution of raw OBIS data (orange) and cell assignment (squares) in the Celtic Sea (blue) and 0.5 degree buffer zone (dotted line). Thirty-eight cells were considered in the analysis. I did not consider cells where less than 50% of their area overlapped the Celtic Sea and buffer zone.*

To ensure that between datasets I could assume similar reporting practices, datasets were grouped based on study methodology, study taxonomic focus, and study habitat focus, based on study metadata (Table 2.1). For example, all benthic surveys specifically targeting gastropods were grouped together, and separately all benthic surveys targeting invertebrates more generally were grouped together. This was because the model formulation used makes inferences on the unrecorded presence of one species based on the recorded presence of others, and therefore makes assumptions about the recording practices of surveyors. As such, in the latter case, I can assume that non-gastropod molluscs were not observed if they were not recorded, however in the former case, if non-gastropod molluscs were not recorded, this could be either because they were not observed or because they were present but not of interest to the study. In grouping datasets by methodology and by taxon and habitat focus, I am able to more confidently make assumptions about the recording practices of the surveyors. In cases where grouping reduced the number of cells modelled in a group to less than the total (38), trends in the subset of groups were taken to represent trends in the region as a whole.

Table 2.1: *Groupings for OBIS data based on the habitat and taxon foci, and methodology of the collectors of the source dataset. Blank cells indicate where no information on focus was supplied in metadata.*

Group	Habitat Focus	Taxon Focus	Methodology
1	Littoral	All taxa	Atlas data
2	-	Invertebrates	Museum collection
3	-	Plankton*	Plankton recorders/surveys
4	Littoral	All taxa	Survey
5	Near-shore benthic	All taxa	Survey
6	-	All taxa	Survey
7	-	Molluscs	Survey
8	-	Fish*	Trawl
9	-	All taxa	Citizen science (diver survey)

* Note that studies may have recorded occurrence data for molluscs incidentally, despite their not being the primary taxon focus.

Additionally, to ensure some level of standardisation in data availability over time, dates within groups were binned such that each time-period bin contained approximately equal numbers of records, while still retaining enough bins to form a coherent analysis. In occupancy modelling terminology, I consider these binned time periods to represent closure periods (usually "years" in traditional implementations of the model) between which occupancy could change, but within which occupancy is static, with three further sub-periods representing groups of "visits" (Figure S1).

Therefore, points on output modelled time series represent the last (or in some cases only) year of the closure period. Of the original dataset, 482 species had sufficient data to be used in the occupancy modelling stage of the analysis. Citations for datasets used in modelling can be found in Table S1.

Following data download and processing, occupancy models were run for each species within each group, with data for each group being considered independently. Each model (Appendix S1) was run using JAGS (Plummer 2003), and convenience functions from the R package "sparta" (August et al. 2015, R Core Team 2017).

2.3.2 Occupancy model

I defined a random walk occupancy model with observation sub-model for unstructured data, as in Outhwaite et al. (2018), where true state of occupancy z at time t and in cell i is drawn from a Bernoulli distribution,

$$z_{it} \sim Bernoulli\ (\psi_{it})$$

Equation 2.1

Here, ψ_{it} is the *logit* linked probability of occurrence, defined by the random walk time-period effect a_t and random cell effect η_i, such that

$$logit(\psi_{it}) = a_t + \eta_i$$

Equation 2.2

The time-period effect a_t is drawn from a normal distribution with mean a_{t-1}, where a at $t=1$ is drawn from a vague normal distribution. Whether a species was observed, y, in cell i and time-period t during time sub-period v was again drawn from a Bernoulli distribution,

$$y_{itv} \sim Bernoulli(\lambda_{itv})$$

Equation 2.3

defined by the reporting probability, λ_{itv}, where

$$\lambda_{itv} = z_{it} \times p_{itv}$$

Equation 2.4

Here, detection probability is equal to the product of occupancy, z, and detection, p_{itv}: a *logit* linked function of the time-period specific probability α_t that a list of length 1 contains the focal species, and the logged list length of time sub-period v, $Log(L_{itv})$, multiplied by l, the parameter describing the relationship between increasing list length and detectability, such that

$$logit(p_{itv}) = \alpha_t + l \times Log(L_{itv})$$

Equation 2.5

Vague normal priors were applied to η and α, and vague uniform priors to l and initial cell occupancy. Occupancy models were run for each species within each group (defined by target taxon, target habitat, and methodology), with data for each group being considered independently. In all, 9 groups were considered, with the number of mollusc species individually modelled in each ranging between 7 and 353, resulting in 1,663 model runs in all. Each model was run with two chains for 45,000 iterations, following a burn-in of 5,000 iterations, using a thinning factor of 3. Vague priors were used so as to provide the model with no initial belief in the value of the parameter, using default vague parameter distributions and values supplied by the package “sparta”. Two chains were used to enable the calculation of the Rhat statistic (Gelman and Shirley 2011, see below), and chain length was chosen to ensure the best compromise between a successful model fit and computational requirements, with burn-in values being chosen as a suitable proportion of total chain length (in this case 10%). Thinning was used to minimise the effect of the inherent correlation in Markov chains, by retaining only every third estimated value from the chain to estimate posteriors (Hobbs and Hooten 2015).

2.3.3 Time series analysis

Model output was in the form of time series of proportional occupancy, which then underwent several quality checks and modifications. Each had the first and last points removed, as these were prone to being highly uncertain and affected strongly by the availability of data at the beginning and end of the study period, and as such only time series that contained 5 or more points before this modification were considered. Time series were also excluded where more than 10% of the points had an Rhat value (a measure of model convergence) of greater than or equal to 1.1 (where values of less than 1.1 imply adequate convergence; Gelman and Shirley 2011). Where the underlying distribution of a point estimate (the posterior distribution) had a standard deviation of greater than 0.2, this generally indicated the point at which the posterior is no longer unimodal but becomes uniform, indicating no additional information than the prior. When 50% of time series values had such posterior standard deviations, the time series was excluded from analysis. The values of 10% and 50% are largely arbitrary, and represent a compromise between ensuring a suitable fit of the model and retaining as many species assessments as possible. Where one species was modelled over several data groups, model outputs across groups were averaged, weighting each output by relative confidence, measured as the proportion of the time-series with posterior standard deviation values of less than 0.2. Temporal changes in species level occupancy were assessed as difference between proportional occupancy in the final time-period compared to initial proportional occupancy.

2.3.4 Assessment of threat status

Data on threat status for the species considered were retrieved from the IUCN Red List (IUCN 2018) and the OSPAR List of Threatened and/or Declining Species and Habitats (OSPAR Commission 2018), and allocated to one of three categories (Table 2.2).

Table 2.2: *Threat assessment status assigned to species considered, and their equivalent assessment status in the IUCN Red List, and OSPAR List of Threatened and/or Declining Species & Habitats.*

Assigned Category	IUCN Assessment Status	OSPAR Assessment Status
Unassessed	Unassessed Data Deficient	-
Not Threatened	Least Concern Near Threatened	-
Threatened	Vulnerable Endangered Critically Endangered Extinct	Included in OSPAR List

2.4 Results

Of the original 867 taxa in the OBIS dataset, 166 species (~19%) had sufficient data availability, and Rhat and posterior SD values I deemed acceptable, to be taken through to further analysis. Most of these were gastropods (N = 100) or bivalves (N = 55), with smaller numbers of Cephalopoda (N = 6), Polyplacophora (N = 4), and Scaphopoda (N = 1). Across all species for which modelled outputs were considered confident, the mean trend in species proportional occupancy over its recording period was a decline of 0.002, or a 0.2% decline in cells occupied. The median trend was a decline of 8.3×10^{-6}, or a 0.0008% decline in cells occupied. However there is a large amount of variation between species (Figure 2.2), with change in species proportional occupancy over their recording period ranging from -0.20 to +0.18, and 50% of species seeing a decrease in occupancy over time, with 50% seeing an increase or no change (Figure 2.3).

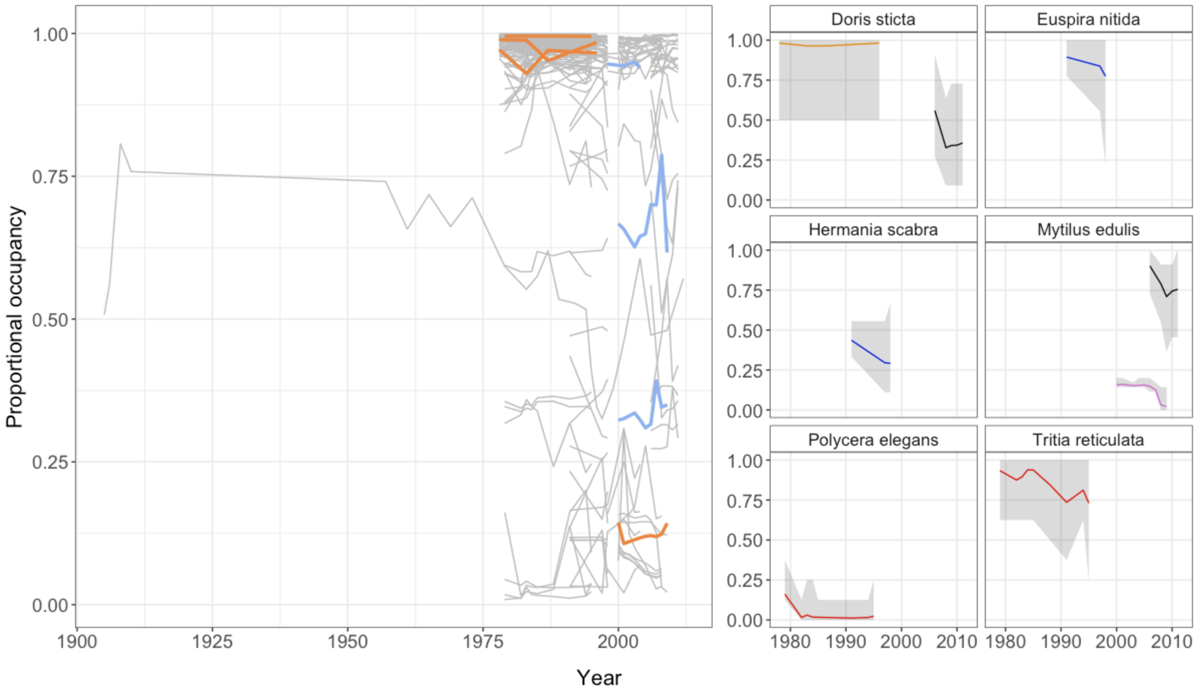

Figure 2.2: *Left: Output time series for 166 species of Celtic Sea mollusc successfully modelled, with previously assessed species highlighted (blue indicating non-threatened and orange indicating threatened species). Right: the 6 mollusc species showing declines in proportional occupancy of 0.1 (10% of surveyed cells over the time-series) or greater.*

I did not find any significant difference in average trend across the major taxonomic groups shown in Figure 2.3 (ANOVA, $F_{4,161} = 0.92$, $P = 0.45$), and there was no difference between orders within the two dominant classes (Gastropoda: $F_{10,89} = 0.91$, $P = 0.53$; Bivalvia: $F_{11,43} = 1.09$, $P = 0.39$). Modelled species time series, after removal of first and last values and in some cases being a combination of time series from 2 or more data groupings, ranged in length from 5 to 107 years. Points per time series ranged from 3 to 26, with a mean of 7. Approximately 59% of species had time series representing 10 or more years, with 43% having time series of 20 or more years, while 53% of species had 5 or more unique points, representing temporal binning periods.

While numerous species showed declines in occupancy over time, the gastropods *Tritia reticulata*, *Hermania scabra*, *Polycera elegans*, *Euspira nitida* and *Doris sticta*, and the bivalve *Mytilus edulis*, demonstrated the most substantial declines (a decrease in estimated proportional cell occupancy of 0.1 or greater over

Figure 2.3: *Change in proportional occupancy (final minus initial proportional occupancy) for 166 mollusc species over five classes, such that a decline of 0.1 represents a 10% decrease in cells occupied over the modelled time series. Larger points indicate more confidence in the time series (defined by the posterior standard deviation of points), and colour indicates species threat status according to IUCN Red List or OSPAR assessments (blue indicating non-threatened, orange indicating threatened).*

the period of recording, Table S2), though none have yet been assessed by the IUCN (IUCN 2018). Six species considered have however been formally assessed by the IUCN or OSPAR, three Cephalopods (*Illex coindetii*, *Sepia officinalis*, and *Todaropsis eblanae*, all non-threatened), two Gastropods (*Patella ulyssiponensis* and *Nucella lapillus*, both threatened in at least one north-east Atlantic region), and one Bivalve (*Ostrea edulis*, threatened in at least one north-east Atlantic region). All threatened species, and one unthreatened Cephalopod (*Sepia officinalis*), fell between the lower quartile and median proportional occupancy change, while *Illex coindetii* falls below the lower quartile, and *Todaropsis eblanae* above the upper quartile of proportional occupancy change (Figure 2.4).

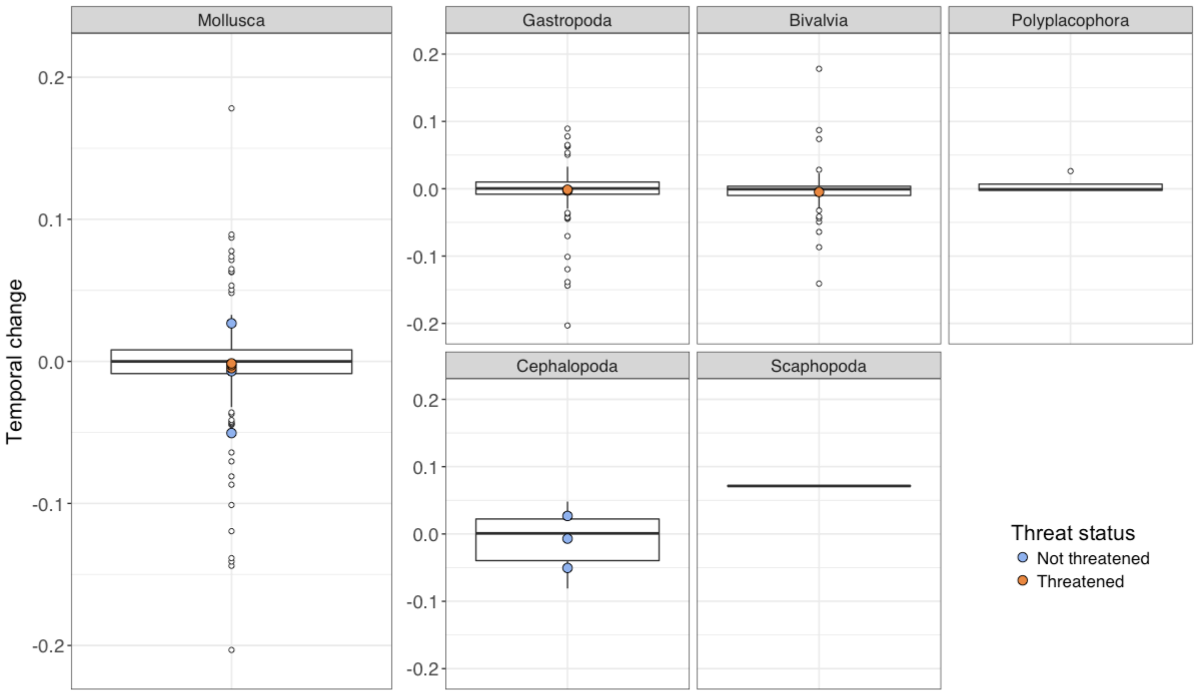

Figure 2.4: *Distribution of temporal change in proportional occupancy (final minus initial proportional occupancy) for 166 mollusc species over 5 groups, such that a decline of 0.1 indicates a 10% decrease in cells occupied over a modelled time series. Coloured points represent species that have been subject to formal conservation assessment, with blue indicating non-threatened and orange indicating threatened species.*

2.5 Discussion

Occupancy modelling was successfully applied to unstructured, aggregated marine biodiversity data to gain insight into the changes in biodiversity of marine molluscs in the Celtic Sea. Robust trends were derived for 166 species, with an overall slight decline in occupancy across species but considerable variability within all major taxonomic groups. Also evident is that despite the wealth of data available for UK waters, more data are needed before comment can be made on changes in most species: while Rhat values were almost universally good, and I was able to successfully model trends in 166 species, for many others the posterior standard deviation values made it clear that no information was gained from the occupancy modelling process. As such, many more species for which OBIS held data could not be considered successfully modelled, and were therefore not presented here. This is despite efforts to present the data in a way amenable to the modelling process, which in turn reduced the number of unique time series data points, resulting in numerous short time series. Despite this, I was able to estimate trends in 19% of the species for which I had data, a significant increase on previous, high profile national assessments (e.g. only 8 marine invertebrates across all taxa in the UK's recent State of Nature report; Hayhow et al. 2016) and a proportion of a similar order to that of other implementations of occupancy modelling for biodiversity studies (e.g. 25% species retention for Woodcock et al. 2016).

The overall trend displayed was a decrease in cells occupied by species over their recording period. Whether this pattern is data driven, or represents an ecological effect, requires further investigation. However, the findings of the State of Nature report (Hayhow et al. 2016) of long term declines in marine biodiversity (excluding fish), levels of threat across the entire phylum (Régnier et al. 2009), and the level of anthropogenic pressure on the Celtic and surrounding seas (ABPmer 2016) suggests that this decline may be ecologically rather than data-driven. Unfortunately, the paucity of specific assessments of marine mollusc biodiversity, population change or threat status means I am unable to speak directly to how my results compare to real world marine mollusc biodiversity change. Potentially a more significant subject of investigation however is the high level of variability between species, which is masked when attempting to draw conclusions of the Phylum as a whole. It is possible that the increases seen in species occupancy are a result of competitive release, invasive species increasing in occupancy, habitats becoming more appropriate for species as a result of climate change, changes in fishing practices, or any combination of these effects, while decreases may be a result of competition, exploitation, or decreasing habitat suitability. Determining which of these factors is operating in any specific case would require further research into the ecology of individual species, but my analysis is a useful first step towards prioritising species for this more detailed investigation. What is clear is that, while broad indices of change may be useful for engagement and policy, even a Phylum level index is likely to mask significant changes in individual species. It is possible that looking at indices of change in functional groups or keystone species may be more useful in a conservation context, while biodiversity monitoring more broadly will require us to consider the underlying variation in indices of change.

This analysis does however allow us to identify potentially at risk, vulnerable, or interesting species for further investigation (Table S2), especially important considering that only 6 of the 166 species considered have had any sort of formal assessment by the IUCN Red List (IUCN 2018) or OSPAR (OSPAR Commission 2018). Despite the fact that molluscs are heavily threatened (Régnier et al. 2009) and there is no *a priori* reason to expect rates of marine mollusc extinction risk to be lower than those of terrestrial mollusc species (Webb and Mindel 2015), marine molluscs remain under assessed, with only 1,377 of 43,600 known species (3.16%) assessed by the IUCN to date (IUCN 2018). In addition, 494 of these assessed species are listed as Data Deficient, a category usually associated with heightened conservation concern (Bland et al. 2014). Consistent with this, all of the most pronounced negative trends that I have derived occur in species with no existing conservation status assessment (Figure 2.3). Considering current investment and the effort required to survey species for threat assessment (Blamford and Gaston 1999, Stuart et al. 2010, Bland et al. 2014), methods such as those presented here, which can highlight potentially threatened or declining species and prioritise assessment and survey efforts, will be hugely valuable to protecting marine biodiversity going forward.

These results suggest that occupancy modelling is a viable method of developing meaningful information on marine biodiversity from unstructured data. While independent validation of the results is difficult, as the model is estimating an unknown, previous detailed assessments (van Strien et al. 2013, Isaac et al. 2014) of the modelling framework lend confidence to the methodology. Comparison to raw trends from the original OBIS data would do little to help this, as it is subject to the aforementioned biases, however examining how changes in the dominant species in OBIS data (i.e. the most often recorded) compare to the changes seen in modelled data could prove an interesting next step to assess model validity. Similarly, future assessment and modelling of a species with known trends may be useful to further add to the evidence base for occupancy modelling.

However, to implement these models successfully the data had to be manipulated extensively, and even having done so the level of data availability remains a significant factor in determining the output estimates of occupancy in some cases. Furthermore, this approach pushes the boundaries of the assumptions that occupancy is static within closure periods (represented by each time series point), since in some cases closure periods were years or even decades long, however such an approach has been employed in previous implementations of occupancy modelling (Boakes et al. 2017), and without improved data this is likely to always be necessary. There is however more that can be done to improve confidence going forward and produce more robust results, including introducing more covariates into the model, as well as implementing other methods such as multispecies modelling (Woodcock et al. 2016). Indeed, the implementation of a random-walk model here (Outhwaite et al. 2018) is already an improvement on a previously implemented dynamic model (not shown). Such modifications and increased complexity will likely be necessary to expand the methodology to further areas, as the seas of northern Europe are among the most data rich in OBIS.

Increasing model complexity, and taxonomic and geographic breadth, will however greatly increase required computational time and power. In this case, the most data rich group required 20-30 minutes of computational time and approximately 10GB of memory per species (single cluster core), though both sub-setting (grouping) the data and data manipulations reduced the raw quantity of model data, resulting in reduced demands. Results will also of course be improved with the collection of new, and mobilisation of existing, species level occupancy data – even in this data rich environment conclusions can only be drawn on 166 species, of the 867 for which I had data.

It is important also to note that this is a geographically restricted study, and decline here may not indicate wider scale declines, and likewise wider scale threats may not necessarily translate to local decreases in occupancy, possibly explaining why species assessed by the IUCN or OSPAR as declining appear in this model as relatively stable, and vice versa. Similarly, note that occupancy is measured here at a coarse scale (1° latitude-longitude grid cells), and as such stability in modelled occupancy at this cell level may mask finer scale local population declines. While it is often observed that local scale abundance is reflected in larger scale occupancy (Freckleton et al. 2005, Soininen and Heino 2005), whether this pattern holds here would need to be the subject of further investigation.

Overall, this methodology substantially increases our ability to document broad scale trends in marine biodiversity by extracting maximum value from large, unstructured aggregations of biodiversity data such as OBIS or GBIF (GBIF.org 2018). This case study of Celtic Sea molluscs has already considerably increased the number of marine invertebrate species for which trends in regional distribution can be estimated. My results also emphasise that while cross-taxon indices of biodiversity change have considerable value as communication tools, they can also mask variation across species, and should be considered as a starting point to identify specific cases requiring further, more detailed research.

3: Global trends in the genus *Conus* from multispecies occupancy models

3.1 Abstract

Marine invertebrates have received less attention than vertebrates when considering changes in marine biodiversity in the face of anthropogenic threats, likely as a result of a historical notion that they are more resilient. Recent studies however have looked to remedy this, notably through the attention given to the genus *Conus*, the most diverse marine genus and the first gastropod genus assessed comprehensively for the IUCN Red List. Work is still required however to increase our understanding of marine invertebrate trends. Here, I assess the utility of multispecies occupancy modelling to fill this knowledge gap and aid in the wider assessment of marine invertebrates, estimating temporal changes in proportional occupancy for 124 species of *Conus*. I find variable trends in occupancy, with most species exhibiting increases in proportion of cells occupied over their time series, broadly supporting the idea that most of the genus is “Least Concern”. I however fail to estimate trends in most *Conus* species considered threatened, indicating that sufficient data to assess the most vulnerable species of the genus are not available, and that assessments at the genus level from occupancy modelling may be conservative, being unable to model the most substantial declines. I conclude by identifying a number of species not currently identified as threatened but exhibiting declines, as possible candidates for future research.

3.2 Introduction

Molluscs are one of the most diverse marine phyla, second only to the Arthropoda in species richness with over 48,000 described species (WoRMS Editorial Board 2018) of a potential 164,000 in total (Appeltans et al. 2012). Almost a quarter of extant marine species are molluscs (Peters et al. 2013), and cephalopod molluscs represent both the largest and most complex invertebrates (Crook and Walters 2011, Paxton 2016). Despite this, we still know little about the current status of, and level of threat faced by marine molluscs, and marine invertebrates in general (McManus 1997, Régnier et al. 2009, Peters et al. 2013), especially when compared to commercially exploited marine vertebrates and many terrestrial groups (Webb and Mindel 2015). Although this lack of attention has been justified in the past by a perception that marine species in general may be less prone to extinction, and less vulnerable to human impacts than terrestrial species (McKinney 1998, Roberts and Hawkins 1999, Peters et al. 2013), as well as more resilient to change than marine vertebrates (Jamieson 1993, Peters et al. 2013), recent work has suggested that marine groups are no less extinction-prone than terrestrial groups that have been subject to a similar amount of study (e.g. Webb and Mindel 2015), and that defaunation of the oceans is well underway (McCauley et al. 2015).

Global extinctions of marine molluscs appear to be rare, with only 4 reported to date (IUCN 2018). However, extinction risk and also extinction rate are likely to be higher than reported. Moreover, declines and local extinctions have been reported in a number of species (e.g. Carlton et al. 1991, Hobday et al. 2001, Dulvy et al. 2003), and the first invertebrate considered for the US endangered species list was a mollusc (*Haliotis sorenseni*, Hobday et al. 2001). Marine molluscs certainly face many of the same anthropogenic threats that are known to have affected other marine groups. Molluscs including gastropods, bivalves, and cephalopods, are exploited by fisheries, with c. 6M tonnes of molluscs landed in 2016 (FAO 2018c). Additionally, ocean acidification poses a threat to those mollusc species that produce calcareous shells (Cooley et al. 2009, 2012, Parker et al. 2013), threatening not only these species but those ecosystems that rely on them as engineers and habitat producers (Gutierrez et al. 2003), and potentially having a significant effect on the availability of molluscs to fisheries in the near future (Cooley et al. 2012). Marine pollution also endangers molluscs, leading to vulnerability to disease (Pipe and Coles 1995) and cellular degeneration (Jebali et al. 2007).

In recognition of the threats experienced by marine molluscs, and the likely gap in our knowledge of their status and trends, recent effort has been directed towards assessing molluscs in a more systematic way. The first full IUCN Red List assessment of a marine gastropod mollusc genus was published for *Conus* by Peters et al. (2013), which is also the most species rich marine animal genus (Duda and Kohn 2005). *Conus* is a venomous sea snail with a global tropical distribution (Bouchet 1990, Peters et al. 2013) of great interest for bio-prospecting, and important economically for local communities (Taylor et al. 1993, Garber 2005, Peters et al. 2013), and of significance as a component of the first human cultures (e.g. Amesbury et al. 1996, Chadwick and Olivera 2009, D'Errico and Backwell 2016). Applying similar rigorous assessments to other mollusc groups will require considerable investment, however the assessment of *Conus* provides an opportunity to test the extent to which aggregated global biodiversity data stored in repositories such as the OBIS (the Ocean Biogeographic Information System, OBIS 2018) can be used to preliminarily assess species trends, and to identify species or groups of conservation concern.

Using OBIS data to assess trends in *Conus* molluscs requires that we account for the biases and structure problems inherent in OBIS. Here, I apply the same occupancy modelling framework (MacKenzie et al. 2006, Isaac et al. 2014) outlined in the previous chapter to derive trends for *Conus* molluscs. Assessing *Conus* is useful in this case as the previous work of Peters et al (2013) presents a point of comparison for trends resulting from this analysis. Furthermore, *Conus* epitomises the data problems inherent in large data repositories such as OBIS, including erroneous location data, numerous incomplete records and variable data availability over the length of the time series, and as such will make an interesting test case. I utilise a multispecies model here, as opposed to the single species model of the previous chapter, as multispecies models enable the sharing of information between species during parameter estimation, and assessing only a single genus makes this information sharing logical, and preferable in cases where data availability is limited (Zipkin et al. 2009, Ruiz-Gutiérrez et al. 2010), as in *Conus*. This model is additionally dynamic, allowing for colonisation and extinction at variable rates over time, enabling us to better model the available data. As such this study not only seeks to derive global trends in an important genus, but also examine the suitability of multispecies occupancy models for aggregated marine biodiversity data, and their potential for the development of an urgently needed global index of marine biodiversity change (Edgar et al. 2016).

3.3 Methods

3.3.1 Data download and processing

The data download and processing procedure here followed closely that of Chapter 2. All available data for the genus *Conus* was downloaded from OBIS using R (R Core Team 2017) and the package "robis" (Provoost et al. 2017). Metadata associated with the studies that collected *Conus* data was also retrieved using the OBIS API and downloaded OBIS resource identifiers. Taxonomy was verified using the package "worrms" (Chamberlain 2017), and records were then binned into 5-degree square cells (Figure 3.1, QGIS Development Team, 2018; shapefiles from naturalearthdata.com). Cells falling entirely on land (with a 1 degree buffer zone), likely a result of for example significant coordinate imprecision or rounding, were excluded from analysis.

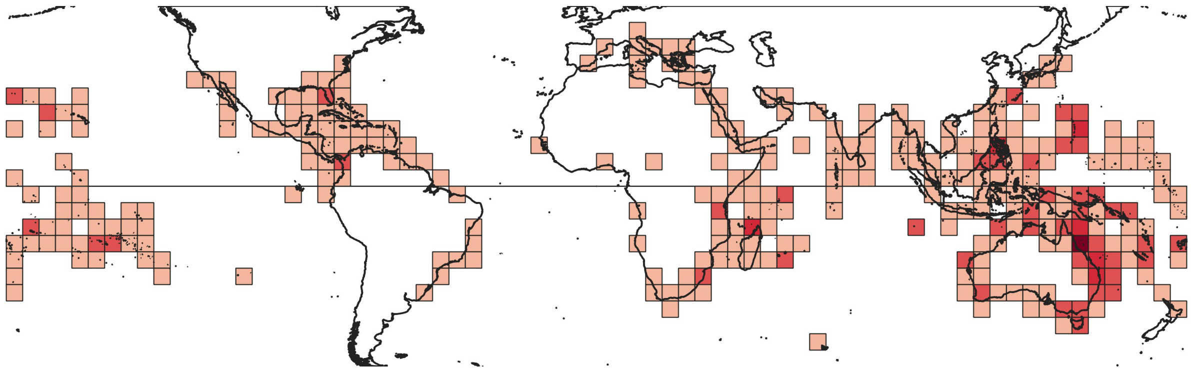

Figure 3.1: *Distribution of* Conus *records from OBIS, assigned to a 5-degree square grid. Darker colours indicate increased record density.*

As previously, data were then assigned to groupings based on the aims of the study that collected them, specifically the habitat targeted by the study, the methodology used and the focal taxa of the study (Table 3.1). In this way, studies within the same group could be assumed to have used similar recording practices having observed a species. For example, I can assume all studies that focused on recording molluscs would have recorded *Conus* if it was observed, however I cannot make the same assumption of studies that may have recorded *Conus* incidentally while focusing on another taxa, e.g. fish. This step is particularly important in this formulation of the occupancy model as the observation sub-model makes inferences on detectability based on species lists and surveyor behaviour, and as such grouping the data to make these behaviours as similar as possible within a group is desirable. Following grouping, data were also temporally binned to produce time-periods of approximately equal data availability (Figure S2), as described previously. Each time period goes on to represent one point on the output time-series of estimated proportional occupancy, or a "closure period" in occupancy modelling terminology. Citations for data used in the modelling process can be found in Table S3. Data were then formatted for occupancy modelling using functions from the R package "sparta", modified to produce data files suitable for multispecies modelling (August et al. 2015). Occupancy models (Appendix S2) were run in R using JAGS (Plummer 2003, R Core Team 2017).

Table 3.1: *Habitat*Taxon*Methodology groupings for modelled* Conus *data. Each group underwent multispecies modelling independently. Blanks represent where sufficient information on study focus was not available in OBIS metadata.*

Group	Habitat Focus	Taxon Focus	Methodology
1	Benthic	Animals	Grab, dredge or trawl
2	-	Animals	Museum collection
3	Benthic	All or unspecified	Grab, dredge or trawl
4	Seamounts	All or unspecified	-
5	-	All or unspecified	Museum collection
6	-	All or unspecified	-
7	-	Invertebrates	Museum collection
8	-	Invertebrates	-
9	-	Molluscs	Museum collection

3.3.2 Multispecies dynamic occupancy model

I defined a dynamic multispecies occupancy model (modified from Ruiz-Gutiérrez et al. 2010, Woodcock et al. 2016), which is formulated in a similar way to the single species model described previously. The true state of occupancy of species *i* in cell *j* at time *t* is defined by

$$z_{i,j,t} \sim Bernoulli(\psi_{i,j,t})$$

Equation 3.1

where $\psi_{i,j,t}$ is the species specific probability of occurrence in cell *j* at time *t* defined by

$$\psi_{i,j,t} = z_{i,j,t-1} \times \varphi_{i,j,t} + (1 - z_{i,j,t-1}) \times \gamma_i$$

Equation 3.2

Here, $\varphi_{i,j,t}$ and γ_i are respectively the *logit* linked species, cell, and time specific persistence probability, and the *logit* linked species specific colonisation probability. $\varphi_{i,j,t}$ is defined by the *logit* linked sum of the species specific persistence intercept ϕ_i and the random cell effect η_j:

$$logit(\varphi_{i,j,t}) = \phi_i + \eta_j$$

Equation 3.3

Observation of species *i* during visit *k* was defined by

$$y_{i,k} \sim Bernoulli(\lambda_{i,k})$$

Equation 3.4

where detection probability $\lambda_{i,k}$ of species *i* at cell *j* and year *t* defined by visit *k* equals

$$\lambda_{i,k} = z_{i,j,t} \times p_{i,k}$$

Equation 3.5

Here, detection probability is the product of state of occupancy and the *logit* linked function of observation probability $p_{i,k}$ defined by the random year effect α_t and $log(L_k) \times l_i$, a term describing the logged length of a cell species list on visit *k* multiplied by the factor l_i describing the relationship between increasing list length and increasing probability of detection of species *i*, such that

$$logit(p_{i,k}) = \alpha_t + log(L_k) \times l_i$$

Equation 3.6

Vague normal priors were applied to η, α, γ and ϕ, and vague uniform priors to l and initial cell occupancy. Occupancy models were run for each grouping separately. Each model was run with two chains for 35,000 iterations, with a burn-in of 15,000 iterations and thinning factor of 3.

3.3.3 Time series analysis

Output time series underwent a number of quality control checks before being analysed. Firstly, as in Chapter 2, the first and last time series values were discarded, as they were prone to high levels of uncertainty. Any time series following this that comprised of fewer than three points (binned time-periods) was discarded. Likewise, time series were discarded when (a) 10% or more of Rhat values for proportional occupancy were greater than 1.1, (b) 50% or more of proportional occupancy values had posterior distribution standard deviations greater than 0.2, and (c) 50% or more of proportional occupancy values had credible interval sizes of greater than 0.5. Rhat is a measure of convergence, where a value of less than 1.1 is generally considered good (Gelman and Shirley 2011), while standard deviations of less than 0.2 indicate that the parameter estimates are informative. Where a single species was modelled in multiple groups, change in proportional occupancy (final occupancy minus initial occupancy) was averaged across groups, weighting the average from each group by (a) confidence (proportion of the time series with posterior SD≤0.2), and (b) confidence and length of time series (number of decades). Species threat status as assessed by the IUCN was retrieved from the IUCN Red List website (IUCN 2018), to act as an indicator of both knowledge of species trends, and the potential direction of trends, by broadly assuming that threatened species would display decreases in proportional occupancy over time.

3.4 Results

Trends were successfully modelled in 124 species of *Conus*, of 632 species in the genus in total (Peters et al. 2013). Only 3 methodological groupings (Table 3.1, groups 3, 7, and 9) of 9 could be modelled successfully and produced results reliable enough to go on to further analysis. One further group (5) ran successfully, but consistent failure of the parameter *p* to converge resulted in it being excluded from analysis. Of these 124 species modelled, 6 had no available assessment status from the IUCN Red List, despite the genus being previously completely assessed (Peters et al. 2013). Of those that did have threat status information, 3 were Data Deficient and 113 were of Least Concern, while one species, *Conus cardinalis*, was listed as Near Threatened and one species, *Conus anabathrum*, was listed as Vulnerable (Figure 3.2). In contrast, Peters et al. (2013) defined 87 Data Deficient species, 478 of Least Concern, 26 Near Threatened species and 27 Vulnerable species, as well as 11 Endangered and 3 Critically Endangered species. Species of Least Concern were significantly over-represented in those I was able to model, with species of every other classification being under-represented (Chi-square, $p < 0.001$).

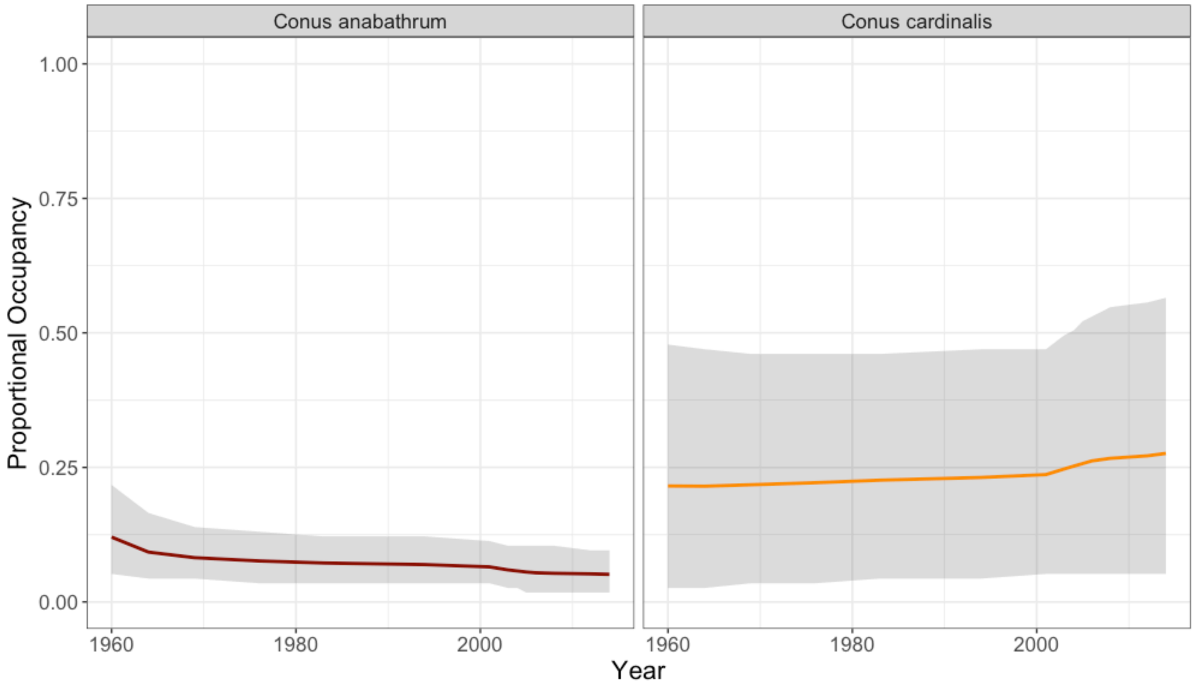

Figure 3.2: *Modelled trends in proportional occupancy for two species of* Conus *identified as Vulnerable* (C. anabathrum) *and Near Threatened* (C. cardinalis).

Of the 124 species successfully modelled, 79 (64%) showed increases in proportional occupancy or no change over their respective study periods, and 45 (36%) exhibited decreases in proportional occupancy. When weighting these changes by time series length, 81 species (65%) experienced increases or no change, while 43 (35%) exhibited decreases in proportional occupancy (Figure 3.3).

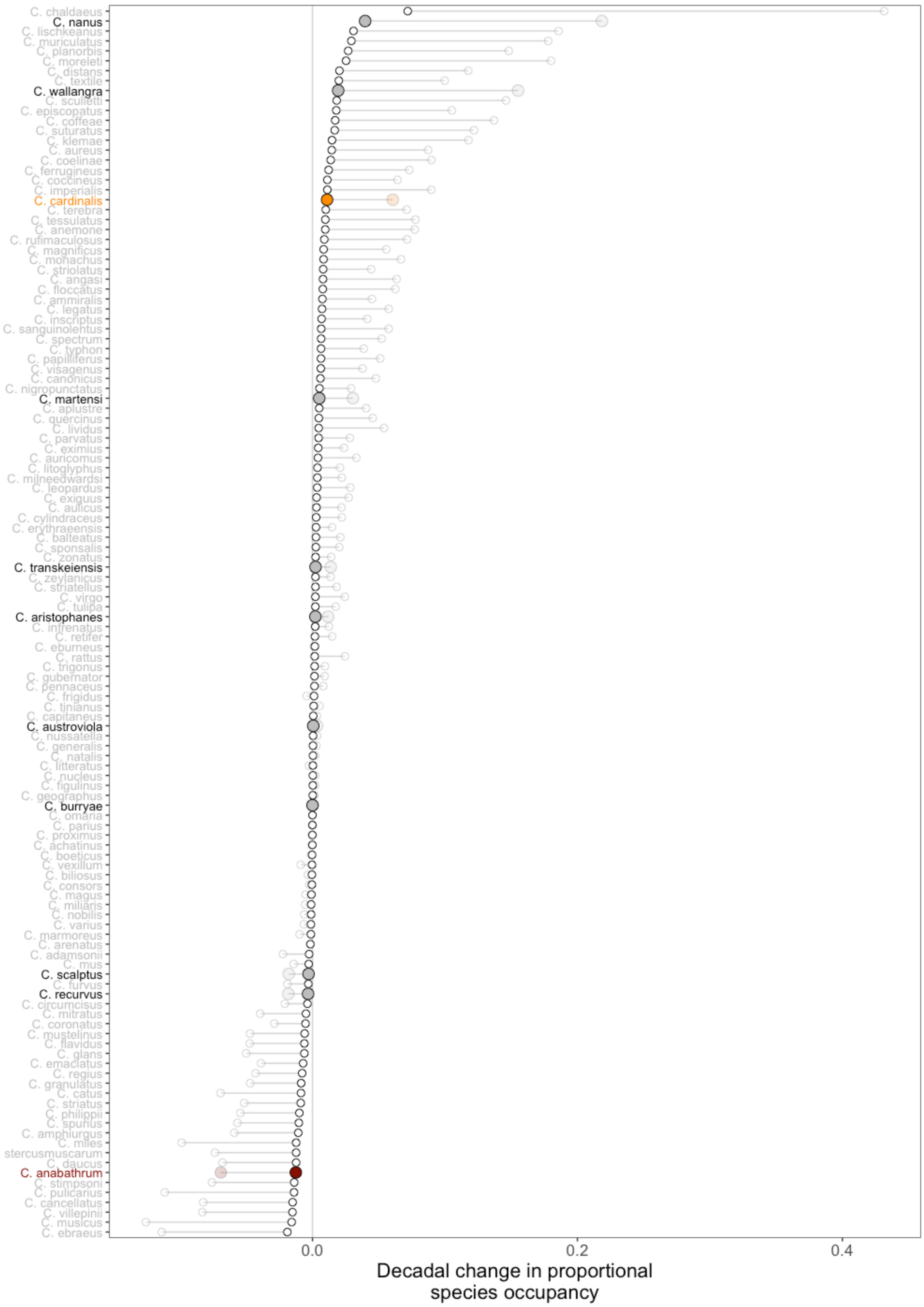

Figure 3.3: *Decadal change in Conus species proportional occupancy (bold), compared to non-weighted change (faint, lines). Species IUCN Red List threat status is represented by point colours: red = vulnerable, orange = near threatened, white = least concern, grey = data deficient or unassessed.*

Mean species decadal change was an increase in proportional occupancy of 0.003, equivalent to gaining occupancy in 0.3% of total cells per decade, and median decadal change exhibited was an increase in proportional occupancy of 0.002, equivalent to gaining occupancy in 0.2% of total cells per decade. *Conus* species display large degrees of variation in temporal occupancy change, with a range in decadal proportional occupancy changes of 0.07 to -0.02.

3.5 Discussion

Multispecies occupancy modelling was successfully employed to generate robust trends in 124 species of the genus *Conus*, or approximately 20% of the genus overall, using global data. I found a large degree of variation between species trends (standardised to decadal change) in proportional occupancy at 5-degree resolution, with most species experiencing decadal increases in occupancy. I was however only able to derive trends for 2 of the 67 *Conus* species identified as any degree of threatened or near threatened by the IUCN (IUCN 2018), indicating that previous field studies of *Conus* have failed to record sufficient data on the species that are most in need of temporal occupancy information. It is notable that this has wider implications in the production of biodiversity indicators, such that broad indexes from occupancy modelling may under-estimate declines by failing to produce trends in the most threatened species.

The two threatened or near threatened species that were successfully modelled (*Conus cardinalis* and *Conus anabathrum*) produced conflicting results. In the case of the vulnerable *C. anabathrum*, this analysis corresponds to that of the IUCN, with declines in both overall occupancy and cell occupancy standardised to decade suggesting this species may be vulnerable. This is not the case for the near threatened *C. cardinalis*, which our models suggest is increasing in occupancy. While this may initially seem counterintuitive, cell occupancy is obviously not the only factor defining threat level. Peters et al. (2013) name pollution, harvesting, disturbance and environmental change as the four leading causes of threat to *Conus* species, and as a shallow water, reef dwelling species (IUCN 2018), it is likely that any cell occupied by *C. cardinalis* is going to experience at least one of these threats, and as such increasing occupancy alone is unlikely to alleviate threat for this species.

Broadly, these results imply stability or increases in cell occupancy in most species. This would therefore agree with the assessment of many of these species as Least Concern, at least if we consider declining trends in cell occupancy as an indicator of threat. It is worth noting however, as in Chapter 2, aspects of this study may be conservative in their estimates of trends. A coarse 5-degree resolution may mask local scale declines in occupancy despite an increase in the number of 5-degree cells occupied. While abundance-occupancy theory suggests that this is unlikely (Freckleton et al. 2005, Soininen and Heino 2005), since large-scale occupancy usually reflects local abundance, we cannot rule out the possibility that spatial binning is masking finer scale declines without further information. Likewise the extended temporal bins used may mask declines that occur suddenly or on short timescales, which have the potential to threaten rarer species or smaller populations with extinction.

Of potential concern are the six species of *Conus* (*C. ebraeus, C. musicus, C. villepinii, C. cancellatus, C. pulicarius, C. stimpsoni*) that demonstrate greater declines than the vulnerable *C. anabathrum* (Figure 3.4, Table S4). While in three cases (*C. ebraeus*, *C. musicus*, and *C. pulicarius*), these declines occur in relatively common species (at least in terms of cells occupied), in the other three cases declines represent a much greater proportional loss of cell occupancy. In all cases, no population trend data is available for these species, and IUCN threat assessment is made based on expert opinion, range, perceived abundance, shell value to collectors, or some combination of these (Peters et al. 2013, IUCN 2018). There is additionally little species-specific literature regarding trends in the three declining and less common species (*C. villepinii, C. cancellatus, C. stimpsoni*), though these species do exhibit commonalities, all occurring in the Western Atlantic (Southern USA, Gulf of Mexico, Central America, in the case of *C. villepinii* ranging as far south as Brazil) and in relatively deep water (25m-475m, 40m-60m, 42m-196m respectively) (Rosenberg 2009). These results suggest that perceived abundance may be masking real-world declines, and that trends in these species warrant further investigation, particularly in the cases of *C. villepinii*, *C. cancellatus* and *C. stimpsoni*, where their similarity in depth preferences and range may enable straightforward collection of data on all three species.

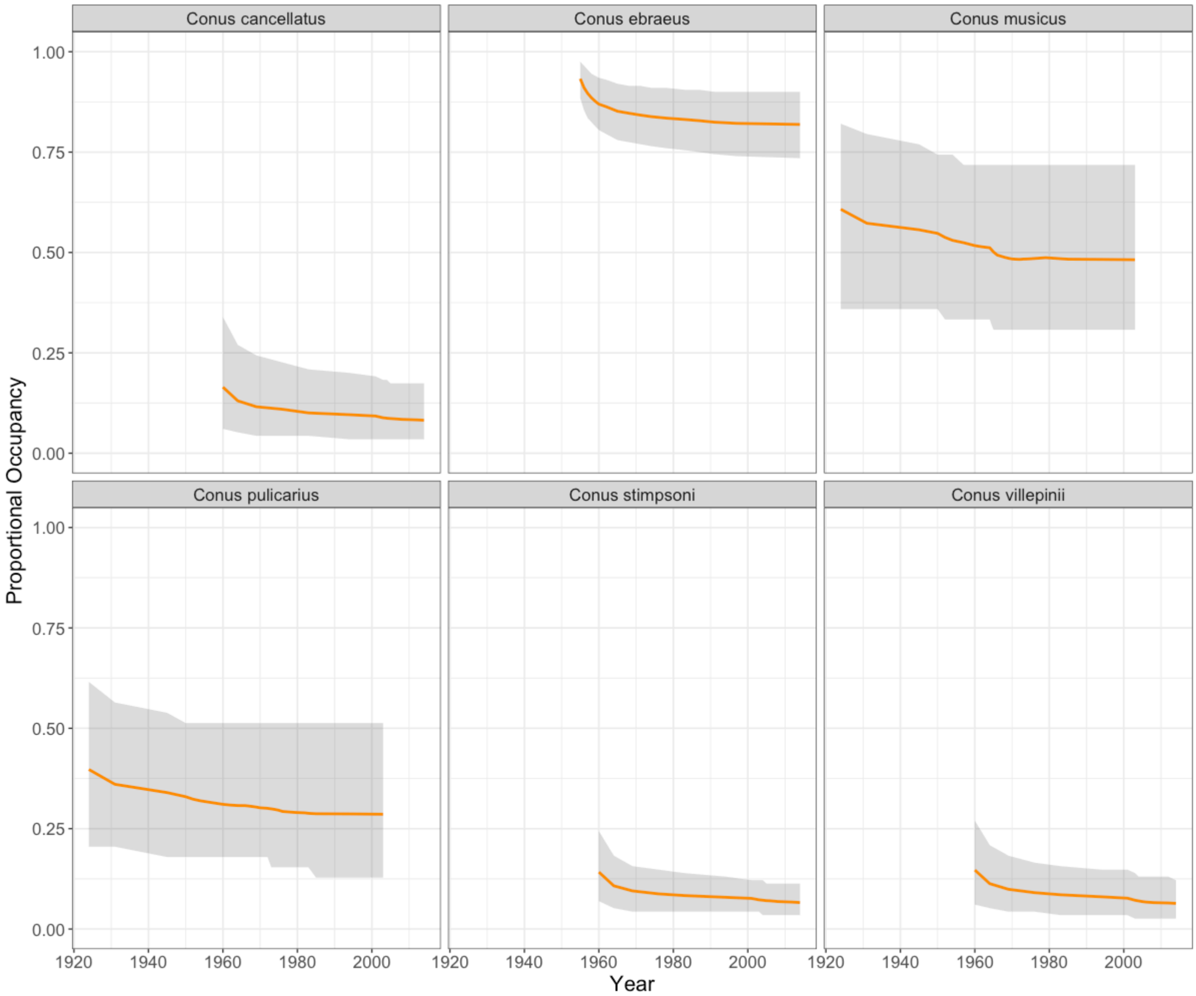

Figure 3.4: *Trends in six species exhibiting declines in proportional occupancy greater than those of* C. anabathrum, *all previously listed as Least Concern by the IUCN.*

One interesting irregularity in the data presented here is the absence of species assessment data for a number of species, despite the complete genus being previously assessed. Taxonomic verification through the World Register of Marine Species (WoRMS Editorial Board 2018) indicated that these taxa were accepted as verified species, and have not been subject to taxonomic revision since the publication of the genus assessment. The genus therefore either has not been fully assessed, or assessment criteria are not publicly available for all species. No matter the case, it is interesting to note that even after a comprehensive, “full” assessment of the genus, there is still unavailable information.

In terms of the modelling framework, multispecies models outperformed the single species models used in Chapter 2 in this case, in that trends in occupancy for 39 more *Conus* species could be successfully modelled (a 46% increase in the number of species successfully modelled). This is likely a function of the multispecies models’ ability to share information across species, improving parameter estimates for single species when data for that specific species may be more limited (Zipkin et al. 2009, Ruiz-Gutiérrez et al. 2010). However, this increased performance came at the cost of greatly increased requirements in terms of computational time and resources. In all model runs (Table 3.1), I was only able to include data for *Conus* species, and not for co-occurring species that may have increased the accuracy of estimates, or the number of *Conus* species successfully modelled. Likewise, in many cases computational limitations meant I was only able to monitor the parameter of interest, namely proportional occupancy, rather than all model parameters, and as such in these cases I was unable to check for convergence in these parameters. When I was able to monitor more parameters however, convergence was observed in all but one case (parameter p in Group 5, which was subsequently removed from analysis), lending confidence to these results, especially since these computational limitations were only experienced when modelling the groups with most data, and therefore those with most information to draw on to estimate parameters. As computational power required is broadly a function of the number of species, cells, closure periods, and iterations, I would therefore suggest that multispecies models such as these are only attempted for datasets with large temporal or spatial dimensions, or a large number of species, when ample computational power is available.

Overall, these results indicate that multispecies occupancy modelling can be successfully implemented in cases where occurrence data for marine species may be limited. However, doing so comes at the cost of greatly increased computational demands, which must be considered when making a decision on which modelling framework to use. In this case, I was able to estimate species level trends in 20% of the genus *Conus*, finding stability or increasing trends in proportional occupancy in a majority of species, broadly agreeing with the recent IUCN Red List assessment of much of the genus as Least Concern. More significantly however, I have found that for the species of *Conus* assessed as most threatened, data is not available to estimate robust trends in occupancy. This has wider implications for occupancy modelling and its use in the production of indicators of biodiversity change, suggesting that the most threatened species may be missed in broad scale studies of trends implementing such models. Despite this, I have identified six species of *Conus* considered to be Least Concern that exhibit changes in proportional occupancy of greater magnitude than those of a species identified as Vulnerable, three of which in particular may benefit from increased study and data collection.

4: Cetacean abundance-occupancy relationships in European waters: how well does aggregated biodiversity data perform?

4.1 Abstract

The generally positive relationship between local abundance and regional occupancy, termed the abundance-occupancy relationship (AOR), is one of the most prevalent in macroecology. Identifying both inter- and intraspecific relationships is useful for numerous reasons, especially in a conservation context where they can be used to infer abundance from more easily collected occupancy data. Here, I derive AORs for 20 species of cetacean in European waters, using data from effort-based surveys. I also apply a multispecies occupancy modelling methodology, to account for detection bias and surveyor effort, to three additional sources of presence-only data and assess the ability of modelled estimates of occupancy both to replicate these AORs, and to estimate abundance. I find significant positive intraspecific AORs for 14 cetacean species, and significant positive interspecific AORs for all years assessed. Interspecific AORs were successfully replicated using occupancy modelled data. Furthermore, I find estimates of abundance produced with modelled occupancy values and known AORs to be positively correlated with known abundance values, indicating an ability to estimate the rank order of species abundance within a given year. These results indicate that occupancy modelling can be combined with already available and easily collectable data to infer abundance in cetacean species, potentially leading to improved and more cost-effective conservation and management. However, intensive effort-based survey data allow for more accurate detection of temporal trends within species.

4.2 Introduction

Abundance-Occupancy Relationships (AORs) (Brown 1984, Gaston et al. 2000), the relationship between regional occupancy and local abundance of a species, are one of the most ubiquitous patterns in macroecology, and have been suggested as one of the few "general rules" of ecology (Lawton 1999, Hall et al. 2010). Positive interspecific AORs, where locally abundant species also tend to be regionally widespread, have been described in numerous taxa in marine and terrestrial systems (see e.g. Gaston et al. 2000, Blackburn et al. 2006, Webb et al. 2011), and are an emergent property of both models of regional population dynamics (e.g. Freckleton et al. 2005) and of microcosm experiments (e.g. Warren and Gaston 1997). AORs are observed between species (interspecifically), but also over space and time within a species (intraspecifically), though intraspecific patterns are usually more variable, and conform less to the "general rule" of positive AORs (Gaston et al. 2000, Webb et al. 2007).

The mechanisms giving rise to AORs are still unclear and repeatedly debated (reviewed in Gaston et al. 2000). However, while we still do not fully understand the reasons that these patterns arise, or why some species deviate from the typical positive pattern (e.g. Blackburn et al. 1998), they are nevertheless useful for a number of reasons, a central theme among these being the ability to infer changes in abundance from changes in occupancy. Whether a species occupies a site is typically much easier to determine than the abundance of a species at a site. As such, using AORs to infer the local abundance of a species based on their recorded occupancy, or at least the trend in changing abundance with changing occupancy, is useful both for conservation and for the managed exploitation of natural resources (Gaston 1999, Gaston et al. 2000, Fisher and Frank 2004, Hall et al. 2010, Frisk et al. 2011, Hui et al. 2012). Moreover, in conservation contexts, a recorded decrease in occupancy under an AOR framework implies a disproportionate decrease in abundance. This results in the so-called "double jeopardy" of threatened species, whereby species that occur in restricted ranges would also have lower density, and therefore be more susceptible to extinction (Lawton 1993, Gaston 1998, 1999, Johnson 1998, Gaston et al. 2000). A clear understanding of how occupancy scales with abundance for a particular species or group is therefore undoubtedly desirable, whether to determine the strength of the relationship or if a taxon is one of the few that deviate from this “general rule”, evidenced by the multitude of studies focusing on describing and explaining the phenomenon in numerous systems and taxa (e.g. Holt and Gaston 2003, Fisher and Frank 2004, Blackburn et al. 2006, Gaston et al. 2006, Foggo et al. 2007, Webb et al. 2007, 2011, Hall et al. 2010, Verberk et al. 2010, Pérez-del-Olmo et al. 2011).

AORs are especially important for groups of species in which gaining accurate abundance estimates is logistically challenging, but determining regional occurrence more straightforward, such that known AORs can be exploited to infer patterns and trends in abundance. One such group is the cetaceans. Comprising of whales, dolphins and porpoises, cetaceans represent a broad and charismatic mammalian clade threatened by numerous factors, including climate change (MacLeod et al. 2005, Simmonds and Isaac 2007, Simmonds and Eliott 2009), past and current exploitation by whaling and fishing industries (e.g. Van Waerebeek et al. 1997, Barbosa-Filho et al. 2018), and a number of other maritime activities resulting in for example ship-strikes, entanglement, and disorientation from underwater noise (e.g. Knowlton and Kraus 2001, Nowacek et al. 2007, Van Waerebeek et al. 2007, Weilgart 2007). Many cetaceans are also long-lived and slow to reproduce (Musick 1999), amplifying the effects of these threats. This is notable not only because cetaceans play an important ecological role as predators of most trophic levels (Bowen 1997, Morissette et al. 2006), but also because cetaceans often represent a flagship group for conservation (Sergio et al. 2008, Parsons et al. 2015), with few other marine groups evoking the same level of public engagement, response, and emotion. Moreover, the status of cetaceans is frequently proposed as an indicator of overall ecosystem state (e.g. Moffat et al. 2011), which requires abundance data that are often lacking. Understanding abundance-occupancy dynamics within and between cetacean species is therefore very useful both from a purely theoretical macroecological perspective, and from a conservation and policy standpoint.

However to date only one study has focused on determining the presence and shape AORs in cetaceans (Hall et al. 2010), and more work is needed to expand beyond the four species considered there.

Here, I derive AORs for 20 species of cetaceans, using occupancy and abundance data from effort-based surveys of European waters, collated as part of the Marine Ecosystems Research Programme (MERP, marine-ecosystems.org.uk). Additionally, I use a dynamic multispecies occupancy modelling methodology (MacKenzie et al. 2006, Ruiz-Gutiérrez et al. 2010, Woodcock et al. 2016) to estimate cetacean occupancy for European waters using aggregated data derived from two other sources: a presence-only occupancy dataset from MERP, and an additional presence-only dataset from OBIS (the Ocean Biogeographic Information System, OBIS 2018), in order to assess the accuracy of these occupancy estimates and AORs derived from them when compared to surveyed occupancy. I chose to assess these 20 species due to their coverage within the MERP effort-based survey dataset, as well as having sufficient data from OBIS and the MERP presence-only dataset to model and take through to AOR analysis. In doing this, I address three questions: (a) how do occupancy and abundance for the 20 species of cetaceans scale in European waters, (b) how well do modelled estimates of occupancy derived from "lower quality" aggregated data sources compare to those from dedicated surveys, and (c) how reliable are these estimates of occupancy when inferring intra- and interspecific AORs and estimating abundance. Doing so will be a useful initial step to both increase our understanding of cetacean AORs, and to determine how well abundance can be inferred from oft collected or freely accessible presence-only data when true abundance estimates may be lacking.

4.3 Methods

4.3.1 Data sourcing, download and processing

Effort-based survey data recording occupancy and abundance (individuals per km^2) of cetacean species on a $50km^2$ grid in European waters (Figure 4.1, QGIS

Development Team, 2018; shapefiles from naturalearthdata.com) was provided by the Marine Ecosystems Research Programme (MERP, marine-ecosystems.org.uk, hereafter the "MERP survey data"). Also provided by MERP was a presence-only dataset for cetaceans in the same area, recording sightings from any source, targeted or opportunistic (hereafter the "MERP presence-only data"). Full details are available in Waggitt and Evans (in prep). OBIS cetacean data was retrieved through the package "robis" in R (Provoost et al. 2017, R Core Team 2017), using the extents defined by the MERP survey data (35 to 65 degrees latitude, -20 to 20 degrees longitude). OBIS data recorded before 1900, without a date of recording, or with coordinate uncertainty (when reported) of greater than 20km were excluded from analysis. Data points in the OBIS or MERP presence-only data falling beyond 1 decimal degree inland were likewise removed from the dataset. All data was assigned a cell identifier based on a $50km^2$ grid following the MERP survey data, and taxonomic names for species from all datasets was verified against the World Register of Marine Species using the package "worrms" (Chamberlain 2017), with unaccepted names being changed to accepted versions where possible. Records with unaccepted names without an accepted variant were removed from the dataset. Records from any dataset not identified to at least species level were removed, and records identified to below species level were normalised to their parent species.

MERP presence-only and OBIS data were then temporally binned to ensure standardised data availability through time. This step was additionally important here as data were highly seasonal. As such, I chose to use years as the smallest period of modelling, or cell-level "visit", and a minimum of three combined years as a temporal bin representing a closure period. Following this, OBIS data were grouped in a similar way to that described in previous chapters, to allow me to assume relatively standard recording practices within groups. Here I chose to use three broad groupings, specifically I group by whether data was from (a) a targeted survey (hereafter the "OBIS targeted survey data"), (b) opportunistic recording (hereafter the "OBIS opportunistic recording data"), or (c) mixed or unknown sources (including museum collections). This is for two reasons. Firstly, to ensure each group had the most possible data to increase confidence in the output estimates of occupancy, and secondly because the MERP presence-only data was supplied with no metadata. The MERP data were collected both in targeted surveys and opportunistically, but lacking record level information about collection method I could not further subset. To ensure relatively standardised treatment across all data, but also allow for reasonably robust model assumptions in OBIS data, I chose not to subset OBIS data further than as described above. Citations for OBIS data used in modelling can be found in Table S5.

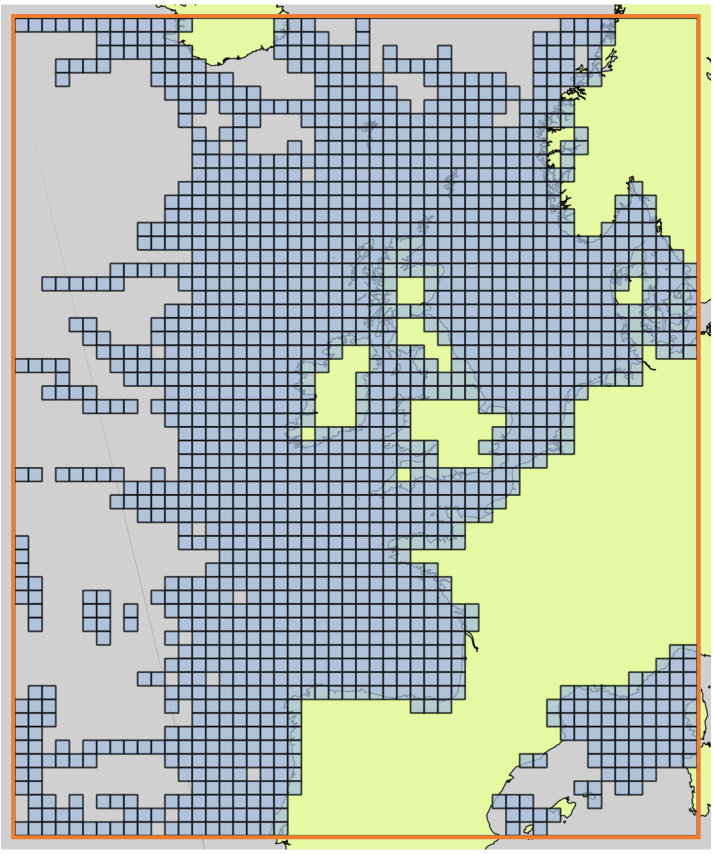

Figure 4.1: *Cells in European waters sampled by MERP effort-based survey data (blue), and the bounding box used for OBIS and MERP presence only data (orange).*

4.3.2 Occupancy modelling

OBIS and MERP presence-only data were modelled using a dynamic multispecies occupancy model as outlined in Chapter 3 (Ruiz-Gutiérrez et al. 2010, Woodcock et al. 2016, Appendix S2). The MERP data and three OBIS sub-groups were modelled independently, for 35,000 iterations following a burn-in of 15,000 iterations, using 2 chains and a thinning factor of 3. All occupancy models were run using R and JAGS (Plummer 2003, R Core Team 2017).

As in Chapter 3, all output occupancy time series were subject to a number of quality control checks, however none failed the quality control assessment outlined previously, namely that any time series (a) had 50% of values with credible intervals of greater than 0.5, (b) had 10% of values with Rhats of greater than 1.1, or (c) had 50% of values with proportional occupancy posterior standard deviation of greater than 0.2. I chose not to remove first and last time series values here to maximise the number of points from which to model AORs, however even with these points included, all time series successfully fulfilled quality control criteria, and as such I felt comfortable including these values in the analysis. One OBIS group, derived from mixed or unknown sources, was excluded from further analysis, as occupancy estimates here failed to correlate with those of the MERP survey data or other occupancy modelled data.

Occupancy estimates from modelled OBIS and MERP presence-only data were then compared to recorded occupancy from effort-based survey data, to assess the ability of occupancy modelling and unstructured data to capture both absolute, and trends in, occupancy change. This was done in two ways. Firstly, trends in proportional occupancy were assessed in effort-based survey data, and modelled MERP presence only and OBIS data, using three methods: (a) final minus initial occupancy, (b) change in mean occupancy between the first and second half of time series, and (c) change in mean occupancy between the first two thirds and last third of time series. These changes were assigned to broad groups based on the direction and magnitude of change in proportional occupancy, specifically (a) increases of more than 0.2 (++), (b) increases of less than 0.2 (+), (c) decreases of less than 0.2 (-), and (d) decreases of greater than 0.2 (--). Following this, percentage agreement between surveyed occupancy and modelled occupancy from MERP and OBIS data was assessed, both in terms of direction of change, and direction and magnitude of change. Additionally, for each modelled group and within each year, second order polynomials were fitted modelling surveyed occupancy against the difference between modelled occupancy estimates and surveyed occupancy, such that polynomial models were assessing the relationship between increasing surveyed occupancy, and the level of over- or underestimation by occupancy modelled estimates.

4.3.3 Abundance-occupancy relationships

Abundance-occupancy relationships, both for each species over time (intraspecific) and every species within a year (interspecific) were modelled using effort-based survey data and binomial GLMs of the form

$$\textit{proportional occupancy} \sim a + b \times \log(\textit{mean maximal abundance})$$

Equation 4.1

where proportional occupancy is the maximum number of unique cells occupied by a species in a given year divided by the maximum number of cells surveyed, and mean maximal abundance is the maximum number of individuals per km^2 recorded in each cell, averaged over all cells surveyed within a given year.

Estimated proportion of cells occupied was extracted from MERP and OBIS occupancy model outputs, and modelled against MERP surveyed occupancy using binomial GLMs of the form above, to assess the ability of occupancy modelled estimates to replicate observed intra- and interspecific AORs. These GLMs were weighted by total number of cells surveyed per year for the MERP survey data, and total number of cells with at least one record for the modelled OBIS and MERP presence-only datasets. The degree of correlation between GLM parameters for surveyed and occupancy modelled data was also assessed.

Predictions of abundance were made first by modelling surveyed occupancy against surveyed abundance for each species using a linear model of the form

$$\log(\textit{mean maximal abundance}) \sim c + m \times \text{logit}(\textit{proportional occupancy})$$

Equation 4.2

Abundance predictions were then made using modelled occupancy values and the coefficients of the above linear model, for each species in each year it was observed. These predictions were then compared to observed abundance values, to assess the ability of occupancy modelled data to predict abundance, given knowledge of AORs.

4.4 Results

4.4.1 Comparing modelled and surveyed occupancy

In all cases, occupancy modelling overestimated proportional occupancy when compared to surveyed occupancy (Figures S3, S4, S5). Occupancy modelling was however often more accurate in predicting surveyed occupancy for more range-restricted species, i.e. those with lower proportional occupancy values. Second order polynomial modelling revealed that there was often a significant relationship between the level of overestimation (i.e. difference between modelled and surveyed proportional occupancy) and increasing surveyed occupancy, with many significant positive first order polynomial terms ($p < 0.05$), and (less often) significant negative second order polynomial terms (Table S6).

Time-series of modelled proportional occupancy more often than not displayed trends similar to those in surveyed occupancy data, for the same time period (Table 4.1, Table S7). OBIS data from targeted surveys consistently had the highest percentage agreement when compared to surveyed occupancy data, both when considering the direction, and the direction and magnitude of trends. MERP data likewise performed well (>50% agreement) in all cases except when considering the direction and magnitude of trends estimated using the final minus initial occupancy metric. OBIS data from opportunistic sources was consistently least successful in replicating the trends in proportional occupancy seen in surveyed data, in all cases failing to reach 50% agreement with effort-based survey data.

Table 4.1: *Percentage agreement between trends in occupancy calculated in three ways (mean occupancy in final third of time series minus mean occupancy in initial two thirds, mean occupancy in final half of time series minus mean occupancy in initial half, final proportional occupancy minus initial proportional occupancy), derived from surveyed occupancy data, and occupancy modelled data from 3 sources (MERP = MERP presence-only, OBIS T = OBIS targeted surveys, OBIS O = OBIS opportunistic recording).*

% Agreement	Final third minus initial two thirds			Final half minus initial half			Final occupancy minus initial occupancy		
	MERP	OBIS T	OBIS O	MERP	OBIS T	OBIS O	MERP	OBIS T	OBIS O
Direction	59	65	47	65	76	35	65	88	47
Magnitude	53	53	41	53	65	29	47	65	24

4.4.2 Intraspecific AORs

I found significant positive intraspecific AORs ($p < 0.001$) for 14 of the 20 species for which I had surveyed occurrence and abundance data (Figure 4.2, Table S8). Of those six species without significant AORs, one was close to significance (*Megaptera novaeangliae*, $p = 0.07$), and four did not have sufficient data to make robust estimates (*Balaenoptera musculus*, N = 3; *Mesoplodon mirus*, N = 2; *Pseudorca crassidens*, N = 1; *Stenella frontalis*, N = 1).

Using the modelled MERP presence-only data (Figure 4.3), I was able to replicate significant positive intraspecific AORs for 6 of the 14 species that displayed them in survey data (*Delphinus delphis*, *Lagenorhynchus acutus*, *Lagenorhynchus acutus*, *Lagenorhynchus albirostris*, *Stenella coeruleoalba* and *Tursiops truncates*). In two further cases (*Balaenoptera acutorostrata* and *Orcinus orca*), I observed significant negative intraspecific AORs when using modelled MERP data, compared to significant positive relationships when using survey data. When using modelled OBIS targeted survey data, I successfully reproduced significant positive intraspecific AORs in 8 of 14 species (*Balaenoptera physalus*, *Delphinus delphis*, *Hyperoodon ampullatus*, *Lagenorhynchus acutus*, *Lagenorhynchus albirostris*, *Orcinus orca*, *Stenella coeruleoalba* and *Tursiops truncatus*). In two further cases (*Balaenoptera acutorostrata* and *Globicephala melas*) I observed significant negative relationships that had been positive in survey data. For modelled OBIS opportunistic recording data, I successfully replicated positive intraspecific AORs in 3 species (*Hyperoodon* *ampullatus*, *Lagenorhynchus albirostris* and *Orcinus orca*), and observed negative intraspecific AORs in 4 species where they had previously been positive (*Balaenoptera acutorostrata*, *Delphinus delphis*, *Globicephala melas* and *Tursiops truncates*).

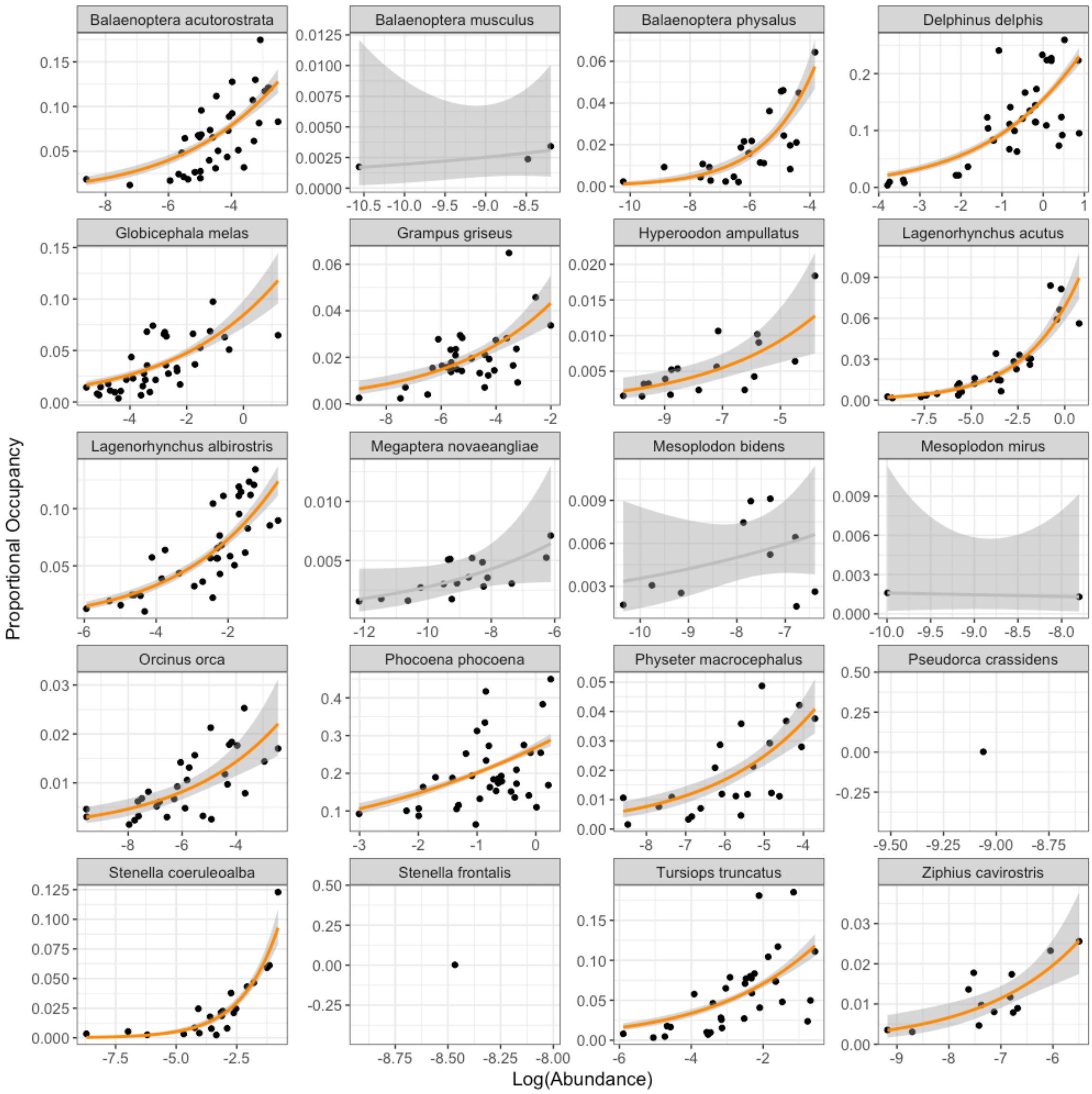

Figure 4.2: *Intraspecific AORs for 20 species of cetacean in European waters derived from MERP abundance survey data. In each panel, each point represents the proportion of cells occupied and mean maximal abundance of the species in a given year. Fourteen species exhibited significant positive AORs (binomial GLM: orange, confidence intervals: grey), while six exhibited non-significant relationships (binomial GLM: grey, confidence intervals: grey) or had too little data to model. Note scales vary on both axes between species.*

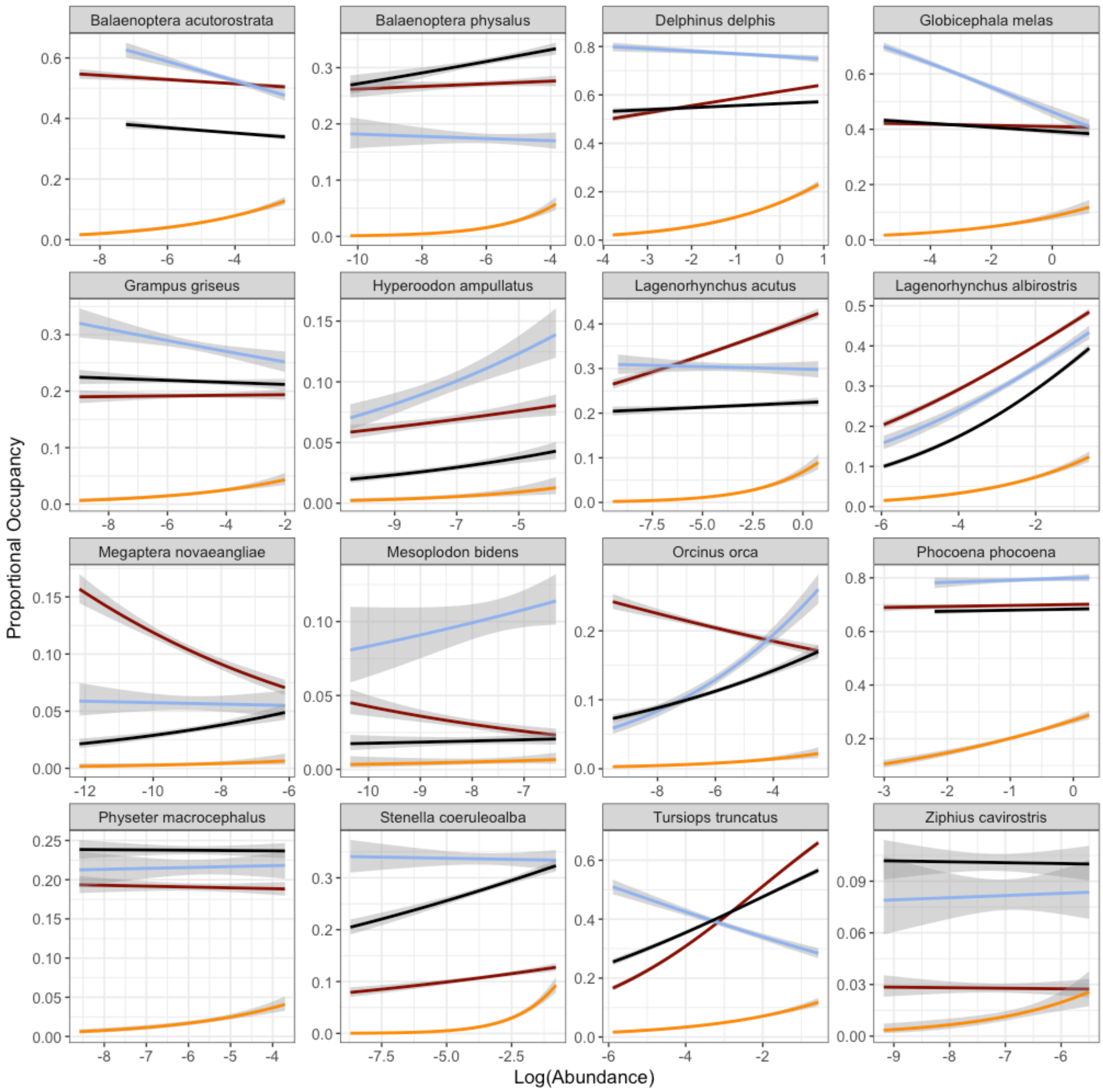

Figure 4.3: *Comparison of intraspecific AORs for 16 species derived from four different estimates of occupancy: MERP effort-based survey occupancy (orange), modelled MERP presence-only occupancy (red), modelled OBIS targeted survey occupancy (black), and modelled OBIS opportunistic recording occupancy (blue). Abundance estimates were all derived from MERP surveyed abundance data. Note scales vary on both axes between species.*

When comparing parameter estimates, *a* parameter values for binomial GLMs on MERP presence-only ($r = 0.78$), OBIS targeted survey ($r = 0.86$), and OBIS opportunistic recording ($r = 0.74$) data were significantly positively correlated with those of GLMs performed on the MERP survey data ($p < 0.05$). However, no significant correlation existed between *b* parameter estimates derived from GLMs on modelled occupancy data when compared to MERP survey data ($p > 0.05$).

4.4.3 Interspecific AORs

I found significant positive interspecific AORs ($p < 0.001$) for all 37 years for which I had sufficient data from the MERP effort-based survey dataset (Figure 4.4, Table S9).

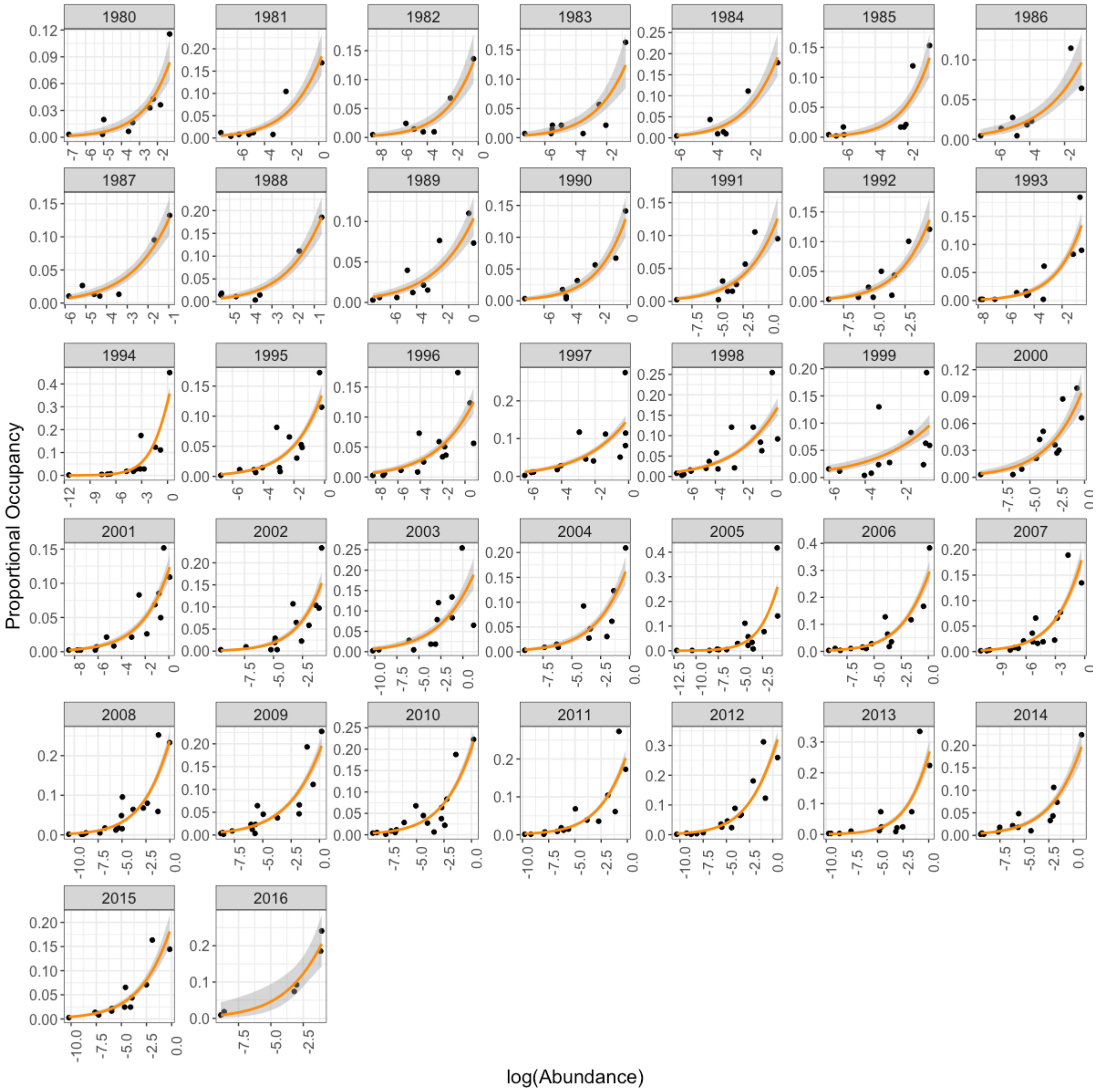

Figure 4.4: *Interspecific AORs for 37 years with recorded abundance in MERP abundance survey data. In each panel, points represents the proportion of cells occupied and mean maximal abundance of a species in that year. All years exhibited significant positive interspecific AORs (binomial GLM: orange, confidence intervals: grey). Note scales vary on both axes between years.*

Significant positive interspecific AORs were replicated in all years when using proportional occupancy values from each of the occupancy modelled datasets (Figure 4.5).

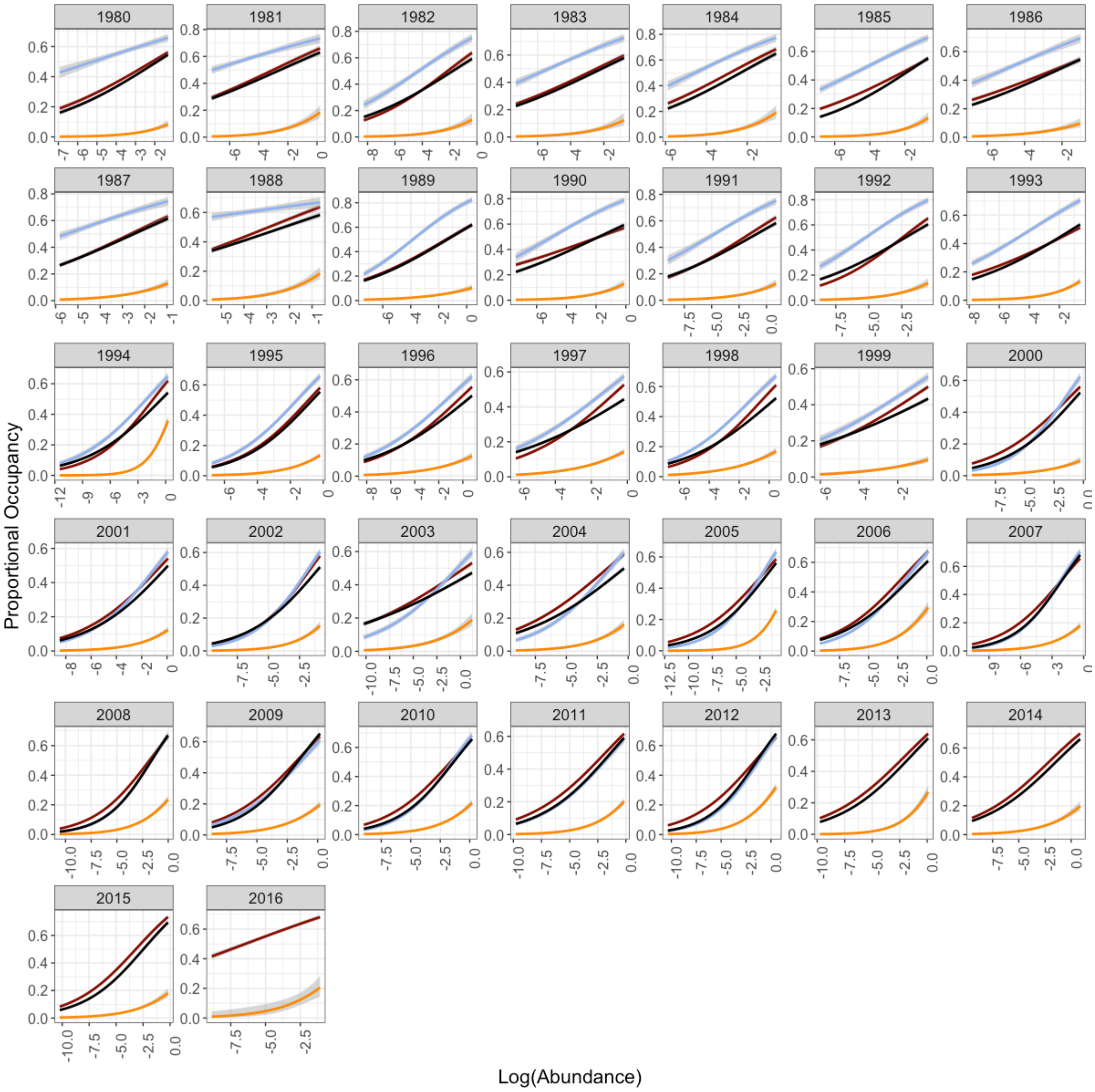

Figure 4.5: *Comparison of interspecific AORs for 37 years derived from four different estimates of occupancy: MERP effort-based survey occupancy (orange), modelled MERP presence-only occupancy (red), modelled OBIS targeted survey occupancy (black), and modelled OBIS opportunistic recording occupancy (blue). Abundance estimates were all derived from MERP surveyed abundance data. Data were available only until 2012 for OBIS opportunistic recording data, and 2015 for OBIS targeted survey data. Note scales vary on both axes between years.*

Significant positive correlations were observed when comparing between *a* parameter values from modelled MERP presence-only data GLMs and survey data GLMs ($r = 0.66$, $p < 0.05$), and when comparing between modelled OBIS targeted survey data GLMs and survey data GLMs ($r = 0.60$, $p < 0.05$). No significant correlation was observed when comparing survey data to modelled OBIS opportunistic recording data. No significant correlation between binomial GLM *b* parameter values was found when comparing survey data to occupancy modelled data, though modelled OBIS opportunistic recording data did exhibit a negative correlation that approached significance ($r = -0.33$, $p = 0.06$).

4.4.4 Predicting abundance from modelled occupancy

When predicting abundance using modelled proportional occupancy, I was unable in most cases to maintain the rank order of abundance between years within a species in any significant way (Figures S6, S7, S8). However, predicting the relative abundance of species within a year was much more successful, at least in the years 1994 and beyond. Significant positive correlations ($p < 0.05$) between recorded cetacean abundance and predicted cetacean abundance were observed within 21 years (57%, Figure 4.6) using modelled MERP data, 24 years (67%, Figure 4.7) using modelled OBIS targeted survey data, and 20 years (60%, Figure 4.8) using modelled OBIS opportunistic recording data. Additionally, in all three cases, almost all non-significant correlations were also positive. As such, occupancy modelling data, modelled using AORs, was able to accurately identify the common and rare cetacean species within a given year, and predict relative abundance of cetaceans, in 57%-67% of cases.

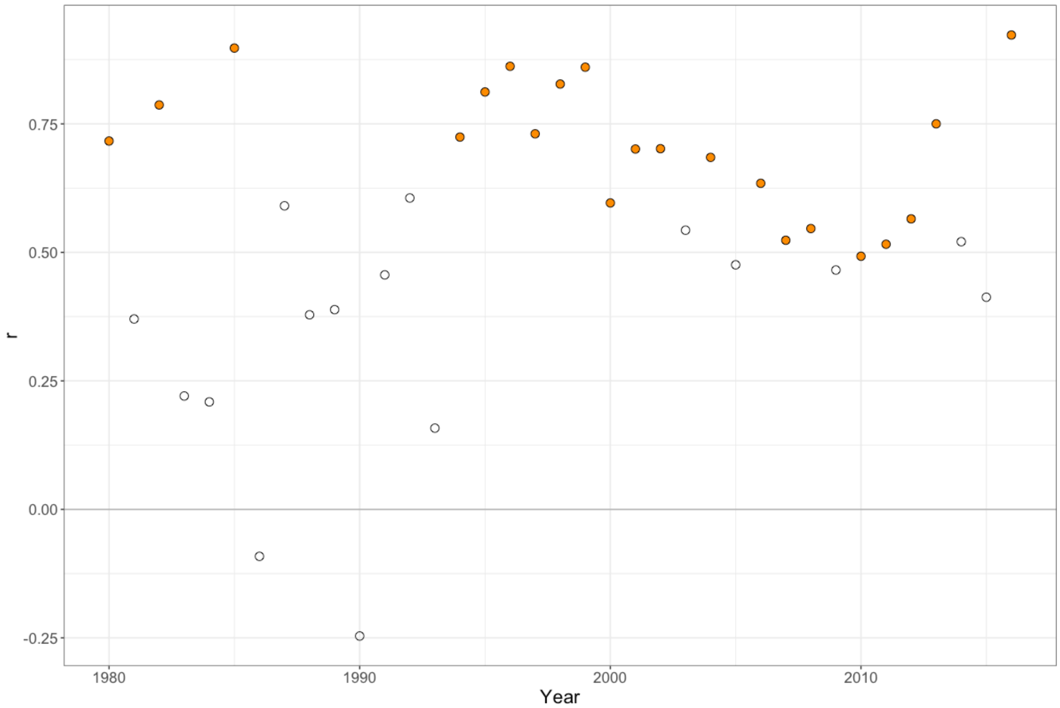

Figure 4.6: *Coefficients of correlation between observed and predicted abundance per year, using abundance estimates derived from interspecific AORs and modelled MERP presence-only data. Orange points indicate significant correlations ($p < 0.05$).*

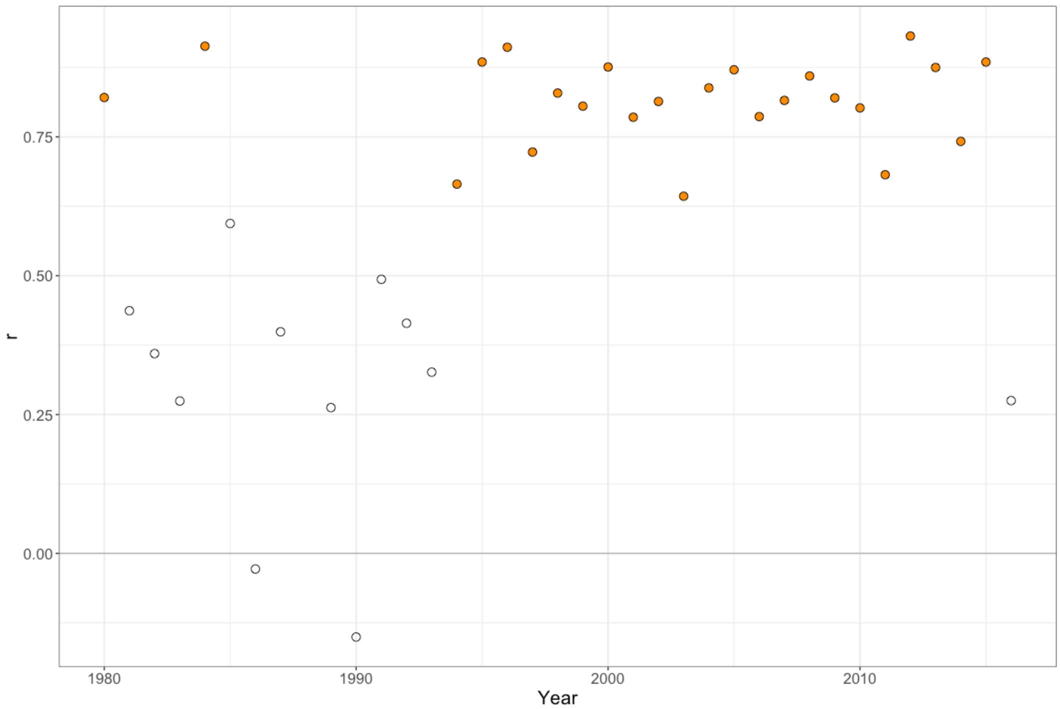

Figure 4.7: *Coefficients of correlation between observed and predicted abundance per year, using abundance estimates derived from interspecific AORs and modelled OBIS data derived from targeted surveys. Orange points indicate significant correlations ($p < 0.05$).*

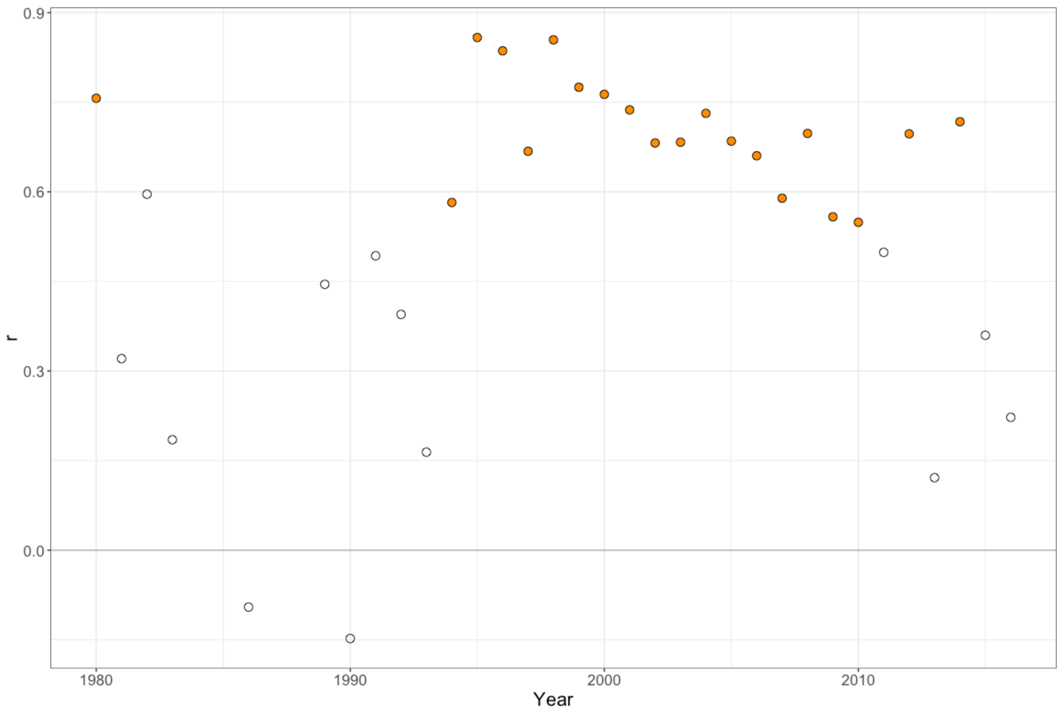

Figure 4.8: *Coefficients of correlation between observed and predicted abundance per year, using abundance estimates derived from interspecific AORs and modelled OBIS data derived from opportunistic recording. Orange points indicate significant correlations (p < 0.05).*

4.5 Discussion

Using occupancy and abundance data derived from effort-based surveys of cetaceans in European waters, I observed significant positive intraspecific abundance-occupancy relationships in 14 species, the most ever observed in this group. These results correspond to those of the one previous study of cetacean AORs (Hall et al. 2010), and conform to the ecological “general rule” of increased regional occupancy with increasing local abundance (Lawton 1999, Hall et al. 2010). Likewise, I observed significant positive interspecific abundance-occupancy relationships between species within years, i.e. the most wide-ranging species, or those with the highest proportional occupancy, are also the most abundant at a local scale. These results are notable in a conservation context, suggesting that we can infer how cetacean abundance is changing if we have knowledge of regional cetacean occupancy, and that knowledge of occupancy in a given year enables us to confidently assess which species are truly common or rare. They also suggest that declines in regional occupancy threaten cetaceans with a “double jeopardy” of disproportionate declines in abundance (Lawton 1993, Gaston 1999).

While interesting in itself, this information is most useful when we have an accurate knowledge of species regional occupancy. Modelled occupancy estimates in all cases overestimated occupancy when compared to survey data, though typically the rank order of species proportional occupancy within a given year was captured (Figures S3, S4, S5, Table S6, Table 4.1). Estimates of proportional occupancy were generally reasonably accurate for the range-restricted species (i.e. those with lower proportional occupancy). This is less true however of more wide-ranging species (i.e. those with higher proportional occupancy), where occupancy models tended to greatly overestimate proportional occupancy. Polynomial models indicated that there was often a significant linear increase in overestimation with increasing proportional occupancy of a species, though in some cases a significant second order polynomial term indicated that estimates became more accurate again for species at the highest levels of occupancy. Whether this is the result of the model overestimating true occupancy, or the effort-based survey data failing to capture true occupancy is unclear. It is unlikely the surveyed occupancy is truly representative of real-world occupancy, as cetaceans spend time at depth, and would thus not be observed by surveys assessing the sea surface, though this problem is likely alleviated somewhat by the temporal aggregation of the data.

Within species, I was generally unsuccessful in capturing the rank order of occupancy across years (not shown), however modelled estimates of occupancy are more often than not able to identify significant cases of decrease or increase within species, at least as observed in the effort-based survey data (Table S7). This failure to capture fine scale intraspecific trends in occupancy is not as a result of model failure; all models successfully ran and passed quality control checks. Rather, it is likely a result of the longer closure periods used here, which I extended to combat variation in data availability, particularly seasonal variation. It is therefore not surprising that within a species I was unable to discern fine scale temporal patterns accurately, and instead only observe the larger scale changes in proportional occupancy.

When using modelled occupancy to estimate AORs, I once again found that interspecific relationships were much better predicted than intraspecific relationships in terms of shape and significance, especially in later years, despite proportional occupancy being overestimated. This also held true for predicting abundance from modelled occupancy, where in c. 60-70% of cases I was able to identify broadly the rank order of abundance across species within a year accurately. The probable explanation for this ability to identify inter- over intraspecific relationships is that, even under low sampling effort, it is likely that the most abundant species in any given year will be recorded more often than the least abundant, and similarly those with greatest proportional occupancy will likely be recorded more often than those with low proportional occupancy. In short, the data passed to the model contains information on the relative abundance or rarity of sampled species. Therefore it is unsurprising that modelled estimates of occupancy reflect this dynamic.

Modelled proportional occupancy data is therefore clearly useful in certain circumstances when considering AORs and abundance in marine species, notably in the case of assessing interspecific relationships between occupancy and abundance, and predicting relative abundance from interspecific relationships. However, the source of the data modelled seems to only have a marginal effect on the quality of output AORs and abundance estimates. Data sourced from OBIS that originated from opportunistic recording were generally poorer in predicting AOR shape, however showed no real difference in ability to predict abundance than the MERP presence-only dataset. Only OBIS data derived from targeted surveys performed better in this regard, but even this improvement was marginal. Consequently, it is notable that freely available data that could be regarded as "poorer quality" has the potential to produce robust and conservation relevant assessments of abundance and AORs, and that data collection methods less structured and more cost effective than effort-based techniques (Evans and Hammond 2004) have the potential when combined with occupancy modelling to provide abundance information useful to marine conservation and macroecology, despite the fact that these methods on their own are considered less useful in estimating abundance (Evans and Hammond 2004). Groupings such as “targeted” or “opportunistic” are however broad, and further work is needed to clarify exactly the type and minimum level of data quality required to produce robust results, to discern for example whether shore-based opportunistic sightings or stranding data reveal similar patterns to at sea opportunistic data, and to effort-based survey data.

There are however particular considerations to make when applying AORs and occupancy modelling to data for groups such as cetaceans, particularly in the case of highly mobile or migratory species. From a technical standpoint, data for highly mobile species are more likely to contain “double counts” of the same individuals or groups over a region, potentially leading to artificially inflated values of proportional occupancy, a risk that will only increase in cases where data are temporal aggregated, as in the case of occupancy modelled data here. Additionally, from an ecological standpoint, the suggested processes that link local abundance to regional occupancy (e.g. metapopulation dynamics, resource availability, Gaston et al. 2000) may not operate in the same ways in species that roam at regional scales, or similarly the study scale used here may be insufficient to accurately capture the ecological processes leading to AORs for species with much greater ranges than considered here. This potentially means that the concept of AORs have less ecological relevance to highly mobile species, either overall or in the case of this study. The degree to which this ecological consideration is true however is difficult to determine without further studying and elucidating the mechanisms potentially leading to AORs in highly mobile cetaceans, though previous studies of migratory bird species (Gaston et al. 2000), and both mobile and migratory bird species (e.g. the negative trend found by Webb et al 2019) suggest that AORs are still ecologically relevant to species of these life histories. Both technical and ecological factors may if present lead to incorrect estimates of occupancy or abundance from AORs, or incorrect range assumptions relating to for example required protected area size, though sedentary or resident species are likely to be more robust to these issues given their more restricted ranges. This is to say that, while positive interspecific AORs were expected and have been found here in cetaceans, they are potentially more robust for sedentary and resident species, and their use in conservation prior to further testing should reflect this, by being considered as part of a suite of tools rather than a sole determinant of management or policy.

Further steps could additionally be taken during occupancy modelling to improve the estimates of intraspecific AORs. Specifically, an investigation into the effect of varying temporal bin length on output occupancy trends and intraspecific AORs could prove very useful in determining whether the choice of closure period, or the data itself, prevented us from accurately replicating observed small scale temporal trends and intraspecific relationships. In this case, closure periods were chosen so as to provide relatively uniform period length across datasets, and relatively uniform data availability across periods (a compromise between removing seasonal signatures in the data and ensuring enough years within a closure period to act as sub-periods or "visits" meant that the shortest closure periods were three years in length). Determining how this seasonality and varying data availability effects estimates when closure periods are for example one year, the typical (but not necessary, MacKenzie et al. 2006) closure period used in occupancy modelling studies of terrestrial data (e.g. Kéry et al. 2010, van Strien et al. 2013), would be an interesting next step in potentially improving these estimates of intraspecific AORs.

I suggest that, at least in cetaceans as implemented here, occupancy models are useful for garnering information on which species may be wide ranging or restricted (i.e. high and low proportional occupancy respectively), and provide information on broad scale changes in species occupancy over long time periods. These models however, as implemented through this methodology, are arguably less useful in providing information about proportional occupancy on a fine temporal scale, and further work is needed to assess the effect of lengthening temporal bins on the accuracy of such estimates. Potentially most interesting, and useful in an applied conservation context, is that occupancy modelling of unstructured and potentially biased data, combined with a prior knowledge of species interspecific

AORs, enables relative commonality and rarity in terms of abundance to be accurately determined between species in a given year, though the degree to which species migration and mobility affect this requires more investigation. Nevertheless, it seems advisable to consider occupancy modelling as an additional tool in marine biodiversity monitoring, and specifically when looking to determine changes in relative abundance in assemblages of marine cetaceans.

5: Examining the marine latitudinal biodiversity gradient using aggregated occurrence data

5.1 Abstract

The shape of latitudinal gradients of diversity in marine systems has been the subject of continued debate. A recent analysis by Chaudhary et al. (2016) using OBIS data reported a bimodal gradient of diversity with an equatorial dip, however this study failed to account for sampling biases with latitude that were significantly correlated with their measure of diversity. Occupancy modelling presents an interesting opportunity to test explicitly the effect of variable data collection effort, by treating sampling bias at latitudinal scales as analogous to bias arising from surveyor effort at the site level in more traditional surveying frameworks. Here I apply occupancy modelling to OBIS data for two contrasting groups previously analysed by Chaudhary et al., finding a bimodal pattern of latitudinal diversity. I argue however that this modelled pattern is unlikely to be robust, considering the naïveté of the model, the latitudinal range considered and the absence of any temperature and depth covariates in the modelling framework. I conclude that, while naïve occupancy models are useful at spatial scales with less environmental variation, such models require added complexity to discern the true pattern of latitudinal diversity in marine systems, and to deal effectively with the effects of sampling effort in aggregated biodiversity databases such as OBIS.

5.2 Introduction

Latitudinal diversity gradients, with species diversity decreasing from the tropics to the poles, are one of macroecology's most well-studied, and some say prevalent, patterns (e.g. Pianka 1966, Gaston 2000), and have often been reported in marine and terrestrial taxa (Gaston 2000, Hillebrand 2004a, 2004b). However, despite a wealth of research, our knowledge of the latitudinal biodiversity gradient is still inadequate in two significant ways, specifically the *cause* of this relationship, and the *shape* of this relationship in marine taxa.

As many as 30 theories have been proposed to explain the idea of decreasing diversity with increasing latitude (see Willig et al. 2003 for a review, Brayard et al. 2005). Many suggest that patterns in biodiversity are a result of how solar energy input varies with latitude, for example because of the idea that temperature increases productivity, therefore leading to higher diversity at lower latitudes (Pianka 1966, Willig et al. 2003, Woolley et al. 2016), or because of increased rates of speciation at the tropics (but see Rabosky et al. 2018) as a result of greater solar energy input leading to increased metabolic rates (Rohde 1992). Alternatively, mid-domain hypotheses suggest that a random distribution of species ranges bounded by environmental or physiological barriers (e.g. two poles, temperature tolerances, landmasses) will result in increased levels of range overlap at the middle of the domains defined by these barriers, resulting therefore in increased diversity there (Willig et al. 2003, Brayard et al. 2005). This theory has however been the subject of some criticism, as has been shown to be unable to produce realistic diversity gradients and distributions of range size amongst species without the addition of other factors such as density dependence, except for under a narrow set of circumstances (Keith and Connolly 2013). In reality, it is likely that a number of causes act simultaneously, and that the relative contribution of these causes vary in different cases and areas.

In marine systems however, potentially a more fundamental gap in our knowledge comes in describing the shape of marine latitudinal diversity gradients (MLDGs), specifically the location of peak diversity. Gradients in species diversity in terrestrial systems have typically been defined as unimodal with an equatorial peak (Gaston 2000), however both unimodal (e.g. Hillebrand 2004a, 2004b, Witman et al. 2004) and bimodal (i.e. a distribution with two peaks of diversity in mid-latitudes and an equatorial dip e.g. Kerswell 2006, Fautin et al. 2013, Chaudhary et al. 2016, Saeedi et al. 2017) distributions have been claimed for MLDGs. Debate therefore continues as to the "general" form of MLDGs, and assessing whether this takes a unimodal or bimodal shape is complicated by a number of factors. First is the methodology used to generate the proposed gradient. For example, a number of studies examine gradients using data from only the northern hemisphere, and finding a peak in diversity just north of the equator conclude a unimodal MLDG, when in fact a similar pattern south of the equator would be equally consistent with a bimodal MLDG (Chaudhary et al. 2016). This is likewise the case for studies that consider even smaller regions. Second is that data availability plays an important role in the ability to develop robust estimates of MLDGs. Specifically, very high levels of sampling in northern mid-latitudes, as well as increased levels of effort in digitizing existing data, and poor sampling at low latitudes, can lead to reports of bimodal or asymmetric unimodal MLDGs as a result of sampling effort (Fernandez and Marques 2017, Menegotto and Rangel 2018). Finally, the reported shape of MLDGs often varies depending on the identity or life history of the taxa studied, for example equatorial peaks in vertebrate richness compared to mid- to high-latitude peaks in invertebrate richness found by Edgar et al. (2017). Such variation between taxa has led some to suggest that attempting to derive a single general pattern of latitudinal diversity is illogical or liable to mask interesting and important patterns (Webb 2012, Fernandez and Marques 2017).

Recently, Chaudhary et al. (2016) reassessed a number of studies examining MLDGs, reclassifying many of those originally thought unimodal as bimodal and often asymmetric. The authors go on to propose that a general pattern of bimodality and asymmetry is a result of a previously studied combination of mid-domain and temperature effects (Brayard et al. 2005). The authors also analysed OBIS (Ocean Biogeographic Information System, OBIS 2018) data for a number of groups, arguing that despite the substantial differences in data availability with latitude across OBIS data (Figure 5.1), sampling effort was not a factor in determining the shape of MLDGs, in part because of the work of previous analyses of bimodal MLDGs (Powell et al. 2012, Fautin et al. 2013), and a perceived similarity of sampling effort across the tropics. When challenged on this point (Fernandez and Marques 2017), the authors conducted further analyses while considering sampling effort, showing that rarefied latitudinal diversity data still exhibit bimodal patterns, and standing by their original conclusions, despite the fact that their original metric of diversity was significantly correlated with sampling effort (Chaudhary et al. 2017). However, further work with OBIS data has since demonstrated significant under-sampling at low latitudes, suggesting that this bimodal pattern may in fact be a result of sampling bias and knowledge gaps after all (Menegotto and Rangel, 2018).

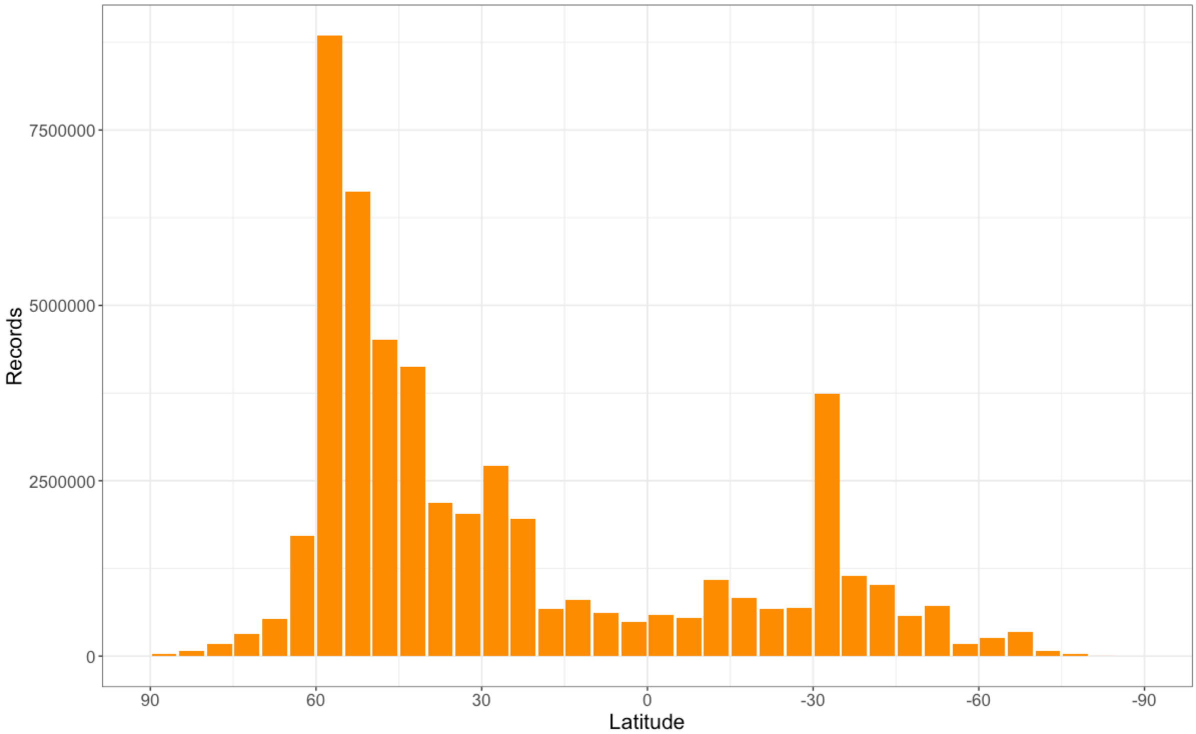

Figure 5.1: *Number of unique records (N = 50,917,822) contained in OBIS per 5-degree latitudinal band. Data is presented as retrieved from OBIS (2018/07/16), and has undergone no cleaning or verification.*

The previous study by Chaudhary et al. (2016) utilised OBIS data to try to discern patterns in marine latitudinal diversity. Indeed, OBIS is an almost ideal candidate for doing so, as it contains data for every major taxonomic group, meaning groups representing a variety of trophic levels, body sizes, and life histories can be assessed for trends in latitudinal diversity, and additionally OBIS has global coverage in terms of data (OBIS 2018). However, more can be done to explicitly account for the geographical biases in sampling effort that Chaudhary et al. (2017) concede are inherent in OBIS (e.g. Menegotto and Rangel, 2018). Occupancy modelling provides us with a potential method to do this, by modelling the occupancy of species unobserved in lesser-sampled areas. Occupancy modelling in a traditional context uses information about surveyor effort at a sampled site to infer if species were present but unrecorded at said site, based on the total number (and indirectly the identity) of species recorded. This problem can be thought of as analogous to that of variable surveyor effort over larger latitudinal scales, where lower effort in some latitudinal bands may lead to species being present though unrecorded.

Here, I apply a multispecies occupancy model to OBIS data to estimate MLDGs while explicitly accounting for sampling effort, using data from the Atlantic Ocean for two taxonomic groups (Gastropoda and Elasmobranchii). I chose to assess these groups because (a) they represent contrasting life histories and habitats (respectively, predominantly benthic invertebrates and vertebrates of varying habitat), (b) they have a broad latitudinal range in the Atlantic Ocean, and (c) they were previously assessed by Chaudhary et al. (2016). In doing this, I aim to explore whether accounting directly for latitudinal bias using occupancy modelled OBIS data reveals a unimodal pattern of latitudinal diversity, of whether the results of Chaudhary et al. (2016) are indeed robust to variable data availability with latitude in OBIS.

5.3 Methods

5.3.1 Data download and processing

All data for the Atlantic Ocean, as defined by the International Hydrographic Organisation (www.iho.int, Figure 5.2, QGIS Development Team, 2018; shapefiles from naturalearthdata.com), for the classes Gastropoda and Elasmobranchii, were retrieved from OBIS using the “robis” package in R (Provoost et al. 2017, R Core Team 2017). Records without a date of recording were removed from analysis. Data points falling on land were also removed from analysis, excluding those within a 1-degree buffer of the coast, to account for variable coordinate precision in OBIS data. Taxonomy was verified using the package “worrms” (Chamberlain 2017). Records with unaccepted taxonomic names had their names changed to accepted versions where possible, or were removed from the dataset. Records not identified to species level were likewise removed, and sub-species level records were allocated to their parent species. This quality control resulted in 144,862 records of 3,144 species of Gastropods, and 410,604 records of 388 species of Elsamobranchs.

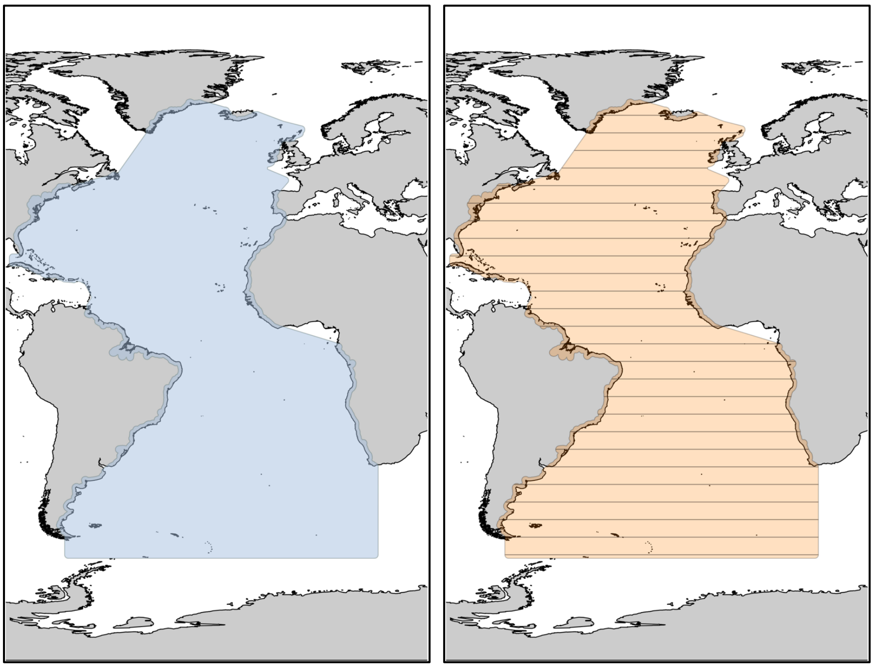

Figure 5.2: *The Atlantic Ocean (as defined by the International Hydrographic Organisation) with 1-degree buffer zone (left), and modelled 5-degree latitudinal bands (right). The most northerly and southerly, incomplete latitudinal bands (for both groups) were removed from model output.*

Records were assigned to 5-degree latitudinal bands (Figure 5.2), and spanned the latitudes c. –61 to 65 for Gastropoda and c. –57 to 67 for Elasmobranchii. The most northerly and southerly latitudinal bands for each group, which did not have full coverage by data and were therefore less than 5 degrees, were modelled, but removed from model output after analysis. As in previous implementations of the occupancy modelling framework, data were assigned to groupings based on the methodology of data collection, and the taxon targeted by the data collectors, to ensure that assumptions about recording practices were more robust. These groupings were assigned separately for the two taxonomic groups, however they differed from previous methods, in that I considered only (a) whether a dataset originated from a targeted survey, opportunistic collection, or mixed or unknown sources (mostly museum specimens), and (b) whether the taxonomic group in question was likely to be recorded if observed, based on the metadata information available about the specified target taxon of the dataset (Table 5.1). Both groups were formatted for occupancy modelling and subsequently modelled independently. Citations for OBIS data used in modelling can be found in Table S10.

Table 5.1: *Methodological groupings for the two taxonomic groups undergoing occupancy modelling. Likelihoods are divided into three classes: A – very likely (e.g. target taxa of recording), B – unknown or not especially likely (e.g. incidental recordings when targeting different taxa), and C – very likely if observed, but methods or objectives mean taxa was not necessarily fully sampled (e.g. a bottom-trawl may record benthic elasmobranchs, but pelagic elasmobranchs would not appear).*

Group	Taxonomic Grouping	Collection Method	Likelihood of Recording
1	Elasmobranchii	Mixed or Unknown Methods	B
2	Elasmobranchii	Mixed or Unknown Methods	C
3	Elasmobranchii	Mixed or Unknown Methods	A
4	Elasmobranchii	Opportunistic Recording	B
5	Elasmobranchii	Opportunistic Recording	C
6	Elasmobranchii	Opportunistic Recording	A
7	Elasmobranchii	Targeted Survey	B
8	Elasmobranchii	Targeted Survey	C
9	Elasmobranchii	Targeted Survey	A
10	Elasmobranchii	Opportunistic Recording	A‡

11	Gastropoda	Mixed or Unknown Methods	C
12	Gastropoda	Mixed or Unknown Methods	A
13	Gastropoda	Opportunistic Recording	C
14	Gastropoda	Targeted Survey	B
15	Gastropoda	Targeted Survey	C
16	Gastropoda	Targeted Survey	A

‡For Whale Sharks and Manta Rays only

5.3.2 Multispecies occupancy model

I used here a modified, non-temporal version of the multispecies model outlined in Chapter 3 (Appendix S3): since I was only concerned with spatial information rather than temporal, the model was run with only one time-period (or "closure period"), within which the data were divided into numerous sub-periods, corresponding to "visits" in traditional occupancy modelling terminology (Figure S1). This is in contrast to previous implementations, which had multiple time-periods, each with three sub-periods. While this may intuitively seem to contradict the idea of closure, or that species are consistently either present or absent at a site with a closure period and across visits, this is less concerning in this case considering that I have no interest in the temporal trends in species, only the overall number of species present in a latitudinal band. Furthermore, modelling the data with only one time-period but multiple sub-periods enabled me to make the most use of the data available, while reducing unnecessary computational pressure.

Additionally, since in this case I model only one time-period, this occupancy model is no longer considered dynamic, as colonisation and extinction probabilities do not factor into an estimate of occurrence if multiple time periods are not modelled. While local level colonisation and extinction may have occurred over the time-period I am using, I considered the latitudinal bands used here large enough that a global scale diversity gradient would be minimally affected by local-scale changes.

Both taxonomic groups were modelled independently, and within both groups the data were further subdivided into the groupings outlined above (Table 5.1), which were in turn modelled independently of each other. Models were run using JAGS and R (Plummer 2003, R Core Team 2017) as before, with 20,000 iterations following a 30,000 iteration burn-in, with 2 chains and a thinning factor of 3. A large burn-in is used here, as in Boakes et al. (2017) to counteract the fact that I only consider one time-period. In my previous uses of occupancy models, the first and last modelled time-periods were removed from analysis due to a higher level of uncertainty, however since in this case I have only one time-period, confidence in estimated occupancy is increased by ensuring adequate time for the model to stabilise and converge.

5.3.3 Assessing occupancy in latitudinal bands

Occupancy models in the form used here estimate occupancy numerous times, and then average across the posterior distribution of occupancy estimates to provide a mean occupancy value, z, of between 0 and 1 for a latitudinal band, which can be thought of as analogous to the likelihood that a particular species occupies that band. As such, I first assigned z values to 1 for species observed in a latitudinal band in OBIS data. I then used three thresholds of z (0.25, 0.5, and 0.75) to assess whether I consider an unobserved species sufficiently likely to occupy a band, and therefore count towards its species richness.

5.4 Results

Occupancy modelling was successful in both taxonomic groups to produce latitudinal band level estimates of species richness. Only in three cases was a specific species*grouping combination unsuccessful in converging (Rhat > 1.1, Gelman and Shirley 2011), which were subsequently removed from analysis. All other monitored parameters likewise were successful in converging (Rhat < 1.1), however Rhat values for *z* were not monitored, as they are not informative for this parameter.

Prior to occupancy modelling, data from OBIS exhibited significant multi-modality in both taxonomic groups (Hartigans' Dip Test, p < 0.05), indicating a bimodal (or at least non-unimodal) latitudinal biodiversity gradient of the type claimed to be characteristic of marine taxa (Figure 5.3, left). Similarly, when using a *z*-threshold of 0.75 (Figure 5.3, right), a significantly multimodal distribution of species richness emerges from occupancy modelled occurrence data (Hartigans' Dip Test, p < 0.05).

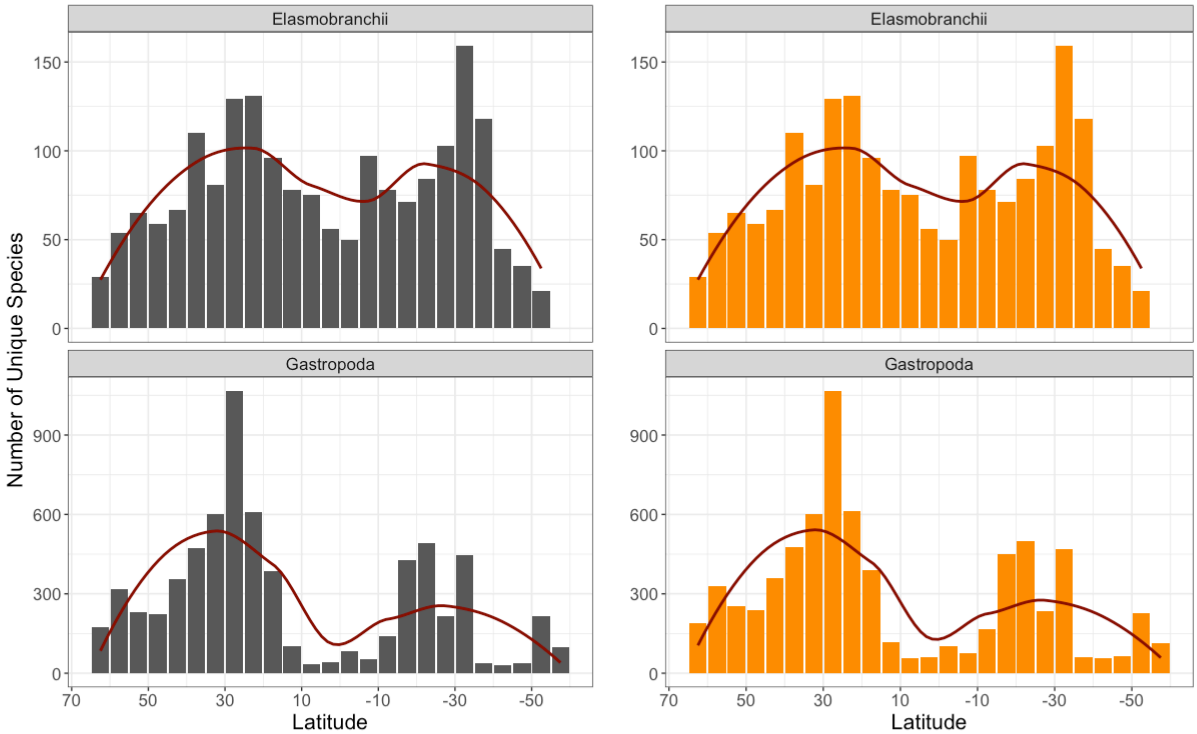

Figure 5.3: *Latitudinal gradient in species richness in raw OBIS data (left) and occupancy modelled OBIS data (z-threshold ≥ 0.75, right) for gastropods and elasmobranchs, with loess curve.*

In gastropods, species richness distribution at a *z*-threshold of 0.75 differed significantly from that of the raw OBIS data (p < 0.05). However, when Chi-squared tests were run on smaller subsamples (N = 1,000), to avoid artificially inflating significance through large sample sizes, modal p-values (N = 500) indicated no significant difference between modelled gastropod species richness distribution and original OBIS distribution. Elasmobranch distribution after modelling and with a 0.75

z-threshold was identical to that of the original OBIS data (p = 1). The distribution of additional species predicted per latitudinal band for each *z*-threshold can be found in Figure S9.

In the case of the two lower *z*-threshold values, 0.25 and 0.5, modelled latitudinal gradients were statistically all significantly non-unimodal (Hartigans' Dip Test, $p < 0.05$), though exhibit almost uniformly high richness across latitude (Figure 5.4).

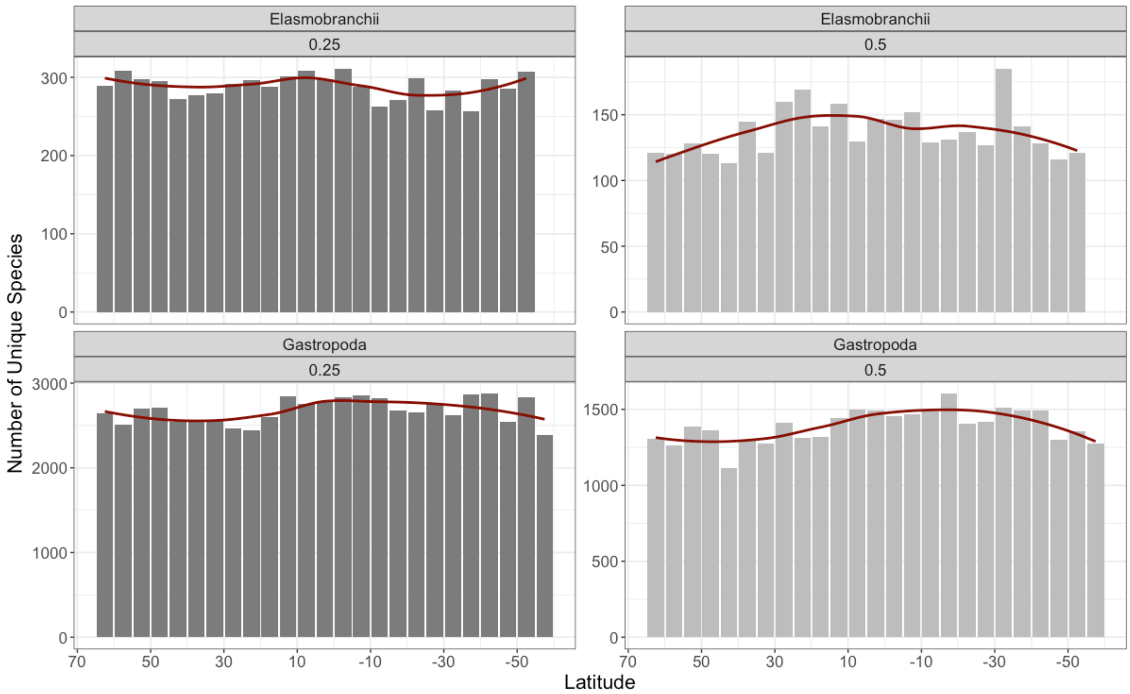

Figure 5.4: *Modelled marine latitudinal diversity gradients based on the lower two z-thresholds: 0.25 (left) and 0.5 (right), for both groups, with loess curve. Note variation in y-axis scale.*

5.5 Discussion

Gradients of species richness were successfully modelled on a global scale for two taxonomic groups: gastropods and elasmobranchs. However, I garnered no additional information from the occupancy modelling process than was present in the raw OBIS data when using a *z*-threshold of 0.75. Rhat values for all species-grouping-parameter combinations assessed were satisfactory in all but three cases, which were subsequently removed, implying that this lack of information is not the result of a poorly converged model. There are at least two possible reasons for this model output being no more informative that the OBIS data. The first and simplest answer is that the OBIS data represents a true pattern in latitudinal species gradients, and further modelling it did little to increase its accuracy. This would be consistent with the findings of Chaudhary et al. (2016), who suggest a bimodal latitudinal diversity gradient, use OBIS data as evidence for this, and consider the effects of sampling bias on band-level estimates of species richness minimal.

The second possible cause is that occupancy models of this type are not effective at discerning the patterns in occupancy I am examining when supplied with limited information. While large-scale occupancy modelling studies have previously been conducted (e.g. Boakes et al. 2017), they typically employ more nuanced versions of the occupancy models used here, so it is possible that this relatively naïve version is insufficient to examine this type of pattern without additional data. This second case I believe is more likely, especially given that the modelled gradients are relatively uniform in shape when using liberal *z*-threshold values, until the *z*-threshold is sufficiently high that it takes the shape of the original data, or the baseline level of information that the model was supplied with. This is particularly evident in the case of elasmobranchs, where a *z*-threshold of 0.75 leaves only species observed in the original data. This is not to say that a bimodal latitudinal diversity gradient is not a possible result of occupancy modelling in OBIS data, but a more nuanced model is likely required before we are able to definitively distinguish between true patterns, or patterns resulting from little information being gained from the modelling process.

A pertinent question to ask then is what further information is required to improve this modelling framework, and make it applicable to the study of MLDGs? The likely answer is the inclusion of information on species temperature preferences or tolerances. Since many of the most supported and most likely hypotheses for the shape of latitudinal gradients of diversity in general are related to increased solar energy at lower latitudes (Rohde 1992), for which temperature has been used as a proxy (Roy et al. 2000), or to the assortment of ranges defined by temperature tolerance (Brayard et al. 2005), it is likely that this driving force needs to be included as a covariate in future modelling attempts to explain and estimate MLDGs. In this naïve implementation, all bands are considered equally habitable for every species, and it is instead whether the species is detected there, and the number (and indirectly the identity) of other species detected there, that inform true presence or absence at the band level. As such, and especially with the large numbers of species modelled here, it is unsurprising that at low to mid *z*-thresholds, the number of species occupying each band remains high and relatively constant, and that only at higher *z*-thresholds do we see a change from a (relatively) uniformly high level of occupancy. The inclusion of temperature data, which is already available for some species (e.g. Comte and Olden 2017, Bennett et al. 2018), would combat this by modifying the probability of species presence in a band depending on the band's suitability for that species in terms of temperature. While increasing the complexity of the models will therefore likely increase the computational time and power required to run them, it will also enable a more informed decision of the ability of the model to successfully estimate true trends in MLSGs. Care needs to be taken however to avoid using temperature affinity estimates inferred from species occurrence records, if these occurrence records are then going to be used to estimate latitudinal diversity. As such, the best data for this task will likely derive from experiments of temperature tolerance and affinity. Further complexity, and potentially accuracy, could additionally be added by using depth as a covariate. Not only will increasing depth moderate the effect of temperature on species, but Chaudhary et al. (2016) cite the larger area of continental shelf in northern mid-latitudes, and thus the larger available habitat for shelf-dwelling species, as one potential reason for their bimodal pattern of latitudinal diversity.

Despite the fact that I gained little information compared to the raw data, the model did run successfully, and converged well almost universally. This is impressive given the number of species assessed, as well as the fact that only one time-period was considered, and that this is geographically and taxonomically the largest scale implementation of occupancy modelling in a marine setting to my knowledge. I therefore feel that this first pass represents a useful baseline from which future studies can work, in order to implement more complex models and gain further insight into large-scale marine latitudinal diversity gradients from aggregated data.

6: Discussion

Throughout the course of this thesis, I have explored how occupancy modelling and unstructured, aggregated, or biased data can be used to garner information on biodiversity change in marine species. In this discussion, I will explore the advantages and problems with implementing occupancy modelling in aggregated marine data, specifically considering OBIS, and suggest where it can be used to gain the most benefit for marine ecology.

6.1 Key findings

a) **Occupancy modelling can be successfully implemented in aggregated marine biodiversity data to produce robust estimates of long-term occupancy change.** However doing so requires extensive data manipulation in order to implement models effectively.

b) **Groups lacking significant formal study, but that are well represented in aggregated biodiversity databases, stand to gain from the implementation of an occupancy modelling methodology.** Chapter 2 of this work assessed long-term temporal trends in 166 species of molluscs in the Celtic Sea, and such an approach has the potential to be applied in future setting to improve the taxonomic representativeness of national and international assessments of biodiversity change. Chapter 3 assessed temporal change in 124 species of *Conus* globally, a genus of gastropod mollusc that has been comprehensively assessed for the IUCN Red List, but for which population trend data is often absent, especially notable for the species we observed as exhibiting the most significant declines.

c) **Occupancy modelling can potentially be used to make broad scale, cost-effective estimates of abundance.** In species for which we have known interspecific abundance-occupancy relationships, occupancy modelling can be used with both aggregated survey data and aggregated opportunistically recorded data to estimate the rank order of species abundance within a year reasonably reliably, as I have demonstrated in Chapter 4. Given the extensive history of study of AORs and the ready availability of existing data, there are potentially numerous candidate species that would make interesting case studies to examine the applicability and reliability of occupancy modelling here further.

d) **Careful consideration should be given to the implementation of naïve occupancy models.** The relatively simple occupancy models I have utilised here, and incidentally the most readily available implementations, are insufficient in certain circumstances which may not be obvious until the modelling process is conducted. In these cases, such as Chapter 5, more complex models will need to be invoked that specifically consider the underlying drivers of occupancy or occupancy change. In the case of latitudinal gradients of marine biodiversity, models explicitly considering the effect of temperature, solar energy, or depth would likely produce much more informative results.

6.2 Unstructured data and occupancy modelling as tools for marine biodiversity monitoring

Aggregated marine biodiversity databases such as OBIS are incredibly useful in the study of marine ecology and biodiversity change, as evidenced by their frequent use in the literature (e.g. iobis.org/library/, references throughout this work), and by our ability here to assess fundamental questions regarding macroecological theory, such as the abundance-occupancy relationship. However, despite the wealth of data available for them, many marine taxa (particularly invertebrates) continue to be absent from the most significant national and international assessments of biodiversity change (e.g. WWF 2015, 2016, Hayhow et al. 2016). The reasons for this are unclear, but one may be that the aggregated data from sources such as OBIS are considered unfit for purpose due to the issues of variable surveyor effort and detection bias outlined in this work, while using only the constituent single datasets can be more restricting in terms of taxonomic coverage, though terrestrial datasets similarly vulnerable to detection bias and surveyor effort are included in such assessments (e.g. amateur recording scheme data, Hayhow et al. 2016). I believe that in this thesis I have demonstrated how we can account for some of these issues to gain robust trends in the regional and global proportional occupancy of marine species that have historically been neglected in previous efforts. In doing so, I have expanded greatly on the number of invertebrates that could potentially be represented in future assessments of marine biodiversity in the UK, as well as demonstrated how unstructured data can be added to the toolbox of threat assessment status in cases where population trend data for a species is lacking. As methods such as occupancy modelling become more popular in marine research, and more accessible to researchers (August et al. 2015), the possibilities presented by aggregated marine data sources will only continue to grow.

Considering its popularity in terrestrial research, it is surprising that occupancy modelling has up to this point only seen a handful of implementations in marine data (MacNeil et al. 2008a, Katsanevakis et al. 2011, Issaris et al. 2012, Coggins et al. 2014), especially considering variable surveyor effort and detection bias are just as problematic, if not more so, in the marine realm as in the terrestrial (Bates et al. 2015), and a similar problem is often addressed in fisheries data through the concept of "catchability" (e.g. Arreguín-Sánchez 1996). There are many potential reasons for this. It may be in part because the concept of occupancy modelling is relatively recent (MacKenzie et al. 2002), and the fact that it was developed in a terrestrial setting has meant it has been slow to cross the boundary into marine research. However, a significant reason occupancy modelling has failed to gain traction in marine research is likely the fundamental differences in the collection of marine and terrestrial data, especially by amateurs. Much of occupancy modelling's popularity has come from its ability to robustly estimate useful information from citizen science, amateur, or opportunistic recording of biodiversity data (van Strien et al. 2013, Isaac et al. 2014). It is possible therefore that the higher incidence on land of widespread and systematic recording schemes by amateurs, as well as high profile citizen science programmes, is the reason occupancy modelling has gained a popularity in terrestrial research that it has yet to see in marine data.

6.3 Considerations when applying occupancy modelling to aggregated marine data

There is no reason however why occupancy modelling should not be used with marine data, as previous studies (MacNeil et al. 2008a, Katsanevakis et al. 2011, Issaris et al. 2012, Coggins et al. 2014) and this thesis exemplify. There are, though, a number of factors to consider when using such methods with marine data, especially data from aggregated sources such as OBIS. The first aspect to consider is that trends gained from occupancy modelling are difficult to verify, precisely because the method is designed to predict the unknowable from imperfect data. That is not to say the method is untrustworthy; not only is the mathematical basis for occupancy modelling sound, but simulation studies comparing occupancy modelling to other methods (Isaac et al. 2014) demonstrate it as the best option to account for detection bias, and in the case of cetaceans presented here, comparison of both occupancy and predicted abundance estimates from modelled data and survey data imply reasonable confidence in the results. But rather it is to caution that naïve occupancy models are not applicable to every situation, as exemplified in Chapter 5, and care should be taken before implementing management decisions based on unverified or un-field-tested modelling results alone. This is particularly true when considering models that assess widely varied habitats. In Chapters 2, 3, and 4, while spatial scales varied, the broad scale environmental factors defining species presence or absence were consistent, either because a small geographic area was considered (e.g. the UK), or because a single broad biome was being assessed (e.g. tropical waters). When naïve occupancy modelling was attempted on scales covering significantly varied habitats, it was unsuccessful. In these cases therefore, it is important to consider the underlying ecology of the trends being investigated, and account for those accordingly with covariates in the model code.

The second is that careful consideration must be given to the assumption of closure, or the idea that when estimating occupancy within a "closure period", presence or absence of a species should be constant. For sessile organisms this assumption can hold as true as it does on land, but for wider ranging, highly mobile organisms, this assumption may be violated, depending on the temporal and spatial resolution chosen. While this is not necessarily a barrier to the implementation of occupancy modelling, and indeed in all cases presented in this thesis the assumption of closure has been relaxed, it is certainly a factor to keep in mind when implementing such a method.

The third key consideration is the level of data manipulation required to achieve robust results from occupancy modelling when using OBIS data. Aside from basic quality control checks (such as the verification of taxonomic and geographic information) in all cases here where occupancy modelling has been implemented, OBIS data has needed to be temporally and spatially binned to ensure model outputs are robust to the most extreme variation in temporal and spatial recording bias, and to emulate the type of site-based data occupancy modelling is designed for. This binning has been context-dependent and sometimes required fine-tuning, inhibiting the possibility at present of a user-friendly implementation of generic occupancy modelling for OBIS data, for example in R package form (R Core Team 2017). Currently too, the effect of these manipulations on output time-series is still relatively unknown. The next step in implementing occupancy modelling in OBIS data, and perhaps the most important, is therefore a thorough sensitivity analysis conducted on simulated data to determine the effect of these manipulations on the accuracy of output time series. Such data would take the form of simulated distribution data (which can be produced easily using R, e.g. with the package "mobsim"; May 2017), temporally replicated, and sampled computationally (as in Isaac et al. 2014) in different ways, then aggregated to produce a database emulating OBIS. This data can then be subjected to occupancy modelling, varying the degree of temporal and spatial binning I have implemented in this thesis, to compare trends in and performance of occupancy modelled data to that of the original simulated data. Doing so would help reveal the true effect of temporal and spatial binning on modelled trends.

Finally, it is important to note that often the most threatened species (e.g. in the case of *Conus*) do not have enough data to be successfully subjected to occupancy modelling, supporting the idea that the best known species are the most common and least threatened (Pimm et al. 2014, Webb and Mindel 2015). Therefore a group or even genus level index created from occupancy modelled trends may under-represent threatened species, and present conservative estimates of change as a result. As such, species level trends are important to consider in any wholesale application of occupancy modelling.

6.4 Computational limitations in occupancy modelling

Computational limitations, and the abundance of available data in OBIS, presented potentially the single largest obstacle in the completion of this work, but have received little attention in literature regarding the implementation of these models (but see Dennis et al. 2017). Occupancy modelling in a Bayesian framework, as used here, requires significant computational power and time, and even while using a high performance computing cluster, a lack specifically of memory often hampered the ability to implement occupancy models in the form that would arguably have been most ideal. These limitations typically take two forms, namely (a) the number of species it is possible to model, and (b) the ability to monitor all model parameters.

Required computational power, and required memory to store model outputs, increase as a result of four factors when implementing occupancy models, namely the number of species, sites or cells, and time periods modelled, and the number of model iterations. As such, for a given area and time period, when a minimum number of iterations is required for model convergence, the number of species possible to model is inherently limited, at least when considering the more robust multispecies models. In the case of *Conus* for example, additional gastropod species could not be modelled alongside *Conus* because of computational constraints, and in this case cells and closure periods were defined on a reasonably coarse scale. Significant thought should therefore be given to implementing multispecies occupancy modelling for large groups of species at fine temporal and spatial resolution, and wholesale implementation of occupancy modelling at a global scale is likely to be almost impossible without significant computational power. This problem is alleviated by using single species methods, as each model run considers only data for a single species and thus computational requirements are smaller. However, the downside of this method is that information sharing between models is not possible, which may in turn reduce the reliability of results, and the number of species successfully modelled, when data availability for a group is low (Zipkin et al. 2009, Ruiz-Gutiérrez et al. 2010).

Constraints on memory additionally required in many cases that numerous model parameters could not be monitored for assessment of convergence. In all cases, the parameter of interest (namely proportional occupancy) was assessed and all presented results required this parameter to meet quality control requirements regarding convergence and information content. However, beyond proportional occupancy, the ability for other model parameters to be monitored varied considerably. In all cases where other parameters could be monitored, they were subjected to the same quality control procedure as proportional occupancy (where this was appropriate), and fortunately the number of parameters modelled typically decreased with increasing quantities of data, which in turn provide the model with more information and theoretically make it more likely to converge successfully. However, while perfect convergence in all model parameters is not necessarily required for robust results, the ability to successfully monitor all parameters should be considered before relying solely on occupancy modelling as an evidence base for real-world action, for example in the implementation of management interventions.

6.5 Future directions

The most important future step arising from this work is a thorough sensitivity analysis examining the effect that both temporal and spatial binning, as described above, and methodological data grouping, have on output time series of occupancy when compared to simulation data. Doing so will alleviate many of the concerns or criticisms raised against using occupancy models and marine data in this way, as well as allow for more informed decisions to be made when data are binned and grouped. Following this, the abundance of data in OBIS and elsewhere, and the taxonomic breadth of this data, means broad but robust temporal trends could be achieved for any number of marine taxa, many of which have received little attention previously. The development of more complex models of occupancy in marine settings will also allow ecologists to answer more fundamental questions regarding marine macroecology, the most obvious examples being those of abundance-occupancy relationships and the marine latitudinal diversity gradient discussed in this work. Finally, and potentially most interestingly, these models could be implemented quickly and cost effectively in taxonomic groups in threatened areas of the globe to give a broad understanding of the species or functional groups of most and least concern, identifying and prioritising which species should be subject to further, on-the-ground assessment.

6.6 Concluding remarks

Unstructured data and occupancy modelling have the potential to greatly increase our knowledge of change in biodiversity (Edgar et al. 2016), particularly for taxonomic groups for which there has been little previous interest, and also our understanding of macroecological patterns. In this thesis, I have demonstrated some of the ways we can address both practical and more theoretical ecological questions using various occupancy modelling methodologies, and data from the world's largest repository of marine biodiversity information, the Ocean Biogeographic Information System. It is my hope that the methodological framework outlined here sees wider use in marine research, and continual improvement and expansion, to further improve our knowledge of, and ability to manage, marine biodiversity in a changing world.

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8: Supporting Information

Figure S1: Methodological schematic.

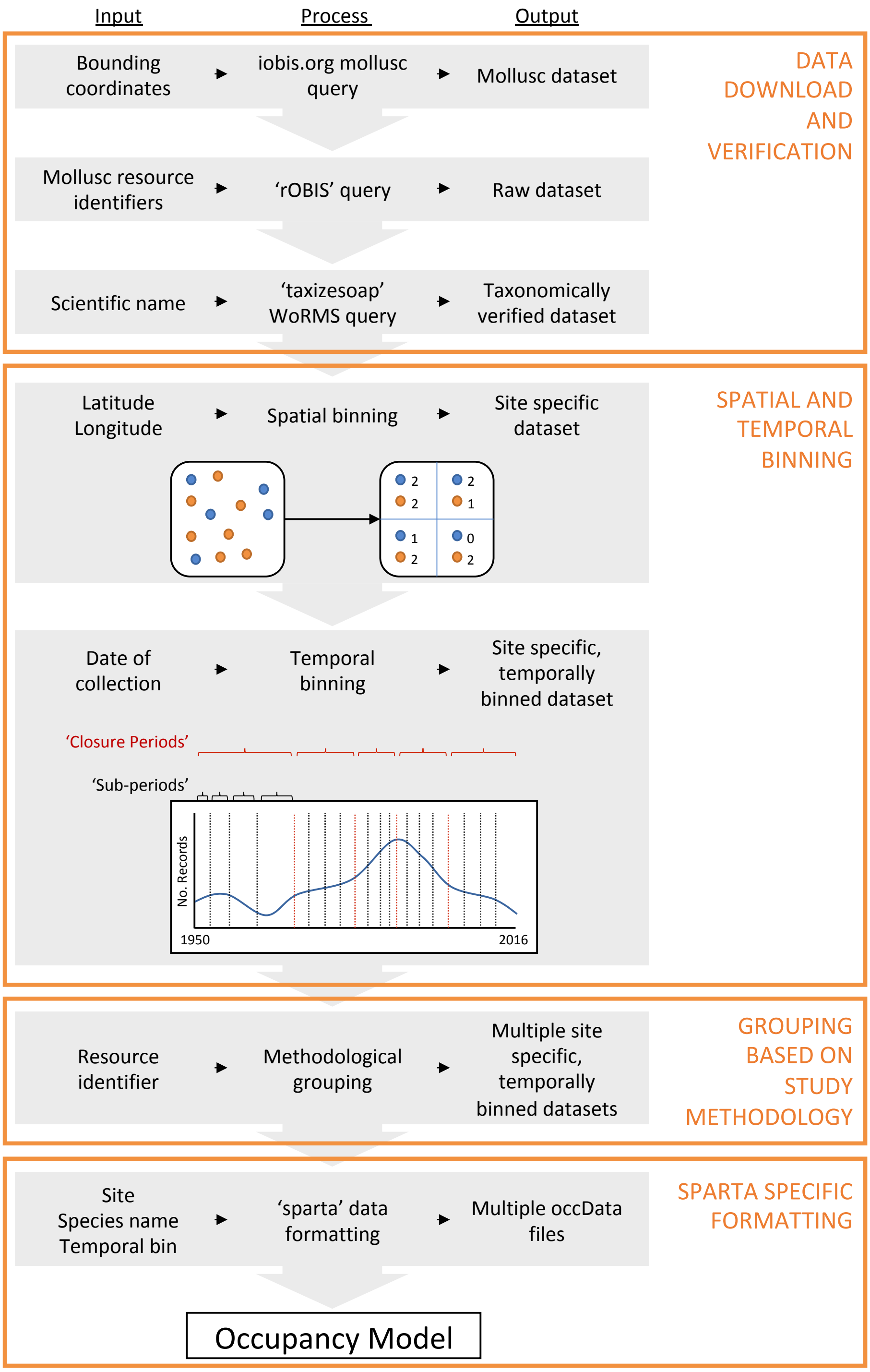

Figure S1: *Schematic demonstrating the data collection, validation and processing required to utilise OBIS data with occupancy models, using convenience functions from "sparta".*

Figure S2: Length of closure periods for the three *Conus* data groupings that produced suitably confident outputs to be used in analysis

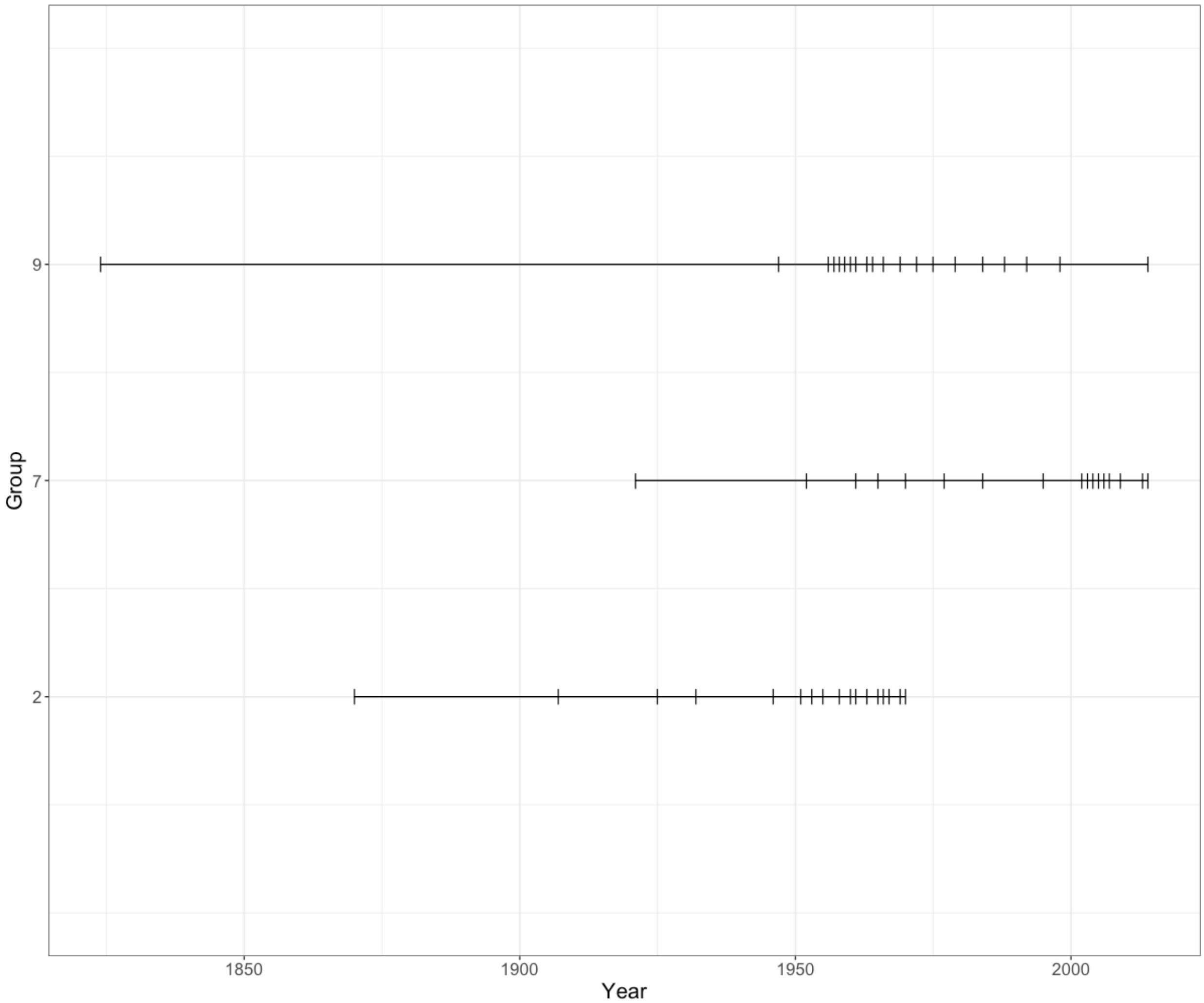

Figure S2: *Length of closure periods for the three* Conus *methodological groupings that produced output suitable for further analysis. Vertical lines represent breaks between closure periods.*

Figure S3: Comparison of surveyed occupancy, and the difference between surveyed occupancy and modelled MERP occupancy estimates, derived from MERP presence-only data, for all species within years.

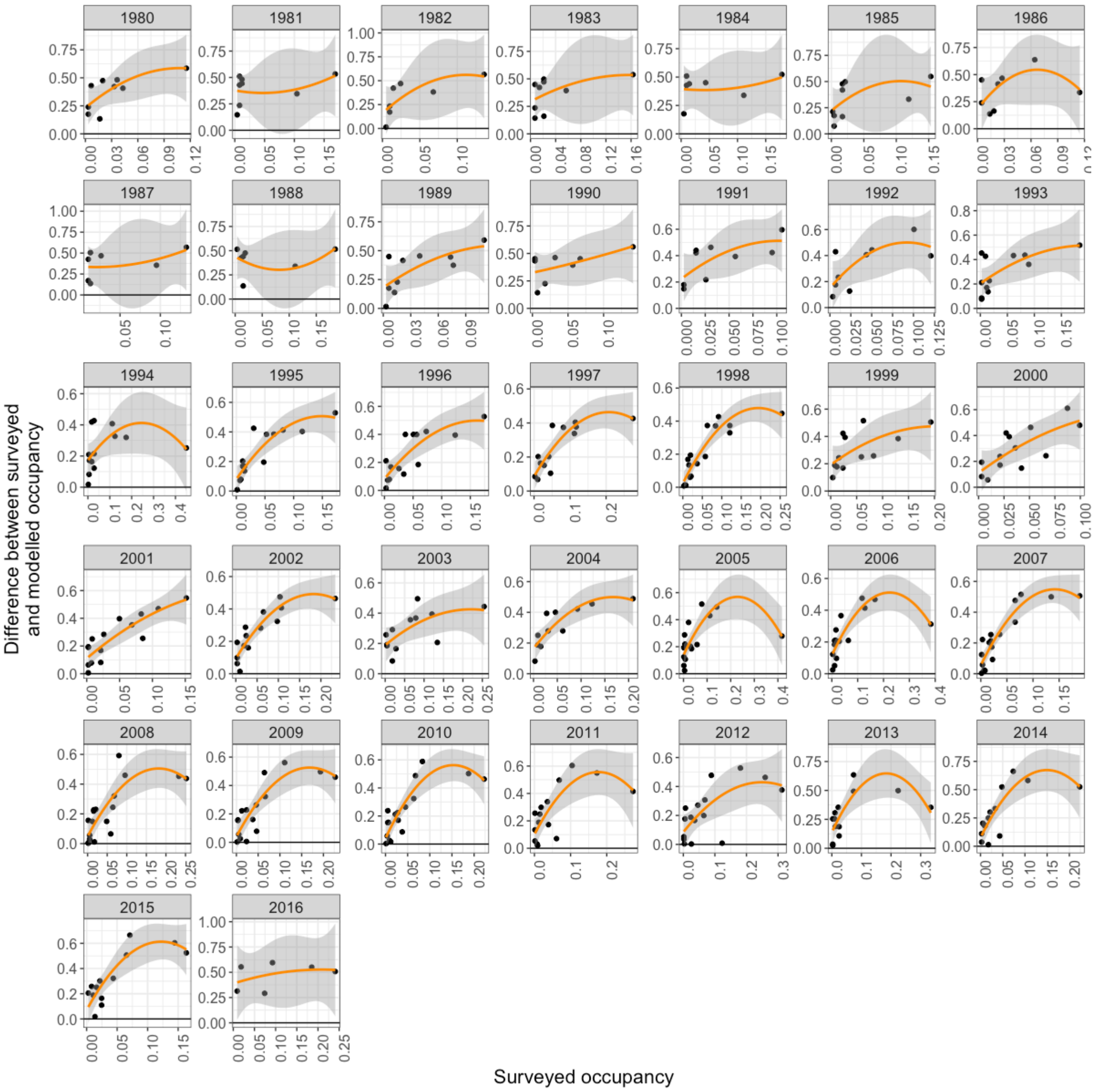

Figure S3: *Relationship between surveyed occupancy from the MERP effort-based surveys, and the difference between surveyed occupancy and modelled occupancy from MERP presence-only data, such that exact predictions of occupancy fall on the black horizontal line, and overestimates fall above the line. Orange lines are the result of a smoothed second order polynomial. Coefficient values and significance levels for all significant polynomial relationships can be found in Table S6.*

Figure S4: Comparison of surveyed occupancy, and the difference between surveyed occupancy and modelled OBIS occupancy estimates, derived from targeted survey data, for all species within years.

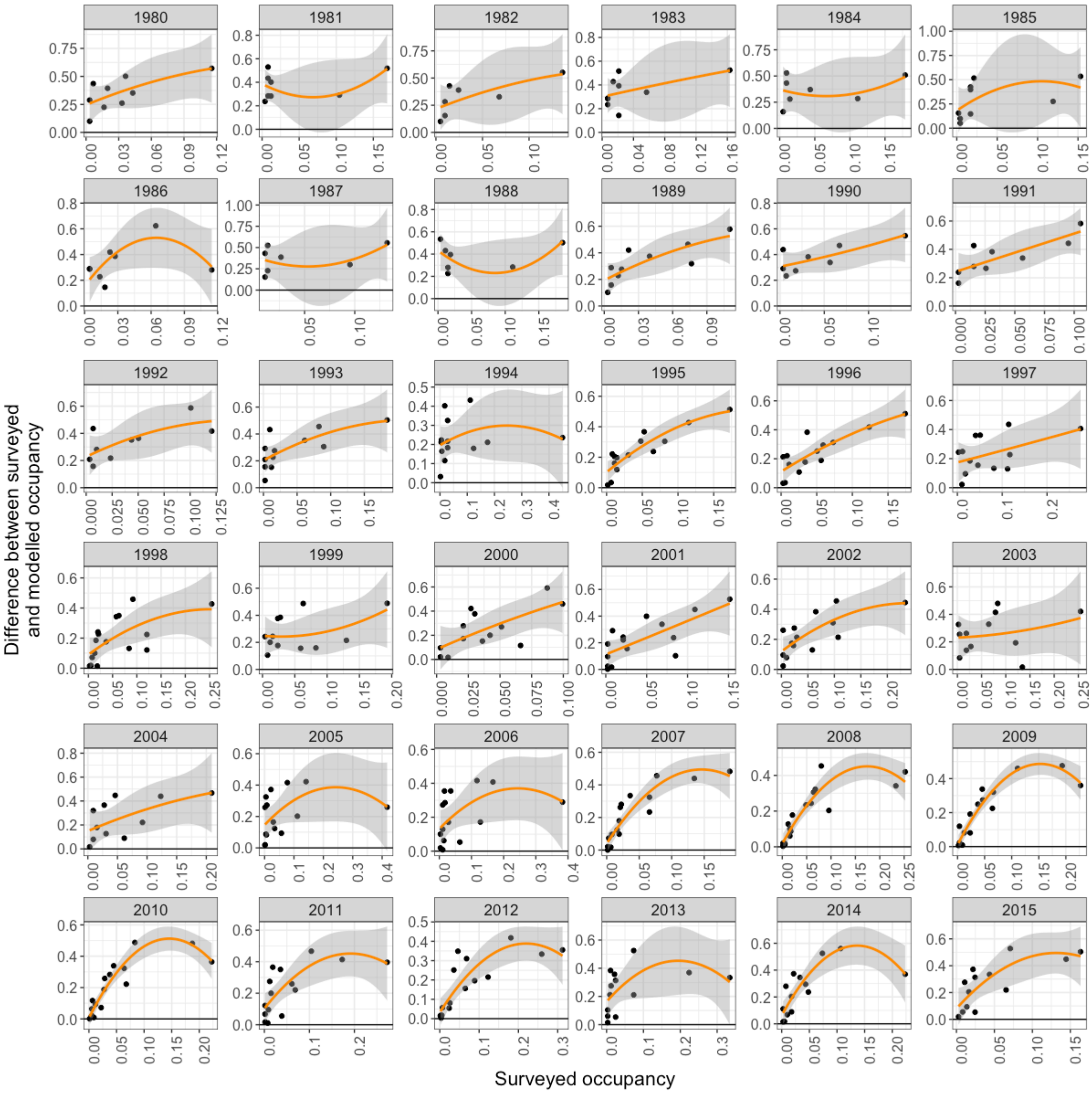

Figure S4: *Relationship between surveyed occupancy from the MERP effort-based surveys, and the difference between surveyed occupancy and modelled occupancy from OBIS data derived from targeted surveys, such that exact predictions of occupancy fall on the black horizontal line, and overestimates fall above the line. Orange lines are the result of a smoothed second order polynomial. Coefficient values and significance levels for all significant polynomial relationships can be found in Table S6.*

Figure S5: Comparison of surveyed occupancy, and the difference between surveyed occupancy and modelled OBIS occupancy estimates derived from opportunistic data, for all species within years.

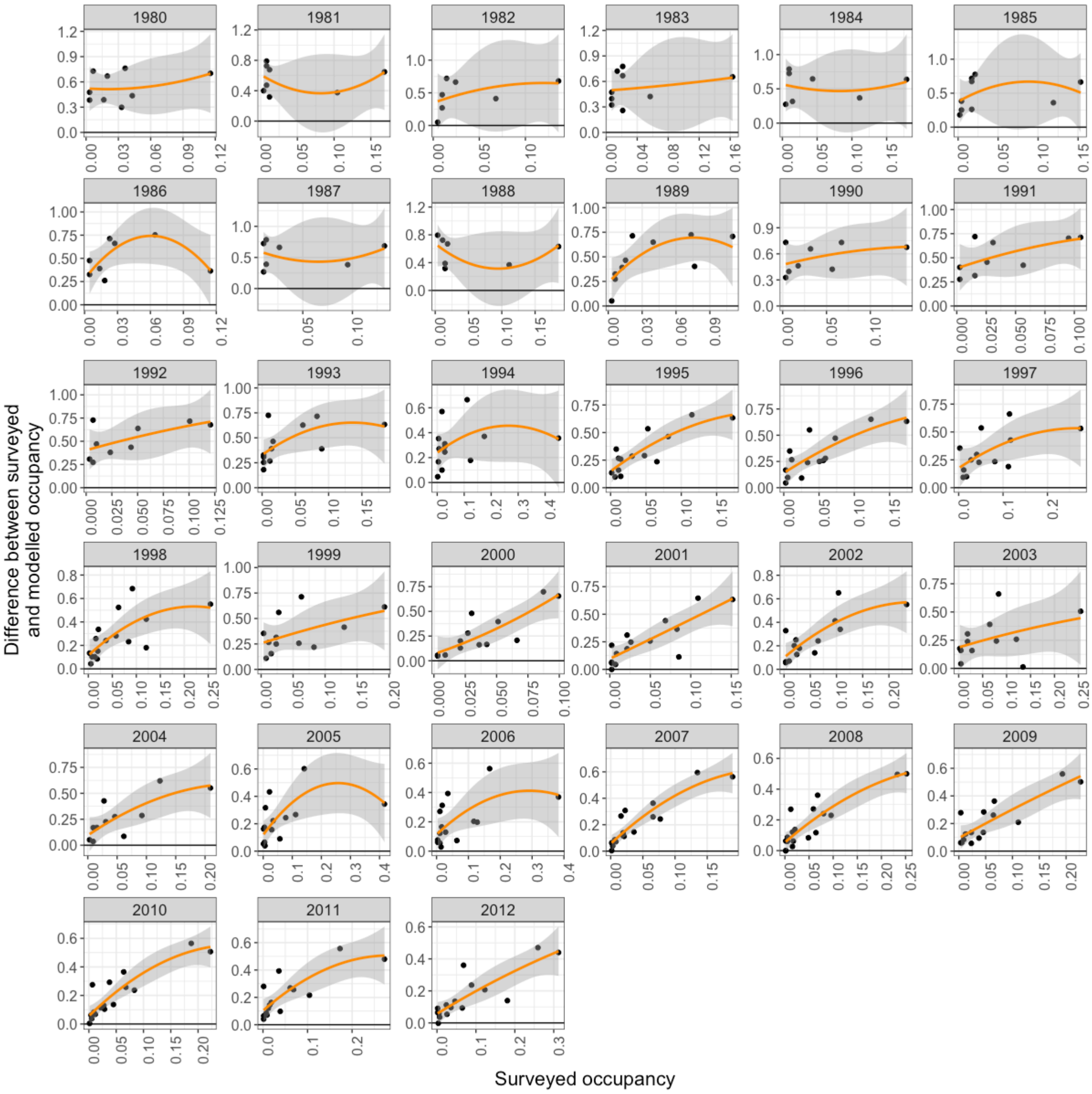

Figure S5: *Relationship between surveyed occupancy from the MERP effort-based surveys, and the difference between surveyed occupancy and modelled occupancy from OBIS data derived from opportunistic recording, such that exact predictions of occupancy fall on the black horizontal line, and overestimates fall above the line. Orange lines are the result of a smoothed second order polynomial. Coefficient values and significance levels for all significant polynomial relationships can be found in Table S6.*

Figure S6: Prediction of abundance for all years within species using occupancy modelled MERP data.

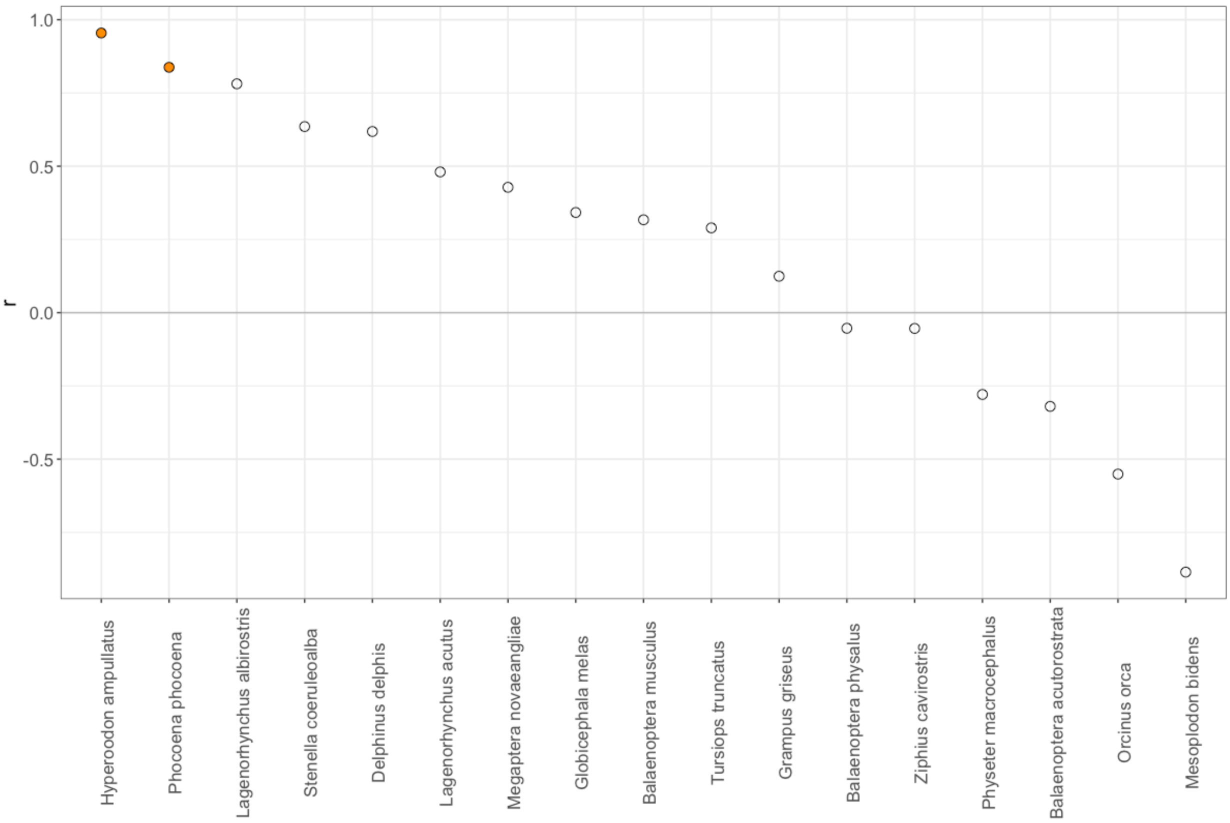

Figure S6: *Coefficients of correlation between observed and predicted abundance per species, using abundance estimates derived from intraspecific AORs and modelled MERP presence-only data. Orange points indicate significant correlations (p < 0.05).*

Figure S7: Prediction of abundance for all years within species using occupancy modelled OBIS targeted survey data.

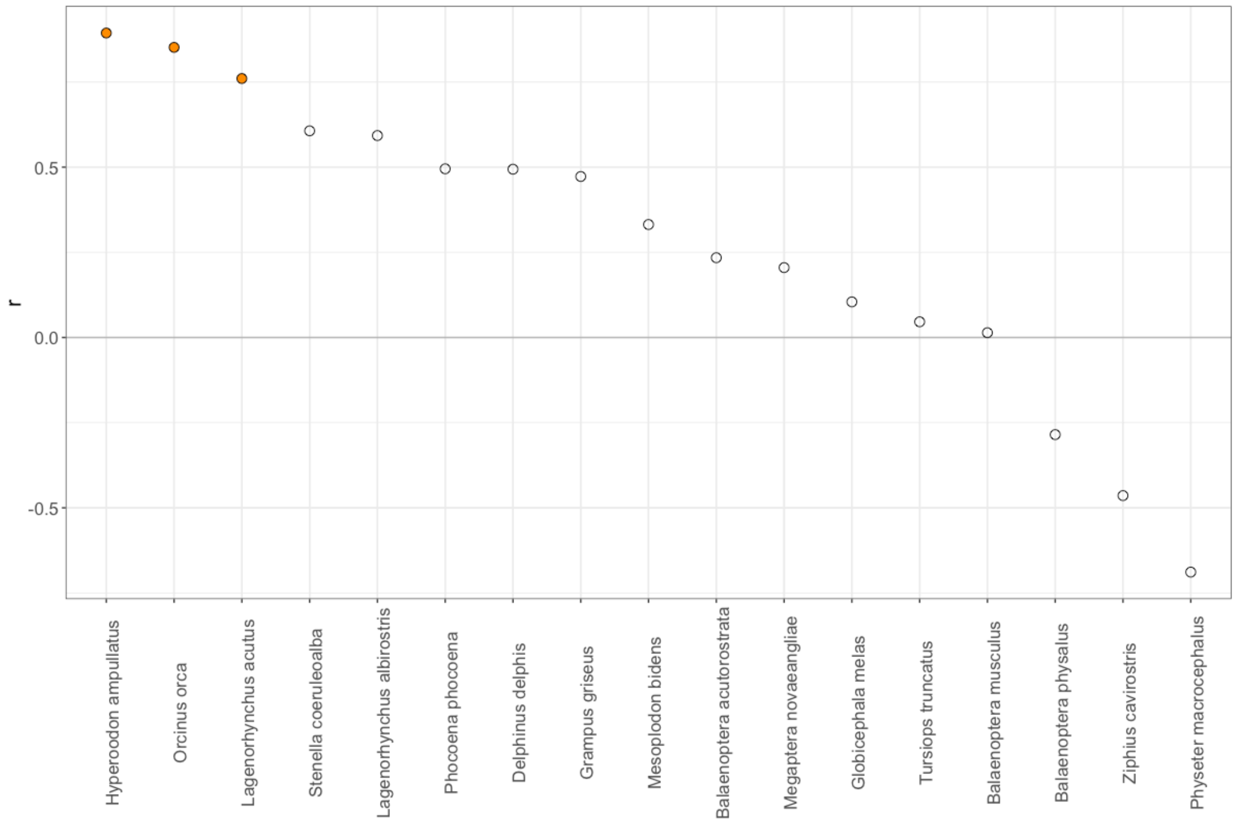

Figure S7: *Coefficients of correlation between observed and predicted abundance per species, using abundance estimates derived from intraspecific AORs and modelled OBIS data derived from targeted surveys. Orange points indicate significant correlations ($p < 0.05$).*

Figure S8: Prediction of abundance for all years within species using occupancy modelled OBIS opportunistic data.

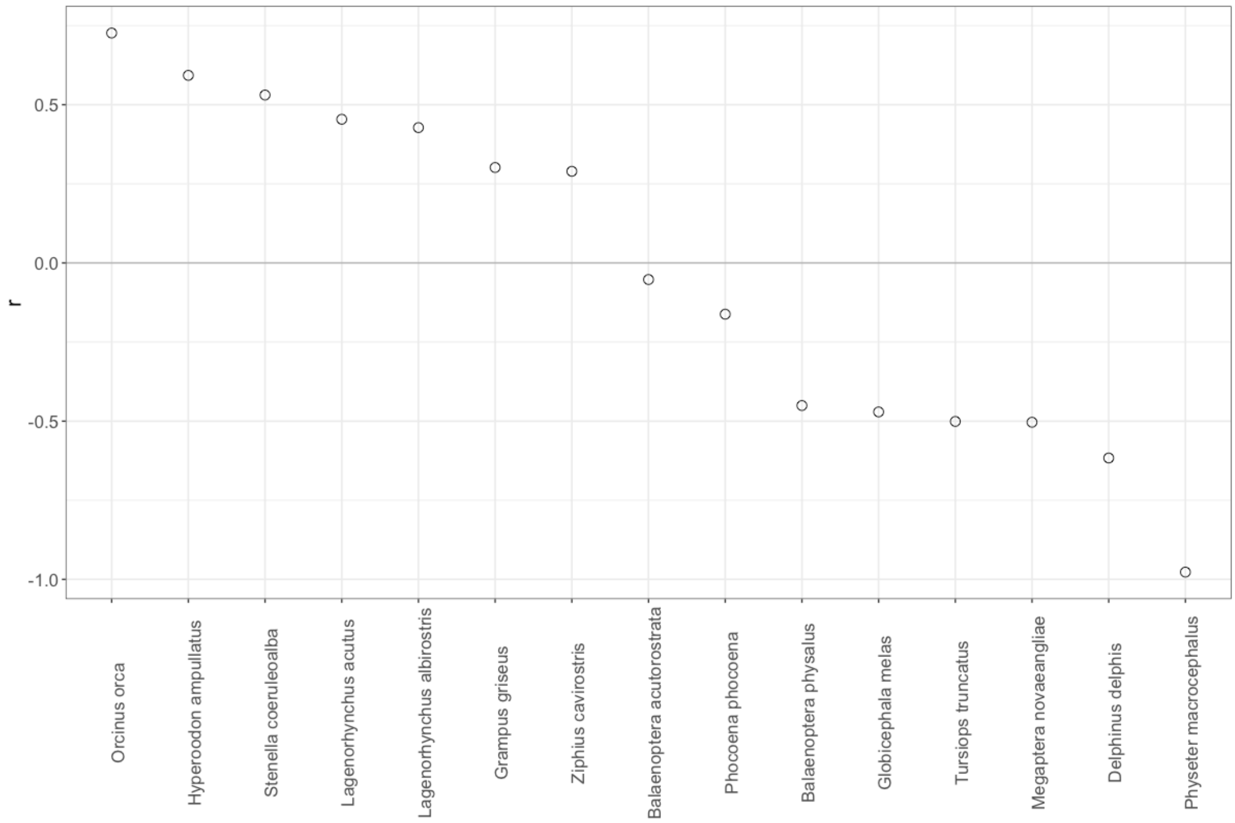

Figure S8: *Coefficients of correlation between observed and predicted abundance per species, using abundance estimates derived from intraspecific AORs and modelled OBIS data derived from opportunistic recording. Orange points indicate significant correlations ($p < 0.05$).*

Figure S9: Number of species gained per latitudinal band after occupancy modelling

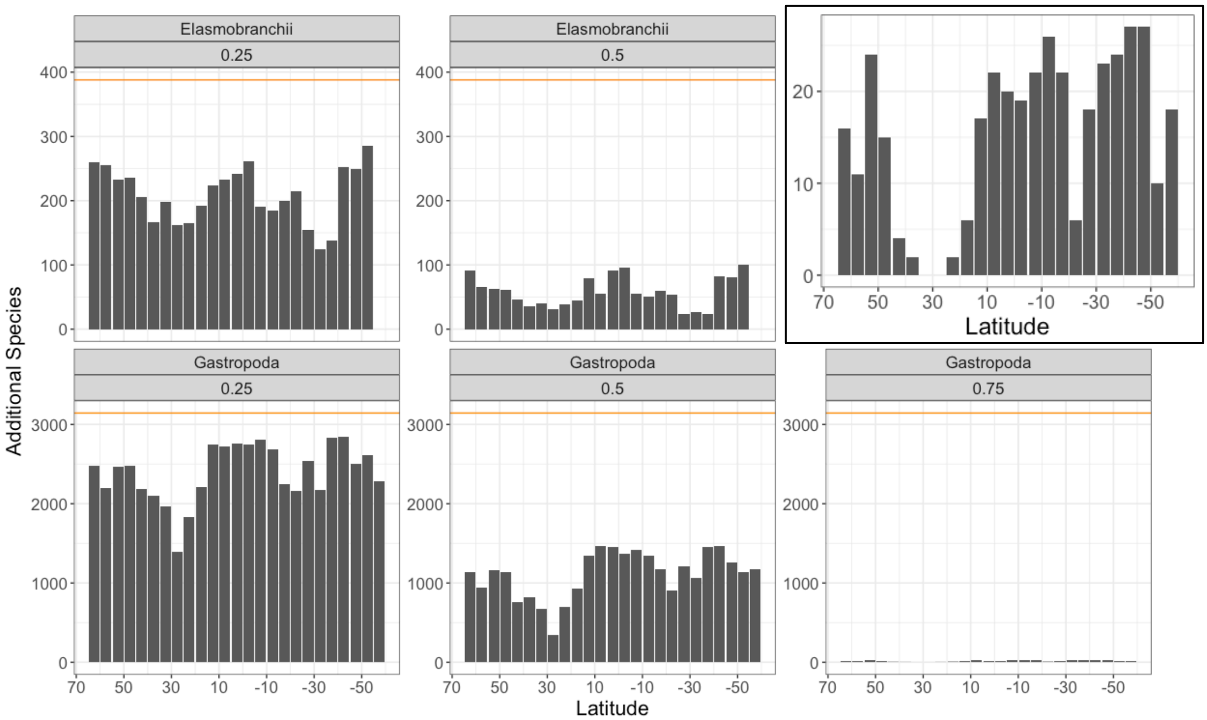

Figure S9: *Number of additional species estimated as present in each latitudinal band after occupancy modelling for two taxonomic groups (gastropods and elasmobranchs), using three z-threshold values (0.25, 0.5, and 0.75). No additional elasmobranch species were predicted to be found using z-threshold = 0.75. Orange lines indicate the maximum number of species possible to be observed in a band, based on the number of species for which data was modelled. Inset (top right): Detailed view of additional gastropod species predicted per latitudinal band at z-threshold = 0.75.*

Appendix S1: JAGS single species random-walk occupancy model code

See Outhwaite et al. (2018) for further details:

```
model {
  # State model
  for (i in 1:nsite){
    for (t in 1:nyear){
      z[i,t] ~ dbern(muZ[i,t])
      logit(muZ[i,t]) <- a[t] + eta[i]
    }
  }

  # Observation model
  for (j in 1:nvisit){
    y[j] ~ dbern(Py[j])
    Py[j] <- z[Site[j],Year[j]]*p[j]
    logit(p[j]) <- alpha.p[Year[j]] + LL.p*logL[j]
  }

  # State model priors
  a[1] ~ dnorm(mu.a, 0.0001)
  mu.a ~ dnorm(0, 0.01)
  tau.a <- 1/(sd.a * sd.a)
  sd.a ~ dt(0, 1, 1)T(0,)
  tau2 <- 1/(sigma2 * sigma2)
  sigma2 ~ dt(0, 1, 1)T(0,)

  for(t in 2:nyear){
    a[t] ~ dnorm(a[t-1], tau.a)
  }

  for (i in 1:nsite){
    eta[i] ~ dnorm(0, tau2)
  }

  # Observation model priors
  for (t in 1:nyear){
    alpha.p[t] ~ dnorm(mu.lp, tau.lp)
  }

  mu.lp ~ dnorm(0, 0.01)
  tau.lp <- 1 / (sd.lp * sd.lp)
  sd.lp ~ dt(0, 1, 1)T(0,)
  LL.p ~ dunif(dtype2p_min, dtype2p_max)

  # Derived parameters
  for (t in 1:nyear){
    psi.fs[t] <- sum(z[1:nsite, t])/nsite
  }
}
```

Appendix S2: JAGS dynamic multispecies occupancy model code

Modified from the dynamic multispecies model of Ruiz-Gutiérrez et al. (2010) and Woodcock et al. (2016):

```
model {
  # State Model
  for (i in 1:nspecies){
    for (j in 1:nsite){
      z[i,j,1] ~ dbern(init.occ[i])
      for (t in 2:nyear){
        logit(phi[i,j,t]) <- alpha.phi[i] + eta[j]
        muZ[i,j,t] <- z[i,j,t-1] * phi[i,j,t] + (1 - z[i,j,t-1]) * gamma[i]
        z[i,j,t] ~ dbern(muZ[i,j,t])

      }
    }
  }

  # Observation Model
  for (i in 1:nspecies){
    for (k in 1:nvisit) {
    logit(p[i,k]) <- alpha.t.p[Year[k]] + LL.p[i]*logL[k]
    Py[i,k]<- z[i,Site[k],Year[k]] * p[i,k]
    y[k,i] ~ dbern(Py[i,k])
    }
  }

  # State model priors
  for (i in 1:nspecies){
    init.occ[i] ~ dunif(0, 1)
    alpha.phi[i] ~ dnorm(mu.alpha.phi, tau.alpha.phi)
    logitgamma[i] ~ dnorm(mu.gamma, tau.gamma)
    logit(gamma[i]) <- logitgamma[i]
  }

  for (j in 1:nsite) {
    eta[j] ~ dnorm(0, tau2)
  }

  mu.alpha.phi ~ dnorm(0, 0.01)
  mu.gamma ~ dnorm(0, 0.01)
  tau.alpha.phi ~ dt(0,1,1)T(0,)
  tau.gamma ~ dt(0,1,1)T(0,)
  tau2 <- 1/(sigma2 * sigma2)
  sigma2 ~ dunif(0, 5)

  # Observation model priors
  for (i in 1:nspecies){
    LL.p[i] ~ dunif(dtype2p_min, dtype2p_max)
  }
```

```
  for (t in 1:nyear) {
    alpha.t.p[t] ~ dnorm(0, tau.lp4)
  }

  tau.lp4 ~ dt(0,1,1)T(0,)

  # Derived parameters
  for (i in 1:nspecies){
    for (t in 1:nyear) {
      psi.fs[i,t] <- sum(z[i,1:nsite,t])/nsite
    }
  }

  for (t in 1:nyear) {
    pdet.alpha[t] <- exp(alpha.t.p[t])/(1 + exp(alpha.t.p[t]))
  }
}
```

Appendix S3: JAGS non-temporal multispecies occupancy model code

Modified from the dynamic multispecies model of Ruiz-Gutiérrez et al. (2010) and Woodcock et al. (2016):

```
model {
  # State model
  for (i in 1:nspecies){
    for (j in 1:nsite){
      z[i,j,1] ~ dbern(init.occ[i])
    }
  }

  # Observation model
  for (i in 1:nspecies){
    for (k in 1:nvisit) {
      logit(p[i,k]) <- alpha.t.p[Year[k]] + LL.p[i]*logL[k]
      Py[i,k]<- z[i,Site[k],Year[k]] * p[i,k]
      y[k,i] ~ dbern(Py[i,k])
    }
  }

  # State model priors
  for (i in 1:nspecies){
    init.occ[i] ~ dunif(0, 1)
  }

  # Observation model priors
  for (i in 1:nspecies){
    LL.p[i] ~ dunif(dtype2p_min, dtype2p_max)
   }

  for (t in 1:nyear) {
    alpha.t.p[t] ~ dnorm(0, tau.lp4)
  }

  tau.lp4 ~ dt(0,1,1)T(0,)

  # Derived parameters
  for (i in 1:nspecies){
    for (t in 1:nyear) {
      psi.fs[i,t] <- sum(z[i,1:nsite,t])/nsite
    }
  }

  for (t in 1:nyear) {
    pdet.alpha[t] <- exp(alpha.t.p[t])/(1 + exp(alpha.t.p[t]))
  }
}
```

Table S1: OBIS citations for datasets modelled in Chapter 2.

Resource ID	Resource Name and Citation	Analysis Grouping
99	**Marine records from Pembrokeshire Marine Species Atlas** Dale Rostron. Marine records from Pembrokeshire Marine Species Atlas. Countryside Council for Wales, Gwynedd, UK.	1
29	**Atlantic Reference Centre Museum of Canadian Atlantic Organisms - Invertebrates and Fishes Data** Van Guelpen, L., 2016. Atlantic Reference Centre Museum of Canadian Atlantic Organisms - Invertebrates and Fishes Data. Version 4 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2017-04-04	2
500	**NMNH Invertebrate Zoology Collections** Department of Invertebrate Zoology, Research and Collections Information System, NMNH, Smithsonian Institution. See: http://www.mnh.si.edu/rc/db/collection_db_policy1.html	2
2280	**Arctic benthic invertebrate collection of the Zoological Institute of the Russian Academy of Science** Sirenko B.I., ed. 2001. List of species of free-living invertebrates of Eurasian Arctic seas and adjacent deep waters. In: Explorations of the fauna of the seas. 51(59). St. Petersburg: 1-132.	2
2505	**ICES Historical Plankton Dataset** ICES Historical Plankton Dataset (1901-1912). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	3
2546	**World Ocean Database 2009** Baranova, O.K, T.D. O'Brien, T.P. Boyer and I.V. Smolyar (2009). Plankton data. Chapter 16 in Boyer, T. P., J. I. Antonov, O. K. Baranova, H. E. Garcia, D. R. Johnson, R. A. Locarnini, A. V. Mishonov, T. D. O'Brien, D. Seidov, I. V. Smolyar, M. M. Zweng, 2009. World Ocean Database 2009. S. Levitus, Ed., NOAA Atlas NESDIS 66, U.S. Gov. Printing Office, Wash., D.C., 216 pp., DVDs	3
2548	**Continuous Plankton Recorder (Zooplankton)** Continuous Plankton Recorder (CPR) data (zooplankton) from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Available from http://iobis.org/, accessed 2017-04-04	3
3046	**Zooplankton in the Bay of Biscay (1995-2004, yearly DEPM surveys)** Zooplankton from the Bay of Biscay (1995-2004 MPDH surveys). Marine Research Unit, AZTI, Spain.	3

702	**2005-Ongoing UK MarLIN Shore Thing timed search results** UK National Biodiversity Network, Marine Biological Association - Ongoing UK MarLIN Shore Thing timed search results.	4
705	**Survey of North Wales and Pembrokeshire Tide Influenced Communities** UK National Biodiversity Network, Countryside Council for Wales - Survey of North Wales and Pembrokeshire Tide Influenced Communities	4
3053	**Marine data from Natural Resources Wales (NRW) Technical Support (Research & Monitoring) Contracts, Wales** UK National Biodiversity Network, Countryside Council for Wales - Marine data from Countryside Council for Wales (CCW) Technical Support (Research & Monitoring) Contracts, Wales	4
3105	**Marine Intertidal Phase 1 species dataset from the Countryside Council for Wales 1996-2005** UK National Biodiversity Network, Countryside Council for Wales - Marine Intertidal Phase 1 species dataset from the Countryside Council for Wales 1996-2005.	4
3125	**Marine flora and fauna records from the North-east Atlantic** Marine flora and fauna records from the North-east Atlantic. Porcupine Marine Natural History Society, UK - UK National Biodiversity Network.	4
96	**Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by English Nature** English Nature. Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by English Nature. English Nature, Peterborough, UK.	5
1987	**Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by JNCC** Ostler, R. Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by JNCC. Joint Nature Conservation Committee, Centre for Ecology and hydrology, Aberdeenshire, UK.	5
89	**Marine Life Survey Data (collected by volunteers) collated by MarLIN** Parr, J. Marine Life Survey Data (collected by volunteers) collated by MarLIN. MarLIN, collated Marine Life Survey Datasets, Marine Biological Association of the UK, Plymouth, UK.	6
248	**Biogeographic data from BODC - British Oceanographic Data Centre** British Oceanographic Data Centre, UK. Biogeographic data from BODC. in: EurOBIS. http://www.marbef.org/data/eurobissearch.php?dataprovider=47, accessed on 2017-04-04.	6

590	**National Marine Monitoring Programme data set** Whomersley, P., 2003: National Marine Monitoring Programme. Benthos data of the North Sea, Irish Sea, English Channel from 2002-2003. CEFAS, Burnham On Crouch, UK	6
1512	**Marine Life List of Ireland** Allen D., Beckett B., Brophy J., Costello M.J., Emblow C., Maciejewska B., McCrea M., Nash R., Penk M. & Tierney A. Marine species recorded in Ireland during field suveys by EcoServe, Ecological Consultancy Services Ltd. Available online at http://www.marbef.org/data/eurobis.php. Consulted on 2017-04-04	6
1986	**Marine Life Information Network (MarLIN) marine survey data (Professional)** Parr, J. Marine Life Information Network (MarLIN) marine survey data (Professional). Marlin, Collated Marine Life Survey Datasets, Marine Biological Association of the UK, Plymouth, UK	6
2586	**PANGAEA - Data from Ocean margin exchange project (OMEX I)**	6
2637	**BIOMÔR 4 The Outer Bristol Channel Marine Habitat Study** Mackie, A.S.Y., James, J.W.C., Rees, E.I.S., Darbyshire, T., Philpott, S.L., Mortimer, K., Jenkins, G.O. & Morando, A., 2006. The Outer Bristol Channel Marine Habitat Study. - Studies in Marine Biodiversity and Systematics from the National Museum of Wales. BIOMÔR Reports 4: 249 pp. & Appendix 228 pp.	6
3096	**Marine records from Skomer Marine Nature Reserve (MNR) Marine Monitoring Programme** Marine records from Skomer Marine Reserve (MNR) Marine Monitoring Programme. Countryside Council for Wales, UK - UK National Biodiversity Network.	6
3475	**NaGISA Project**	6
4374	**The UK Archive for Marine Species and Habitats Data** Marine Biological Association of the UK (MBA); (2016): DASSH: The UK Archive for Marine Species and Habitats Data	6
8	**Academy of Natural Sciences OBIS Mollusc Database** Rosenberg et al., 2002	7
1985	**Mollusc (marine) data for Great Britain and Ireland** UK National Biodiversity Network, Conchological Society of Great Britain & Ireland - Mollusc (marine) data for Great Britain and Ireland.	7
1576	**ICES contaminants and biological effects** ICES Contaminants and biological effects database (DOME - Biota). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	8

2493	**Irish Ground Fish Survey for commercial fish species** Fish trawl survey: Irish Ground Fish Survey for commercial fish species. ICES Database of trawl surveys (DATRAS). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk	8
2530	**ICES Beam Trawl Survey for commercial fish species** Fish trawl survey: ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	8
2537	**ICES French Southern Atlantic Bottom Trawl Survey for commercial fish species** Fish trawl survey: ICES French Southern Atlantic Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	8
2538	**Northern Irish Ground Fish Trawl Survey** Fish trawl survey: Northern Irish Ground Fish Trawl Survey. ICES Database of trawl surveys (DATRAS). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	8
103	**Seasearch Marine Surveys** Marine Conservation Society. Seasearch Marine Surveys. Marine Conservation Society, Ross-on-Wye, UK.	9
3064	**Marine species distributions in Irish coastal waters** National Biodiversity Data Centre: Marine species distributions in Irish coastal waters, 2013-11-20. Accessed via http://www.gbif.org/dataset/0d83ea43-5afb-4c50-af9c-fd22674338bb on 2017-04-04	9
3422	**Diveboard - Scuba diving citizen science observations** Diveboard - Scuba diving citizen science observations. Online at http://www.diveboard.com and http://ipt.diveboard.com/resource.do?r=diveboard-occurrences. http://dx.doi.org/10.15468/tnjrgy http://dx.doi.org/10.15468/tnjrgy	9

Table S2: Magnitude of change in proportional occupancy for the 166 species assessed in Chapter 2, as well as Class-level classification and assessment status (derived from IUCN and OSPAR assessments).

Change	Species	Class	Assessment Status
-2.031625e-01	*Tritia reticulata*	Gastropoda	Unassessed
-1.439407e-01	*Hermania scabra*	Gastropoda	Unassessed
-1.409487e-01	*Mytilus edulis*	Bivalvia	Unassessed
-1.385208e-01	*Polycera elegans*	Gastropoda	Unassessed
-1.195741e-01	*Euspira nitida*	Gastropoda	Unassessed
-1.011371e-01	*Doris sticta*	Gastropoda	Unassessed
-8.681111e-02	*Limaria loscombi*	Bivalvia	Unassessed
-8.096667e-02	*Octopus vulgaris*	Cephalopoda	Unassessed
-7.039259e-02	*Emarginula fissura*	Gastropoda	Unassessed
-6.411534e-02	*Pecten maximus*	Bivalvia	Unassessed
-5.045619e-02	*Illex coindetii*	Cephalopoda	Not threatened
-4.920833e-02	*Limecola balthica*	Bivalvia	Unassessed
-4.470833e-02	*Rissoa lilacina*	Gastropoda	Unassessed
-4.435833e-02	*Barleeia unifasciata*	Gastropoda	Unassessed
-4.385926e-02	*Pandora pinna*	Bivalvia	Unassessed
-4.339167e-02	*Berthella plumula*	Gastropoda	Unassessed
-4.246667e-02	*Gibbula tumida*	Gastropoda	Unassessed
-4.130833e-02	*Loripes orbiculatus*	Bivalvia	Unassessed
-3.710238e-02	*Diaphana minuta*	Gastropoda	Unassessed
-3.593704e-02	*Euspira fusca*	Gastropoda	Unassessed
-3.220417e-02	*Spisula solida*	Bivalvia	Unassessed
-2.971921e-02	*Bittium reticulatum*	Gastropoda	Unassessed
-2.950000e-02	*Kellia suborbicularis*	Bivalvia	Unassessed
-2.674167e-02	*Heteranomia squamula*	Bivalvia	Unassessed
-2.335000e-02	*Lacuna vincta*	Gastropoda	Unassessed
-2.167407e-02	*Parvicardium minimum*	Bivalvia	Unassessed
-2.156250e-02	*Lacuna pallidula*	Gastropoda	Unassessed

-2.128476e-02	*Magallana gigas*	Bivalvia	Unassessed
-1.924444e-02	*Hemilepton nitidum*	Bivalvia	Unassessed
-1.841111e-02	*Erato voluta*	Gastropoda	Unassessed
-1.732222e-02	*Diodora graeca*	Gastropoda	Unassessed
-1.351667e-02	*Melarhaphe neritoides*	Gastropoda	Unassessed
-1.276667e-02	*Ocenebra erinaceus*	Gastropoda	Unassessed
-1.201111e-02	*Nucula nitidosa*	Bivalvia	Unassessed
-1.141852e-02	*Epitonium trevelyanum*	Gastropoda	Unassessed
-1.135455e-02	*Okenia elegans*	Gastropoda	Unassessed
-1.085625e-02	*Buccinum undatum*	Gastropoda	Unassessed
-1.078333e-02	*Melanella lubrica*	Gastropoda	Unassessed
-1.029491e-02	*Timoclea ovata*	Bivalvia	Unassessed
-1.019167e-02	*Diaphorodoris luteocincta*	Gastropoda	Unassessed
-9.729630e-03	*Saxicavella jeffreysi*	Bivalvia	Unassessed
-8.625000e-03	*Limacia clavigera*	Gastropoda	Unassessed
-8.508333e-03	*Ensis magnus*	Bivalvia	Unassessed
-7.979167e-03	*Odostomia unidentata*	Gastropoda	Unassessed
-7.970833e-03	*Cochlodesma praetenue*	Bivalvia	Unassessed
-7.795833e-03	*Thecacera pennigera*	Gastropoda	Unassessed
-7.574074e-03	*Alvania beanii*	Gastropoda	Unassessed
-7.433333e-03	*Polycera faeroensis*	Gastropoda	Unassessed
-6.914493e-03	*Sepia officinalis*	Cephalopoda	Not threatened
-6.062500e-03	*Turritella communis*	Gastropoda	Unassessed
-5.460417e-03	*Doto pinnatifida*	Gastropoda	Unassessed
-4.783333e-03	*Ostrea edulis*	Bivalvia	Threatened
-4.737500e-03	*Calyptraea chinensis*	Gastropoda	Unassessed
-3.662500e-03	*Gari fervensis*	Bivalvia	Unassessed
-3.583333e-03	*Papillicardium papillosum*	Bivalvia	Unassessed
-2.967424e-03	*Acanthodoris pilosa*	Gastropoda	Unassessed
-2.850000e-03	*Spisula subtruncata*	Bivalvia	Unassessed
-2.662500e-03	*Patella ulyssiponensis*	Gastropoda	Threatened

-2.491667e-03	*Acanthochitona crinita*	Polyplacophora	Unassessed
-2.233333e-03	*Ensis siliqua*	Bivalvia	Unassessed
-2.233333e-03	*Acanthochitona fascicularis*	Polyplacophora	Unassessed
-2.173380e-03	*Polititapes rhomboides*	Bivalvia	Unassessed
-1.948148e-03	*Jujubinus striatus*	Gastropoda	Unassessed
-1.900000e-03	*Polycera quadrilineata*	Gastropoda	Unassessed
-1.821212e-03	*Limaria hians*	Bivalvia	Unassessed
-1.616667e-03	*Modiolus barbatus*	Bivalvia	Unassessed
-1.616667e-03	*Trivia monacha*	Gastropoda	Unassessed
-1.537037e-03	*Kurtiella bidentata*	Bivalvia	Unassessed
-1.433333e-03	*Euspira catena*	Gastropoda	Unassessed
-1.400952e-03	*Nucella lapillus*	Gastropoda	Threatened
-1.196591e-03	*Janolus cristatus*	Gastropoda	Unassessed
-1.145833e-03	*Littorina saxatilis*	Gastropoda	Unassessed
-1.116667e-03	*Doto coronata*	Gastropoda	Unassessed
-1.066667e-03	*Facelina annulicornis*	Gastropoda	Unassessed
-7.606061e-04	*Lutraria lutraria*	Bivalvia	Unassessed
-6.500000e-04	*Nucula nucleus*	Bivalvia	Unassessed
-6.416667e-04	*Abra alba*	Bivalvia	Unassessed
-5.166667e-04	*Chamelea gallina*	Bivalvia	Unassessed
-4.333333e-04	*Favorinus blianus*	Gastropoda	Unassessed
-4.333333e-04	*Myosotella myosotis*	Gastropoda	Unassessed
-3.333333e-04	*Onchidoris muricata*	Gastropoda	Unassessed
-1.666667e-04	*Clausinella fasciata*	Bivalvia	Unassessed
-1.666667e-05	*Vitreolina philippi*	Gastropoda	Unassessed
0.000000e+00	*Hyala vitrea*	Gastropoda	Unassessed
5.000000e-05	*Myrtea spinifera*	Bivalvia	Unassessed
1.000000e-04	*Calliostoma zizyphinum*	Gastropoda	Unassessed
3.166667e-04	*Tritonia plebeia*	Gastropoda	Unassessed
4.000000e-04	*Lepidochitona cinerea*	Polyplacophora	Unassessed
5.000000e-04	*Fjordia browni*	Gastropoda	Unassessed

5.833333e-04	*Philine quadripartita*	Gastropoda	Unassessed
6.030303e-04	*Edmundsella pedata*	Gastropoda	Unassessed
6.222222e-04	*Lutraria angustior*	Bivalvia	Unassessed
7.333333e-04	*Lasaea adansoni*	Bivalvia	Unassessed
8.500000e-04	*Mangelia attenuata*	Gastropoda	Unassessed
1.066667e-03	*Retusa truncatula*	Gastropoda	Unassessed
1.281481e-03	*Turbonilla lactea*	Gastropoda	Unassessed
1.316667e-03	*Dendronotus frondosus*	Gastropoda	Unassessed
1.337037e-03	*Arcopagia crassa*	Bivalvia	Unassessed
1.394108e-03	*Aplysia punctata*	Gastropoda	Unassessed
1.418056e-03	*Tritia incrassata*	Gastropoda	Unassessed
1.620833e-03	*Bela nebula*	Gastropoda	Unassessed
1.825000e-03	*Tricolia pullus*	Gastropoda	Unassessed
2.208333e-03	*Cerastoderma edule*	Bivalvia	Unassessed
2.571759e-03	*Abra prismatica*	Bivalvia	Unassessed
2.690114e-03	*Rissoa parva*	Gastropoda	Unassessed
2.807295e-03	*Mimachlamys varia*	Bivalvia	Unassessed
2.814815e-03	*Colus gracilis*	Gastropoda	Unassessed
2.971212e-03	*Venus casina*	Bivalvia	Unassessed
3.146759e-03	*Lucinoma borealis*	Bivalvia	Unassessed
3.562500e-03	*Dosinia exoleta*	Bivalvia	Unassessed
3.868116e-03	*Nucula sulcata*	Bivalvia	Unassessed
4.024769e-03	*Mya truncata*	Bivalvia	Unassessed
4.118056e-03	*Limapontia capitata*	Gastropoda	Unassessed
4.851852e-03	*Raphitoma purpurea*	Gastropoda	Unassessed
4.893519e-03	*Fabulina fabula*	Bivalvia	Unassessed
5.151268e-03	*Tectura virginea*	Gastropoda	Unassessed
5.693939e-03	*Steromphala cineraria*	Gastropoda	Unassessed
5.722222e-03	*Aegires punctilucens*	Gastropoda	Unassessed
6.124242e-03	*Cadlina laevis*	Gastropoda	Unassessed
6.440741e-03	*Manzonia crassa*	Gastropoda	Unassessed

7.250000e-03	*Patella vulgata*	Gastropoda	Unassessed
7.362963e-03	*Musculus subpictus*	Bivalvia	Unassessed
7.801515e-03	*Eubranchus tricolor*	Gastropoda	Unassessed
8.000000e-03	*Cerithiopsis tubercularis*	Gastropoda	Unassessed
8.141667e-03	*Hiatella arctica*	Bivalvia	Unassessed
8.700000e-03	*Eledone cirrhosa*	Cephalopoda	Unassessed
9.604348e-03	*Adalaria proxima*	Gastropoda	Unassessed
9.900000e-03	*Favorinus branchialis*	Gastropoda	Unassessed
1.016250e-02	*Ennucula tenuis*	Bivalvia	Unassessed
1.016667e-02	*Calliostoma granulatum*	Gastropoda	Unassessed
1.080072e-02	*Eatonina fulgida*	Gastropoda	Unassessed
1.088841e-02	*Mangelia costata*	Gastropoda	Unassessed
1.376458e-02	*Nuculana minuta*	Bivalvia	Unassessed
1.416001e-02	*Crepidula fornicata*	Gastropoda	Unassessed
1.418395e-02	*Peringia ulvae*	Gastropoda	Unassessed
1.434815e-02	*Dikoleps nitens*	Gastropoda	Unassessed
1.485000e-02	*Barnea candida*	Bivalvia	Unassessed
1.634537e-02	*Moerella donacina*	Bivalvia	Unassessed
1.640000e-02	*Onchidoris sparsa*	Gastropoda	Unassessed
1.866667e-02	*Elysia viridis*	Gastropoda	Unassessed
1.913750e-02	*Cylichna cylindracea*	Gastropoda	Unassessed
2.041515e-02	*Catriona gymnota*	Gastropoda	Unassessed
2.056667e-02	*Doto tuberculata*	Gastropoda	Unassessed
2.059568e-02	*Rissoella diaphana*	Gastropoda	Unassessed
2.275000e-02	*Pododesmus patelliformis*	Bivalvia	Unassessed
2.370370e-02	*Armina loveni*	Gastropoda	Unassessed
2.617407e-02	*Leptochiton asellus*	Polyplacophora	Unassessed
2.678667e-02	*Todaropsis eblanae*	Cephalopoda	Not threatened
2.812917e-02	*Macomangulus tenuis*	Bivalvia	Unassessed
2.891667e-02	*Ammonicera rota*	Gastropoda	Unassessed
2.904074e-02	*Littorina obtusata*	Gastropoda	Unassessed

3.201212e-02	*Fjordia lineata*	Gastropoda	Unassessed
3.237576e-02	*Trapania pallida*	Gastropoda	Unassessed
3.275000e-02	*Aporrhais pespelecani*	Gastropoda	Unassessed
4.815333e-02	*Loligo forbesii*	Cephalopoda	Unassessed
5.033801e-02	*Patella pellucida*	Gastropoda	Unassessed
5.335758e-02	*Rostanga rubra*	Gastropoda	Unassessed
6.275417e-02	*Skeneopsis planorbis*	Gastropoda	Unassessed
6.326228e-02	*Clione limacina*	Gastropoda	Unassessed
6.493636e-02	*Tritonia nilsodhneri*	Gastropoda	Unassessed
7.135507e-02	*Antalis entalis*	Scaphopoda	Unassessed
7.380417e-02	*Sphenia binghami*	Bivalvia	Unassessed
7.766667e-02	*Phorcus lineatus*	Gastropoda	Unassessed
8.710000e-02	*Thracia villosiuscula*	Bivalvia	Unassessed
8.925556e-02	*Littorina fabalis*	Gastropoda	Unassessed
1.781167e-01	*Thyasira flexuosa*	Bivalvia	Unassessed

Table S3: OBIS citations for datasets modelled in Chapter 3.

Resource ID	Resource Name and Citation	Analysis Grouping
56	**REVIZEE Score Sul / Bentos** REVIZEE South Score / Benthos - Amaral, A.C.Z. e Rossi-Wongtschowski, C.L.D.B. (eds.) 2004. Biodiversidade bentônica da região sudeste-sul do Brasil, plataforma externa e talude superior. São Paulo : Instituto Oceanográfico da USP, 2004 (Série Documentos Revizee - Score Sul). 216 p. ISBN 85-98729-08-6.	1
613	**Macro- and megafauna from the North Aegean Sea from 1997-1998** Antoniadou C. (1998). Macro- and megafauna from the North Aegean Sea from 1997-1998. Aristotle University of Thessaloniki, Department of Biology, Laboratory of Zoology, Greece.	1
2343	**South TX Outer Continental Shelf and MI, AL, and FL Outer Continental Shelf benthic organism sampling 1974-1978** US National Oceanographic Data Center. 2011. South TX Outer Continental Shelf and MI, AL, and FL Outer Continental Shelf benthic organism sampling 1974-1978. US National Oceanographic Data Center, Silver Spring, Maryland, USA. Retrieved from http://www.usgs.gov/obis-usa/.	1
2827	**Namdeb Diamond Corporation Limited Marine Monitoring Programme** Pulfrich, A. (2013). Namdeb Diamond Corporation Limited Marine Monitoring Programme: Offshore licences. Dataset published by AfrOBIS; consulted via iOBIS	1
3424	**Aegean macrobenthic fauna** Koukouras A., 2000: Northern Aegean dataset. Aristotelian University of Thessaloniki Department of Zoology and Zoological Museum, School of Biology, Greece	1
3554	**CSIRO, Cruise SS200510, Benthic Biodiversity, Western Australia, 2005** CSIRO - Southern Surveyor voyage SS 10/2005, benthic biodiversity of the deep continental shelf and slope in Australia's SW region	1
73	**Australian Museum**	2
151	**Benthic biodiversity along the central coast in the Brazilian EEZ (OBIS South America, BRAZIL)** Lavrado, H.P. e Ignacio, B.L. (eds.) 2006. Biodiversidade bentônica da costa central da Zona Econômica Exclusiva brasileira. Rio de Janeiro : Museu Nacional, 2006.(Série Livros; 18) 389 p. ISBN 85-7427-014-8	3
264	**Benthic species from the tropical Pacific surrounding New Caledonia** Bertrand RICHER DE FORGES (IRD) & Philippe BOUCHET (MNHN). 1998. Benthic species from the tropical Pacific. IRD-Noumea	3

1492	**NBI** http://www.nbi.noaa.gov	3
3550	**CSIRO, Cruise SS200705, Benthic Biodiversity, Northwest Australia, 2007** CSIRO - Southern Surveyor Voyage SS 05/2007, benthic biodiversity of the deep continental shelf and slope in Australia's NW region	3
3557	**CSIRO, Benthic Plant Invertebrate and Fish Biodiversity, Great Barrier Reef, Northeast Australia, 2003-2006** CSIRO - Great Barrier Reef seabed biodiversity study 2003-2006	3
3962	**National Benthic Infaunal Database**	3
10	**SeamountsOnline (Seamount Biota)** Stocks, K. 2003. SeamountsOnline: an online information system for seamount biology. Version 3.1. seamounts.sdsc.edu	4
500	**NMNH Invertebrate Zoology Collections** Department of Invertebrate Zoology, Research and Collections Information System, NMNH, Smithsonian Institution. See: http://www.mnh.si.edu/rc/db/collection_db_policy1.html	5
1502	**Marine and Coastal Research Institute - INVEMAR, Colombia, IABIN** INVEMAR. SIBM en línea: Sistema de Información sobre Biodiversidad Marina. Santa Marta: Instituto de investigaciones Marinas y Costeras José Benito Vives de Andréis,. http://www.invemar.org.co/siam/sibm/index.htm	5
4681	**Tasmanian Museum and Art Gallery provider for OZCAM - marine records** Webmaster O (2017): Tasmanian Museum and Art Gallery provider for OZCAM - marine records. v1.0. CSIRO Oceans and Atmosphere. Dataset/Occurrence. http://ogc-act.csiro.au/ipt/resource?r=tmag_marine&v=1.0	5
25	**EPA'S EMAP Database** Some of the data described in this chapter were produced by the U.S. Environmental Protection Agency through its Environmental Monitoring and Assessment Program (EMAP), http://www.epa.gov/emap/.	6
42	**Mediterranean Ocean Biogeographic Information System** Hellenic Centre For Marine Research, MedOBIS - Mediterranean Ocean Biogeographic Information System. Hellenic Centre for Marine Research; Institute of Marine Biology and Genetics; Biodiversity and Ecosystem Management Department, Heraklion, Greece. Http://www.medobis.org/	6
71	**IndOBIS, Indian Ocean Node of OBIS** Chavan, VIshwas and C. T. Achuthankutty (editors), IndOBIS Catalogue of Life, Available at http://www.indobis.org/, Retrived 12/03/2018	6
77	**MV Marine Invertebrates**	6
3475	**NaGISA Project**	6

3851	**IndOBIS Dataset (70001-72000)** Indian Ocean Biogeographic Information System (IndOBIS)- Distribution records of marine organisms from the Indian Ocean	6
3853	**IndOBIS Dataset (64001-66000)** Indian Ocean Biogeographic Information System (IndOBIS)- Distribution records of marine organisms from the Indian Ocean	6
3862	**IndOBIS Dataset (34001-36000)** Indian Ocean Biogeographic Information System (IndOBIS)- Distribution records of marine organisms from the Indian Ocean	6
3869	**IndOBIS Dataset (48001-50000)** Indian Ocean Biogeographic Information System (IndOBIS)- Distribution records of marine organisms from the Indian Ocean	6
3893	**IndOBIS Dataset (1-2000)** Indian Ocean Biogeographic Information System (IndOBIS)- Distribution records of marine organisms from the Indian Ocean	6
3900	**IndOBIS Dataset (86001-88000)** Indian Ocean Biogeographic Information System (IndOBIS)- Distribution records of marine organisms from the Indian Ocean	6
4442	**University of Florida Museum of Natural History Invertebrate Zoology Collection**	7
4727	**Museums Victoria Marine Invertebrates Collection**	7
508	**The Southeast Regional Taxonomic Center** Marine Resources Research Institute, South Carolina DNR	8
1583	**CRED Rapid Ecological Assessment of Invertebrate in the Pacific Ocean** Coral Reef Ecosystem Division (CRED), NOAA Pacific Island Fisheries Science Center, 2008-05-08, CRED Rapid Ecological Assessment of Invertebrate in the Pacific Ocean, from 2002 to 2008	8
8	**Academy of Natural Sciences OBIS Mollusc Database** Rosenberg et al., 2002	9
127	**Natal Museum - Mollusc Collection**	9
142	**iziko South African Museum - Mollusc Collection**	9
2332	**East London Museum** East London Museum - Mollusc Collection	9
3206	**Moluscos del Museo de Ciencias Naturales de la Universidad Simón Bolivar**	9
4539	**Museum and Art Gallery of the Northern Territory Malacology Collection - marine records**	9

4689	**Queensland Museum Molluscs - Marine records** Healy J (2017): Queensland Museum Molluscs - Marine records. v1.0. CSIRO Oceans and Atmosphere. Dataset/Occurrence. http://ogc-act.csiro.au/ipt/resource?r=qm_molluscs&v=1.0	9
4730	**Australian Museum Malacology Collection - Marine records** Reid M (2017): Australian Museum Malacology Collection - Marine records. v1.0. CSIRO Oceans and Atmosphere. Dataset/Occurrence. http://ogc-act.csiro.au/ipt/resource?r=am_malacology&v=1.0	9

Table S4: Total and decadal change in proportional occupancy for the 124 species of *Conus* assessed in Chapter 3, and IUCN threat assessment status.

Total Change	Decadal Change	Species	Assessment Status
-1.137966e-01	-1.896610e-02	*Conus ebraeus*	Least Concern
-1.257448e-01	-1.571809e-02	*Conus musicus*	Least Concern
-8.312483e-02	-1.511361e-02	*Conus villepinii*	Least Concern
-8.247826e-02	-1.499605e-02	*Conus cancellatus*	Least Concern
-1.115232e-01	-1.394040e-02	*Conus pulicarius*	Least Concern
-7.590081e-02	-1.380015e-02	*Conus stimpsoni*	Least Concern
-6.922200e-02	-1.258582e-02	*Conus anabathrum*	Vulnerable
-6.795756e-02	-1.235592e-02	*Conus daucus*	Least Concern
-7.359825e-02	-1.235311e-02	*Conus stercusmuscarum*	Least Concern
-9.870267e-02	-1.233783e-02	*Conus miles*	Least Concern
-5.903161e-02	-1.073302e-02	*Conus amphiurgus*	Least Concern
-5.661677e-02	-1.029396e-02	*Conus spurius*	Least Concern
-5.449559e-02	-9.908288e-03	*Conus philippii*	Least Concern
-5.153071e-02	-8.863918e-03	*Conus striatus*	Least Concern
-6.942219e-02	-8.677774e-03	*Conus catus*	Least Concern
-4.707369e-02	-8.558852e-03	*Conus granulatus*	Least Concern
-4.293530e-02	-7.806417e-03	*Conus regius*	Least Concern
-3.888821e-02	-7.070583e-03	*Conus emaciatus*	Least Concern
-5.003891e-02	-6.152174e-03	*Conus glans*	Least Concern
-4.742269e-02	-6.111859e-03	*Conus flavidus*	Least Concern
-4.715689e-02	-5.894612e-03	*Conus mustelinus*	Least Concern
-2.879210e-02	-5.234927e-03	*Conus coronatus*	Least Concern
-3.940547e-02	-4.925683e-03	*Conus mitratus*	Least Concern
-2.085294e-02	-3.791444e-03	*Conus circumcisus*	Least Concern
-1.824395e-02	-3.317082e-03	*Conus recurvus*	Unassessed
-1.893203e-02	-3.155338e-03	*Conus furvus*	Least Concern
-1.790842e-02	-2.984736e-03	*Conus scalptus*	Data Deficient

-1.424557e-02	-2.846397e-03	*Conus mus*	Least Concern
-2.236109e-02	-2.568121e-03	*Conus adamsonii*	Least Concern
-1.670502e-03	-1.591403e-03	*Conus arenatus*	Least Concern
-9.767853e-03	-1.220982e-03	*Conus marmoreus*	Least Concern
-6.488759e-03	-1.179774e-03	*Conus varius*	Least Concern
-6.262750e-03	-1.043792e-03	*Conus nobilis*	Least Concern
-5.596983e-03	-1.017633e-03	*Conus miliaris*	Least Concern
-5.193210e-03	-8.007063e-04	*Conus magus*	Least Concern
-2.467756e-03	-4.486828e-04	*Conus consors*	Least Concern
-3.465835e-03	-4.332294e-04	*Conus biliosus*	Least Concern
-8.852183e-03	-3.578597e-04	*Conus vexillum*	Least Concern
-8.966946e-04	-3.157477e-04	*Conus boeticus*	Least Concern
-5.224136e-04	-8.706894e-05	*Conus achatinus*	Least Concern
-3.614804e-04	-6.572370e-05	*Conus proximus*	Least Concern
-1.531633e-04	-2.784788e-05	*Conus parius*	Least Concern
-5.552636e-05	-1.009570e-05	*Conus omaria*	Least Concern
1.360210e-04	2.473108e-05	*Conus burryae*	Unassessed
1.523033e-03	1.903792e-04	*Conus geographus*	Least Concern
2.018624e-03	2.523280e-04	*Conus figulinus*	Least Concern
2.134005e-03	2.667506e-04	*Conus nucleus*	Least Concern
-2.674128e-03	3.133898e-04	*Conus litteratus*	Least Concern
2.100797e-03	3.501329e-04	*Conus natalis*	Least Concern
2.897719e-03	3.622149e-04	*Conus generalis*	Least Concern
3.481219e-03	4.351524e-04	*Conus nussatella*	Least Concern
3.441330e-03	5.735550e-04	*Conus austroviola*	Data Deficient
3.263758e-03	5.934105e-04	*Conus capitaneus*	Least Concern
5.331491e-03	8.885818e-04	*Conus tinianus*	Least Concern
-4.461328e-03	1.157012e-03	*Conus frigidus*	Least Concern
8.170574e-03	1.485559e-03	*Conus pennaceus*	Least Concern
9.199060e-03	1.515936e-03	*Conus gubernator*	Least Concern
9.369003e-03	1.619415e-03	*Conus trigonus*	Least Concern

2.448730e-02	1.662699e-03	*Conus rattus*	Least Concern
1.153900e-03	1.792485e-03	*Conus eburneus*	Least Concern
1.480617e-02	1.850771e-03	*Conus retifer*	Least Concern
1.235215e-02	2.058691e-03	*Conus infrenatus*	Least Concern
1.184761e-02	2.154111e-03	*Conus aristophanes*	Unassessed
1.750829e-02	2.188536e-03	*Conus tulipa*	Least Concern
2.441811e-02	2.194066e-03	*Conus virgo*	Least Concern
1.816102e-02	2.270127e-03	*Conus striatellus*	Least Concern
1.366675e-02	2.277792e-03	*Conus zeylanicus*	Least Concern
1.380175e-02	2.300291e-03	*Conus transkeiensis*	Unassessed
1.406596e-02	2.344326e-03	*Conus zonatus*	Least Concern
2.025098e-02	2.560970e-03	*Conus sponsalis*	Least Concern
2.101259e-02	2.626573e-03	*Conus balteatus*	Least Concern
1.468430e-02	2.669873e-03	*Conus erythraeensis*	Least Concern
2.218178e-02	2.772723e-03	*Conus cylindraceus*	Least Concern
2.187380e-02	3.016018e-03	*Conus aulicus*	Least Concern
2.733122e-02	3.103451e-03	*Conus exiguus*	Least Concern
2.854204e-02	3.567755e-03	*Conus leopardus*	Least Concern
2.207680e-02	3.679466e-03	*Conus milneedwardsi*	Least Concern
2.072749e-02	3.794243e-03	*Conus litoglyphus*	Least Concern
3.309576e-02	4.136970e-03	*Conus auricomus*	Least Concern
2.375783e-02	4.319606e-03	*Conus eximius*	Least Concern
2.819223e-02	4.627060e-03	*Conus parvatus*	Least Concern
5.402843e-02	4.681560e-03	*Conus lividus*	Least Concern
4.548253e-02	4.784199e-03	*Conus quercinus*	Least Concern
4.044500e-02	5.055625e-03	*Conus aplustre*	Least Concern
3.049006e-02	5.081676e-03	*Conus martensi*	Unassessed
2.908426e-02	5.288048e-03	*Conus nigropunctatus*	Least Concern
4.782061e-02	5.977576e-03	*Conus canonicus*	Least Concern
3.781649e-02	6.302748e-03	*Conus visagenus*	Least Concern
5.113370e-02	6.391713e-03	*Conus papilliferus*	Least Concern

3.866932e-02	6.444887e-03	*Conus typhon*	Least Concern
5.216774e-02	6.520968e-03	*Conus spectrum*	Least Concern
5.750226e-02	6.564096e-03	*Conus sanguinolentus*	Least Concern
4.124154e-02	6.873589e-03	*Conus inscriptus*	Least Concern
5.757528e-02	7.196910e-03	*Conus legatus*	Least Concern
4.488065e-02	7.480108e-03	*Conus ammiralis*	Least Concern
6.257404e-02	7.821755e-03	*Conus floccatus*	Least Concern
6.349819e-02	7.937273e-03	*Conus angasi*	Least Concern
4.431488e-02	8.057251e-03	*Conus striolatus*	Least Concern
6.676622e-02	8.345778e-03	*Conus monachus*	Least Concern
5.572985e-02	8.399094e-03	*Conus magnificus*	Least Concern
7.140016e-02	8.925020e-03	*Conus rufimaculosus*	Least Concern
7.722307e-02	9.652884e-03	*Conus anemone*	Least Concern
7.767580e-02	9.709475e-03	*Conus tessulatus*	Least Concern
7.113321e-02	1.004063e-02	*Conus terebra*	Least Concern
6.059119e-02	1.101658e-02	*Conus cardinalis*	Near Threatened
8.969744e-02	1.121218e-02	*Conus imperialis*	Least Concern
6.410360e-02	1.121364e-02	*Conus coccineus*	Least Concern
7.307406e-02	1.217901e-02	*Conus ferrugineus*	Least Concern
8.974871e-02	1.374739e-02	*Conus coelinae*	Least Concern
8.724201e-02	1.454033e-02	*Conus aureus*	Least Concern
1.177922e-01	1.472403e-02	*Conus klemae*	Least Concern
1.219049e-01	1.677901e-02	*Conus suturatus*	Least Concern
1.370170e-01	1.712712e-02	*Conus coffeae*	Least Concern
1.051284e-01	1.794359e-02	*Conus episcopatus*	Least Concern
1.460596e-01	1.825745e-02	*Conus sculletti*	Least Concern
1.551857e-01	1.939821e-02	*Conus wallangra*	Data Deficient
9.983588e-02	1.987542e-02	*Conus textile*	Least Concern
1.175997e-01	2.032783e-02	*Conus distans*	Least Concern
1.801085e-01	2.533003e-02	*Conus moreleti*	Least Concern
1.481469e-01	2.693581e-02	*Conus planorbis*	Least Concern

1.779438e-01	2.935594e-02	*Conus muriculatus*	Least Concern
1.857744e-01	3.096240e-02	*Conus lischkeanus*	Least Concern
2.184713e-01	3.972205e-02	*Conus nanus*	Unassessed
4.314552e-01	7.190920e-02	*Conus chaldaeus*	Least Concern

Table S5: OBIS citations for datasets modelled in Chapter 4.

Resource ID	Resource Name and Citation	Analysis Grouping
76	**MV Mammals**	1
99	**Marine records from Pembrokeshire Marine Species Atlas** Dale Rostron. Marine records from Pembrokeshire Marine Species Atlas. Countryside Council for Wales, Gwynedd, UK. http://doi.org/10.15468/42yudm	1
1695	**Taxonomic Information System for the Belgian coastal area** Flanders Marine Institute (VLIZ). Taxonomic Information System for the Belgian coastal area. 10 Aug 2004, Oostende, Belgium, Accessed on 2018-06-25.	1
2170	**Allied Humpback Whale Catalogue, 1976 – 2003** Stevick, P. 2006. Allied Humpback Whale Catalogue, 1976 - 2003. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/73) on 2018-06-25.	1
2375	**Cetacean occurrence off the west central Portugal coast from boat-based surveys 2007-2008** Brito, C. 2011. Cetacean occurrence off the west central Portugal coast from boat-based surveys 2007-2008. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/726) on 2018-06-25.	1
2553	**HMAP Dataset 04: World Whaling** T.D. Smith ed. 'World Whaling Database: Individual Whale Catches, North Atlantic' in M.G Barnard and J.H Nicholls (comp.) HMAP Data Pages (www.hull.ac.uk/hmap).	1
2749	**Historical distribution of whales shown by logbook records 1785-1913** Woolmer, G. 2013. Historical distribution of whales shown by logbook records 1785-1913. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/885) on 2018-06-25.	1
2832	**DFO Maritimes Region Cetacean Sightings** DFO. (2017). DFO Maritimes Region Cetacean Sightings. Version 7 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-06-25	1
3117	**Norman and Florence Hammond records. Seawatch and coastal survey records** Norman and Florence Hammond records. Seawatch and coastal survey records. Cumbria Biodiversity Data Centre, UK - UK National Biodiversity Network.	1

3125	**Marine flora and fauna records from the North-east Atlantic** Marine flora and fauna records from the North-east Atlantic. Porcupine Marine Natural History Society, UK - UK National Biodiversity Network. http://doi.org/10.15468/pcmg9q	1
4292	**Asia-Pacific Dataset** Jintsu-Uchifune, Y., Yamamoto, H. (2016) Marine organism occurrence data of the Asia-Pacific region extracted from literature. Available at http://www.godac.jamstec.go.jp/bismal/e/S9-5_Asia-Pacific. Accessed on 2018-06-25.	1
4678	**Museums Victoria Mammalogy Collection**	1
567	**National Whale and Dolphin Sightings and Strandings Database** Raymond, B. National Whale and Dolphin Sightings and Strandings Database. See Metadata record: http://data.aad.gov.au/aadc/metadata/metadata_redirect.cfm?md=AMD/AU/DB_Cetaceans_NSSD	2
2137	**New record of the humpback whale in the Adriatic Sea in 2009** Genov, T., P. Kotnjek, and L. Lipej. 2009. New record of the humpback whale (*Megaptera novaeangliae*) in the Adriatic Sea. Annales, Series Historia Naturalis. 19(1):25-30	2
2156	**BLM CETAP OPP Sightings** Kenney, R. 2013. BLM CETAP OPP Sightings. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/284) on 2018-06-25.	2
2172	**UK Royal Navy Marine Mammal Observations** Maughan, B. and K. Arnold. 2010. UK Royal Navy Marine Mammal Observations. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/64) on 2018-06-25.	2
2377	**United Kingdom National Whale Stranding Database 1913-2008** Officer, S. 2011. United Kingdom National Whale Stranding Database 1913-2008. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/731) on 2018-06-25.	2
2436	**Porpoises (NRM)** Swedish Museum of Natural History: Porpoises (NRM), 2013-09-11. Accessed via http://www.gbif.org/dataset/6aa7c400-0c66-11dd-84d2-b8a03c50a862 on 2018-06-25 http://doi.org/10.15468/yrxfxp	2
2493	**Irish Ground Fish Survey for commercial fish species** Fish trawl survey: Irish Ground Fish Survey for commercial fish species. ICES Database of trawl surveys (DATRAS). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	2

2709	**Historical strandings of cetaceans on the Portuguese coast** Sousa, A. 2012. Historical strandings of cetaceans on the Portuguese coast. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/829) on 2018-06-25.	2
3064	**Marine species distributions in Irish coastal waters** National Biodiversity Data Centre: Marine species distributions in Irish coastal waters, 2013-11-20. Accessed via http://www.gbif.org/dataset/0d83ea43-5afb-4c50-af9c-fd22674338bb on 2018-06-25	2
3113	**Biodiversity of the North Sea - Sylt** GEO-Tag der Artenvielfalt, Artenvielfalt der Nordsee - Sylt (accessed through GBIF data portal, http://data.gbif.org/datasets/resource/2839, 2018-06-25) http://doi.org/10.15468/nvhjkx	2
3127	**RECORD Cetacean data up to current day** UK National Biodiversity Network: Record, the Biodiversity Information System for Cheshire, Halton, Warrington and the Wirral - RECORD Cetacean data up to current day. Accessed via http://www.gbif.org/dataset/64cd76db-9879-46ab-955b-0bc64a769978 on 2018-06-25	2
3422	**Diveboard - Scuba diving citizen science observations** Diveboard - Scuba diving citizen science observations. Online at http://www.diveboard.com and http://ipt.diveboard.com/resource.do?r=diveboard-occurrences. http://dx.doi.org/10.15468/tnjrgy	2
3633	**Short-beaked common dolphin in the northern Adriatic Sea 2010-2011** Genov, T., G. Bearzi, S. Bonizzoni and M. Tempesta. 2012. Long-distance movement of a lone short-beaked common dolphin *Delphinus delphis* in the central Mediterranean Sea. Marine Biodiversity Records. 5:e9. doi:10.1017/S1755267211001163	2
4584	**Observatoire Pelagis sightings from fishery surveys 2004-2009** Doremus, G. 2016. Observatoire Pelagis sightings from fishery surveys 2004-2009. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1405) on 2018-06-25.	2
103	**Seasearch Marine Surveys** Marine Conservation Society. Seasearch Marine Surveys. Marine Conservation Society, Ross-on-Wye, UK.	3
1512	**Marine Life List of Ireland** Allen D., Beckett B., Brophy J., Costello M.J., Emblow C., Maciejewska B., McCrea M., Nash R., Penk M. & Tierney A. Marine species recorded in Ireland during field suveys by EcoServe, Ecological Consultancy Services Ltd. Available online at http://www.marbef.org/data/eurobis.php. Consulted on 2018-06-25	3

1576	**ICES contaminants and biological effects** ICES Contaminants and biological effects database (DOME - Biota). The International Council for the Exploration of the Sea, Copenhagen. 2010. Online source: http://ecosystemdata.ices.dk.	3
1625	**MAR-ECO 2004 - Mammals and birds** Skov,H, T. Gunnlaugsson, W.P. Budgell, J. Horne, L. Nøttestad, E. Olsen, H. Søiland, G. Víkingsson and G. Waring (2008) Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. Deep-sea Research II. 55: 254-268.	3
1986	**Marine Life Information Network (MarLIN) marine survey data (Professional)** Parr, J. Marine Life Information Network (MarLIN) marine survey data (Professional). Marlin, Collated Marine Life Survey Datasets, Marine Biological Association of the UK, Plymouth, UK	3
1987	**Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by JNCC** Ostler, R. Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by JNCC. Joint Nature Conservation Committee, Centre for Ecology and hydrology, Aberdeenshire, UK.	3
2002	**JNCC seabird distribution and abundance data (all trips) from ESAS database** Dunn, T. 2012. JNCC seabird distribution and abundance data (all trips) from ESAS database. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/427) on 2018-06-25.	3
2019	**Harbour porpoises, white-beaked dolphins and minke whales in North Sea - Land surveys** Weir, C. 2007. Harbour porpoises, white-beaked dolphins and minke whales in North Sea - Land surveys -. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/423) on 2018-06-25.	3
2085	**YoNAH Encounter** Stevick, P. 2013. YoNAH Encounter. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/274) on 2018-06-25.	3
2125	**Alnitak-Alnilam Cetaceans and sea turtles surveys off Southern Spain** Cañadas, A. 2013. Alnitak-Alnilam Cetaceans and sea turtles surveys off Southern Spain. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/429) on 2018-06-25.	3
2162	**Harbour porpoises, white-beaked dolphins and minke whales in North Sea - Vessel surveys** Weir, C. 2011. Harbour porpoises, white-beaked dolphins and minke whales in North Sea - Vessel surveys -. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/425) on 2018-06-25.	3

2192	**Bottlenose dolphins in Slovenian and adjacent waters (north Adriatic Sea) in 2002-2008** Genov, T., P. Kotnjek, J. Lesjak, A. Hace and C.M. Fortuna. 2008. Bottlenose dolphins (*Tursiops truncatus*) in Slovenian and adjacent waters (northern Adriatic Sea). Annales, Series Historia Naturalis. 18(2):227-244, http://www.cetaceanalliance.org/download/literature/Genov_etal_2008.pdf; Genov , T., A. Wiemann and C.M. Fortuna. 2009. Towards identification of the bottlenose dolphin (*Tursiops truncatus*) population structure in the north-eastern Adriatic Sea: preliminary results. Varstvo narave. 22:73-80, http://www.zrsvn.si/dokumenti/63/2/2009/Genov_1574.pdf	3
2202	**SMRU Small Cetacean Abundance NS 1994** P.S. Hammond P. Berggren H. Benke D.L. Borchers A. Collet M.P. Heide-Jørgensen S. Heimlich A.R. Hiby M.F. Leopold N. Øien. 2002. Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology. 39:361-376, http://www.vliz.be/imisdocs/publications/133116.pdf	3
2245	**PIROP Northwest Atlantic 1965-1992** Hyrenbach, D., F. Huettmann and J. Chardine. 2012. PIROP Northwest Atlantic 1965-1992. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/280) on 2018-06-25.	3
2251	**Baltic Porpoise Sightings 01-02** Moscrop, A. 2011. Baltic Porpoise Sightings 01-02. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/344) on 2018-06-25.	3
2354	**CRRU Cetacean sighting in Scotland waters 1997-2010** Robinson, K.P., N. Baumgartner, S.M. Eisfeld, N.M. Clark, R.M. Culloch, G.N. Haskins, L. Zapponi, A.R. Whaley, J.S. Weare and M.J. Tetley. 2007. The summer distribution and occurrence of cetaceans in the coastal waters of the outer southern Moray Firth in northeast Scotland (UK). Lutra. 50(1): 19-30, http://www.crru.org.uk/cust_images/pdfs/robinson_etal_Lutra2007.pdf; Robinson, K.P., M.J. Tetley and E.G. Mitchelson-Jacob. 2009. The distribution and habitat preference of coastally occurring minke whales (*Balaenoptera acutorostrata*) in north-east Scotland. Journal of Coastal Conservation. 13(1): 39-48, http://www.crru.org.uk/cust_images/pdfs/robinson_etal_JCC_2009.pdf; Robinson, K.P., S.M. Eisfeld, M. Costa, and M.P. Simmonds. 2010. Short-beaked common dolphin (*Delphinus delphis*) occurrence in the Moray Firth, northeast Scotland. Marine Biodiversity Records. 3:e55, http://www.crru.org.uk/cust_images/pdfs/robinson_etal_MBR_2010.pdf	3
2356	**OceanCare cetacean sightings 2001-2014** Frey, S. 2015. OceanCare cetacean sightings 2001-2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/662) on 2018-06-25.	3

2363	**Hebridean Dolphin and Whale Trust killer whale sightings 1990-2006** Koetter, S. 2010. Hebridean Dolphin and Whale Trust killer whale sightings 1990-2006. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/694) on 2018-06-25.	3
2365	**Marine Awareness North Wales, Wildlife Trust harbor porpoise baseline surveys on the north coast of Anlesey, Wales, UK** Shucksmith, R. 2011. Marine Awareness North Wales, Wildlife Trust harbor porpoise baseline surveys on the north coast of Anlesey, Wales, UK. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/703) on 2018-06-25.	3
2384	**University of Algarve and ICNB Cetacean Sightings 1999** Faustino, C. 2011. University of Algarve and ICNB Cetacean Sightings 1999. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/755) on 2018-06-25.	3
2389	**Acquario di Genova, Delfini Metropolitani Project, cetacean sightings 2001-2009** Bellingeri, M. 2011. Acquario di Genova, Delfini Metropolitani Project, cetacean sightings 2001-2009. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/761) on 2018-06-25.	3
2439	**CE.TU.S. research cetacean sightings in the North Tuscany and Tuscan Archipelago waters, 1997-2011** Bedocchi, D. and S. Nuti. 2011. CE.TU.S. research cetacean sightings in the North Tuscany and Tuscan Archipelago waters, 1997-2011. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/732) on 2018-06-25.	3
2452	**OCEAMM harbor porpoise sightings in the North Sea** Bouveroux, T. 2011. OCEAMM harbor porpoise sightings in the North Sea. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/779) on 2018-06-25.	3
2462	**SMRU sperm whale distribution around the Balearic Islands 2003-2008** Pirotta, E. and L. Rendell. 2011. SMRU sperm whale distribution around the Balearic Islands 2003-2008. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/807) on 2018-06-25.	3
2463	**Jonian Dolphin Conservation di Taranto marine mammal sightings 2009-2012** Fanizza, C. 2012. Jonian Dolphin Conservation di Taranto marine mammal sightings 2009-2012. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/812) on 2018-06-25.	3
2636	**Small Cetaceans in the European Atlantic and North Sea (SCANS II) - 2005**	3

2656	**CWS-EC Eastern Canada Seabirds at Sea (ECSAS)** Fifield, David A. and Gjerdrum, Carina. 2015. CWS-EC Eastern Canada Seabirds at Sea (ECSAS). Version 4 (2015-Oct). In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-06-25	3
2690	**Lamont-Doherty/LGL/NSF cruises** Holst, M., O. Lee and H. Smith. 2014. Lamont-Doherty/LGL/NSF cruises. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/511) on 2018-06-25.	3
2710	**Bottlenose Dolphin Research Institute (BDRI) cetacean sightings 2011** Diaz Lopez, B. 2012. Bottlenose Dolphin Research Institute (BDRI) cetacean sightings 2011. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/830) on 2018-06-25.	3
2718	**CIRCE Marine mammals off Spain 2001-2012** Verborgh, P. 2012. CIRCE Marine mammals off Spain 2001-2012. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/840) on 2018-06-25.	3
2732	**Adriatic Shipping Company marine mammal sightings in the Adriatic Sea 1988-2000** Giovagnoli, L. 2013. Adriatic Shipping Company marine mammal sightings in the Adriatic Sea 1988-2000. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/865) on 2018-06-25.	3
2743	**University of Valencia cetacean surveys in the Spanish Mediterranean 2000-2003** Gozalbes, P. 2012. University of Valencia cetacean surveys in the Spanish Mediterranean 2000-2003. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/876) on 2018-06-25.	3
2912	**Cetacean sightings along the Catalan coast** Giralt, O. 2013. Cetacean sightings along the Catalan coast. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1030) on 2018-06-25.	3
2920	**Visual contacts from research cruises in the Med sea, 1994-2001** Fossati, C. and G. Romè. 2014. Visual contacts from research cruises in the Med sea, 1994-2001. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1078) on 2018-06-25.	3
2951	**NAFO/ICNAF - Environmental Surveys - NORWESTLANT 1-3, 1963: Marine mammals observations** NAFO 2014. NAFO/ICNAF - Environmental Surveys - NORWESTLANT 1-3, 1963: Marine mammal observations. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-06-25	3

3035	**Acoustic detections of sperm whales from research cruises in the Med sea, 1994-2001** Fossati, C. and G. Romè. 2014. Acoustic detections of sperm whales from research cruises in the Med sea, 1994-2001. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1116) on 2018-06-25.	3
3051	**WDC Shorewatch Sightings** UK National Biodiversity Network, Whale and Dolphin Conservation Society - WDC Shorewatch Sightings.	3
3057	**Visual sightings from Song of the Whale 1993-2013** Boisseau, O. 2014. Visual sightings from Song of the Whale 1993-2013. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1158) on 2018-06-25.	3
3065	**National Inventory of the Natural Heritage: Data from the air monitoring campaigns of marine megafauna (SAMM) in the French metropolitan area** SPN - Service du Patrimoine naturel, Muséum national d'Histoire naturelle, Paris: Inventaire National du Patrimoine Naturel : Données des campagnes de Suivi Aérien de la Mégafaune Marine (SAMM) de France métropolitaine, 2013-06-20. Accessed via http://www.gbif.org/dataset/489cf485-b8de-4d38-a01a-6f426c658222 on 2018-06-25 http://doi.org/10.15468/dylxhs	3
3100	**ESAS cetacean sightings from 1980 to 2003** National Biodiversity Data Centre: ESAS cetacean sightings from 1980 to 2003. 2011-08-18. Accessed via http://www.gbif.org/dataset/4bbd3033-4777-4786-bd4e-81e4c0e233d4 on 2018-06-25	3
3118	**Sea Trust Stena Europe Survey of Cetaceans in the St George's Channel, April 2004 - April 2011** Sea Trust Stena Europe Survey of Cetaceans in the St George’s Channel, April 2004 - April 2011. West Wales Biodiversity Information Centre, UK - UK National Biodiversity Network.	3
3161	**SCANS II cetacean sightings on tracker platform of vessel surveys 2005** Lacey, C. 2014. SCANS II cetacean sightings on tracker platform of vessel surveys 2005. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1152) on 2018-06-25.	3
3218	**British Antarctic (Terra Nova) Expedition, 1910-1913** Southwestern Pacific OBIS (2014). British Antarctic (Terra Nova) Expedition, 1910-1913. Southwestern Pacific OBIS, National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand, 1779 records, Online http://nzobisipt.niwa.co.nz/resource.do?r=terranova released on July 29, 2014	3

3285	**SCANS II cetacean sightings from aerial surveys 2005** Lacey, C. 2014. SCANS II cetacean sightings from aerial surveys 2005. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1153) on 2018-06-25.	3
3293	**SCANS II cetacean sightings on primary platform of vessel surveys 2005** Lacey, C. 2014. SCANS II cetacean sightings on primary platform of vessel surveys 2005. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1150) on 2018-06-25.	3
3625	**Marine mammal monitoring from coastal sites in Cardigan Bay, UK, 2004-2009** Allan, L. 2011. Marine mammal monitoring from coastal sites in Cardigan Bay, UK, 2004-2009. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/716) on 2018-06-25.	3
3966	**Cetacean coordinated transborder monitoring using ferries as platforms of observation off Tunisia 2013-2014 - Atutax** Aissi, M. 2015. Cetacean coordinated transborder monitoring using ferries as platforms of observation off Tunisia 2013-2014 - Atutax. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1263) on 2018-06-25.	3
4003	**CODA cetacean sightings on tracker platform of vessel surveys 2007** Lacey, C. 2015. CODA cetacean sightings on tracker platform of vessel surveys 2007. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1182) on 2018-06-25.	3
4084	**Cetacean coordinated transborder monitoring using ferries as platforms of observation off Tunisia 2013-2014 - Ketos** Letteri Tingali, M. 2015. Cetacean coordinated transborder monitoring using ferries as platforms of observation off Tunisia 2013-2014 - Ketos. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1264) on 2018-06-25.	3
4097	**CODA cetacean sightings on primary platform of vessel surveys 2007** Lacey, C. 2015. CODA cetacean sightings on primary platform of vessel surveys 2007. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1180) on 2018-06-25.	3
4217	**SCANS I cetacean sightings 1994** Lacey, C. 2015. SCANS I cetacean sightings 1994. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1183) on 2018-06-25.	3

4261	**POPA- Fisheries Observer Program of the Azores: Marine mammal sightings in the Azores tuna fishery from 1998 on: during navigation or search mode** Machete, M.; Institute of Marine Research (IMAR), Portugal; Department of Oceanography and Fisheries, University of the Azores (DOP/UAC), Portugal; (2016): POPA- Fisheries Observer Program of the Azores: Marine mammal sightings in the Azores tuna fishery from 1998 on: during navigation or search mode. https://doi.org/10.14284/19	3
4416	**Tethys Research Institute shipboard survey cetacean sightings 1986-2012** Lanfredi, C. and G. Notarbartolo di Sciara. 2014. Tethys Research Institute shipboard survey cetacean sightings 1986-2012. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/774) on 2018-06-25.	3
4439	**Tethys Research Institute aerial survey cetacean sightings 2009-2011** Lanfredi, C. and G. Notarbartolo di Sciara. 2011. Tethys Research Institute aerial survey cetacean sightings 2009-2011. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/776) on 2018-06-25.	3
4490	**European Seabirds at Sea - data collected by the Research Institute for Nature and Forest (INBO), Belgium** Research Institute for Nature and Forest (INBO). European Seabirds at Sea - data collected by the Research Institute for Nature and Forest (INBO). INBO Seabird distribution data (all trips).	3
4516	**Observatoire Pelagis boat surveys 2003-2016** Doremus, G. 2016. Observatoire Pelagis boat surveys 2003-2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1403) on 2018-06-25.	3
4532	**Observatoire Pelagis - Reseau National Echouage (French stranding network) strandings 1934-2015** Dabin, W. 2016. Observatoire Pelagis - Reseau National Echouage (French stranding network) strandings 1934-2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1406) on 2018-06-25.	3
4546	**Observatoire Pelagis aerial surveys 2002-2015** Van Canneyt, O. 2016. Observatoire Pelagis aerial surveys 2002-2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1404) on 2018-06-25.	3

Table S6: Model parameter estimates (est) and significance levels (sig) from 2nd order polynomial LMs of surveyed occupancy against difference between surveyed and modelled occupancy.

Only significant first (Coef 1) and second (Coef 2) order polynomial terms are presented. All intercept terms were positive and significant ($p < 0.05$). Significance levels: *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$), . ($p < 0.1$). See Figures S3-S5 for more information on models.

Year	MERP Presence-only				OBIS Targeted Surveys				OBIS Opportunistic Recording			
	Coef 1		Coef 2		Coef 1		Coef 2		Coef 1		Coef 2	
	Est	Sig	Est	Sig	Est	Sig	Est	Sig	Est	Sig	Est	Sig
1980		.			0.28	.						
1986							-0.26	.			-0.37	.
1989	0.38	*			0.35	**			0.42	*		
1990					0.22	*						
1991	0.29	.			0.29	*			0.32	.		
1992	0.33	.			0.27	*						
1993	0.34	*			0.32	*			0.35	.		
1994			-0.23	.								
1995	0.49	***	-0.18	.	0.44	***			0.56	***		
1996	0.46	***			0.42	***			0.56	**		
1997	0.35	***	-0.21	*					0.35	*		
1998	0.49	***	-0.26	**	0.33	*			0.47	**		
1999	0.29	*										
2000	0.43	**			0.42	*			0.64	***		
2001	0.52	***			0.44	**			0.63	***		
2002	0.42	***	-0.21	*	0.34	**			0.50	**		
2003	0.25	*										
2004	0.32	**	-0.15	.	0.31	.			0.47	**		
2005	0.21	.	-0.40	**					0.28	.	-0.27	.
2006	0.29	**	-0.35	***					0.31	*		
2007	0.59	***	-0.28	**	0.55	***	-0.24	**	0.63	***		
2008	0.52	***	-0.30	*	0.47	***	-0.30	***	0.56	***		
2009	0.55	***	-0.27	*	0.49	***	-0.32	***	0.52	***		
2010	0.55	***	-0.34	**	0.50	***	-0.36	***	0.58	***		
2011	0.45	**	-0.33	*	0.37	**	-0.21	.	0.46	***		
2012	0.44	**			0.42	***	-0.23	*	0.47	***		
2013	0.30	*	-0.41	**								
2014	0.51	**	-0.38	*	0.37	**	-0.40	**				
2015	0.53	***	-0.26	*	0.43	**						

Table S7: Direction and magnitude of trends in proportional occupancy measured using 3 indices derived from 4 methods of occupancy estimation.

Positive changes in proportion of cells occupied are indicated by blue (+ indicates increase of between 0 and 0.2, ++ indicates increase of >0.2), and negative changes in proportion of cells occupied by orange (- indicates decrease of between 0 and 0.2, -- indicates decrease of >0.2). Percentage agreement between surveyed occupancy trends (S), and occupancy modelled trends from different data sources (M = MERP Modelled, OT = OBIS Targeted Surveys, OO = OBIS Opportunistic Recording) are shown, both as agreement in direction of change, and agreement in direction and magnitude of change. Three indices are used to measure trends: occupancy in final 1/3 of time-series minus occupancy in initial 2/3 of time-series, occupancy in final 1/2 of time-series minus occupancy in initial 1/2 of time-series, and final minus initial proportional occupancy (as in the rest of this thesis).

Species	Final third minus initial two thirds				Final half minus initial half				Final occupancy minus initial occupancy			
	S	M	OT	OO	S	M	OT	OO	S	M	OT	OO
Balaenoptera acutorostrata	+	+	-	--	+	+	-	--	-	+	-	--
Balaenoptera musculus	+	-	+	-	+	-	+	-	+	-	+	-
Balaenoptera physalus	+	+	+	+	+	+	+	+	+	+	++	-
Delphinus delphis	+	+	+	-	+	+	+	-	++	++	+	-
Globicephala melas	+	-	-	--	+	-	-	--	+	-	-	--
Grampus griseus	+	+	-	-	+	+	-	-	-	+	-	--
Hyperoodon ampullatus	-	-	-	-	-	-	-	-	-	-	-	-
Lagenorhynchus acutus	-	--	-	-	-	--	-	-	-	--	-	-
Lagenorhynchus albirostris	-	-	--	--	-	-	--	--	-	--	--	--
Megaptera novaeangliae	+	+	-	+	-	+	-	+	-	+	-	+
Mesoplodon bidens	-	+	-	-	-	+	-	-	+	+	-	-
Orcinus orca	-	+	-	-	-	+	-	-	-	+	-	--
Phocoena phocoena	+	-	-	-	+	-	-	-	-	-	-	-
Physeter macrocephalus	+	+	+	-	+	+	+	-	+	+	+	--
Stenella coeruleoalba	+	+	+	-	+	+	+	-	+	+	+	+
Tursiops truncatus	+	++	++	-	+	++	++	-	+	++	++	-
Ziphius cavirostris	-	+	+	-	+	+	+	-	+	+	+	-
% Agreement direction		59	65	47		65	76	35		65	88	47
% Agreement magnitude		53	53	41		53	65	29		47	65	24

Table S8: Binomial GLM coefficients and significance levels for intraspecific AORs in 18 species of cetaceans in European waters.

AORs from the MERP abundance survey are shown in bold. Abundance values from this survey were combined with modelled occupancy values from OBIS Targeted Survey Data (Grp1) and OBIS Opportunistic Data (Grp2), and modelled MERP presence only data, to estimate the same AORs. Coefficients for two species (*Pseudorca crassidens* and *Stenella frontalis*) are not shown due to having single records of abundance. Continued overleaf.

Species	*a*			
	MERP		OBIS	
	Mod	**Surv**	Grp1	Grp2
Balaenoptera acutorostrata	-0.053239	**-1.0094902**	-0.7615945	-0.4208465
Balaenoptera musculus	-4.602685	**-3.6852074**	-5.0765291	-5.971331
Balaenoptera physalus	-0.9168274	**-0.3906424**	-0.5068388	-1.6386197
Delphinus delphis	0.46340823	**-1.6973703**	0.25782076	1.14838632
Globicephala melas	-0.3652825	**-2.3825856**	-0.4356706	-0.1493382
Grampus griseus	-1.4183495	**-2.5409373**	-1.3351563	-1.1854377
Hyperoodon ampullatus	-2.239917	**-3.3350275**	-2.6448616	-1.388894
Lagenorhynchus acutus	-0.3612355	**-2.6107024**	-1.2458061	-0.8532881
Lagenorhynchus albirostris	0.08625939	**-1.7024735**	-0.2281886	-0.1078242
Megaptera novaeangliae	-3.485828	**-3.7052825**	-2.1010385	-2.9143011
Mesoplodon bidens	-4.8470182	**-3.9078905**	-3.5892971	-1.4376629
Mesoplodon mirus	-5.4896575	**-7.3870689**	-6.2707995	-5.2526668
Orcinus orca	-1.7299524	**-3.0984324**	-1.2569288	-0.4508395
Phocoena phocoena	0.84937207	**-1.0010636**	0.7692992	1.37918796
Physeter macrocephalus	-1.4874279	**-1.6822356**	-1.1782828	-1.2503898
Stenella coeruleoalba	-1.8700506	**-1.7135931**	-0.6757825	-0.6935051
Tursiops truncatus	0.89982177	**-1.7923038**	0.40563673	-1.0241011
Ziphius cavirostris	-3.6341613	**-0.6077714**	-2.2282519	-2.3019849

Table S8: Cont.

b				Significance			
MERP		OBIS		MERP		OBIS	
Mod	**Surv**	Grp1	Grp2	Mod	**Surv**	Grp1	Grp2
-0.0280371	**0.36168753**	-0.0378513	-0.1297395	***	*******	***	***
0.02514547	**0.255055**	0.01374508	0.05311133				
0.01188723	**0.62743897**	0.04814546	-0.0134528		*******	***	
0.11985966	**0.55951206**	0.03378287	-0.0602602	***	*******	***	***
-0.0090451	**0.30548674**	-0.0296706	-0.1789732		*******	***	***
0.00351985	**0.27690075**	-0.0108205	-0.0480621		*******		***
0.05145218	**0.26643431**	0.12067353	0.1143621	***	*******	***	***
0.06957039	**0.37879175**	0.01193616	-0.0053246	***	*******	*	
0.24356894	**0.41728202**	0.33103031	0.26204761	***	*******	***	***
-0.1482502	**0.21788895**	0.14151653	-0.0117082	***	**M**	***	
-0.1734691	**0.17285933**	0.04282215	0.09610003	***			M
-0.0204698	**-0.0954696**	0.00862085	-8.29E-16				
-0.0617367	**0.28335804**	0.1347209	0.24290879	***	*******	***	***
0.01730377	**0.3770989**	0.01833265	0.04637377		*******		
-0.0069574	**0.3975664**	-0.002033	0.00688815		*******		
0.06724184	**0.70970291**	0.07826007	-0.0039873	***	*******	***	
0.42676757	**0.39119199**	0.25113548	-0.1803052	***	*******	***	***
-0.0114816	**0.55050257**	-0.0056267	0.01683857		*******		

Table S9: Binomial GLM coefficients for interspecific AORs for cetaceans in European waters across 37 years.

AORs from the MERP abundance survey are shown in bold. Abundance values from this survey were combined with modelled occupancy values from OBIS Targeted Survey Data (Group 1) and OBIS Opportunistic Data (Group 2), and modelled MERP presence only data, to estimate the same AORs. All relationships were significant (binomial GLM, $p < 0.001$).

Year	*a*				*b*			
	OBIS		MERP		OBIS		MERP	
	Group 1	Group 2	Modelled	**Surveyed**	Group 1	Group 2	Modelled	**Surveyed**
1980	0.614	0.875	0.646	**-1.426**	0.327	0.168	0.303	**0.733**
1981	0.487	0.982	0.617	**-1.604**	0.193	0.136	0.205	**0.512**
1982	0.468	1.203	0.679	**-1.718**	0.265	0.283	0.316	**0.498**
1983	0.505	1.142	0.577	**-1.522**	0.237	0.215	0.235	**0.554**
1984	0.821	1.402	0.971	**-1.026**	0.352	0.307	0.341	**0.719**
1985	0.440	1.005	0.369	**-1.396**	0.329	0.249	0.260	**0.711**
1986	0.426	1.043	0.403	**-1.742**	0.243	0.226	0.211	**0.482**
1987	0.758	1.296	0.847	**-1.329**	0.306	0.235	0.322	**0.608**
1988	0.472	0.758	0.721	**-1.017**	0.211	0.088	0.248	**0.717**
1989	0.377	1.408	0.397	**-2.296**	0.275	0.367	0.270	**0.364**
1990	0.402	1.344	0.300	**-1.849**	0.223	0.272	0.169	**0.542**
1991	0.171	0.935	0.330	**-2.264**	0.188	0.197	0.212	**0.369**
1992	0.549	1.506	0.792	**-1.620**	0.248	0.288	0.324	**0.447**
1993	0.299	1.030	0.182	**-1.501**	0.262	0.266	0.219	**0.600**
1994	0.105	0.543	0.414	**-0.755**	0.245	0.262	0.312	**0.680**
1995	0.310	0.744	0.421	**-1.749**	0.465	0.466	0.471	**0.586**
1996	-0.187	0.279	0.006	**-2.204**	0.246	0.278	0.286	**0.336**
1997	-0.180	0.358	0.175	**-1.708**	0.263	0.325	0.375	**0.445**
1998	-0.064	0.528	0.249	**-1.779**	0.340	0.398	0.433	**0.402**
1999	-0.172	0.342	0.122	**-2.097**	0.223	0.280	0.285	**0.355**
2000	0.187	0.615	0.324	**-2.169**	0.333	0.425	0.296	**0.352**
2001	-0.029	0.293	0.140	**-1.997**	0.318	0.378	0.314	**0.474**
2002	0.348	0.805	0.674	**-1.248**	0.357	0.453	0.418	**0.538**
2003	-0.272	0.086	-0.064	**-1.836**	0.131	0.242	0.154	**0.312**
2004	0.092	0.518	0.444	**-1.500**	0.241	0.350	0.258	**0.443**
2005	0.497	0.853	0.573	**-0.561**	0.314	0.391	0.280	**0.614**

2006	0.409	0.665	0.689	**-0.930**	0.318	0.393	0.338	**0.517**
2007	0.898	1.021	0.759	**-1.377**	0.435	0.466	0.355	**0.441**
2008	0.715	0.718	0.668	**-1.162**	0.440	0.442	0.364	**0.447**
2009	0.552	0.375	0.485	**-1.494**	0.404	0.347	0.335	**0.411**
2010	0.565	0.681	0.582	**-1.370**	0.415	0.453	0.357	**0.465**
2011	0.417	0.386	0.519	**-1.294**	0.314	0.314	0.287	**0.470**
2012	0.550	0.469	0.481	**-0.983**	0.398	0.403	0.308	**0.444**
2013	0.419		0.548	**-1.050**	0.296		0.278	**0.582**
2014	0.424		0.605	**-1.739**	0.283		0.279	**0.389**
2015	0.889		1.080	**-1.431**	0.360		0.340	**0.399**
2016			0.911	**-0.897**			0.141	**0.426**

Table S10: OBIS citations for datasets modelled in Chapter 5.

Including grouping identifiers for elasmobranch (E) and gastropod (G) groupings.

Resource ID	Resource Name and Citation	E.	G.
8	**Academy of Natural Sciences OBIS Mollusc Database** Rosenberg et al., 2002	1	12
10	**SeamountsOnline (Seamount Biota)** Stocks, K. 2003. SeamountsOnline: an online information system for seamount biology. Version 3.1. seamounts.sdsc.edu	2	11
11	**ZooGene A DNA Sequence Database for Calanoid Copepods and Euphausiids** Zooplankton genomic database (ZooGene) project: integrating molecular, taxonomic, and oceanographic data. Bucklin,A.; Wiebe,P. H.; Frost,B. W.; Groman,R. G.; Fogarty,M. J.	1	11
12	**Southampton Oceanography Center Discovery Collections Midwater Database**	1	11
25	**EPA'S EMAP Database** Some or all of the data described in this article were produced by the U.S. Environmental Protection Agency through its Environmental Monitoring and Assessment Program (EMAP), http://www.epa.gov/emap/.	8	15
27	**Biocean** Fabri, M-C. et al., Ifremer BIOCEAN database (Deep Sea Benthic Fauna). Institut Français de Recherche pour l'Exploitation de la Mer, Ifremer, Issy-les-Moulineaux, France. World Wide Web electronic publication, http://www.ifremer.fr/isi/biocean	8	15
29	**Atlantic Reference Centre Museum of Canadian Atlantic Organisms - Invertebrates and Fishes Data** Van Guelpen, L., 2016. Atlantic Reference Centre Museum of Canadian Atlantic Organisms - Invertebrates and Fishes Data. Version 4 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	2	11
30	**Electronic Atlas of Ichthyoplankton on the Scotian Shelf of North America** EAISSNA - An Electronic Atlas of Ichthyoplankton on the Scotian Shelf of North America	2	11
38	**ECNASAP - East Coast North America Strategic Assessment** East Coast North America Strategic Assessment Project, Groundfish Atlas for the East Coast of North America	9	14

47	**BioMar - Ireland: benthic marine species survey** Picton, B.E., C.S. Emblow, C.C. Morrow, E.M. Sides, P. Tierney, D. McGrath, G. McGeough, M. McCrea,P. Dinneen, J. Falvey, S. Dempsey, J. Dowse, and M. J. Costello, 1999: Marine sites, habitats and species data collected during the BioMar survey of Ireland. Environmental Sciences Unit, Trinity College, Dublin, Ireland	8	15
49	**Grand Manan Basin Benthos** Grand Manan Basin - Deep Water Sediment Community	8	15
51	**A comparison of benthic biodiversity in the North Sea, English Channel and Celtic Seas - Epifauna** Rees, H.L. et al. A comparison of benthic biodiversity in the North Sea, English Channel and Celtic Seas - Epifauna. Centre for Environment, Fisheries and Aquaculture Science; Burnham Laboratory, 12 Apr 2005, Essex, UK.	7	15
56	**REVIZEE Score Sul / Bentos** REVIZEE South Score / Benthos - Amaral, A.C.Z. e Rossi-Wongtschowski, C.L.D.B. (eds.) 2004. Biodiversidade bentônica da região sudeste-sul do Brasil, plataforma externa e talude superior. São Paulo : Instituto Oceanográfico da USP, 2004 (Série Documentos Revizee - Score Sul). 216 p. ISBN 85-98729-08-6.	8	15
67	**North Pacific Groundfish Observer**	8	15
71	**IndOBIS, Indian Ocean Node of OBIS** Chavan, VIshwas and C. T. Achuthankutty (editors), IndOBIS Catalogue of Life, Available at http://www.indobis.org/, Retrived 2018-07-11	2	11
75	**MV Ichthyology**	3	
77	**MV Marine Invertebrates**	1	11
86	**Paranaguá Bay - Plankton and Benthos Database** Paranaguá Bay - Plankton and Benthos Database	7	15
89	**Marine Life Survey Data (collected by volunteers) collated by MarLIN** Parr, J. Marine Life Survey Data (collected by volunteers) collated by MarLIN. MarLIN, collated Marine Life Survey Datasets, Marine Biological Association of the UK, Plymouth, UK.	2	11

90	**REVIZEE South Score / Pelagic and Demersal Fish Database** REVIZEE South Score / Pelagic and Demersal Fish Database – Figueiredo, J. L.; Santos A. P.; Yamaguti, N.; Bernardes, R. A., Rossi-Wongtschowski, C. L. B. 2002. Peixes da Zona Econômica Exclusiva da região Sudeste-Sul do Brasil. São Paulo : Editora da Universidade de São Paulo: Imprensa Oficial do Estado, 2002. 244 p. ISBN: 85-314-0726-5 (Editora da Universidade de São Paulo), ISBN: 85-7060-126-3 (Imprensa Oficial do Estado). Haimovici, M.; Ávila-da-Silva, A. O.; Rossi-Wongtschowski, C. L. D. B. 2004. Prospecção pesqueira de espécies demersais com espinhel-de-fundo na Zona Econômica Exclusiva da região Sudeste-Sul do Brasil. São Paulo : Instituto Oceanográfico da USP, 2004. (Série Documentos Revizee: Score Sul). 112 p. ISBN 85-98729-01-9.	9	14
91	**SINBIOTA - marine data** Marine Benthos - BIOTA/FAPESP	2	11
97	**Marine species data for Scottish waters held and managed by Scottish Natural Heritage, derived from benthic surveys 1993 to 2012** Scottish Natural Heritage. Marine species data for Scottish waters held and managed by Scottish Natural Heritage, derived from benthic surveys 1993 to 2012. Scottish Natural Heritage, Edinburgh, UK. http://doi.org/10.15468/xm622i	8	15
103	**Seasearch Marine Surveys** Marine Conservation Society. Seasearch Marine Surveys. Marine Conservation Society, Ross-on-Wye, UK.	8	15
105	**REVIZEE South Score / Pelagic and Demersal Fish Database II** Bernardes, R. A.; Rossi-Wongtschowski, C. L. D. B.; Wahrlich, R.; Vieira, R. C.; Santos, A. P.; Rodrigues, A. R. 2005. Prospecção pesqueira de recursos demersais com aramadilhas e pargueiras na Zona Econômica Exclusiva da Região Sudeste-Sul do Brasil. São Paulo: Instituto Oceanográfico da USP (Série Documentos Revizee: Score Sul). 112 p. ISBN 85-98729-13-2. Bernardes, R. A.; Figueiredo, J. L.; Rodrigues, A. R.; Fischer, L. G.; Vooren, C. M.; Haimovic, M.; Rossi-Wongtschowski, C. L. B. 2005. Peixes da Zona Econômica Exclusiva da Região Sudeste-Sul do Brasil: levantamento com aramadilhas, pargueiras e rede de arrasto de fundo. São Paulo: Editora da Universidade de São Paulo. 295p. ISBN 85-314-0890-3.	9	14
125	**Marine and Coastal Management - Copepod Surveys** Marine and Coastal Management - Copepod Surveys	7	14
127	**Natal Museum - Mollusc Collection** Natal Museum - Mollusc Collection	1	12
128	**South African Institute for Aquatic Biodiversity - Fish Collection** South African Institute for Aquatic Biodiversity - Fish Collection	3	

129	**iziko South African Museum - Fish Collection** iziko South African Museum - Fish Collection	3	
138	**iziko South African Museum - Crustacean Collection** iziko South African Museum - Crustacean Collection	1	
139	**iziko South African Museum - Shark Collection** iziko South African Museum - Shark Collection	3	
142	**iziko South African Museum - Mollusc Collection** iziko South African Museum - Mollusc Collection	1	12
144	**Southern Ocean Continuous Zooplankton Recorder (SO-CPR) Survey** See Metadata record for details http://data.aad.gov.au/aadc/metadata/metadata_redirect.cfm?md=AMD/AU/AADC-00099	7	15
151	**Benthic biodiversity along the central coast in the Brazilian EEZ (OBIS South America, BRAZIL)** Lavrado, H.P. e Ignacio, B.L. (eds.) 2006. Biodiversidade bentônica da costa central da Zona Econômica Exclusiva brasileira. Rio de Janeiro : Museu Nacional, 2006. (Série Livros; 18) 389 p. ISBN 85-7427-014-8	8	15
161	**Marine and Coastal Management - Demersal Surveys (AfrOBIS)** Marine and Coastal Management - Demersal Surveys	8	15
168	**Marine and Coastal Management - Linefish Dataset (AfrOBIS)** Marine and Coastal Management - Linefish Dataset	2	
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3962	**National Benthic Infaunal Database**	8	15
3971	**UNCW JAX Aerial Survey - Left side - 2015** McLellan, W. 2016. UNCW JAX Aerial Survey - Left side - 2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1362) on 2018-07-11.	7	14
3979	**AFTT Cape Hatteras Aerial Survey -Left side- 2014** McLellan, W. 2015. AFTT Cape Hatteras Aerial Survey -Left side- 2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1237) on 2018-07-11.	7	14
3983	**AMAPPS Northeast Aerial Cruise Spring 2012** Josephson, B. 2015. AMAPPS Northeast Aerial Cruise Spring 2012. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1247) on 2018-07-11.	7	14
3990	**AFTT JAX Aerial Survey -Left side- 2014** McLellan, W. 2015. AFTT JAX Aerial Survey -Left side- 2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1241) on 2018-07-11.	7	14
3993	**AMAPPS Northeast Aerial Cruise Summer 2010** Josephson, B. 2015. AMAPPS Northeast Aerial Cruise Summer 2010. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1249) on 2018-07-11.	7	14
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4031	**Elasmobranch sightings along the South African coastline** Schroeter, L.S. 2016. ELMO (South African Elasmobranch Monitoring). Citizen Science	6	

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4057	**UNCW Norfolk Canyon Aerial Survey - Left side - 2015** McLellan, W. 2016. UNCW Norfolk Canyon Aerial Survey - Left side - 2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1354) on 2018-07-11.	7	14
4060	**UNCW Norfolk Canyon Aerial Survey - Right side - 2015** McLellan, W. 2016. UNCW Norfolk Canyon Aerial Survey - Right side - 2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1356) on 2018-07-11.	7	14
4088	**Virginia CZM Wind Energy Area Survey - Left side - May 2014 through December 2014** Barco, S. 2015. Virginia CZM Wind Energy Area Survey - Left side - May 2014 through December 2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1229) on 2018-07-11.	7	14
4120	**UNCW Hatteras Aerial Survey - Left side - 2015** McLellan, W. 2016. UNCW Hatteras Aerial Survey - Left side - 2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1350) on 2018-07-11.	7	14
4133	**FRB: Zooplankton data collected during two surveys of the Inner Bay of Fundy in 1920 and 1951** Jermolajev, E. G. (2016) FRB: Zooplankton data collected during two surveys of the Inner Bay of Fundy in 1920 and 1951. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	7	15
4138	**AMAPPS Northeast Shipboard Cruise Summer 2011** Josephson, B. 2015. AMAPPS Northeast Shipboard Cruise Summer 2011. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1269) on 2018-07-11.	8	14
4151	**AMAPPS Northeast Aerial Cruise Summer 2011** Josephson, B. 2015. AMAPPS Northeast Aerial Cruise Summer 2011. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1233) on 2018-07-11.	7	14

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4199	**Gastropoda distribution data from: Deep-sea fauna of European seas - an annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe** Sysoev, A.V.; (2016). Gastropoda distribution data from: Deep-sea fauna of European seas - an annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe.	1	12
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4221	**Virginia CZM Wind Energy Area Survey - Right side - May 2014 through December 2014** Barco, S. 2015. Virginia CZM Wind Energy Area Survey - Right side - May 2014 through December 2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1231) on 2018-07-11.	7	14
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4243	**AFTT JAX Aerial Survey -Left side- 2012-2013** McLellan, W. 2014. AFTT JAX Aerial Survey -Left side- 2012-2013. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1128) on 2018-07-11.	7	14
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4245	**UNCW PAX Aerial Survey - Left side - 2015** McLellan, W. 2016. UNCW PAX Aerial Survey - Left side - 2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1358) on 2018-07-11.	7	14
4248	**UNCW Right Whale Aerial Survey 05-06** McLellan, W. 2011. UNCW Right Whale Aerial Survey 05-06. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/360) on 2018-07-11.	7	14
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4269	**Dry Tortugas Reef Visual Census 2000** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4279	**USGS Patuxent Wildlife Research Center Seabirds Compendium**	7	14
4281	**Florida Keys Reef Visual Census 2014** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14

4296	**ImageDOP Bentic Video Annotations in the Faial-Pico Channel in 2011** Gomes-Pereira JN; Institute of Marine Research (IMAR - Azores), Portugal; Department of Oceanography and Fisheries (DOP) - UAC, Portugal (2016). ImageDOP Bentic Video Annotations in the Faial-Pico Channel in 2011 https://doi.org/10.14284/209	8	15
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4313	**Florida Keys Reef Visual Census 2004** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4316	**Dry Tortugas Reef Visual Census 1999** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4318	**Florida Keys Reef Visual Census 2001** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4320	**Florida Keys Reef Visual Census 1995** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4321	**Florida Keys Reef Visual Census 2000** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4327	**Florida Keys Reef Visual Census 2008** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4333	**Florida Keys Reef Visual Census 2005** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4337	**Dry Tortugas Reef Visual Census 2012** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4338	**Florida Keys Reef Visual Census 1997** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14

4340	**Dry Tortugas Reef Visual Census 2014** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4343	**Dry Tortugas Reef Visual Census 2006** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4347	**Florida Keys Reef Visual Census 2006** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4354	**Florida Keys Reef Visual Census 2003** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4355	**Acadia University: Invertebrates from mudflats in the Minas Basin (Bay of Fundy), collected for the NaGISA project July 2008** Gibson, Glenys and Anna Redden. (2016). Acadia University: Invertebrates from mudflats in the Minas Basin (Bay of Fundy), collected for the NaGISA project July 2008. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	7	15
4361	**Dry Tortugas Reef Visual Census 2010** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4364	**Florida Keys Reef Visual Census 1998** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4365	**Dry Tortugas Reef Visual Census 2004** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4367	**Florida Keys Reef Visual Census 2010** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4368	**Florida Keys Reef Visual Census 2007** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14
4370	**Florida Keys Reef Visual Census 2011** South Florida Reef Visual Census; http://www.sefsc.noaa.gov/rvc_analysis20/samples/index	9	14

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4378	**Canadian Field-Naturalist: Fishes stranded during extreme low tides in Minas Basin, Nova Scotia** Bleakney, J.S. and McAllister, D.E. (2016) Canadian Field-Naturalist: Fishes stranded during extreme low tides in Minas Basin, Nova Scotia. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	5	13
4391	**ACER: Temporal patterns in Minas Basin intertidal weir fish catches** Baker, M., Reed, M. and Redden, A. M. (2017) ACER: Temporal patterns in Minas Basin intertidal weir fish catches. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	9	14
4407	**Acadia University: Juvenile Fish Assemblages collected in bays along the Atlantic Coast of mainland Nova Scotia during summers of 2005 and 2006** O'Connor, S.E. (2017) Acadia University: Juvenile Fish Assemblages collected in bays along the Atlantic Coast of mainland Nova Scotia during summers of 2005 and 2006. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	9	14
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4441	**VIMS Chesapeake Bay Multispecies Monitoring and Assessment Program**	9	14
4442	**University of Florida Museum of Natural History Invertebrate Zoology Collection**	1	11
4479	**UWFC Ichthyology Collection**	3	
4512	**UNCW Hatteras Aerial Survey - Left side - 2016** McLellan, W. 2017. UNCW Hatteras Aerial Survey - Left side - 2016. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1471) on 2018-07-11.	7	14

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4539	**Museum and Art Gallery of the Northern Territory Malacology Collection - marine records**	1	12
4546	**Observatoire Pelagis aerial surveys 2002-2015** Van Canneyt, O. 2016. Observatoire Pelagis aerial surveys 2002-2015. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1404) on 2018-07-11.	9	14
4547	**Florida Keys Reef Visual Census 2016**	9	14
4561	**Florida Keys Reef Visual Census 1996**	9	14
4566	**AMAPPS Northeast Aerial Cruise Winter 2014** Josephson, B. 2016. AMAPPS Northeast Aerial Cruise Winter 2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1381) on 2018-07-11.	7	14
4567	**Virginia CZM Wind Energy Area Survey- Right side - January 2014 through March 2016** Mallette S.D., Lockhart G G., McAlarney R.J., Cummings E.W., Pabst D. A., McLellan W.A., Barco S.G. 2016. Offshore Energy Planning: Documenting Megafauna off Virginia's Coast Using Aerial Surveys. VAQF Scientific Report. 2016-04.	7	14
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4573	**Australian National Fish Collection**	3	
4594	**ACER: Benthic fish recorded as part of the 1989 Littoral Investigation of Sediment Properties project in the Minas Basin** Daborn, G.R. (2017) ACER: Benthic fish recorded as part of the 1989 Littoral Investigation of Sediment Properties project in the Minas Basin. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	9	14
4613	**Florida Keys Reef Visual Census 2009**	9	14
4614	**UNCW Norfolk Canyon Aerial Survey - Left side - 2016** McLellan, W. 2017. UNCW Norfolk Canyon Aerial Survey - Left side - 2016. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1479) on 2018-07-11.	7	14

4630	**Acadia University: Ectoparasites on Atlantic sturgeon (*Acipenser oxyrinchus* Mitchill, 1814) in the Minas Basin** Munroe, Samantha E.M. (2017) Acadia University: Ectoparasites on Atlantic sturgeon (*Acipenser oxyrinchus* Mitchill, 1814) in the Minas Basin. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	7	14
4634	**ImagDOP Benthic Video Annotations in Condor seamount in 2010** Gomes-Pereira JN; Institute of Marine Research (IMAR - Azores), Portugal; Department of Oceanography and Fisheries (DOP) - UAC, Portugal (2017) ImagDOP Benthic Video Annotations in Condor seamount in 2010. https://doi.org/10.14284/304	8	15
4639	**Florida Keys Reef Visual Census 2002**	9	14
4645	**Dry Tortugas Reef Visual Census 2016**	9	14
4665	**Aerial Survey Baseline Monitoring in the Continental Shelf Region of the VACAPES OPAREA: January 2016 - December 2016 (left side)** Mallette, S.D., R.J. McAlarney, G.G. Lockhart, E.W. Cummings, D.A. Pabst, W.A. McLellan, and S.G. Barco. 2017. Aerial Survey Baseline Monitoring in the Continental Shelf Region of the VACAPES OPAREA: January 2016 - December 2016. (left side data). Prepared for U.S. Fleet Forces Command. Submitted to Naval Facilities Engineering Command Atlantic, Norfolk, Virginia, under Contract No. N62470-15-D-8006, Task Order 05. issued to HDR, Inc., Virginia Beach, Virginia. 1 February 2016.	7	14
4667	**UNCW Hatteras Aerial Survey - Right side - 2016** McLellan, W. 2017. UNCW Hatteras Aerial Survey - Right side - 2016. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1473) on 2018-07-11.	7	14
4671	**Aerial Survey Baseline Monitoring in the Continental Shelf Region of the VACAPES OPAREA: January 2016 - December 2016 (right side)** Lockhart, G. and S. Barco. 2017. Aerial Survey Baseline Monitoring in the Continental Shelf Region of the VACAPES OPAREA: January 2016 - December 2016 (right side). Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1495) on 2018-07-11.	7	14
4676	**Florida Keys Reef Visual Census 2012**	9	14
4686	**Australian Museum Ichthyology Collection** McGrouther M (2017): Australian Museum Ichthyology Collection. v1.0. CSIRO Oceans and Atmosphere. Dataset/Occurrence. http://ogc-act.csiro.au/ipt/resource?r=am_ichthyology&v=1.0	3	

4688	**Virginia CZM Wind Energy Area Survey- Left side - January 2014 through March 2016** Mallette S.D., Lockhart G G., McAlarney R.J., Cummings E.W., Pabst D. A., McLellan W.A., Barco S.G. 2016. Offshore Energy Planning: Documenting Megafauna off Virginia's Coast Using Aerial Surveys. VAQF Scientific Report. 2016-04.	7	14
4698	**UNCW JAX Aerial Survey - Right side - 2016** McLellan, W. 2017. UNCW JAX Aerial Survey - Right side - 2016. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1477) on 2018-07-11.	7	14
4705	**Florida Keys Reef Visual Census 1994**	9	14
4706	**AMAPPS Northeast Shipboard Cruise Spring 2014** Josephson, B. 2016. AMAPPS Northeast Shipboard Cruise Spring 2014. Data downloaded from OBIS-SEAMAP (http://seamap.env.duke.edu/dataset/1377) on 2018-07-11.	8	14
4713	**ACER: Marine Resource Inventory of the Seaside Adjunct, Kejimkujik National Park** Brylinksy, M, P. Crawford-Kellock and G.R. Daborn (2017) ACER: Marine Resource Inventory of the Seaside Adjunct, Kejimkujik National Park. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/. Accessed on 2018-07-11	8	15
4727	**Museums Victoria Marine Invertebrates Collection**	1	11
4730	**Australian Museum Malacology Collection - Marine records** Reid M (2017): Australian Museum Malacology Collection - Marine records. v1.0. CSIRO Oceans and Atmosphere. Dataset/Occurrence. http://ogc-act.csiro.au/ipt/resource?r=am_malacology&v=1.0	1	12
4731	**Dry Tortugas Reef Visual Census 2008**	9	14
4732	**Florida Keys Reef Visual Census 1999**	9	14