The spatial and trophic ecology of seabirds in the western North Sea: developing the evidence base for ecologically sustainable fisheries and marine spatial planning

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"God becomes man becomes fish becomes barnacle goose becomes featherbed mountain."

– James Joyce, Ulysses

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Declaration

The following people were involved in this research project:

Sylvan Ray Benaksas, Dr. Tom Webb, Dr. Chris Lynam, Dr. Francis Daunt, Dr. Chibuzor Nnanatu, Dr. Jeroen Van der Kooij, Dr. Sophie Smout, Dr. Janneke Ransijn

Chapter 2: Seabird prey in space and time: Joining multiple datasets to model the distribution of sandeel (Ammodytes marinus) and sprat (Sprattus sprattus) in the North Sea

S.R.B, T.W, C.L, F.D & C.N conceived the idea for the study;

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J.V.D.K provided acoustic data processing training;

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Chapter 3: Identifying critical prey thresholds for successful guillemot chick survival in the face of a shifting prey base

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Chapter 4: Lower impact risk but higher spatial overlap of seabirds and anthropogenic stressors in a changing North Sea

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I, Sylvan Ray Benaksas, the author, confirm that this Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not previously been presented for an award at this, or any other, university.

Abstract

Seabirds along the Eastern coast of Britain have been declining over the past three decades, alongside their main breeding season prey sandeel (*Ammodytes marinus*). Seabird productivity is a critical aspect of a healthy population, and this is highly sensitive to prey availability near to seabird colonies. To understand drivers, outcomes and potential conservation actions of these seabird declines, it is necessary to study the spatial, temporal and trophic ecology of seabirds and their main prey fish. In this thesis I contribute to this understanding by first modelling the fine-scale spatio-temporal distribution of sandeel together with another key prey species, sprat (*Sprattus sprattus*) across the North Sea over the past two decades. Due to the lack of single comprehensive surveys for these two species, I take a novel approach by combining different available survey datasets with different strengths and weaknesses to extend the coverage and statistical power of the model. These maps allow for the identification of hotspots of biomass, population trends, and important environmental drivers for both prey species. Next, I modelled the specific predator-prey interactions of parent guillemots (*Uria aalge*) while provisioning their chicks on the Isle of May with their main breeding season prey, sprat and sandeel. I parameterised multi-species functional response models, which show that that guillemot chick provisioning was far more sensitive to changes in sprat availability than sandeel. My results are broadly in agreement with the widely cited ‘one third for the birds’ proposal - i.e., that prey fish should be maintained at least at one third of historical maximum biomass in order to avoid negative impacts on seabirds. However, my flexible multi-species modelling approach showed that high levels of sandeel biomass have the potential to buffer low years of sprat biomass. Finally, I performed habitat risk mapping to identify hotspots where multiple anthropogenic pressures overlap with key seabird foraging areas. I found that two changes in how we use the ocean over the next decade, the cessation of sandeel fishing in the UK EEZ and the large expansion of offshore wind developments, will likely decrease the overall impact risk but increase the spatial overlap of key seabird foraging habitat and anthropogenic stressors. Overall seabirds and their prey are experiencing significant changes and here I lay the groundwork of quantitative evidence with a comprehensive cover of many aspects of seabird ecology that will aid and improve manager’s decisions in relation to commercial fishing, marine spatial planning and seabird conservation.

1. Introduction

1.1 Seabird declines

Seabirds are an enigmatic and ubiquitous group of species, highly visible and audible even in the 21st century yet only representing ~ 3.5% of bird species globally (Croxall et al., 2012). In Northern Europe seabirds and their eggs have been a source of food likely from the earliest beginnings in the Mesolithic (Best & Mulville, 2016), until the modern era (Merkel, 2010), while their feathers have been a commercial commodity (Thomas et al., 2019). This exploitation reached significantly higher levels during the industrial era that led to the extinction of the great auk (*Pinguinus impennis*) in the 19th Century (Thomas et al., 2019). Following the cessation of direct exploitation around Europe, seabird populations had been making recoveries over the 20th Century (Grandgeorge et al., 2008; Serjeantson, 2001). However, seabirds face many threats in the 21st century, both on land and at sea. These include competition for resources from commercial fisheries, mortality in fisheries bycatch, predation from invasive species, habitat degradation, pollution, marine coastal development, interactions with offshore renewable energy infrastructure, and climate change (Croxall et al., 2012; Dias et al., 2019). The UK now supports many internationally important seabird breeding colonies, however, populations around the UK have declined over the last 3 decades (Burnell et al., 2023). Understanding and addressing these threats will be key to successful seabird conservation over the next decades.

Many seabirds are colonial breeders, attending large colonies up to several hundred thousand in the UK (Burnell et al., 2023). The breeding season begins in spring when adults return to colonies and extends into the summer (June to July), when chicks fledge in preparation for their first winter (Keogan et al., 2021). This is a critical period of time in the annual cycle with high demands for energy for the growing chicks (Collins et al., 2016). During the breeding season seabirds are central place foragers, tied to localised environmental and foraging conditions around the seabird colony which makes them more vulnerable to fluctuations in the availability of appropriate prey (Burke & Montevecchi, 2009).

Forage fish are small pelagic fish named after their ecological role in ecosystems worldwide. They are dominated by the order Clupeiformes with most being planktivorous, forming large pelagic schools (Hastings et al., 2015). Sandeel in the family Ammodytidae are notable forage fish in northern latitudes, and are particular abundant in the North Sea (Green, 2017). They are important mid-trophic fish, linking higher and lower trophic levels of pelagic food webs. Forage fish often display "boom-bust" population dynamics, however, in the North Sea, which is a wide and relatively shallow shelf sea, this is likely to be less dramatic than in upwelling systems (Szuwalski et al., 2019). There are several species of sandeel occurring across the North Sea, most focus has centred on the commercially and ecologically dominant lesser sandeel (*Ammodytes marinus*). We will focus on this species and hereafter refer to this species as “sandeel”. Seabird chick diets on the Eastern coast of the UK have historically been reliant upon sandeel, however, these fish have also been undergoing a concurrent decline with seabird populations and there is major concern for the impacts on dependent predators (Anderson et al., 2014; ICES, 2022a). There has been a varied response to this decline, with some species such as the surface feeding kittiwake still targeting sandeel, while diving auk species - guillemots (*Uria Aalge*) and razorbills (*Alca torda*) - have increasingly switched to sprat (S*prattus sprattus*), another small pelagic fish (Wanless et al., 2018).

Recent studies of puffins (*Fratercula arctica*) have shown that decreased food availability has led to increased foraging costs, distances travelled, and time spent away from the chick by breeding adults which has resulted in reduced breeding success (Fayet et al., 2021). This is a major concern, as across the seabird community breeding success has been declining in the North Sea region over recent decades (Searle et al., 2023b). As seabirds are long lived species, they have some capacity to sustain short term losses in productivity, however, over longer periods of time this will eventually lead to population declines as the population turnover is not able to match mortality (Wanless et al., 2023). There appears to be synchronicity in the decline of seabird productivity in the region (Lahoz-Monfort et al., 2013), and this may even extend globally (Sydeman et al., 2021), which suggests large-scale impacts may be driving these patterns. It is therefore well established that prey depletions greatly impact seabird productivity, however, understanding the underlying causes and mechanistic predator-prey relationships remains a challenge.

1.2 Seabird Threats

There are many direct threats that impact seabird populations, including the recent avian influenza outbreak (Lane et al., 2024). Two of the major threats of concern, climate change and overfishing, impact seabirds only indirectly, but can substantially influence prey availability and thus seabird breeding success. These threats and impacts on seabirds have classically been considered as either “bottom-up” (climate driven) or “top-down” (predation – including fishing - driven) forces that structure food webs (Perkins et al., 2018). However, the forage fish on which seabirds depend occupy mid-trophic positions, and are likely influenced by both (Bakun, 2006; Cury et al., 2000; Lynam et al., 2017) which implies that both threats can be impacting seabirds through the food web.

Climate change in this context is generally considered to exert a bottom-up indirect effect that has a cascading impact starting at the lowest trophic level and knock-on effects through the food web to the small pelagic fish that compose the diet of seabirds. The North Sea has seen a decline in productivity and zooplankton abundance over recent decades, particularly along the east coast of the UK (Capuzzo et al., 2018; Hays et al., 2005), and has undergone drastic changes, with a regime shift occurring in the late 1980s completely restructuring the pelagic food web (Beaugrand, 2004; Edwards et al., 2002). The plankton copepod community has undergone major changes, with spring developing *Calanus finmarchicus* being largely replaced by summer developing *Calanus helgolandicus* (Frederiksen et al., 2013; Planque & Fromentin, 1996). This has affected planktivorous fish, such as sandeel (Van Deur et al., 2009), by a mechanism called the match-mismatch hypothesis, which is the ability (or inability) of predator phenology to match that of its prey, which may be exacerbated by rapid environmental change (Edwards & Richardson, 2004; Régnier et al., 2017), which has serious impacts on the energy content of short-lived fish (Frederiksen et al., 2011; Régnier et al., 2019) with cascading effects up from the bottom of the food web (Wanless et al., 2004). In addition, further up the food web phenological mismatch has been observed between seabirds and sandeel (Burthe et al., 2012), however, the phenological mismatch was not shown to impact seabird breeding success, suggesting they are sufficiently able to adapt their behaviour.

Direct links of climate change cascading up to affect seabirds have shown reduced fish energy content (Frederiksen et al., 2011; Wanless et al., 2005), have been linked to poor recruitment of fish and lower production (Lindegren et al., 2018) with potentially reduced over-winter fish survival (MacDonald et al., 2018). The changes in fish productivity, energy content and survival are very serious impacts that can have strong negative effects on dependent seabird populations. Despite these negative effects, recent climate forecasting has predicted increased spatial overlap between seabirds and sandeels in the North Sea over the next 30 years, suggesting a complex picture of impacts under future climate change (Sadykova et al., 2020).

Fishing is considered a top-down process, directly impacting the fish populations. Overfishing and the collapse of target fish populations are the most obvious and dramatic effects of poorly managed commercial fishing, however, there are other significant effects. Commercial fishing has been shown to change the composition (Daan et al., 2005), alter the age and genetic structure, increase recruitment variability (Botsford et al., 2011) and alter distributions (Cury et al., 2000) of fish populations and communities. Many fish populations are largely shaped by fishing pressure (Boyd et al., 2020; Lynam et al., 2017). Through its impacts on the age structure and reproductive cycles, commercial fishing can lead to fish populations tracking environmental conditions more closely (Perry et al., 2010).

Understanding the effects of commercial fishing resource competition on seabird populations has been difficult (Frederiksen et al., 2008b) because of the complex underlying interactions (Frederiksen et al., 2007; Lynam et al., 2017), the confounding effects of environmental change (Engelhard et al., 2014b), and population fluctuations of predatory fish which compete with seabirds for prey (Cury et al., 2000; Engelhard et al., 2014a; Furness, 1982), as well as the scale of data required for a robust analysis (Frederiksen et al., 2005; Matthiopoulos et al., 2008; Sydeman et al., 2017; Wright et al., 2019). Nonetheless, impacts of sandeel overfishing and resource competition with seabirds in the North Sea have been observed throughout the North Sea, starting in the Shetland islands in the late 1980s (Monaghan, 1992), followed by the east coast of Scotland in the late 1990s (Daunt et al., 2008) and a North Sea wide decline in the population since 2002 (ICES, 2023b). Conservation concerns over predators, including seabirds, in the region led to an area off the coast of Scotland being closed to sandeel fishing (Searle et al., 2023b). This closure positively impacted the kittiwake (*Rissa tridactyla*) population (Daunt et al., 2008), which has a high sensitivity to sandeel depletions (Furness & Tasker, 2000). The breeding success of kittiwakes further south in England has also been linked to sandeel fishing intensity on the Dogger Bank (Cook et al., 2014). However, positive effects of the Scottish sandeel closure for other seabird species in the area have not been observed (Searle et al., 2023b). The uncertainties in the impact of area closures on seabird breeding success limit the ability to directly study the impacts of fishery declines. More generally, there is a need for mechanistic studies of the interactions between seabirds and their predators, which may form complex non-linear relationships, before it is possible to fully determine the further impacts of fishing.

1.3 A changing prey-scape

Energy transfer is key component of ecology that structures food webs, and for predators this requires the detection and capture of prey. The availability of different prey species and patches to a predator can be described as a prey-scape, a conceptualisation relating the available prey populations and species to the undulating hill and valleys of a landscape, however, a prey-scape is dynamic unlike the landscape (on short timescales) and may be better related to a choppy sea surface. Many pelagic ecosystems have a ‘wasp-waist’ food web, where one or two species of forage fish dominate mid-trophic levels, occupying a vital role mediating energy transfer through the ecosystem and linking more diverse higher and lower trophic levels (Lynam et al., 2017). Such forage fish populations are highly variable

(Toresen & Østvedt, 2008; Watanabe, 2007), owing to their short life span and tight coupling to lower trophic levels (Alder et al., 2008), and this has led to difficulty in their management (Holling & Meffe, 1996). Furthermore, because of their population variability and their impact both up and down the food web, fishing small pelagic fish can have effects on the wider ecosystem (Smith et al., 2011). The attempt to understanding variability in fish recruitment has been a century-long investigation (Hjort, 1914), and quantifying the structuring roles of recruitment variability versus extraction still poses a major challenge to sustainable fisheries management (Beddington et al., 2007).

Forage fish populations occur in huge numbers and constitute up to 30% of the global fish catch (Alder et al., 2008), thus their effective management is of great consequence economically and socially as well as ecologically. Forage fish are generally not for direct human consumption but largely used in reduction as feed for aquaculture and pig and poultry livestock, with the expansion of forage fisheries being driven by the rapid growth of global aquaculture (Alder et al., 2008; Froehlich et al., 2018). The North Sea is one of the most heavily fished regions in the world, where many pelagic fish stocks have collapsed in the recent past due to overfishing. For instance, herring and mackerel stocks became severely depleted in the 1970s (Dickey-Collas et al., 2010; Sherman et al., 1981). It has been suggested that sandeel population expansions in the North-East Atlantic occurred subsequently as a result of replacing depressed mackerel and herring stocks in the food web (Sherman et al., 1981), highlighting the dynamic nature of pelagic food webs. In the North Sea in the 1990s sandeel became the target of the largest single-species industrial fishery in the region (Frederiksen et al., 2004). Sandeel catches peaked in excess of 1.2 million tonnes annually and since the early 2000s, sandeel populations have collapsed and failed to fully recover (ICES, 2023b). One hypothesis is that fishing caused the recent sandeel crashes and climate change has trapped the stocks in this depleted state (Lindegren et al., 2018). The same mechanisms have been suggested for North Sea cod and mackerel (Jansen, 2014). Forage fish productivity has significantly decreased in the North Sea, and fishing levels that would achieve MSY (defined as the maximum fish catch that would preserve fish productivity) have nearly halved since the 1980s with a specific shift around 1993 (Clausen et al., 2018). As well as this, forage fish populations have become less stable under the current low productivity regime (Clausen et al., 2018). All of these impacts raise serious concerns for forage fish in the North Sea, which in addition to seabirds, are also key resources for many predator populations such as marine mammals, many species of elasmobranchs and other commercially important piscivorous fish, highlighting the need to further study the population dynamics of these small fish (Engelhard et al., 2013; Ransijn et al., 2021; Wilson & Hammond, 2019).

It has been recognised since the 2000s that there are regionally distinct sandeel populations within the North Sea, and that understanding this population structure is key to effective management (Jensen et al., 2011; Rindorf et al., 2016). In 2011 the regional North Sea ICES management advice for sandeels was split into seven management areas based on separate, independent stocks (ICES, 2022a). This is vitally important for sandeel management in the North Sea as the regional variation in growth rate (MacDonald et al., 2019), length-at-age (Rindorf et al., 2016) and fecundity (Boulcott & Wright, 2011), as well as their patchy distribution makes the species especially vulnerable to localised depletions. The management advice is evolving with the best scientific evidence, and there were further changes to management area delineation in 2016 (ICES, 2022a). Stock assessments occur for four of the seven areas, areas 1 – 4, which is where the commercial fishing occurs. The fishery and assessment in area 7, around the Shetland islands, ceased permanently in the mid-2000s following a second sandeel population crash. Area 1, covering the Dogger Bank, and area 3, within the Norwegian EEZ, are the major fishing areas of the entire North Sea, together constituting an average 75% of the total historic sandeel catch. Area 2 along the German and Danish coasts are the next most important areas followed by area 4, along the East coast of Scotland. Area 4 includes the permanently closed sandeel habitat in the firth of forth, however since 2011 fishing has recommenced in the remaining part of this management area. Area 4 has constituted an average of 5% of the total North Sea sandeel catch, however this is highly variable, and in some years has been as high as 25%, with the catch increasing significantly since 2017. Denmark is the major sandeel fishing nation in the North Sea, comprising 73% of the historic catch, followed by Norway and then small efforts by Scotland, Germany and Sweden (ICES, 2020a).

Sprat is another important forage fish in the North Sea region. After high levels of fishing the population crashed in the early 1980s, but it has since made some recovery with favourable climatic conditions, as it is a warmer-water species compared to sandeel (Frisk et al., 2015). However, there is still uncertainty to the extent of this recovery, with sprat fishing still prohibited in the Firth of Forth region following declines in the 1990s (Jennings et al., 2012). Given their recovery and warmer water affinity, sprat have the potential to buffer the impacts of the sandeel declines for predators in a changing North Sea prey-scape. Sprat have declined less in productivity compared to other North Sea forage fish such as sandeel and herring (Clausen et al., 2018). Indeed, some seabirds and marine mammals have increased their consumption of sprat in recent decades (Ransijn et al., 2021; Wanless et al., 2018). However, this replacement of one prey species for another has not been universal, as only some species of birds, such as guillemots and razorbills, have a large portion of sprat in the chick diet, while most species still have varying levels of sandeel in the diet (Wanless et al., 2018). Predator diet changes are influenced by complex factors and could simply be caused by a decline in preferential prey rather than an increase in alternative prey. As such quantitative studies of sprat populations are necessary to understand sprat population dynamics on a regional, localised level.

A key requirement in order to understand the impacts of this changing prey-scape on seabirds is detailed information on the distribution of prey species in time and space. Given their ecological importance there is a surprising lack of information on the fine-scale distributions of either sandeel or sprat. Attempts to link prey metrics to seabird breeding success at the local scale (Isle of May) have relied on measures such as local sea surface temperature (SST) (Frederiksen et al., 2004; Harris et al., 2005) and productivity (Frederiksen et al., 2013), which can be considered as proxies of prey abundance, however the relationship between fish abundance and those ecosystem metrics is likely to be complex.

The large-scale, intensive bottom trawl surveys required to study a fish population across the North Sea were originally designed and targeted towards commercially important fish, such as herring or flatfish. Over the decades they have expanded to cover a much broader range of species as ecological importance has also been taken into consideration (Andersens, 2020). However, for small pelagic fish like sandeel and sprat, their small size and shape are less suited to these surveys, that often target larger fish. Sprat have a wider shape and larger fish a considered to be reliable caught by the international bottom trawl survey (IBTS) for example. However, due to their unusual burrowing behaviour, patchy distribution, size and shape, sandeels are poorly sampled by standardized bottom trawl surveys, having been shown to have a low and variable catchability (Johnsen & Harbitz, 2013). The same is also true for acoustic surveys used for other pelagic fish as sandeel lack swim bladders required for effective reflectance in acoustic monitoring (van der Kooij et al., 2008). Since the 1990s intermittent localised dredge surveys have been conducted to monitor sandeel populations (ICES, 2022a). These occur on known sandeel banks which are targeted by the fishery and are conducted in the winter when sandeel are usually buried in the sediment, which maximises catchability (Johnsen & Harbitz, 2013). Data are available from 2008 for area 4 (Scottish region) and from 2012 for the rest of the North Sea. However, these surveys are highly localised in their spatial coverage and only target commercially important habitat (Jensen et al., 2011), and furthermore have only a short time series available. Thus, despite their enormous ecological importance, the large-scale data required to study the spatio-temporal dynamics of sandeel across the whole North Sea is lacking. **To address this knowledge gap, the first aim of my thesis is to combine the large-scale but less reliable bottom trawl surveys with the sandeel specific but small-scale dredge**

surveys into a single Bayesian modelling framework which can draw strengths from the respective datasets while increasing the spatial and temporal coverage of the data and the statistical power of the analysis. This combined approach is completely novel in the study of sandeel, and to test its reliability I compare the results to those obtained from other studies of sandeel distributions and dynamics. While sprat is well captured by both bottom trawl surveys and acoustic surveys, to the best of my knowledge they have never been combined in a spatial model. The existence of overlapping but very different data sources allows me to test merging multiple datasets, and to improve the spatial coverage in order to obtain the best model of sprat biomass (Isaac et al., 2020).

1.4 Linking predators and prey: critical prey thresholds

Seabird breeding colonies occur on only specific islands and coastal cliffs where they are inaccessible to predators. As seabird density within colonies can be high, there is also high inter- and intra-specific competition for prey (Barger et al., 2016), with the depletion of prey over the breeding season in an area extending outwards from the colony known as Ashmole's halo (Birt et al., 1987). This occurs as adult seabirds must forage and return to the central breeding location, with a pair alternating foraging trips without leaving the chick alone for too long (Harris & Wanless, 1997). Because of this they are highly sensitive to changing prey availability (Regular et al., 2014), and added competition (e.g., from fishing boats operating in the area) may have a large effect on prey resources because of the already high predation demands.

Previous work has shown that prey depletion impacts puffin breeding success (Fayet et al., 2021) and that industrial sandeel fishing impacts vulnerable kittiwakes (Cook et al., 2014; Searle et al., 2023b). However, quantifying the relationship between seabirds and their prey, and identifying the critical prey thresholds at which seabirds would begin to be impacted is important for both future seabird and prey fish management. Ecosystem based fisheries management is a move away from single-species fisheries management, where sustainability is defined only as the preservation of adequate biomass of the target fish, to a system where the wider ecosystem impacts, and the needs of dependent predators are considered when defining what is a sustainable fishing level (Hill et al., 2020). There has been limited implementation of EBFM frameworks in active fish management advice, however, if we are to move towards them in the future, we need accurate evidence on the relationship between predators and the target fish species, as well as on threshold levels of prey biomass at which impacts on predators become evident (Free et al., 2021).

Much work on seabird diets has focused on what parents bring back to the colony to provision chicks (Barrett et al., 2006), due to the difficulty in measuring adult diets and the ease in observing provisioned meals. As a result, the diet of adults and young juveniles outside of the breeding season is relatively unknown. However, young chicks represent a particularly vulnerable and critical life stage, during which provisioning has a significant impact on chick survival and thus on annual population dynamics. Therefore, focusing on chick provisioning rates is likely a good choice for investigating predator prey thresholds.

Holling (1959) first described the functional response of a predator, as the variation in predation rate or behaviour in relation to prey density. Functional responses are generally divided into three types, dependent on the form of the relationship, with a type I response displays a linear relationship between predator consumption rates and prey density, a type II relationship declines monotonically, and a type III relationship is sigmoidal. These simple functional response relationships have since been extended to include multiple prey species (Ransijn et al., 2021). Functional response models allow for realistic representations of predation that can quantify top-down impacts of the predator as well as bottom-up effects of changing prey availability, the latter of which is of prime interest for this thesis. Multispecies functional responses account for attack rates, with high consumption predicted for strong predator-prey interactions, and they allow for prey switching, i.e. the change in prey preference in relation to prey density when a prey type becomes sparse. Parameterizing such a model is difficult because it requires extensive data on both predation rates and prey availability through time, which is very difficult to quantify in the field. As such, many applications have been limited to laboratory studies of insects (Holling, 1959). However, the use of Bayesian methods using Markov-Chain Monte-Carlo sampling (MCMC) has enabled the development of a framework that can handle data sparsity for predators such as seabirds (Ransijn et al., 2021).

A global analysis of the relationship between seabird productivity and their prey proposed that one third of historical biomass of the prey species was the critical limit to prevent declines in seabird productivity ("One Third for the Birds"; Cury et al., 2011). For the North Sea region, this analysis only focused on the Shetlands islands and a single prey species, sandeel. As outlined above, further south in the North Sea seabirds have at least some potential to switch to alternative prey, namely sprat, complex behaviour that a single-prey analysis will ignore. **The second aim of this thesis is to develop multi-species functional response models that allow us to model a more realistic representation of seabird foraging in the North Sea, accounting for the abundance of alternative prey (sprat) and allowing identification of critical thresholds of prey for seabird chick rearing that can inform future sustainable fisheries management.**

1.5 The future of seabirds in a changing North Sea

The North Sea is undergoing widespread environmental and anthropogenic changes beyond seabird and prey fish populations that have reshaped the ecosystem over recent decades and will continue to do so into the near future. These pressures have specific spatial distributions and determining how they relate to seabird populations and their foraging grounds will be key to understanding the potential impacts of these pressures. Research on the cumulative effects of stressors across space and time has shown that there is an increase in the number and intensity of activities occurring in the marine realm (Halpern et al., 2015)h. As a consequence, the fact that any individual pressure might not be having serious effects on seabird populations needs to be considered in the wider context of spatially overlapping pressures, and the possibility of cumulative impacts. Several studies have looked at the impacts of anthropogenic pressures on seabirds in the North Sea, but they have either had a limited scope in their selection of pressures, or have had a local focus (Andersen et al., 2020; Bradbury et al., 2014; Burthe et al., 2014; Gușatu et al., 2021; Leopold et al., 2015).

The North Sea has a very extensive fishing industry with a history of centuries of exploitation (Holt & Raicevich, 2018). Landings from the North Sea peaked between 3 and 4 million tonnes annually between the 1960s and the mid 1990s, after which they have declined, however, fishing using a wide range of gears still occurs at significant levels and poses a strong anthropogenic pressure (ICES, 2021). As set out above, sandeel fishing occurred at very high levels peaking at 1.2 million tonnes in 1997, and North Sea populations are sensitive to local depletions due to regional population differences (see section 1.2 Seabird Threats). The two regions where there is the greatest concern for sandeel declines and impacts on the wider ecosystem have been in Scotland. The First was in the Shetland Islands beginning in the late 1980s (Monaghan, 1992), which ultimately ended with the cessation of commercial fishing as the reduced stock became uneconomical to fish (ICES, 2020a). The second region of concern was along the East coast of mainland Scotland, which led to the closure of sandeel fishing grounds in an area extending offshore from the Scottish-English border north to Fraserborough south of the Moray Firth (See Figure 2A, Chapter 2). This signifies that there is concern for seabird prey resources along the East coast of the UK and together with the uncertainty around seabird recoveries following area closures (Searle et al., 2023b), and further analysis of the spatial interaction of fishing pressure with seabird foraging across the region is needed.

The climate of the region has been changing with the North Sea identified as one of the top 20 global marine climate change hotspots over the past 60 years (Hobday & Pecl, 2014). As mentioned in the previous section, there have been significant changes in the North Sea ecoregion due to climate change over the past decades. This has led to large scale changes with a regime shift occurring in 1989, altering the plankton community and the pelagic ecosystem and this in turn has had knock on effects for mid-trophic prey of seabirds (see section 1.2 Seabird Threats for details). Climate Change can act in several ways, in addition to altering the food web as already mentioned, climate change can increase the intensity and occurrence of marine heat waves (Nauw et al., 2015), which strongly affected the Northeast Atlantic in 2023 (Berthou et al., 2024). Climate change is altering the patterns of winter storms (Woollings et al., 2012), which can strongly affect seabirds causing mass mortality events known as “wrecks” (Clairbaux et al., 2021).

Marine traffic occurs across large ranges of the marine environment, where global large has seen a four-fold increase between 1992 and 2012 (Robbins et al., 2022). In addition, the North Sea contains some of the busiest shipping ports in the world (OSPAR, 2018). Marine traffic is generally associated with a low risk of direct mortality for seabirds, however, given its intensity and spatial restriction within designated shipping channels, there is a strong risk for disturbance of seabirds accessing the column for foraging (Schwemmer et al., 2011). Assessing the potential impact of shipping disturbance on seabirds has been difficult due to the practicalities of measuring the interaction, however, studies have shown that disturbance can be energetically costly and that seabird reactions are highly variable between species (Fliessbach et al., 2019). Thus, spatial analyses need to be species specific when assessing the impact of shipping.

Offshore windfarms are a central part of the clean energy transition and due to the shallow, sandy seabed the North Sea is projected to be a major hotspot for offshore wind development (WindEurope, 2023). Windfarms are recognized as a threat to seabird populations due to mortality from direct collision and the effects of displacement from foraging grounds or migration routes (Bradbury et al., 2014), despite uncertainty in species-specific differences in these impacts (Garthe et al., 2023). Because of these risks significant work has been done looking into the potential impacts of windfarms on seabirds (Garthe et al., 2023) and the spatial distribution of windfarm pressures (Bradbury et al., 2014; Gușatu et al., 2021). However, there has been limited scope in how these effects have been assessed with other co-occurring stressors across the region.

All of these pressures are potential threats to seabirds and their effective foraging, and while studies have looked at single stressor impacts a cumulative spatial risk analysis is needed for seabirds in the North Sea region. Looking to the future, the identified pressures are likely to continue. However, there are two large changes underway for the North Sea region. The first is the rapid increase in offshore windfarms over the coming decade as part of the rapid energy transition that will ramp up construction of offshore windfarms in the North Sea region. The recent Esbjerg Declaration in 2022 by Denmark, Belgium, Germany, and the Netherlands aims to make the North Sea a “green power plant for Europe” (Norrth Sea Governments, 2022). This is being driven to combat climate change and increase energy security following Russia’s invasion of Ukraine. Building on this, The North Seas energy Cooperation recently announced in 2022 an ambitious goal of 260GW of marine wind energy capacity by 2050, which will constitute 85% of the total EU wind generation targets (North Seas Energy Cooperation, 2022).

The second large change is the recent prohibition of sandeel fishing inside the UK EEZ taking effect in March 2024 (https://www.gov.uk/government/consultations/consultation-on-spatial-management-measures-for-industrial-sandeel-fishing/outcome/government-response for English waters and https://www.gov.scot/publications/sandeel-prohibition-fishing-scotland-order-2024-final-business-regulatory-impact-assessment/ for Scottish waters). While a legal challenge has been raised by the EU in relation to this and there is large uncertainty to the future of the policy, it has the potential for large impacts on the marine ecosystems of the Western North Sea. Concurrent to all of these environmental and anthropogenic changes, there is also a global push to increase marine protected area coverage, with the 2022 Kunming-Montreal Global Biodiversity Framework Target 3 sets out a target of 30% of sea, land and inland water area protected by 2030 (CBD, 2022), which is a rapid scaling up from the CBD 2010 target of 10% by 2020 (Coates, 2018), showing the growing awareness and pressure tackle the twin climate and biodiversity targets. All of these vastly contrasting impacts and uses of space necessitate strong marine spatial planning to ensure all of the needs can be met.

The third aim of this thesis is to analyse how seabird foraging is interacting with anthropogenic stressor across the North Sea over the past decade and under future scenarios. Additionally, I aim to test how the large-scale fisheries management change of sandeel fishing cessation in the UK EEZ will interact with other stressors in the region to provide necessary insight and evidence to the validity of the policy.

1.6 Structure of this Thesis

In this thesis I contribute new knowledge to contribute towards the conservation of North Sea seabirds and the sustainable management of fisheries by addressing the following three key aims:

1. Map the spatio-temporal distributions of sandeel and sprat biomass across the North Sea for the past 2 decades (Figure 1, process 2).
2. Parameterize the multi-species functional response model of guillemot chick provisioning on the Isle of May and quantify prey population levels that would negatively affect breeding success in inform ecosystem-based fisheries management (Figure 1, process 3).
3. Map the overlap of seabird foraging hotspots with anthropogenic stressors across the Western North Sea and examine the impacts of future scenarios to inform marine spatial planning (Figure 1, process 4).

Work to meet these three aims is presented across three interconnected chapters, in which I first map the spatio-temporal distributions of key seabird prey species, then use these maps of prey availability to construct multi-species functional response models for seabirds on the Isle of May, and finally I combine these prey distributions with seabird distributions into a foraging index and map how relates to known anthropogenic stressors throughout the western North Sea. This work fills in key gaps on fine-scale distributions of prey fish for the North Sea regions and opens up the possibility for a great amount of future research, by later chapters in this thesis, as well as other researchers of the North Sea ecosystem who will have access to this dataset in the future.

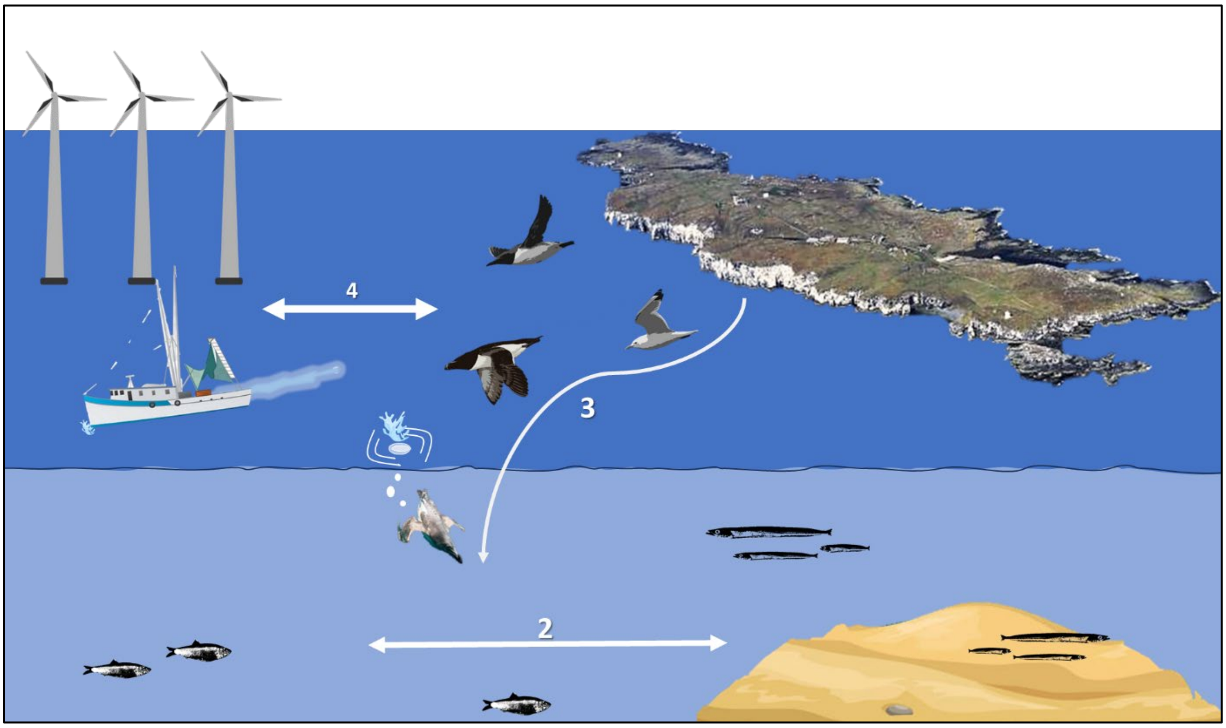


Figure 1. Infographic depicting the processes of seabird foraging ecology and interactions studied in this Thesis. Chapter 2 modelling the prey spatio-temporal distributions corresponds to the process labelled 2, chapter 3 modelling the predator-prey interactions corresponds to the process labelled 3 and chapter 4 mapping the spatial risk assessment corresponds to the process labelled 4. Labels are intended to match chapter numbers for ease of understanding and there is no process 1.

Chapter 2: Seabird prey in space and time: Joining multiple datasets to model the distribution of sandeel (*Ammodytes marinus*) and sprat (*Sprattus sprattus*) in the North Sea

In this chapter I address the need for better spatio-temporal information on the distribution of seabird prey by modelling the distribution of sprat and sandeel on a fine spatial scale (10km grid) across the entire North Sea for the past 2 decades. This involves pooling data from different surveys to create a novel dataset for each species. For sandeel this comprised the beam trawl survey, the international bottom trawl survey and the targeted sandeel dredge survey. For sprat this dataset was composed of the international bottom trawl survey and the herring acoustic survey. Modelling involved cutting-edge Bayesian methods using Integrated Nested Laplace Approximation (INLA) that provide robust estimates and account for spatial and temporal autocorrelation by including smoothed spatial random fields. In addition, fixed effects were included to enable the different survey data to be combined into a single modelling framework. The resulting spatial and temporal distributions and dynamics are examined and compared against other modelling results. These fine-scale datasets fill in a key knowledge gap in our understanding of pelagic ecology and set down the analytical basis for the following two data chapters.

Chapter 3: Identifying critical prey thresholds for successful guillemot chick survival in the face of a shifting prey base

In this Chapter I use the new predictions of sandeel and sprat availability across space and time from Chapter 2 to quantify the predator-prey relationship between seabirds and their prey, and to provide evidence for ecologically sustainable fisheries management. For this analysis I used the exceptional data available for the Isle of May guillemot population. I related seabird chick provisioning rates to estimated prey abundances by parameterising a multi-species functional response model using Markov Chain Monte Carle (MCMC) methods with Stan. The resulting model provides realistic representation of predatory consumption rates by also accounting for alternative prey. The model identified a Type III functional response which is indicative of prey switch and upper predation levels limited by handling time. By combining the functional response curves with unpublished data from Norway on prey energetics, I quantify chick provisioning rates in relation to prey availability and identify critical prey thresholds, below which chick survival is impacted. Finally, I compare this identified threshold to the “One Third for the Birds” global analysis of Cury et al. (2011).

Chapter 4: Lower impact risk but higher spatial overlap of seabirds and anthropogenic stressors in a changing North Sea

The final chapter had the aim of accessing key seabird foraging area overlap with anthropogenic stressors and quantifying a risk impact index. I do this by combining the prey fish predictions from Chapter 1 with published predictions of at sea seabird distributions to create a foraging index score across the Western North Sea for guillemots, kittiwakes, and razorbills breeding in the UK. A second stressor index was created by joining the identified stressors of climate change, sandeel fishing, shipping and offshore windfarms, weighted by species-specific sensitivity scores. An impact risk index was created as the product of the foraging and stressor index. I identified the hotspots of this impact risk index and the overlap with the existing MPA network was quantified. Lastly three future scenarios, two with planned windfarms and sandeel fishing and one with planned windfarms and no sandeel fishing added to the stressor index, were conducted to inform future marine spatial planning policy.

Chapter 5: General Discussion

In this section I summarise my key findings, place them in the context of the wider literature and consider possible future directions of studies.

2. Seabird prey in space and time: Joining multiple datasets to model the distribution of sandeel (*Ammodytes marinus*) and sprat (*Sprattus sprattus*) in the North Sea

2.1 Abstract

Many seabird populations along the East coast of the UK have been declining over the past 3 decades. Concerns exist that declines in their main prey in the breeding season, sandeel (*Ammodytes marinus*), have contributed to declines in seabirds. Some seabird populations have partially switched to sprat (*Sprattus sprattus*) but this is not universally the case. Fine scale estimates of prey fish distributions throughout the foraging range of seabirds are required to study these shifting predator-prey interactions, but these prey distributions are currently either lacking or not tailored to the predators needs for specific sizes of prey during specific time periods. For sandeel, this has largely been due to difficulty sampling this fish and data are limited at appropriate spatial and temporal scales. We test the utility of large-scale ICES-coordinated bottom trawl surveys to estimate the spatial distribution of sandeel, combining them with the winter dredge surveys designed specifically for sandeel. For sprat, we combine bottom trawl surveys with the Herring acoustic Survey. We employ Bayesian spatio-temporal models using R-INLA to model the biomass of small sandeel (<16cm) and sprat at fine spatial resolution across the entire North Sea for the years 2000-2020, accounting for spatial and temporal autocorrelation. We justify the use of bottom trawl surveys for estimating sandeel biomass by comparing our models with other modelling work and with outputs from ICES stock assessments. Sandeel displayed variable temporal trends across the region reflecting their regional sub-population structure. Sandeel area 3 in the Norwegian EEZ was the only region predicted to have a clear upward trend in population size, while Sandeel areas 1 and 2 declined. Sandeel area 4 displayed variable biomass. Sprat were predicted to have an increasing population size with a small northward expansion. This study provides the first North Sea wide estimates of fine-scale distribution of the biomass of key seabird prey, sandeel and sprat, across two decades while identifying the important drivers of these populations.

2.2 Introduction

Globally, seabirds are a particularly endangered group of birds, and among the most threatened groups of vertebrates on the planet (Phillips et al., 2023). Seabirds consistently face a multitude of pressures, namely invasive species, bycatch, climate change and overfishing (Dias et al., 2019). Many seabird species feed on filter feeding small pelagic fish, also called forage fish, which generally form large schools (Alder et al., 2008). Overfishing of these forage fish puts commercial fishing in direction competition with wild predator populations, such as seabirds for dwindling food resources, and despite global declines in seabird populations, this resource competition remains a world-wide issue (Grémillet et al., 2018). Forage fish, due to their short life cycle and low trophic level are known for highly variable abundance (Alder et al., 2008; Cury et al., 2000; Engelhard et al., 2014a). Detailed understanding of such “boom and bust” dynamics in forage fish populations is therefore required for a comprehensive study to link seabird predators to prey fish declines.

At a regional scale, many seabird populations have been declining in the North Sea in recent decades leading to conservation concern (Burnell et al., 2023). Similar to the global picture, there are multiple potential reasons for these more localised declines, including climate change (Burton et al., 2023), as well as prey availability and the impact of commercial fisheries, which have been a major concern in the region for over three decades (Mitchell et al., 2018; Searle et al., 2023). These impacts may be especially important during seabird breeding seasons, when energy demands are highest and when seabirds are tied to and highly dependent on localised environmental and foraging conditions around their colonies (Rindorf et al., 2000). Localised prey shortages have been major factors in the recent breeding failures of seabird populations across the North-East Atlantic, with adult birds having to travel further and expend more energy on foraging trips (Fayet et al., 2021). Fully understanding the extent to which seabird population changes in the North Sea are driven by prey availability requires accurate information on the distribution of both the seabirds and their key prey species over large geographic regions at a fine spatial and temporal resolution.

In the Western North Sea, the spatial distributions of seabirds, including where they forage during the breeding season, are relatively well known (Waggitt et al., 2020; Wakefield et al., 2017), but similarly detailed knowledge of their small pelagic fish prey is lacking (Searle et al., 2022; Wright et al., 2019). Previous studies attempting to link seabird population status and prey availability have thus relied on either environmental proxies (e.g. primary productivity) or coarse-scale regional estimates of abundance from stock assessments

(Cook et al., 2014; Lynam et al., 2017; Searle et al., 2022), limiting the scope for possible scientific studies.

Seabird diets during the breeding season along the North Sea coast of the UK are dependent on two dominant forage fish species: lesser sandeel (*Ammodytes marinus*), hereafter sandeel, and European sprat (*Sprattus sprattus*) (Anderson et al., 2014; Wanless et al., 2018). Both species have been impacted by overfishing in this region (Dickey-Collas et al., 2010; Sherman et al., 1981): following the collapse of sprat populations in the 1980s, sandeel became the target of the largest single-species commercial fishery in the region (Frederiksen et al., 2004), with annual catches peaking in excess of 1.2 million tonnes in 1997 (Alder et al., 2008). Sandeels are also impacted by a range of other factors including climate change (Carroll et al., 2017; Lynam et al., 2013) and increases in piscivorous fish populations (Engelhard et al., 2014a), and since the early 2000s, sandeel populations have significantly declined and failed to recover to historic levels (ICES, 2023b). As a result, the dominance of sandeel in the diet of many seabirds has decreased since the 1980s (Wanless et al., 2018). While sandeel have been replaced by sprat for seabirds in more southern colonies, with juvenile gadids constituting an increasing, but still minor proportion, of the diets of seabirds in more northern colonies (Anderson et al., 2014). Nonetheless, sandeel remain vital prey for many seabird species as well as many other predators in the region (Ransijn et al., 2021; Searle et al., 2023; Wilson & Hammond, 2019).

In recognition of the importance of sandeel to dependent predators, an area off the coast of Scotland was closed to sandeel fishing in 2000 as a precautionary measure (Rindorf et al., 2000). Subsequent surveying of this area has produced mixed conclusions about its efficacy (Greenstreet et al., 2006), with only kittiwakes (*Risa tridactyla*) showing recoveries in productivity (Searle et al., 2023b). To further investigate the relationship between seabirds and their prey, finer-scale information is required to study local dynamics and interactions with predators, which in turn can aid in developing an ecosystem-based approach to the management of this species (Hill et al., 2020). However, current understanding of sandeel spatio-temporal dynamics is typically limited to stock assessments at the scale of the seven regional sandeel management areas (Figure 2A) (Rindorf et al., 2016), as well as from commercial catch data (Jensen et al., 2011). This stems from the difficulty in studying sandeel (Greenstreet et al., 2010; Johnsen & Harbitz, 2013): pelagic fish are generally monitored using acoustic surveys; however, because of their lack of swim bladders sandeel are difficult to detect (Johnsen et al., 2009). Special acoustic algorithms detect sandeel, and this is used by Norway to manage sandeel in area 3r (Figure 2A), but this has not been implemented across large spatial scales (van der Kooij et al., 2008). Dredge surveys targeting sandeel have been conducted in a few localised areas across the North Sea since

1999 for use in stock assessments (ICES, 2022a), and localised acoustic and grab surveys have been conducted on the East coast of Scotland (Greenstreet et al., 2010), but there remain large gaps in our knowledge of sandeel distributions outside of core fishing grounds.

Sprat in the North Sea are at the northernmost part of their range in the Northeast Atlantic (Peck et al., 2015). North Sea sprat biomass collapsed in the 1980s due to intense overfishing, and it is still well below historic levels, although a subsequent decrease in fishing effort has enabled it to partially recover (ICES, 2020b). In the southern and western North Sea it has been increasing in the diet of seabird and cetacean predators (Ransijn et al., 2021; Wanless et al., 2018); however, due to a lack of fine scale data it is unclear whether this is driven by an increase in the local sprat population size. Sprat form one continuous population across the North Sea, except for the isolated Norwegian fjords (Lindegren et al., 2022; McKeown et al., 2020), which is managed as one stock (ICES, 2020b), meaning annual sprat population estimates are on an even coarser scale than sandeel. Sprat are relatively well sampled in the North Sea by both bottom trawl and acoustic trawl surveys. Sprat data from the bottom trawl have been modelled spatially at a fine scale by Ransijn et al. (2021) in their study porpoise prey fields, but only in the southern North Sea (i.e. up to 56°N and excluding the key foraging areas of seabirds from key colonies such as the Isle of May and Shetland). The resulting trawl data for the summer period have not been explicitly analysed with the acoustic information in a spatiotemporal context, although time-series from both feed into the regional stock assessment. Thus for sprat, and as is the case for sandeel, finer scale information on their distribution in space and time relevant for seabird foraging is lacking.

Attempts to overcome the lack of detailed spatial data for these key forage fish species have included combining high quality but small scale survey data with environmental covariates to model sandeel distribution at the scale of the UK EEZ (Langton et al., 2021). however, this relies on surveys from only a small fraction of the sandeel range, this can result in very high uncertainty when predicting fish density for areas and environmental conditions not observed in sample data (Langton et al., 2021). Spatial models lacking a temporal dimension also neglect a key component of sandeel population ecology, their high annual variability in abundance (ICES, 2023b).

Recent work modelling sprat distributions in the North Sea has been either at a coarse spatial scale, focused on winter distributions, or developed to provide an index of habitat suitability (Lenoir et al., 2011; Lindegren et al., 2022; Schickele et al., 2021). Indeed, Lindgren (2022) identified the lack of a fine scale spatio-temporal model of sprat biomass, including environmental covariates, as a major gap in knowledge of this species (Lindegren et al., 2022). For both species models combining broad spatial extent across the North Sea with the temporal resolution to track interannual changes are lacking.

To address these gaps in understanding of the distribution of key forage fish species in the North Sea, in this study we aim to make best use of a range of data sources. We adopt a modern Bayesian spatial statistical approach that allows us to join targeted surveys with limited spatial or temporal coverage (e.g. dredge surveys for sandeel, acoustic surveys for sprat) with the extensive fisheries-independent demersal trawl surveys available for the North Sea, the International Bottom Trawl Survey (IBTS) and Beam Trawl Survey (BTS). These trawl surveys reliably catch sprat but have usually been considered an unreliable source of data on sandeel, which have low and variable catchability due to their small size, long and thin shape and daytime mid-water distribution (Johnsen et al., 2017; Winslade, 1974). However, the sandeel that they do catch provide valuable information about sandeel distributions with the advantage of excellent spatial and temporal coverage, especially when combined with catchability estimates (Walker et al., 2017). We therefore consider these data sources to be complementary to those previously relied upon to model sprat and sandeel distributions, and we aim to formally test their utility in modelling sandeel and sprat distributions. We use Integrated Nested Laplace Approximation (INLA) that can effectively account for spatial and temporal autocorrelation and robustly estimate uncertainty (Rue et al., 2009b), as well as accounting for differences between characteristics (including catchability) of the different surveys, allowing them to be joined into a single modelling framework. Our models include a wide array of static and dynamic environmental variables that can capture and estimate the highly variable nature of these small pelagic fish populations required to model the fine scale distribution of sandeel and sprat biomass in the North Sea over the past two decades at the scales necessary to study predator-prey interactions (e.g. the foraging distance of a breeding seabird) (Wright et al., 2019). Given the large concern and uncertainty in understanding the possible impacts industrial fishing has had on the sandeel populations, we also aim to compare fishing pressure to the sandeel predictions to explore this relationship. In doing so, we also aim to identify the underlying environmental or anthropogenic conditions driving these patterns, which can inform future work on how they may respond under future climate change, and what the implications might be for the seabird species that depend on them.

2.3 Materials and Methods

2.3.1 Fish Survey Data

The International Bottom Trawl Survey (IBTS) and the Beam Trawl Survey (BTS) are the main fisheries-independent bottom trawl surveys that cover the entire Greater North Sea (Figure 2C and 2B). The surveys are fully described in ICES (2022), but in brief the IBTS uses an otter trawl and the BTS employs a beam trawl, and both surveys are designed to target demersal fish species. They do catch pelagic fish in the water column near the seabed and during deployment and recovery, but the catchability (the proportion of fish present that are caught) of sandeel in particular is known to be variable and potentially quite low, because the demersal trawls only sample a portion of the water column, the fish are small and thin and liable to escape the net, and the fraction of fish that are buried in the sediment is unknown (Fraser et al., 2007). To account for the differences in gear efficiency between surveys and catchability issues in the IBTS and BTS data, we corrected biomass values using the gear efficiency correction estimates from Walker et al. (2017). Further justification for our use of these trawl surveys for sandeel is provided in Chapter 2 Supplementary Material. The surveys have been running using a consistent methodology at standardised times of the year since 1990, but here we use data only from the years 2000-2020 as there were fewer than 5 sandeel catches per year recorded between 1990 and 1999. It is unclear whether these reflect genuinely low catches or a change in how sandeel were recorded, but as these years contribute little relevant data, we decided to exclude them. As we were interested in the prey available to most seabirds during the breeding season, an upper fish length limit of 16cm was selected based on a review of available diet literature of small to medium sized bird seabird chick provisioning (Harris & Hislop, 1978; Harris & Wanless, 1986; Thaxter et al., 2013; Wanless et al., 2004, 2005, 2018).

To achieve the closest temporal match with the seabird breeding season, we used data from the Q3 surveys, which covers July until September. Because sandeels are scarce in the Q3 surveys, we combined these with the specific sandeel dredge survey (Figure 2D) which occurs during the winter to target sandeel when they should be buried in the sediment and the winter (Q1) IBTS (Figure 2E). We grouped these with data from the previous summer, because sandeel post-settlement have low mobility, do not perform migrations between grounds (Jensen et al., 2011), and spend the autumn and winter buried in the sediment, thus their winter distribution is likely representative of their distribution at the end of summer. The dredge survey is carried out using a modified scallop dredge. Dredge survey data was only available starting from 2008 for sandeel area 4 and from 2012 for the areas 1r, 2r and 3r. For a full description of the sandeel dredge survey, see Johnsen & Harbitz (2013). To improve the data coverage for sprat, we used data from the Herring Acoustic Survey (HERAS) which covers the entire North Sea from 2009-2020 (Figure 2F), with surveys conducted during the end of June and most of July. Full details of HERAS are provided by ICES (2022), and specific details of the data processing protocols we employed to deal with issues including species partitioning and different protocols employed by different participating countries are provided in Appendix S1. To our knowledge, these datasets have never been joined to conduct a single spatiotemporal analysis of either sandeel or sprat.

All trawl and dredge survey data were obtained from the ICES DATRAS data portal (ICES, 2023a) and the HERAS acoustic data was obtained from the ICES Acoustic Trawl Survey portal (https://www.ices.dk/data/data-portals/Pages/acoustic.aspx). A summary of the data coverage of the five individual surveys described above is provided in Table 1. We corrected biomass by raising it to the equivalent value at 100% gear efficiency, based on catchability estimates for the different sources. HERAS acoustic data was assumed to have close to full efficiency (ignoring the acoustic dead zones at the top and bottom of the water column) and no correction was applied. Dredge survey catchability for sandeel is estimated at 5-8 % with no variance by length (Johnsen & Harbitz, 2013; Langton et al., 2021; Mackinson et al., 2005a). We assumed 8% efficiency in our analysis and so raised biomass from dredge surveys by a factor of 12.5. For IBTS and BTS data the species-specific raising factor varied by 1cm length class where efficiency increased with length, based on gear efficiency corrections from Walker et al. (2017). To join survey data into a single model we included fixed effects for survey type to account for differences between surveys. The biomass efficiency corrections and fixed effect for survey enabled us to minimise differences between surveys.

Table 1. *Summary of survey data sources. For each of the five survey datasets, we provide the range of years that we consider, the season and month in which it is conducted, the number of trawl or detection points in the dataset and whether the dataset was included in the sandeel or sprat model. Temporal shift indicates if a winter sandeel survey was shifted to August.*

Dataset	start year	end year	years	season	months	temporal shift	data points	sandeel	sprat
BTS	2000	2020	21	Summer	July-Sept	×	4,961	✓	×
Q3 IBTS	2000	2020	21	Summer	July-Sept	×	5,334	✓	✓
Q1 IBTS	2000	2019	20	Winter	Jan-March	✓	6,943	✓	×
Dredge	2008	2020	13	Winter	Nov-Dec	✓	3,979	✓	×
HERAS	2008	2020	13	Summer	June-July	×	89, 058	×	✓

2.3.2 Environmental Data

We combined the consolidated fish biomass data with a range of relevant environmental variables to model sandeel and sprat distribution. Sandeel have low dispersal and a very close relationship with the sea floor (Holland et al., 2005), and so physical seabed habitat characteristics are an important factor in their distribution. To characterise these, we use the seabed sedimentary environment data product of Wilson et al. (2018), which maps sediment properties throughout the north-west European shelf at 1/8° (approximately 13km) resolution using a combination of survey data and statistical modelling. Specifically, we used percentage silt content and percentage sand content from this dataset. Gaps in the Skagerrak region were filled using predicted values from Mitchell et al. (2019). Depth data was recorded for most Datras trawls, missing data was filled in from EMODNET bathymetric data layer (https://emodnet.ec.europa.eu/en/bathymetry). Bathymetric slope (degrees) was obtained from the MARSPEC dataset (Sbrocco & Barber, 2013) using the R package *smdpredictors* (Bosch & Fernandez, 2022).

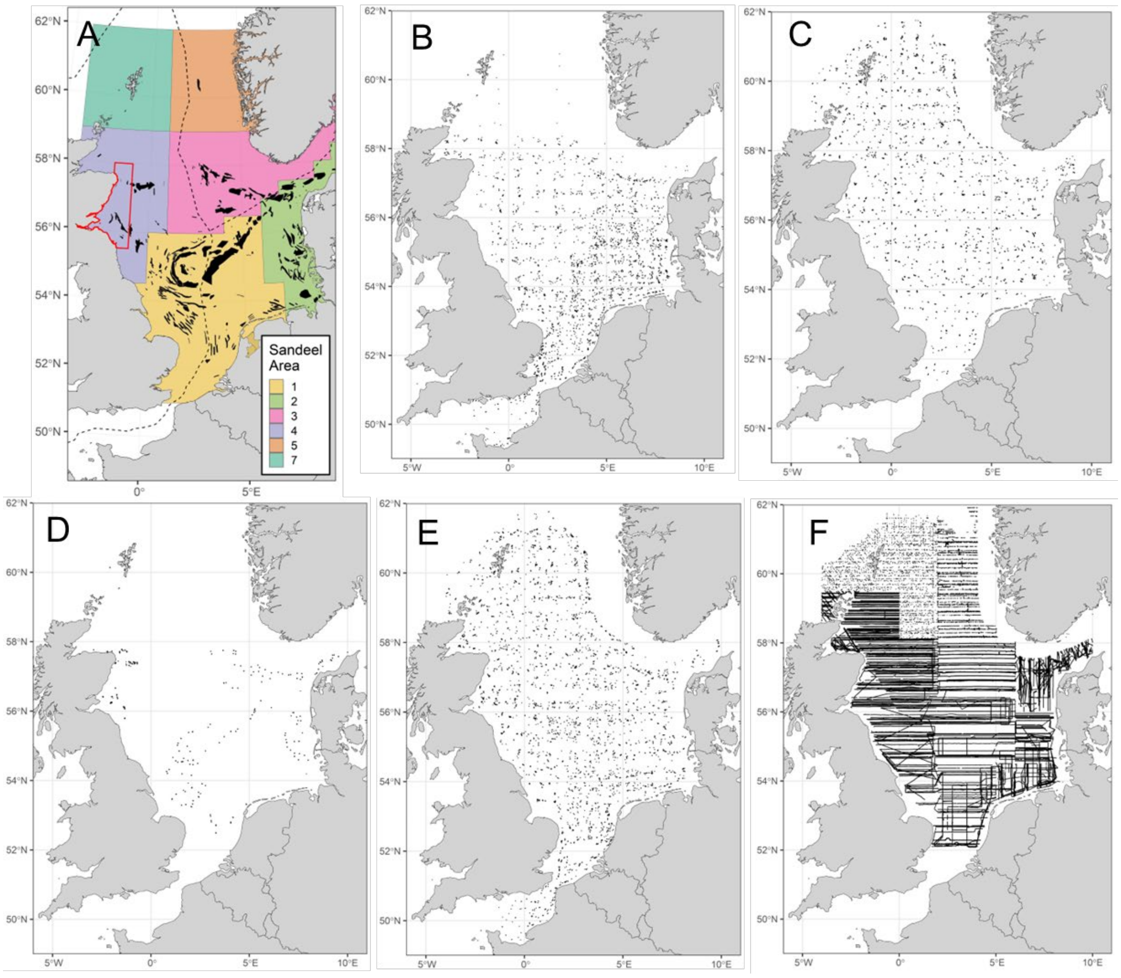


Figure 2. A) Map of sandeel management areas by colour; the solid black shapes denote the core sandeel fishing grounds estimated from Jensen (2011), the red line shows the area closed to sandeel fishing and the dashed lines show the EEZ of the UK, Norway and the EU. Map of survey locations in the North Sea for B) BTS, C) Q3 IBTS, D) Sandeel dredge survey, E) Q1 IBTS data and F) HERAS. The HERAS survey map shows the dataset after thinning the northern 0 points.

Dynamic oceanographic variables were available as mean monthly values from Copernicus (https://www.copernicus.eu/en): mixed layer depth and sea bottom water velocity data were retrieved from the Atlantic-European North-West Shelf-Ocean Physics Reanalysis, while sea bottom dissolved oxygen, sea surface net primary production and phytoplankton concentration were downloaded from the Atlantic-European North-West Shelf-Ocean Biogeochemistry Reanalysis. Sea bottom water velocity is available as separate northward and eastward vectors, where an overall velocity value is calculated as the square root of the sum of squares of the two vector components. Copernicus data were available for the years 2000-2020 on a 7km scale. Correlation between environmental variables was checked using a pairwise global Pearson's correlation test. Where any variables had a high correlation ($r > 0.7$), only one variable was used, for example depth instead of water bottom temperature. Covariate values were mean standardised by subtracting the mean and dividing by the standard deviation, this reduces numerical issues and puts the effects on the same scale. Additional environmental data processing, including dealing with outliers, is described in Chapter 2 Supplementary Material.

2.3.3 Model Fitting

Models were fit in a Bayesian framework using INLA (Integrated Nested Laplace Approximation) using the R package *R-INLA* (Håvard Rue et al., 2023; Håvard Rue et al., 2009a). An alternative to MCMC (Markov Chain Monte Carlo) simulation techniques, INLA approximates Bayesian inference reducing computational costs (Lindgren & Rue, 2015). A major advantage of INLA is its ability to account for spatio-temporal autocorrelation in a computationally efficient manner. Recent studies have shown that using INLA for modelling fish distributions results in more realistic predictions than conventional models (Lezama-Ochoa et al., 2020; Redding et al., 2017).

Fishery survey data is often highly zero-inflated due to the patchy distribution of the fish species because of specific habitat requirements or shoaling behaviour of pelagic fish. In our data, over 82.5% of trawls did not catch sandeel (increasing to 95.5% if the dredge survey is excluded), and 93.5% of survey points did not catch or detect sprat. Zero-inflation is often dealt with by using a two-step hurdle model. To handle this zero-inflation, we fitted models with a Tweedie distribution error structure (Foster & Bravington, 2013; Lecomte et al., 2013), a compound Poisson-Gamma distribution which can model a non-negative continuous response that has a large point mass at 0. Unlike hurdle models (e.g. Zeileis et al., 2008), this allows us to model the data in one continuous process with a single output, avoiding issues with propagating both sources of error (Thorson, 2018). We modelled fish biomass using Tweedie Generalized Additive Models (GAMs) with a log link, allowing us to model non-linear continuous responses by fitting smooth functions to some predictor variables. For both sandeel and sprat, depth was modelled as a non-linear effect using a 1-dimensional SPDE smoother (similar to the basis-penalty smoothing approach; Wood, 2017), and for sprat, phytoplankton concentration was also modelled as a non-linear smoother (Krainski et al., 2018). Survey source was included as a fixed effect, encoded as dummy variables. In the sprat model we applied an autoregressive model of order 1 (AR1) random effect for the year variable and a dummy fixed effect was included for the month variable. The model is defined as a spatiotemporal process Y(s,t) (the response) over spatial locations s and time points t following a Tweedie distribution.

The response is modelled as a combination of covariates, fixed effects, and spatiotemporal random effects:

$$Y(s,t) = \beta 0 + \beta 1.X(s,t) + \delta_{survey} + U_{spatio\text{-}temporal}(s,t)$$

where β0 is an intercept term, β1 is the vector of regression parameters, X(s,t) is the matrix of covariates, δ_{survey} is a dummy fixed effect accounting for survey source, $U_{spatio\text{-}temporal}(s,t)$ represents the spatial-temporal random effect. Backwards model selection was performed using Deviance Information Criterion (DIC) (Spiegelhalter et al., 2014).

2.3.4 Model Validation

The final models were validated by randomly splitting the data into training and validation datasets and rerunning the models on the training datasets, predicting the biomass values for the validation dataset. 85% of the data was used to train the model and 15% of the data were used to test the model. Normalized Root Mean Square Error (NRMSE) was then calculated by subtracting the predicted biomass values from the true biomass values from the validation data and dividing by the spread of observed biomass (min-max) (Bell & Schlaepfer, 2016). For sandeel we also compared our results to the outputs of two independent models as well as polygons of sandeel fishing grounds from Jensen et al. (2011) to assess our predictions spatially and temporally. Firstly, we correlated our spatial predictions (hereafter INLA) with those from Langton et al. (2021) (hereafter Langton) across the UK EEZ. As the Langton predictions have no temporal component, we took the sum of predicted biomass per pixel across all 21 years from the INLA predictions, while this removes a lot of variation, it identifies the core sandeel grounds and enables comparison of the two datasets. We then log scaled and standardised each output from 0 to 100 to enable comparison as the Langton predictions were abundance in numbers. The Langton predictions were on a much finer resolution, therefore we rescaled this to match our predictions to a spatial scale of 10 km. We then compared both our results and the Langton predictions, by subtracting the Langton predictions from the INLA predictions and overlaying the sandeel fishing ground polygons to identify the areas where the model predictions diverged and how these related to identified core sandeel fishing grounds. Secondly, we correlated our INLA temporal trend predictions by sandeel management area with those estimated from the ICES annual stock assessment models (ICES, 2022a). For sprat we are not aware of any published summer distributions on the appropriate spatial scale to compare against. We correlated our sprat temporal trend predictions with those estimated from the ICES annual stock assessment model, which is on the scale of the North Sea.

2.3.5 Fine-scale predictions of seabird prey distribution in space and time

Annual spatial-temporal predictions were made for the years 2000-2020 using the best model for each species, which included the spatial-temporal random effect. These fine scale predictions were made on a 10-km grid covering the entire North Sea. Predictions were made for July, the earliest summer month for which we had data for both species of fish. As sandeel biomass is habitat-specific but variable through time, summing predictions over years gives a good indication of the total habitat of the North Sea populations. For consistency we performed the same for the sprat predictions. Temporal trends could then be calculated by summing the predictions across regional populations. For sandeels, this was the sub-regional sandeel management areas and for sprat this was the entire North Sea. As the final sandeel model did not include swept area, the predictions are a relative index of biomass. In contrast the sprat predictions do include swept area and approach absolute estimates. It is therefore not appropriate to compare the biomass estimates. but only possible to compare the general patterns and maps between the species.

2.3.6 Accounting for spatial and temporal autocorrelation

Accounting for spatial and temporal dependence is a central concern for a spatiotemporal model, given that almost all ecological data will contain spatial and temporal autocorrelation, and failing to take account of this can lead to less accurate results and unrealistically small estimates of error (Václavík et al., 2012). However, this can also be a highly informative property and when modelled properly can greatly improve a model's predictions, in this case of fish biomass (Dormann, 2007). INLA accounts for spatial correlation by using the stochastic partial differential equation (SPDE) method, by approximating a continually indexed zero-mean Gaussian Markov Random Field (GMRF), where a Matérn covariance function applies the correlation between two given points (Bakka et al., 2018). The SPDE with Matérn correlation is applied across a “mesh” generated using a Delauney triangulation covering the study region (Figure S1). Mesh step length, which is the length of the triangle side, was set at 30km for sandeel and 40km for sprat, balancing computation time and the need to capture the spatial scale of population drivers. The mesh is clipped to the North Sea coastline applying a non-stationary model to avoid estimating the spatial effect across land. The spatial random effect is controlled by two parameters, the range and variance parameters. We applied penalised-complexity priors for these parameters as they are informative flexible priors that reduce overfitting (Simpson et al., 2017).

By linking the mesh nodes across each time step, INLA can estimate the temporal correlation between years. For this we used a first order auto-regressive (AR1) process with a time step for every year fit as a separable spatio-temporal model. The spatial effect essentially captures spatially structured variation that cannot be explained by the selected environmental covariates and is applied to the predictions. One potentially important spatially and temporally structured variable that we do not include in our models is fishing pressure (F). As a preliminary test of whether fishing may explain some of the spatial effect in the sandeel model, we compared the temporal trend in the spatial random effect (i.e. the variability unexplained by the model) of each management area that has a stock assessment (areas 1r, 2r, 3r and 4) with estimates of F.

2.4 Results

2.4.1 Model validation

The sandeel model produced sensible predictions largely in agreement with other models. For the sandeel model, model predictions for the validation dataset compared to observed biomass values from that data had an NRMSE value of 0.02. Our spatial predictions were largely in agreement with those of Langton et al. (2021) (Figure 3), with a correlation coefficient of 0.75 ($p < 0.001$) between the two model outputs. The INLA model generally predicted higher biomass that the Langton model except for the western dogger bank and sand banks due south as well as a small part of the Moray Firth (Figure 3). The areas where the Langton model predicted higher sandeel biomass were generally outside of the core fishing grounds (which are indicative of sandeel biomass) (Figure 3C). Comparing our temporal predictions for sandeel areas 1 to 4 with the ICES stock assessments, areas 3r (Skagerrak, northern and central North Sea) and 2r (Skagerrak, central and southern North

Sea) had the greatest similarity to our predictions, with correlation coefficients of 0.79 ($p < 0.001$) and 0.44 ($p = 0.04$) respectively (Figure 4A). Area 4 (northern and central North Sea) had a correlation of 0.19 ($p=0.4$) while area 1 (central and southern North Sea, Dogger Bank) had a correlation of -0.12 ($p = 0.62$). Looking at the fixed effect coefficients for sandeel the dredge had the highest biomass values (posterior mean = -3.25), followed by Q3 IBTS (posterior mean = -4.21) and then Q1 IBTS (posterior mean = -5.70) and biomass was typically much lower in the BTS (posterior mean = -10.24) (Figure 5).

The sprat model had moderate agreement with other model outputs. For the sprat model, model predictions for the validation dataset compared to real observed biomass values from that data had an NRMSE value of 0.003. Comparing our temporal estimates of biomass to the stock assessment, for sprat in the Skagerrak, Kattegat, and North Sea, there was a correlation coefficient of 0.555 ($p = 0.009$) (Figure 4B). The temporal trends show a similar pattern; however, our model predicts lower biomass from 2000 to 2007, and predicts considerably higher biomass in 2009/2010, with a closer agreement from 2011 to 2020. Looking at the fixed effect coefficients sprat biomass was highest in June (-0.89), followed by July (-1.49), then August (-1.91) and lowest in September. (-2.27) The model estimated lower biomass in the HERAS survey (posterior mean = -3.63) compared to the IBTS (posterior mean = -2.93) (Figure 7).

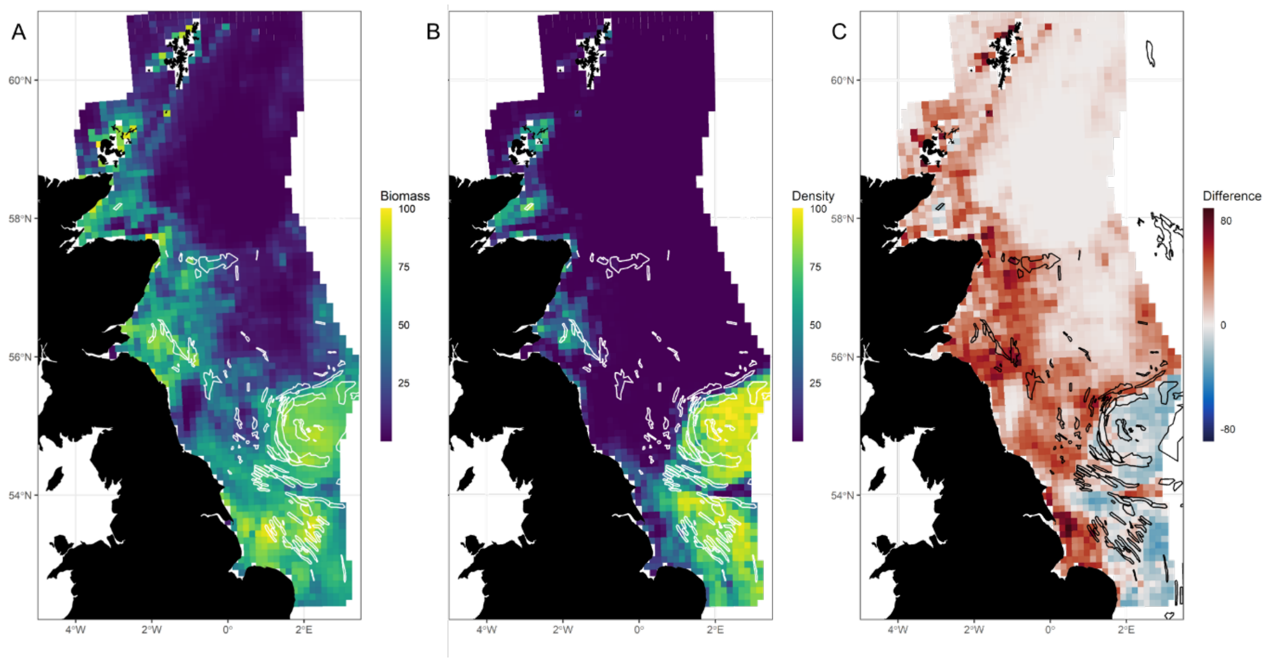


Figure 3. Comparison of predictions of (A) sandeel biomass from the INLA model with (B) density from the Langton model. (C) shows the difference between them as the Langton predictions subtracted from the INLA predictions after both datasets have been converted to a log scale and each standardised between 0 and 100 to make them comparable. Areas in red were predicted to have higher biomass in the INLA model and areas in blue higher abundance in the Langton model. Core fishing grounds from Jensen (2011), which are a proxy for sandeel habitat, are overlayed in white for (A) and (B) and black for (C). Values are on a log scale and standardised to 100 to make the models comparable.

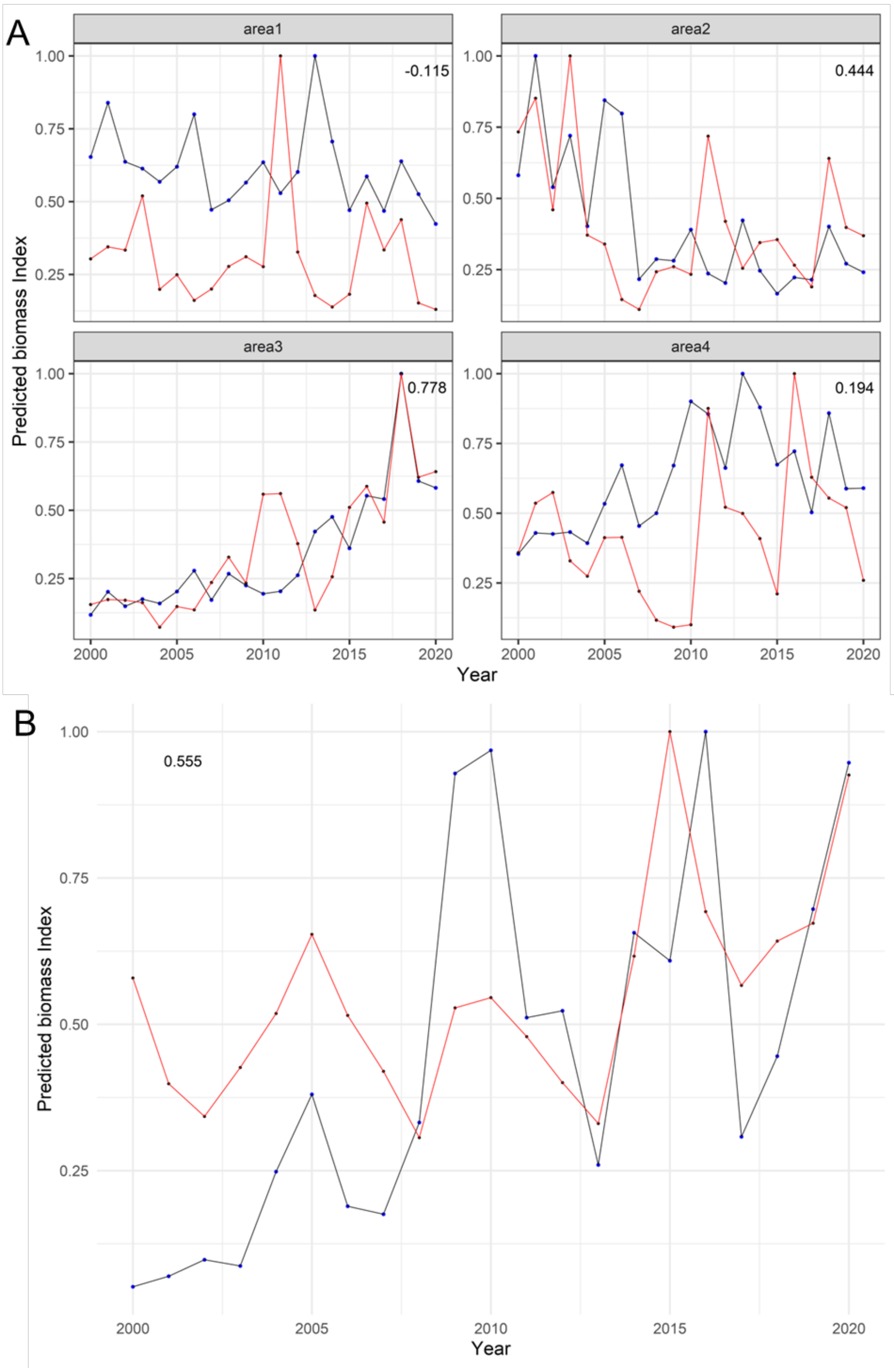


Figure 4. Comparison between time series of biomass predicted our models (black) with biomass estimates from the ICES stock assessments (red) for (A) sandeel areas 1-4 and (B) sprat. Pearson's correlation coefficient shown in the top right corner for sandeel and top left corner for sprat.

2.4.2 Environmental drivers

Sandeel biomass was negatively associated with silt content of the sediment, net primary productivity, mixed layer depth and sand content of the sediment, and positively associated with dissolved oxygen and seafloor slope (Figure 5). Sandeel biomass was predicted to be higher at depths less than 75m (Figure 7A). Sprat biomass was negatively associated with bottom water velocity and positively associated with seafloor slope and mixed layer depth (Figure 6). Highest sprat density was predicted at depths less than 175m (Figure 7B) and at mid-levels of phytoplankton concentrations (8-15 mmol/m^3) (Figure 7C).

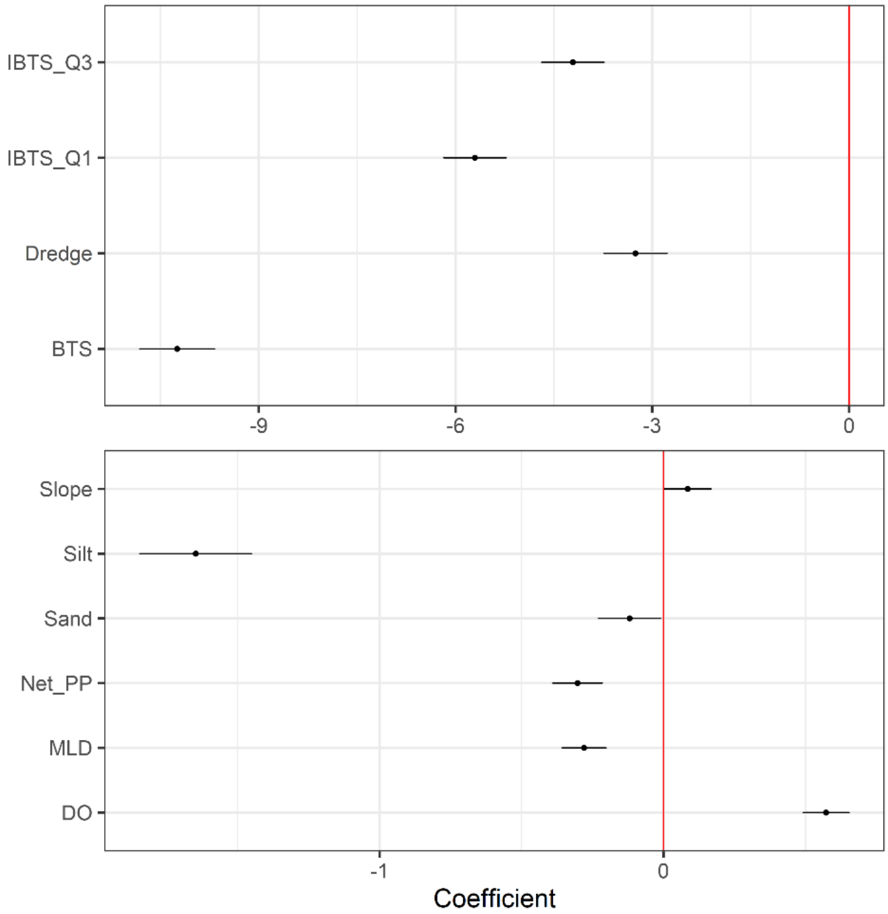


Figure 5. Fixed effect coefficient estimates from the sandeel model. Points represent the mean while the horizontal bars represent the 95% credible interval. The vertical red line denotes 0. IBTS = International Bottom Trawl Survey, BTS = Beam Trawl Survey, Net_PP = Net Primary Productivity, MLD = Mixed Layer Depth, DO = Dissolved Oxygen.

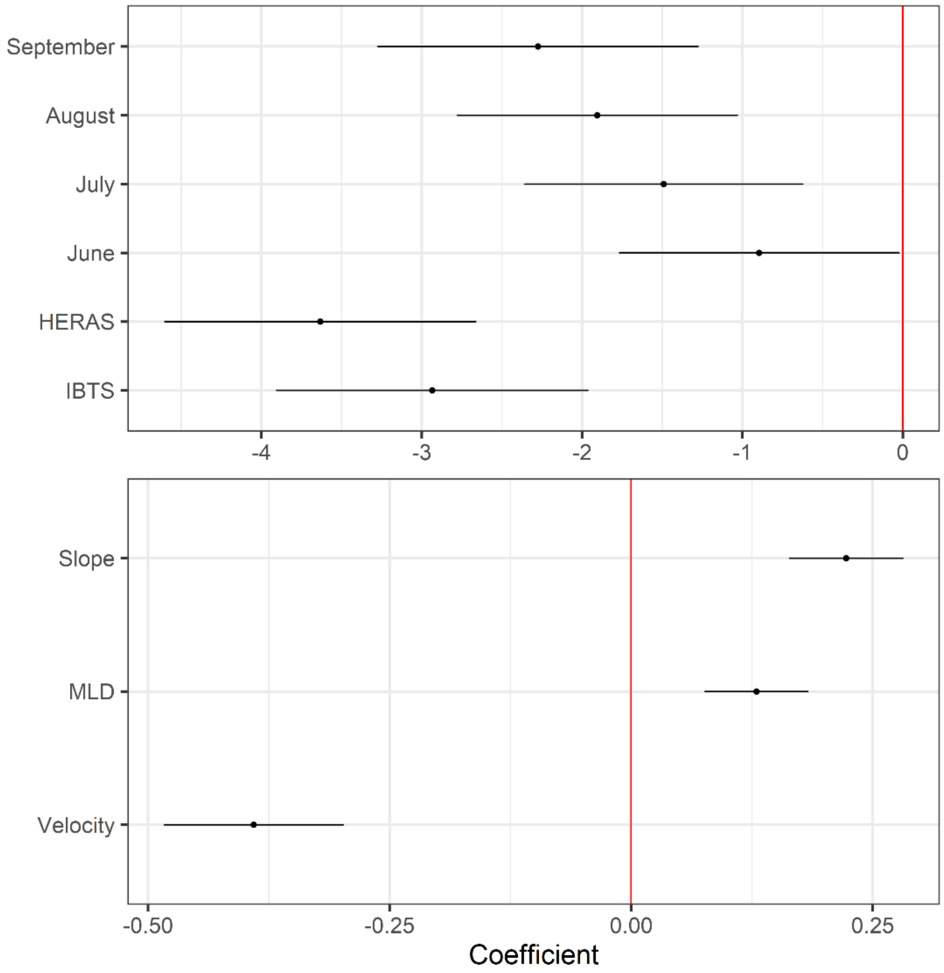


Figure 6. Fixed effect coefficient estimates from the sprat model. Points represent the mean while the horizontal bars represent the 95% credible interval. The vertical red line denotes 0. HERAS = Herring Acoustic Survey, IBTS = International Bottom Trawl Survey, MLD = Mixed Layer Depth.

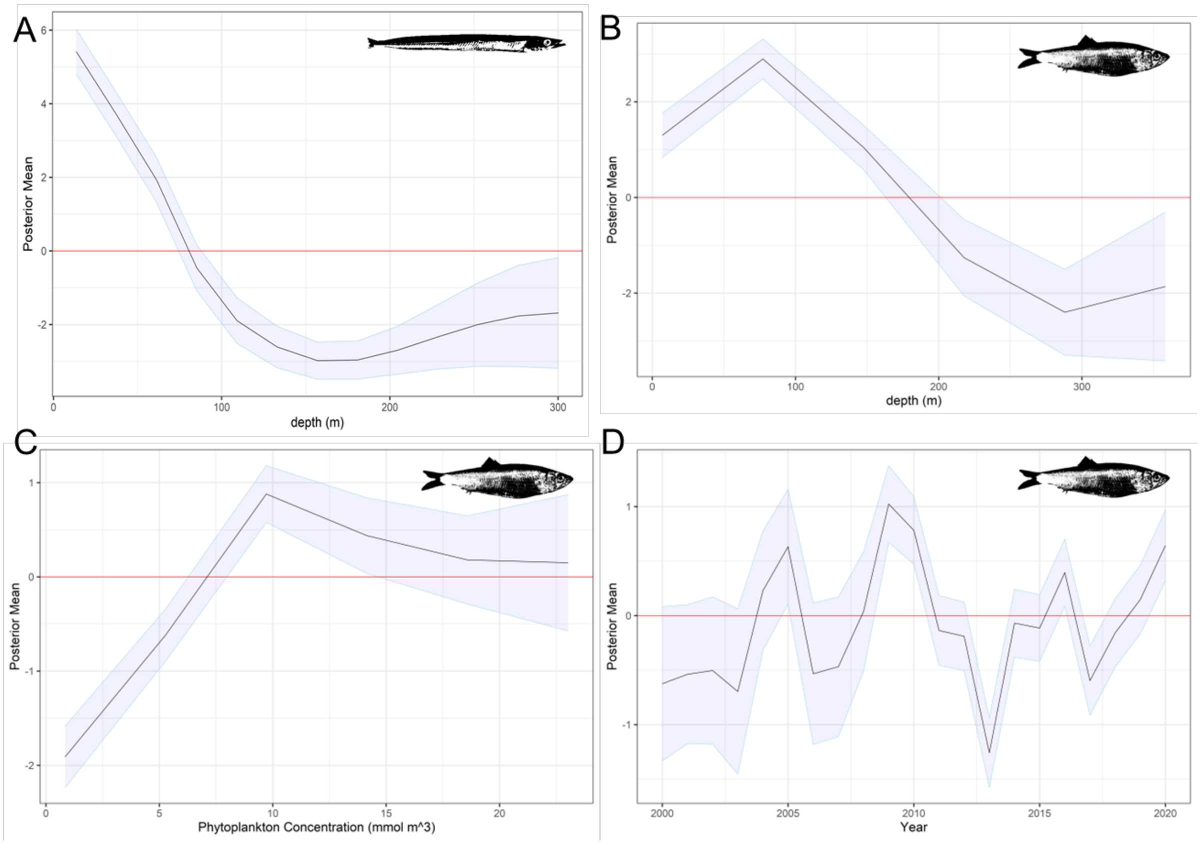


Figure 7. Smoothed non-linear random effects showing the modelled relationship between (A) sandeel biomass and depth (B) sprat biomass and depth and (C) sprat biomass and phytoplankton concentration. (D) The AR1 effect for year for sprat. The red lines denote 0 with points above showing a positive and points below a negative effect.

2.4.3 Fine-scale spatial-temporal predictions

Our model predicts that sandeel biomass is distributed throughout the main sandbank habitats of the North Sea region (Figure 8B), broadly in alignment with core sandeel fishing grounds (Jensen et al., 2011). Our model predicted high biomass in all of the large fishing grounds, with only a couple of very small and isolated fishing grounds that were not predicted to contain sandeel biomass, and a decreasing gradient of sandeel biomass outside of the core fishing grounds (Figure 8B).

Temporal trends in sandeel biomass in each sandeel management area are shown in Figure 9A. All sandeel areas displayed interannual variation consistent with small pelagic fish boom and bust population dynamics. We also made predictions for area 5 (northern North Sea, Viking and Bergen banks) and 7 (northern North Sea, Shetland), as well as the channel, which do not have currently have stock assessments performed and thus these predictions represent the only estimate of regional sandeel population size in these areas. Area 5 was predicted to have very low but variable biomass over the time period, while area 7 initially decreased but then recovered at the end of the timeseries.

There are clear trends in the spatial distribution of sprat biomass over the time period covered by our study (Figure 10A). The model predicts that sprat biomass is initially mostly distributed in the south-eastern North Sea, extending further west over time towards the UK coast, with population increases also seen off the East coast of Scotland, concentrated in southern Moray Firth and south around the headland in Aberdeen Bay (Figure 10A). The central southern region sees an expansion northward, with a noticeable absence from the Dogger Bank area. Our results predict that sprat were found as far north as Scotland at the beginning of the assessment period, but they have increased in density over the past two decades. Looking at the overall temporal trend, sprat biomass tended to increase across the North Sea over the 21 year study period with an oscillating cycle of higher and lower biomass roughly every 3-4 years (Figure 7D; Figure 9B).

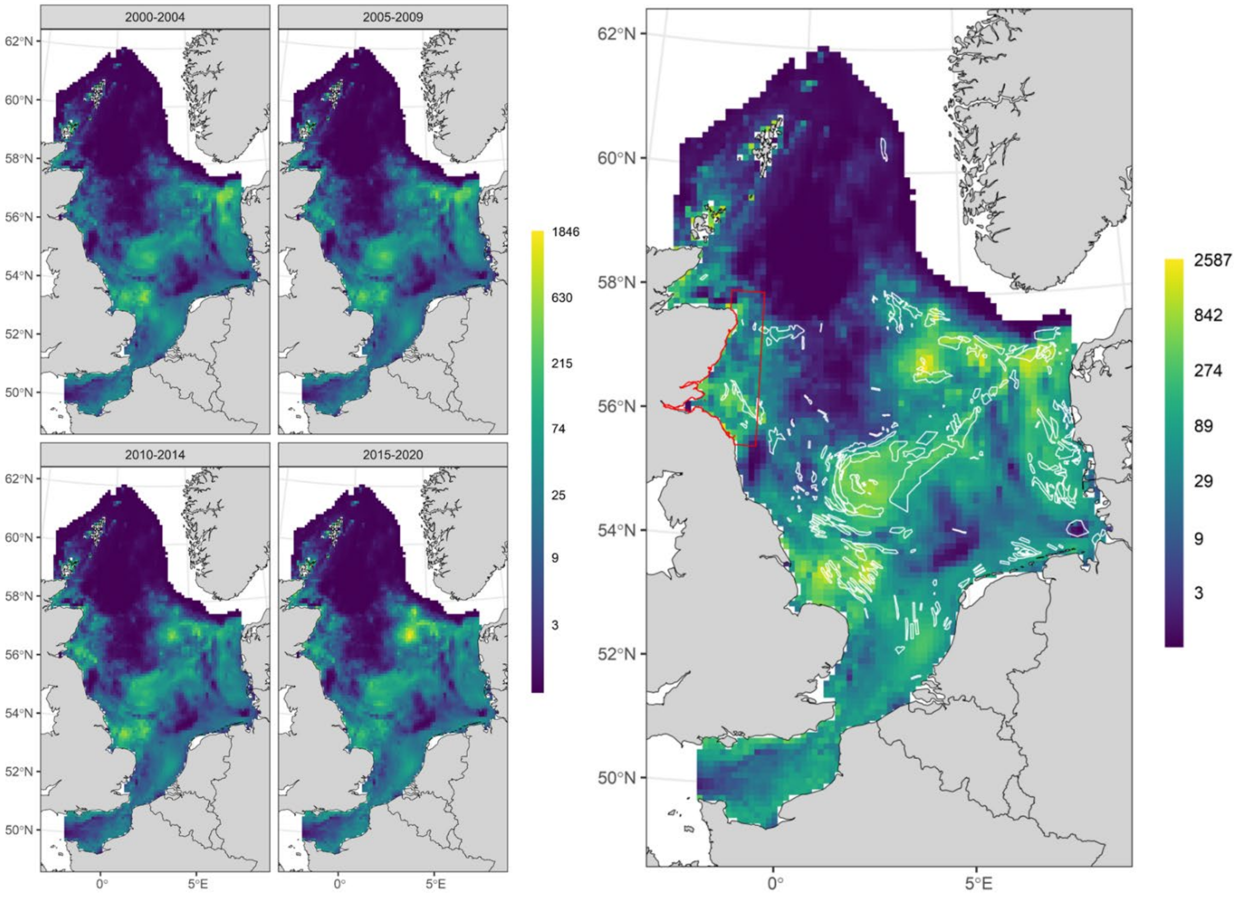


Figure 8. Predicted sandeel biomass (A) summed into four five-year periods over the full timeseries and (B) Summed for the 21-year time period White lines denote major sandeel fishing grounds from Jensen et al., 2011. The red line shows the area closed to sandeel fishing off of the East coast of Scotland. Biomass values are shown on log scale in kg per 10km grid cell.

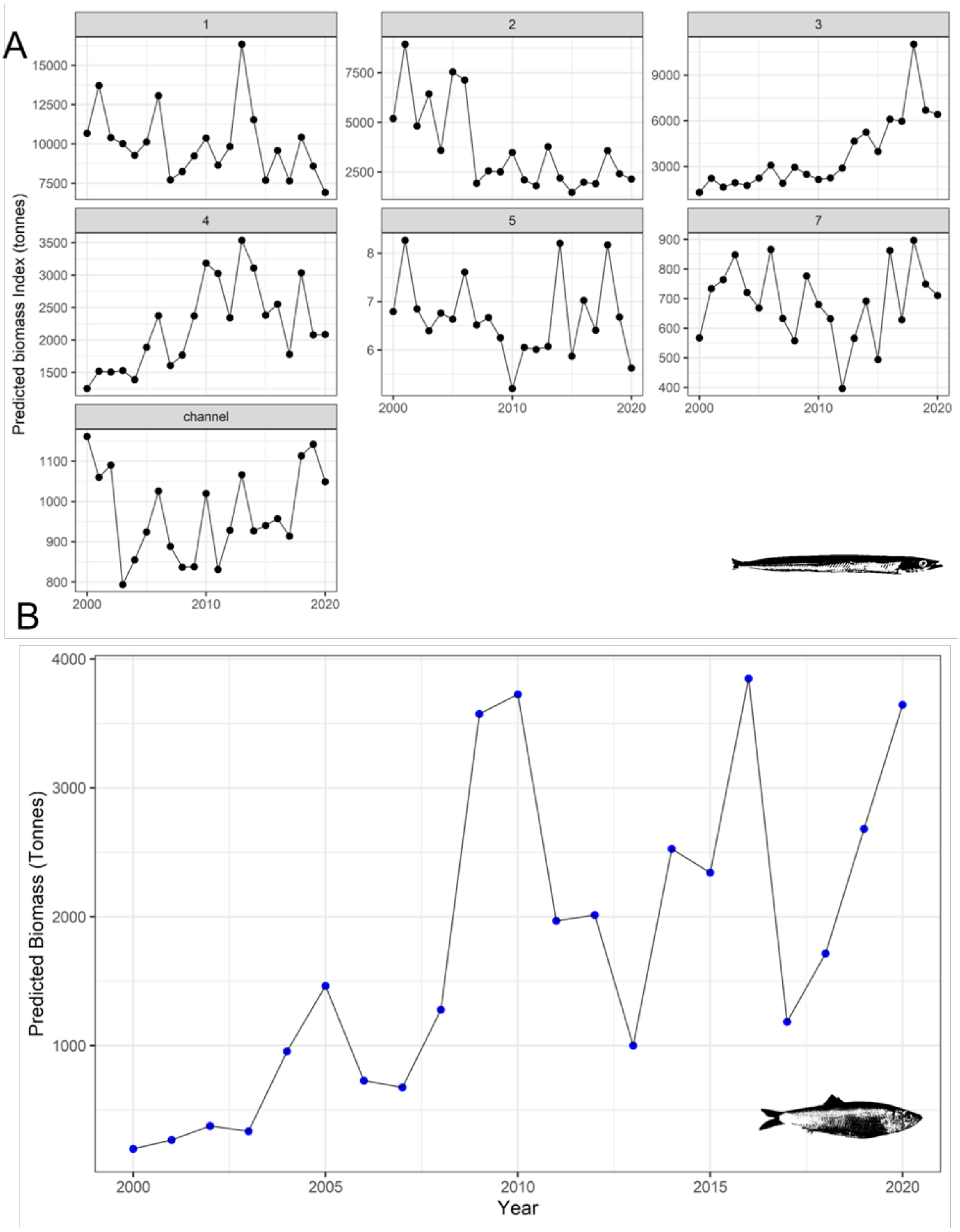


Figure 9. timeseries of biomass for (A) sandeel across the 7 Management Areas with additional category for the English Channel and (B) sprat across the greater North Sea and the Scottish coast north of the firth of forth. Note the sandeel model is relative biomass

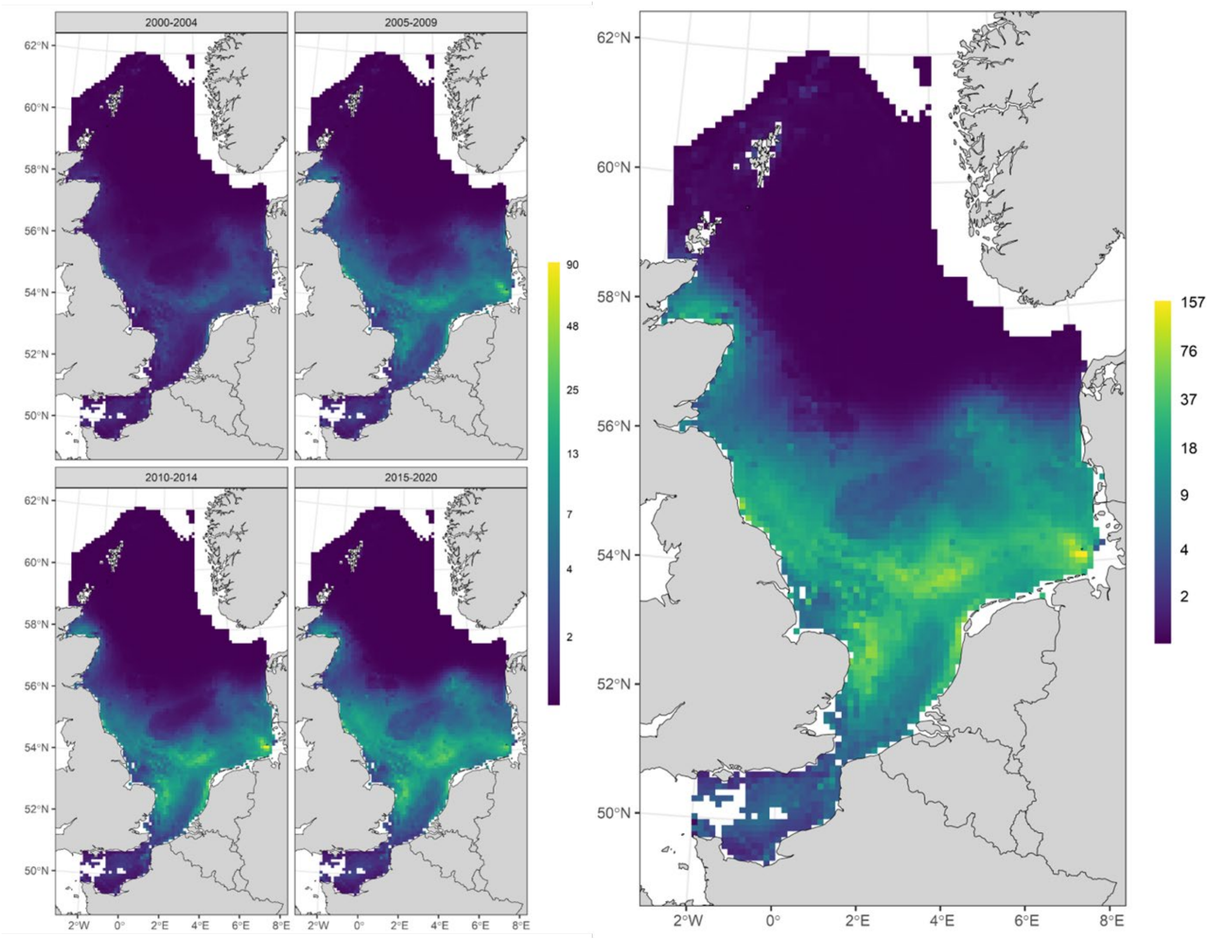


Figure 10. Predicted sprat biomass (A) summed into four five-year periods over the full timeseries and (B) Summed for the 21-year time period. Biomass values are shown on log scale.

2.4.4 Spatial temporal effect

There was residual spatially structured variation in both the sprat and sandeel models which was effectively captured by the spatial random effect. The spatial effect in the sandeel model varied over time (Figure 11A and 11B). The spatial effect predicted higher than average biomass over the southern and western North Sea (sandeel areas 1r and 2r, respectively) at the beginning of the timeseries. This reversed over time and in later years the spatial effect was highest over northern central North Sea (sandeel areas 3r and 4), with the spatial effect changing to negative over sandeel areas 1r and 2r. For sprat the spatial effect had a relatively stable distribution across the study period, however there was a considerable strengthening of the magnitude of the spatial effect throughout the timeseries (Figure 11C and 11D). The sprat spatial effect had a distinct north-south distribution, with positive values in the southern North Sea and negative values in the north. Annual maps of spatial random fields for both species are provided in the supplementary material.

Area 4 was the only region to show a strong negative correlation between the spatial effect and fishing pressure (r = -0.6, p < 0.001) (Figure 12). The spatial effect increases from 2000. There is a distinct change in pattern with a decrease in the spatial effect from 2012. The spatial effect decreases further as fishing pressure increases until a 2018, after which fishing pressure drops and the spatial effect increases slightly. In sandeel areas 1 (r=0.53, p=0.01) and 2 (r=0.44, p=0.05) the spatial effect temporal trend was moderately correlated with F for the respective management areas. The was only a weak positive correlation for area 3 (r=0.096, p=0.67) For sprat there was no correlation between the spatial effect and fishing pressure.

2.5 Discussion

Detailed forage fish distribution data across large spatial and temporal scales in the North Sea are vital to future work understanding predator dynamics, the ecosystem effects of commercial fishing and impacts from climate change. These fish are not fully sampled across their full range by any specific survey, and thus require appropriate modelling that can join surveys together and properly account for sources of uncertainty. Here, we gathered available large scale survey data and employed modern Bayesian modelling techniques using R-INLA to join these surveys together and produce detailed fish biomass estimates across space and time over the past two decades. We were able to produce robust models that were moderately correlated with other analyses, however this varied by region and time (ICES, 2022a; Langton et al., 2021), suggesting that were we able to appropriately join different datasets together. We further discuss instances where our predictions diverged from other models and methods to improve the methodological framework. In addition, by accounting for catchability and joining with the higher accuracy dredge data for the sandeel data, bottom trawl data was able to be included in a model that produced sensible predictions, providing biomass estimates for sandeel and sprat at more widespread spatial and temporal scales than previous work (Jensen et al., 2011; Langton et al., 2021; Lindegren et al., 2022). These outputs fill a vital knowledge gap of the North Sea marine ecosystem and lay the foundation for future ecological work.

Importantly our model makes predictions for areas where no sandeel stock assessments or commercial catch occur, providing novel estimates of the spatial distribution and temporal trends of sandeel around the Shetland and Orkney Islands which are important to seabirds and cetaceans (Waggitt et al., 2020), as well as sandeel area 5, off the West coast of Norway, and the English Channel (Figure 8B).

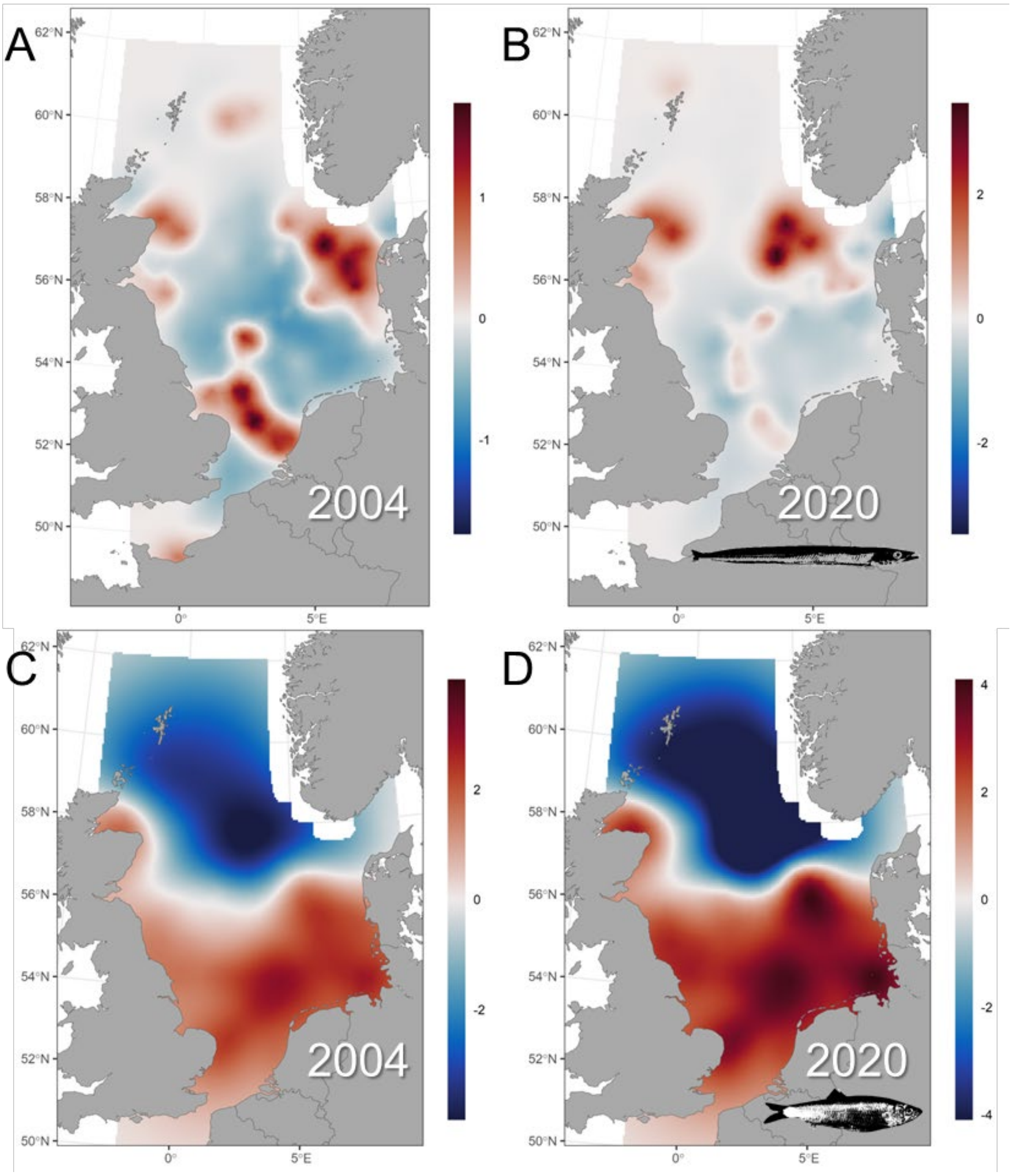


Figure 11. Smoothed spatial random field (dimensionless on the log scale) of the spatial effect for sandeel for (A) 2004 and (B) 2020, and for sprat for (C) 2004 and (D) 2020. The spatial random field approximates the spatial structures residual variation in the model, with red areas containing above average and blue areas below average residual biomass. Non-random spatially structured colours suggest spatial autocorrelation in the data not fully accounted for by the environmental covariates. Notice the colour bars are on different scales.

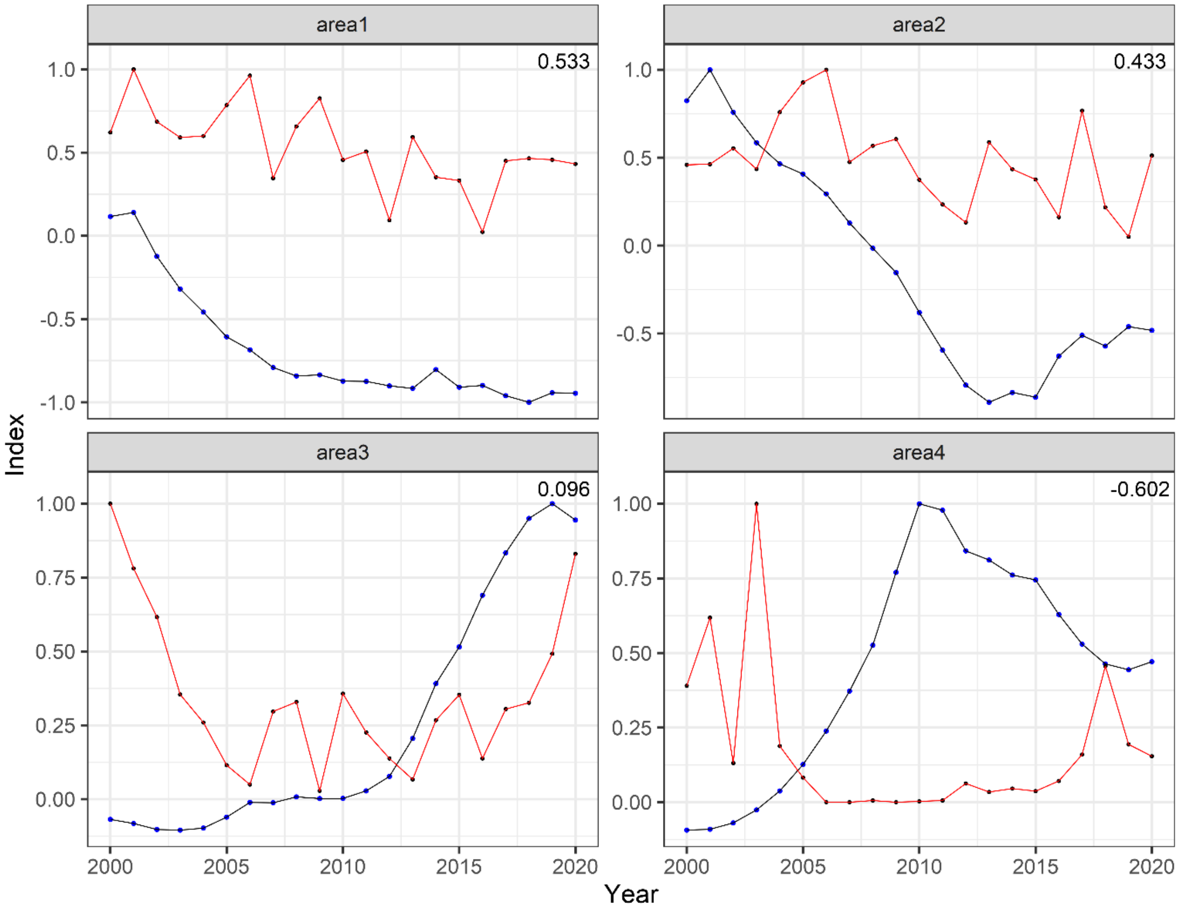


Figure 12. Comparison of the spatial effect temporal trend (black) with fishing pressure from ICES stock assessment (red) for four sandeel areas that have a stock assessment conducted. Pearson's correlation coefficient shown in the top right corner.

Results from our model showed that hotspots of sandeel biomass occurred in areas already identified as major fishing grounds, a proxy for sandeel habitat (Jensen et al., 2011), however there were also areas adjacent to these that were predicted to contain moderate levels of sandeel biomass that are likely important to local predators. The low predicted biomass for sandeel area 5 across the past two decades agrees with monitoring work by Norwegian Institute of Marine Research (IMR) (Falkenhaug et al., 2016). The sandeel fishery in the Shetland region closed in the early 2000s because the low variable catch became uneconomical (ICES, 2022a). This region was also the first to see seabird breeding season food shortages in the North Sea as far back as the 1980s (Monaghan et al., 1989). Having information on the distribution and trend of vital prey in this area is a large benefit and could hopefully improve understanding and management of both prey and predators in the area.

The dredge survey caught the highest amount of sandeel followed by the summer IBTS. The winter IBTS catches were lower, this is likely due to sandeels being buried in the sediment

(Winslade, 1974). Finally, the BTS catches were markedly lower than the other surveys, likely due to its smaller nets with a lower vertical opening. The sprat model predicted lower sprat biomass in the HERAS survey than the Q3 IBTS. This may seem counterintuitive as HERAS has higher values of biomass when sprat does occur; however, it is not unexpected due to the much higher number of absences (i.e. 0 biomass points) due to the very high density of acoustic data, which has a value for every square nautical mile. The results for the sandeel data are relatively straight forward, the dedicated survey caught the most sandeel. However, they also show that the summer IBTS survey caught the next most amount of sandeel and when modelled properly can provide important information on the species. The results for the sprat datasets were less intuitive and this is likely caused by the complexity of joining two fundamentally different survey types (acoustic vs bottom trawl).

Comparing our sandeel predictions to the ICES stock assessment was not straightforward, as the stock assessment includes catch data and considers all sandeel lengths, whereas our model was for sandeel up to and including 16cm, which was chosen to represent the maximum size of prey edible by chicks of the medium sized auks and black legged kittiwake (*Risa tridactyla*) which dominate the seabird community in this region (Thaxter et al., 2013). However, there was strong agreement for certain areas. Area 3 have a very strong correlation while area 2 had good correlation, showing a similar general pattern. Area 4 and 1 had low overall temporal correlation to the stock assessment timeseries, however, there were certain periods with strong similarities, such as the first half of the timeseries for area 4 or 2015 to 2020 in area 1. It is not clear why the strength of this temporal relationship varies between areas.

Area 3 was the only sandeel management area to show a clear upward trend in population size (Figure 9). In 2011, in addition to North Sea wise stock division, Norway implemented an area-based management plan that subdivides management area 3 to provide finer scale management and in-season dynamic advice (Johannessen & Johnsen, 2015). We were not able to test the sub-management area population dynamics but given the limited post-settlement connectivity of sandeel this may suggest finer scale management is beneficial for the species. However, area 3 is relatively small compared to the rest of the North Sea and scaling this up for the whole region may not be possible due to the cost involved. This also raises questions related to the impacts of fishing effort displacement in the case of closures. A large part of area 4 off the coast of Scotland has been closed since 2000, and a portion of the Dogger Bank since 2022, but ICES does not take this into account when estimating fishing quotas recommendations (total allowable catch) and the fishing pressure is then condensed into the open part of the management area (ICES, 2022a).

Our estimate of sprat biomass was moderately correlated to the stock assessment model outputs, which is to be expected as both HERAS and IBTS Q3 survey data are components in both models. However, our model does not contain catch data and does not cover the Kattegat or Skagerrak areas which since 2019 have been included in the greater North Sea sprat assessment and these differences may be a source of divergence between our model trends and that of the stock assessment. The IBTS and the HERAS surveys both collect data on sprat, however, they have very different methodologies and survey differing portions of the water the water column. This is evident as the raw biomass values in the data display different temporal trends across the timeseries. This large variation between surveys has likely led to uncertainty of the true population size. More advanced data integration techniques would be of huge benefit to the study of sprat distributions and dealing with these informative but fundamentally different datasets. Future research should focus on applying these methods (Paradinas et al., 2023).

Our model estimates that sprat biomass has been increasing across their known hotspots with a steady expansion north over the past 20 years. This could be either due to slow recovery from past overfishing in the 1980s, with competition forcing fish to occupy sub optimal habitat on the edge of their northern range or expansion of favourable conditions. We observed the spatial effect north-south boundary pushes slowly north and east. This could potentially be a range expansion northward with climate change. We found no correlation between the spatial effect (residual variation in biomass) and fishing pressure estimated from the stock assessment. This suggests fishing may not be the main driver of sprat stock dynamics in the North Sea over the past two decades. However, this evidence does not enable us to comment on the effects of sprat fishing on intra-annual food availability to dependent predators such as seabirds. Thus, our selection of environmental variables was also not able to capture the driver of this range expansion and further work is needed to investigate this.

Comparing the temporal trend of the spatial effect (residual spatially structure variation) of the sandeel model with fishing pressure found a negative correlation only in area 4. Here the spatial effect increases from 2000 to 2010, however, the direction of change (increase) does not signify an increase in pressure only a change in the effect size of the spatial effect (dimensionless). This pattern aligns with the designation of the sandeel fishing closed area off the coast of Scotland in 2000 and the complete cessation of fishing in the remainder of area 4 in 2005. There is a distinct change in pattern with a decrease in the spatial effect from 2012, which coincides with the resumption of fishing in area 4. Sandeel area 4 has been identified as the most isolated sub population through otolith analysis, biophysical models and genetic analysis (Jiménez-Mena et al., 2020; Wright et al., 2018) . As well as this area 4 has been identified as having the slowest growth rate and lowest productivity of the North Sea regional populations (Boulcott & Wright, 2011; Rindorf et al., 2016). While this comparison is only a simple broad scale correlation, these factors could explain why this was the only region we observed the spatial random effect to be correlated with fishing pressure, as the reproductive isolation and low productivity may increase the vulnerability to localised overfishing, and certainly warrants further study.

Our estimation of sandeel relationships with seabed characteristics strongly agree with previous studies on this topic (Holland et al., 2005). We identified bottom dissolved oxygen as an important driver of sandeel biomass. Studies of closely related *Ammodytes tobianus* have identified that seasonal bottom oxygen deficiencies have been increasing but annually variable, possibly limiting available sandeel habitat (Behrens et al., 2009). This may negatively impact sandeel in the future as shelf seasonal oxygen depletion is projected to increase with increased stratification due to climate change (Holt et al., 2010).

Sprat are known to be able to tolerate a wide range of environmental conditions and it has been difficult to link sprat to particular habitat (Engelhard et al., 2013). The strong spatial random field indicates the distribution is not fully described by the selected variables and other effects may be influencing the distribution of sprat across the North Sea. While we cannot at present describe these unknown drivers of the sprat population, the spatial random field successfully captured the effect across space and time and significantly improved our predictions.

Future modelling work will most certainly improve as finer-scale environmental raster layers become available, especially important for animals such as sandeel that are highly habitat specific. The data pooling methods we employed would likely benefit greatly from applying novel integrated species distribution modelling techniques (Isaac et al., 2020), as there was large uncertainty in the models, especially for sprat due to the different trends in the underlying datasets. Integrated modelling techniques that can join datasets together in a more sophisticated way than we were able to do here, that can account for the observation process as well as the biological process will likely be a huge leap forward for studying these important but understudied fish (Chadwick et al., 2023; Paradinas et al., 2023). Despite this, our work lays down a foundational step forward for understanding the North Sea pelagic ecosystem across ecologically relevant spatial and temporal scales.

Conservation science, particularly in well-studied regions such as the North Sea and for

groups such as seabirds, is less limited by simple data availability now than it was in the recent past. The next challenge is the availability of data integration methods, often for potentially overlapping but different forms of data, to enable us to draw reliable inference from different data sources. Our methods presented here address these exact issues, and the flexible statistical approach can be applied as is or updated and applied to most other animal species. This could be for seabirds themselves, which often have diverse datasets available including GPS tracking and ship-based distance sampling. Our methods also have significant potential in developing countries, which often lack the resources for intensive national surveying programmes and can potentially draw inference by piecing together smaller or disparate datasets that might already exist from other sources.

2.6 Conclusion

Data on forage distributions is a key missing link in studying the ecosystems of the North Sea. Here we have gone some way towards filling this gap by creating fine scale predictions of sandeel and sprat biomass at the North Sea scale across the past two decades. We show that, contrary to common assumptions for sandeel, bottom trawl survey data can inform models that produced sensible results, with the advantage that resulting predictions are at greater spatial and temporal scale than previous work. Our modelled datasets are openly available to inform future work on the North Sea ecosystem, such as the trophic dynamics of seabirds and other predators.

2.7 Chapter 2 Supplementary Material

2.7.1 Justification for use of bottom trawl survey data for sandeel

Bottom trawl surveys such as the IBTS and BTS are generally considered unreliable for sandeel, however they are a hugely important source of fisheries independent data for fish research in the North Sea and the use of these datasets for sandeel would be of great benefit for a fish species that is both difficult to study and undergoing large population change. To the best of our knowledge an analysis using sandeel data from these survey datasets to model their spatiotemporal distribution has never been published. We aim to test if we can extract useful information for this species by minimises the biases. We try to do this in two ways, first by using gear efficiency estimates from Walker et al. (2017) to account for length vary catch efficiency of the fishing gear. We cannot account for uncertainties in the distribution of fish in the water column or sediment for sandeel. However, acoustic work in Norway has shown that sandeel schools form continuous distributions from the seabed up into the water column, suggesting that they are likely to be at least partially sampled by demersal trawls (Johnsen et al., 2017). Post-juvenile sprat tend to be closer to the seabed during the day (Plirú et al., 2012) and this is evident from the much greater catch rates of sprat in the IBTS than for sandeel.

Secondly, we aim to combine these trawl surveys with the sandeel dredge survey, to borrow strength from this more reliable specific sandeel survey while the resulting model has greatly increased temporal and spatial coverage, which the dedicated sandeel survey lacks. However, as sandeel are inactive and buried in the sediment during the winter surveys (Winslade, 1974), and the effect of winter conditions is not our primary interest, we assigned the location and biomass values from the winter surveys to the previous summer, with associated August environmental conditions. We believe this is justified for two reasons. First, as sandeel post-settlement have low mobility and do not perform migrations (Jensen et al., 2011), the time of year is less relevant for estimating the spatial distribution for this sedentary fish. Second, the environmental conditions at the end of summer likely represent the conditions experienced by the sandeel just before they overwinter in the sediment, without subsequently moving from these same locations.

2.7.2 Data Processing

We grouped the winter surveys together with the data from the previous summer to match the sandeel lifecycle; this means the dredge survey was included in the model as the same calendar year as the data was recorded, while the Q1 IBTS was recorded as t-1, so that 2019 data was included in the model as 2018 and there was no 2020 Q1 data (which would have required data from 2021 Q1 which we did not include).

As we were interested in the prey available to most seabirds during the breeding season, an upper sandeel length limit of 16cm was selected for small to medium sized bird species based on a review of available diet literature of seabird chick provisioning (Harris & Hislop, 1978; Harris & Wanless, 1986; Thaxter et al., 2013; Wanless et al., 2004, 2005, 2018). Different seabirds across different time periods target young of the year fish or 1+ group sandeel, with a general transition to young fish around June as the older fish become less available, presumably as they begin to bury in the sediment for winter (Daunt et al., 2008). However, given the variability in size-at-age of sandeel over recent decades (MacDonald et al., 2019), we did not age-stratify our models and included all biomass within the edible size range. We repeated our analyses including all sandeel sizes (up to *c.*25cm) to check what effect the 16cm cut-off had on our results. No size filtering was required for sprat as they very rarely grow larger than 16cm. Sandeel biomass was estimated from fish length using length-weight relationships that account for seasonal body condition (Rindorf et al., 2016). Sprat biomass was estimated using derived seasonal length-weight relationships from Wilhelms (2013). The total biomass (kg) per species was then summed per trawl. As there was no relationship between sandeel biomass and swept area for any of the surveys we did not include swept area in the model. However, for sprat, because the data were joined with the HERAS acoustic survey (see below) which averages biomass estimates over a square nautical mile, IBTS biomass values were raised to biomass per square mile. This was done by dividing the biomass by the swept area in km^2 and scaling this up to the equivalent value per square nautical mile to make the datasets comparable, making the response variable for sprat equivalent to catch-per-unit-effort (CPUE).

Full details of HERAS are provided by ICES (2022), but in common with other acoustic surveys it is caried out using echosounders mounted on the hull, a drop-keel or on a towed body. Because of the mounting position and noise environment at the surface, the top *c.*8-10m of the water column is unobservable. The pingrate of the echosounder is in an average once every second and the rebounded backscatter values, Nautical Area Scattering Coefficient (NASC), are averaged over a square nautical mile. Fish of different species and lengths have different reflectance properties, and by using species and length specific Target Strength formulas NASC can be converted to abundance and biomass. This requires that several pelagic trawls are also conducted each survey for each of the biologically similar areas or ‘strata’ into which the North Sea is divided, in order to derive strata-level estimates of the species composition and length distributions. HERAS implemented updated strata in 2017 (ICES, 2022c) and we use these for all years. HERAS data available on the ICES online database is missing accompanying pelagic trawl data for several older surveys, specifically for Norway (2010-2014 and 2017), Denmark (2010-2015) and Germany (2010-2016) which is necessary to process the acoustic data. To estimate species composition in these cases we used IBTS trawls from July and August. This is imperfect because IBTS targets demersal rather than pelagic fish and there is a several week time-lag between the surveys. To investigate whether we could use IBTS data when we are missing pelagic trawl data, we compared the percentage composition by weight of clupeids per trawl for IBTS and HERAS annually across each strata for years and areas for which we have HERAS pelagic trawls. We found the species composition between these was moderately correlated (Pearson's correlation, $r = 0.59$). Accordingly, we used the IBTS trawl data to supplement the HERAS survey when we lack pelagic trawls.

Acoustic surveys work best for fish with a swim bladder to reflect the echo. Because sandeel lack swim bladders, we use the HERAS survey only for sprat. Scotland, the Netherlands and Norway have pre-processed their data to provide separate NASC values for sprat and herring (*Clupea harengus*), removing all other data. Germany have uploaded data labelled as clupeids, but do not distinguish NASC values between sprat and herring. Denmark do not differentiate NASC values between clupeids, mackerel (*Scomber scombrus*) and gadoids. Because mackerel (like sandeel) lack a swim bladder and are thus poorly detected at the target echosounder frequency of 38hz (the standard used in HERAS), we ignore mackerel in the further acoustic data processing (van der Kooij et al., 2016). Acoustic surveys are mostly done during the daylight when clupeids aggregate in dense schools. During these hours, most gadoids are found in the demersal zone, and so are usually also disregarded during NASC allocation, the exception being whiting which is active in the water column. Non-whiting Gadoids can generally be excluded in acoustic partition even when detected in significant numbers in the trawls due to an acoustic dead zone which extends to approximately 1m above the seabed (Doray et al., 2021), meaning that they will not be reliably detected in the acoustic backscatter (Mackinson et al., 2005b). The exception to this in the HERAS survey is the Danish portion, which is conducted continuously over 24hrs because of different herring behaviour in the area. As such, Danish data recorded during the night was removed to avoid the inclusion of gadoid backscatter. Large parts of the northern North Sea around the Shetland Islands and east to the coast of Norway detected no sprat as this is likely beyond sprat's northern range, and so to avoid biasing the model we thinned the data points and only included a random 10% of these very northern absence records.

2.7.3 Effect of temporal mismatch of surveys

As we joined survey datasets together that has a mismatch in temporal coverage, we did sensitivity analyses to check the effect of this on the model. We examined the effect of the start time of the sandeel dredge survey and HERAS in the sandeel and sprat models, respectively, on the trend of the spatial random effect (Figure S7). Sandeel area 3 was the only component to show a change in spatial random effect following the introduction of extra data into the model, given this limited extent across both models we consider the effect negligible and continued without accounting for this.

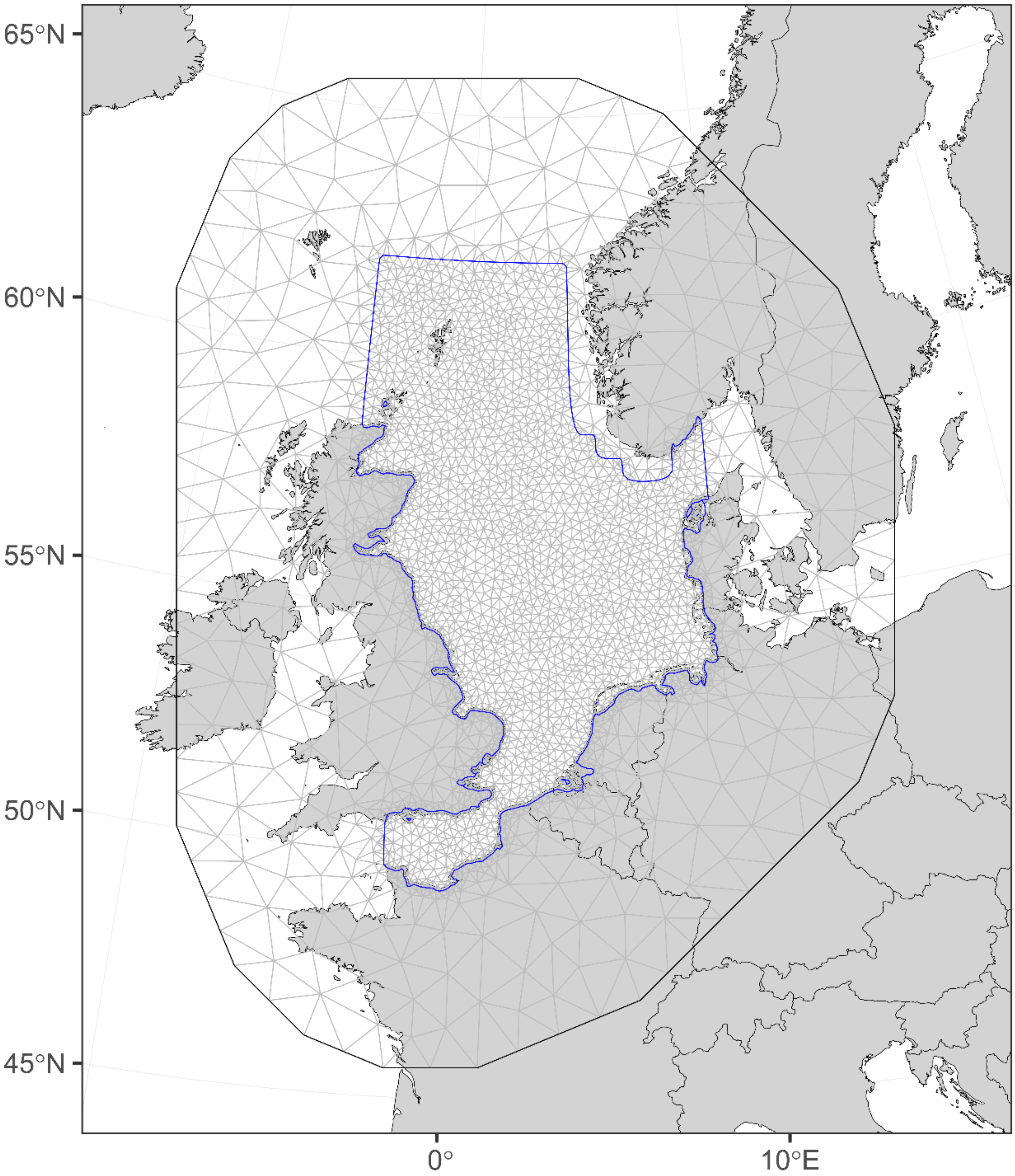


Figure S1. Map of the mesh used for approximating the spatial random field covering the North Sea region, enclosed by the blue line. The mesh boundary is coarsely clipped to the North Sea coastline to avoid estimation across land masses. There is an outer boundary enclosed by the black line that contains large triangles to avoid edge effects.

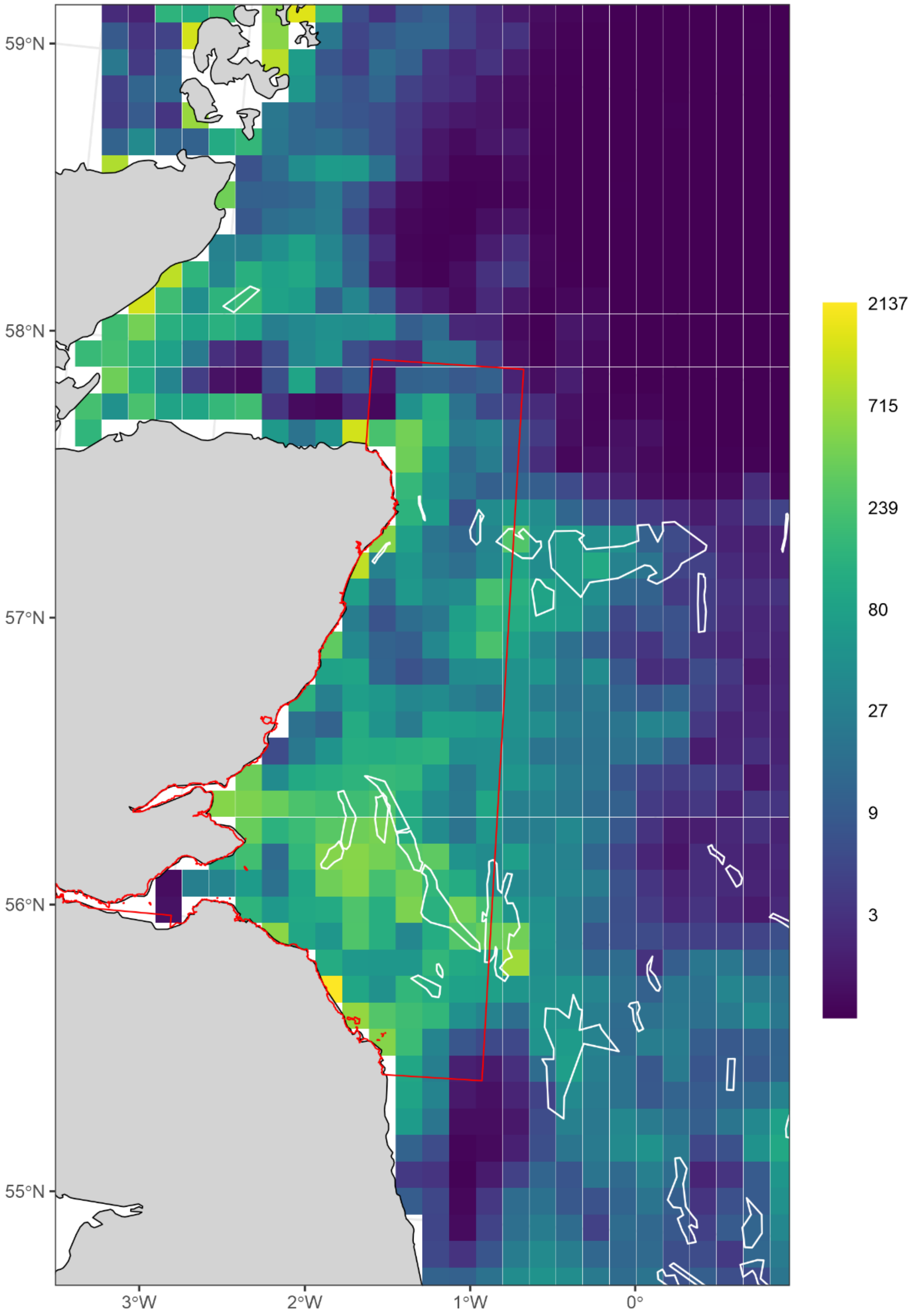


Figure S2. Sum of all sandeel biomass for the 21-year time period for sandeel area 4 along the coast of Scotland and North England. White lines denote major sandeel fishing grounds from Jensen et al., 2011. The red line shows the area closed to sandeel fishing off of the East coast of Scotland. Values are shown on log scale.

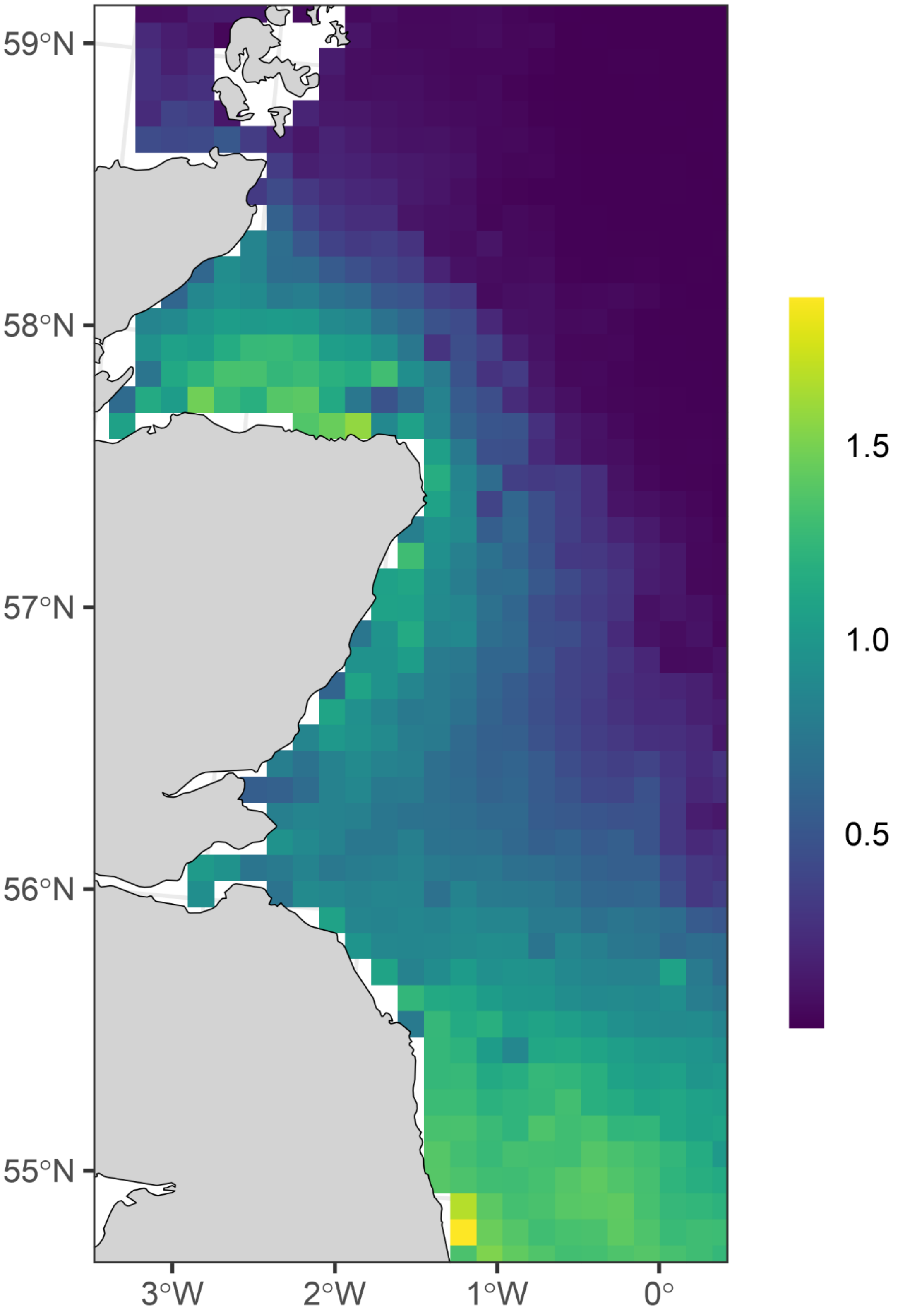


Figure S3. Sum of all sprat biomass for the 21-year time period along the coast of Scotland and North England. Values are shown on log scale.

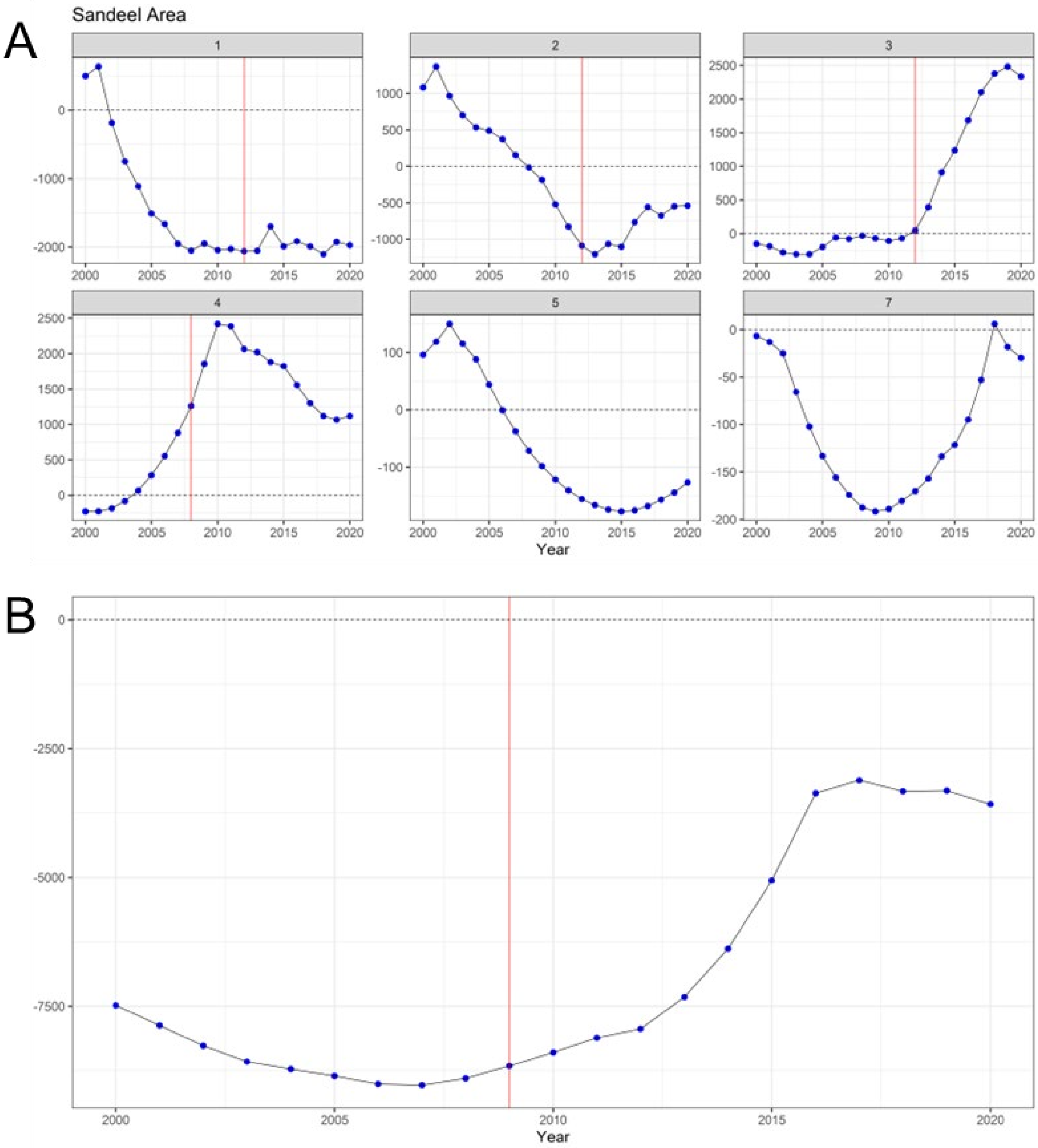


Figure S4. Temporal correlation for (A) each sandeel management area with vertical red line showing the year that dredge data commences in the sandeel model (there is no dredge data for areas 5 and 7) and (B) sprat across the North Sea with the vertical red line showing the year HERAS data commences in the sprat model.

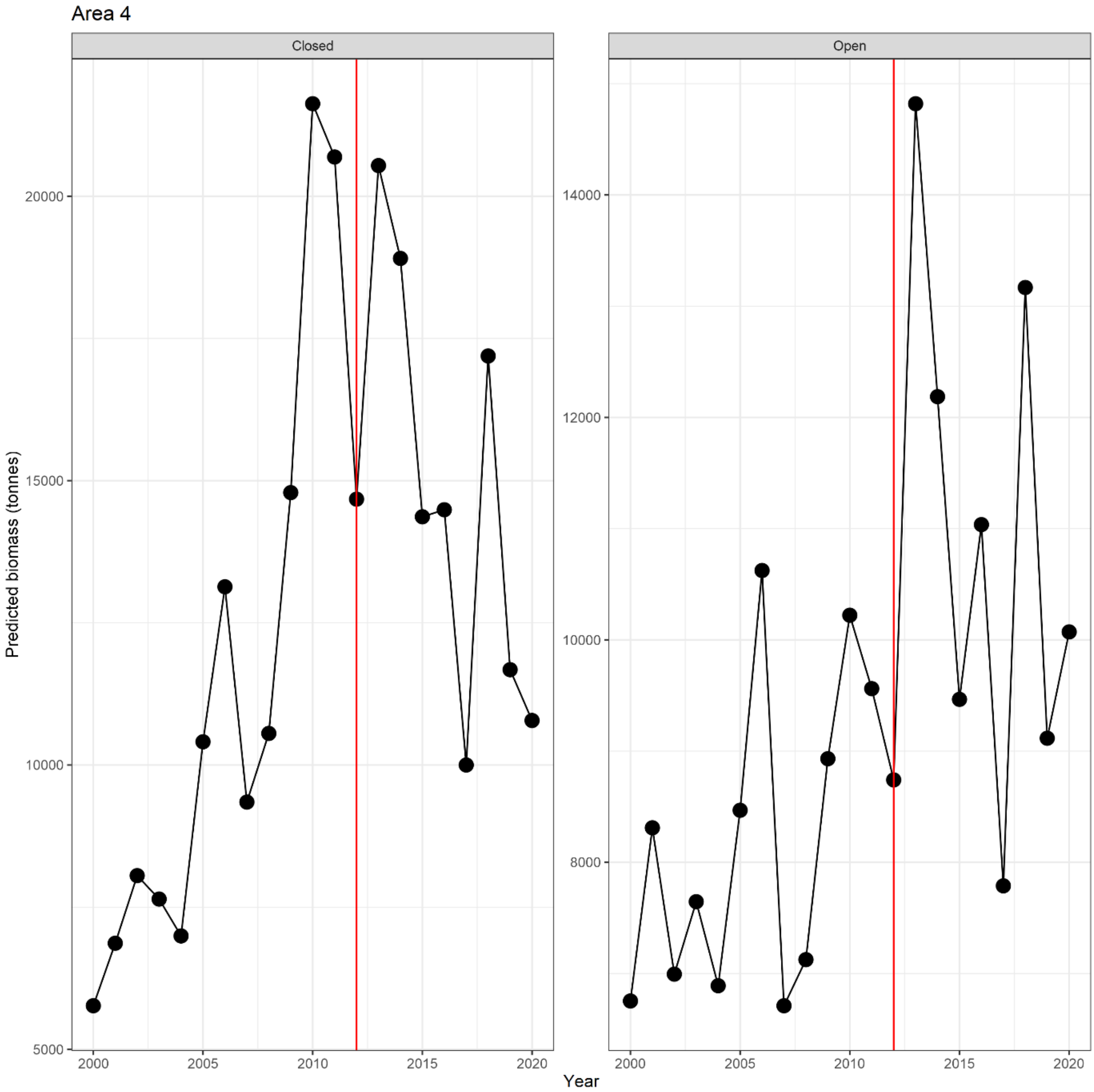


Figure S5. Timeseries of predicted sandeel biomass for area 4 for (A) inside the area closed to sandeel fishing and (B) outside the area closed to sandeel fishing. The red line denotes when fishing recommenced in sandeel area 4 in 2012.

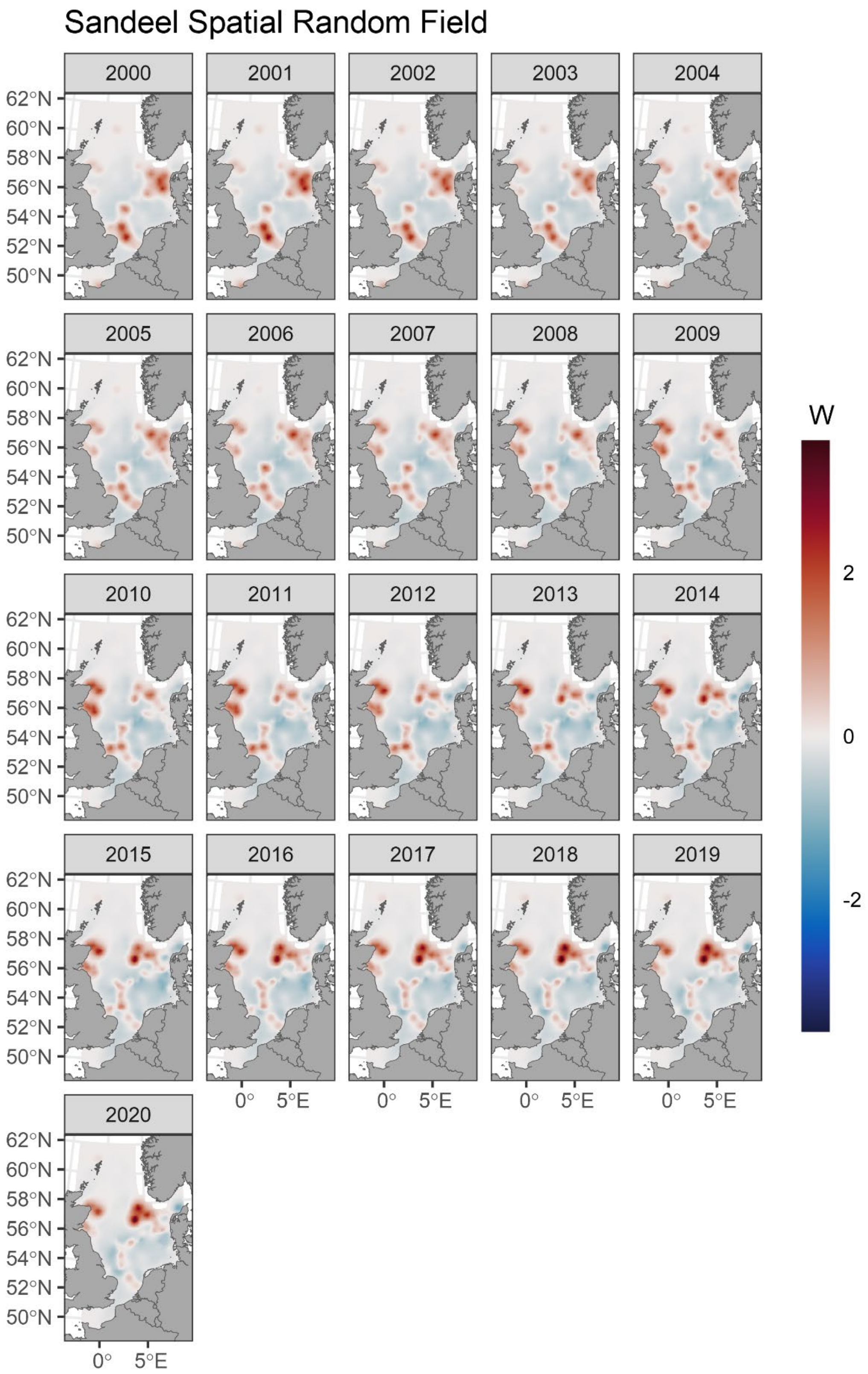


Figure S6. Annual spatial random fields for the sandeel model. W is the spatial effect parameter and is on the log scale

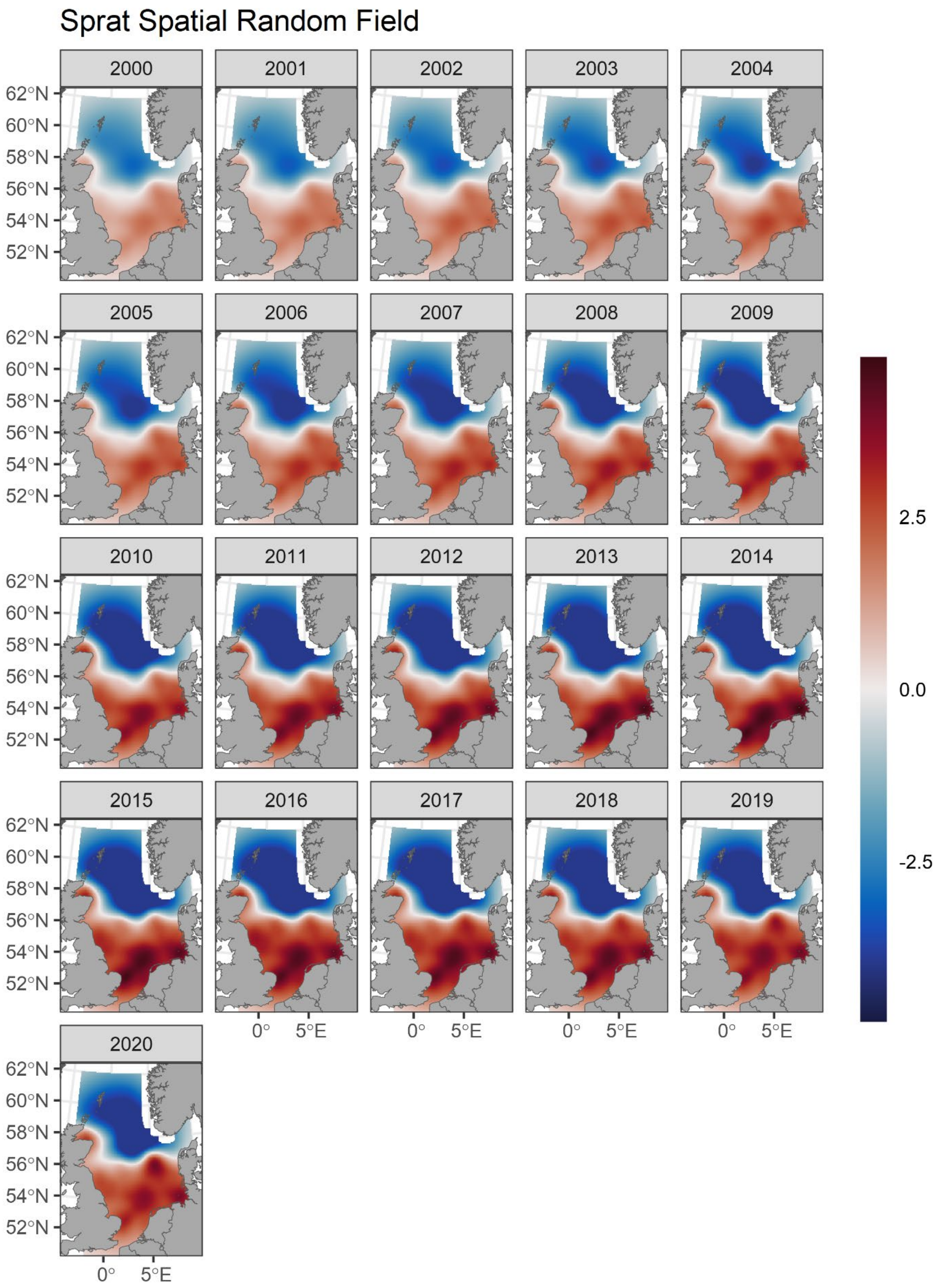


Figure S7. Annual spatial random fields for the sprat model. W is the spatial effect parameter and is on the log scale

3. Identifying critical prey thresholds for successful guillemot chick survival in the face of a shifting prey base

3.1 Abstract

Understanding the foraging dynamics and provisioning strategies of seabirds is crucial for effective conservation and management, particularly in the face of changing prey abundances. This study utilized a multi-species functional response (MSFR) model to investigate the provisioning rates of common guillemots (*Uria aalge*) on the Isle of May over a 20-year period from 2000 to 2019. By applying Bayesian methods to account for variability and uncertainty in prey abundance, we examined how guillemots adapt their feeding strategies in response to varying levels of sprat (*Sprattus sprattus*) and sandeel (*Ammodytes marinus*). Our findings indicate that guillemots exhibit a type III functional response, with a significantly higher preference for sprat (attack rate, a = 0.188) compared to sandeel (a = 0.078). The model predicted that successful chick provisioning depends more heavily on sprat availability, with critical daily energy thresholds estimated at 156 kJ/day for 10-day old chicks, which was estimated to be achieved at 29% of historical sprat biomass or 70% of historical sandeel biomass. Our results partially support the 'One-Third for the Birds' rule, suggesting that maintaining prey abundance at one-third of its historical maximum can support seabird productivity. However, the ability of guillemots to switch to alternative prey mitigates the impact of low abundances of their preferred prey, highlighting the importance of a dynamic multi-species consumption threshold, as defined in this study, for seabirds. Despite recent UK policies banning sandeel fishing and reducing sprat fishing pressures, ongoing monitoring and adaptive management remain essential to address potential future challenges, particularly as climate change and other environmental pressures evolve. This study highlights the importance of long-term, high-quality data for understanding predator-prey dynamics and underscores the need for continued and expanded monitoring to inform conservation strategies across varying ecological contexts.

3.2 Introduction

Seabirds have been declining globally and are under pressure from multiple different stressors (Dias et al., 2019). One of these pressures is declining and variable abundance of key prey species (Sydeman et al., 2021), including during the breeding season when energetic demands are high (Dänhardt & Becker, 2011; Erikstad et al., 2013). Studies in several regions around the world have linked seabird declines to low prey fish biomass (Cook et al., 2014; Cury et al., 2011), with several demonstrating direct links with competing industrial fishing impacting seabird foraging (Bertrand et al., 2012; Fayet et al., 2021) and survival (Crawford et al., 2011; Jahncke et al., 2004). These studies highlight the tight link between seabirds and their prey fish (Davoren & Montevecchi, 2003). A greater understanding of exactly how seabirds respond to changes in prey availability would therefore be of great benefit for conservation planning and management.

On the East coast of Scotland, seabirds have been declining alongside their main breeding season prey lesser sandeel (*Ammodytes marinus*) over the past 3 decades (Burnell et al., 2023; ICES, 2023b; Wanless et al., 2018). Policy responses to this have included closing a large area along the East coast of Scotland to sandeel fisheries (Searle et al., 2023b). This closure has had mixed success, with only Kittiwakes (*Rissa tridactyla*) – known to be highly vulnerable to sandeel declines (Furness & Tasker, 2000) - having shown a positive response (Searle et al., 2023). Responses of other seabird species to changes in prey populations may be more complicated if they are able to adapt through prey switching (Wanless et al., 2018), or by increasing their foraging effort (Fayet et al., 2021). However, this can result in greater energetic costs (Fayet et al., 2021) ultimately leading to long-term declines in adult survival and productivity (Wanless et al., 2023).

Common Guillemots (*Uria aalge*) are a widespread seabird with a circumpolar distribution. The population that breeds on the Isle of May in the Firth of Forth region of Scotland (Figure 13) has been intensively studied since 1982, resulting in one of the longest time series of a seabird breeding colony globally (Wanless et al., 2023). Previous studies have demonstrated a shift in chick diet for this population from sandeel-dominated up to 1997, then since 1998 a predominance of sprat (*Sprattus sprattus*), with sandeel now a minor component (Wanless et al., 2018). Importantly, this dataset contains sufficient detail over a long period of time to help to uncover the mechanistic relationship between predator consumption and prey availability across a period of significant change in the North Sea food web and the environment (Capuzzo et al., 2018; Wanless et al., 2005, 2018).

Understanding the mechanistic relationship between predators and their prey is vital for predicting the effects of varying prey availability on the predator population (Matthiopoulos et al., 2008). In situations where predators may vary their consumption of multiple prey species, multi-species functional response (MSFR) models allow realistic modelling of predation, saturation and prey preference while accounting for prey switching (Smout et al., 2013). Prey preference may change with changing prey abundance, and this can be described as switching. Most functional response studies have focused on laboratory settings as data on predator consumption rates and prey abundance are required to parameterise MSFR models which are rarely available for wild populations (Chan et al., 2017). However, modern Bayesian methods can be used to deal with data availability issues, while also accounting for uncertainty in the models (Ransijn et al., 2021), opening up the possibility of fitting MSFR models to appropriate ecological time series, such as the Isle of May guillemot data.

Smout et al. (2013) previously modelled functional responses of provisioning guillemots in relation to prey availability at the Isle of May. However, this analysis was limited by the spatial resolution of available prey distribution and abundance estimates. Stock assessments exist for sandeel at the scale of the ICES stock assessment Area 4, which covers the east coast of Scotland and central North Sea, and for sprat at the scale of the entire North Sea. These broad scale estimates may not represent the conditions within a guillemot's foraging range around the Isle of May. Sandeel are monitored directly in a dedicated dredge survey, but this does not have sufficient temporal or spatial coverage needed to examine interactions at the scales relevant to foraging seabirds (Chapter 2). To overcome this, Smout et al. (2013) used commercial catch data for sandeels, but fishery-dependent data are not randomised and are biased in their sampling. Here, we overcome these challenges by building Bayesian spatiotemporal models of sandeel and sprat biomass, joining different available datasets to provide annual fine scale estimates of fish biomass over the past two decades at a spatial scale that is aligned to the foraging range of guillemots. We therefore expand upon Smout et al. (2013), which covers the years 1992 to 2005 by combining these finer scale estimates of prey abundance with more recent chick diet data over the years 2000-2019, which includes an overlap period from 2000 to 2005, incorporating a period of substantial changes in both seabird and prey populations. In addition to the work of Smout et al. (2013), we compare our predictions of provisioning rates to breeding success to try and link prey abundances to seabird productivity. We use the data to fit MSFR with the goal of understanding how provisioning guillemots have responded to changes in prey availability over 20 years.

Reproduction is a major driver of population dynamics in long-lived seabirds (Wanless et al., 2023), it is also more directly correlated with prey population dynamics when compared to population abundance, which tends to have a lagged response (Cook et al., 2014). Linking prey availability to seabird breeding success is therefore an important goal. By combining our mechanistic MSFR model relating guillemot chick diet to the availability of alternative prey species with data on guillemot breeding success, we are able to relate chick provisioning to a key demographic rate that shapes seabird population dynamics, accounting for prey switching. This requires quantifying the (likely non-linear) relationship between seabird chick consumption rates and prey availability. To do this, we estimate a threshold of the minimum consumption required for chick survival based on chick energetics, and then use the MSFR model to calculate the combinations of sprat and sandeel abundance that this threshold occurs at. Cury et al., (2011) proposed the idea of 'One-Third for the Birds', with one third of historical maximum prey fish abundance required for healthy seabird populations to maintain productivity. Their study of multiple seabird species on a global scale did not account for the fact that generalist predators, such as guillemots, may switch prey in the face of environmental change. We use our estimated critical prey thresholds to test whether the 'One-Third for the Birds' threshold applies in a multi-species context. We link our estimated critical prey thresholds to breeding success in order to quantify the relationship between prey shortages and a vital rate of seabird populations.

3.3 Methods

3.3.3 Guillemots on the Isle of May

The Isle of May National Nature Reserve is located 8 km off the Eastern coast of Scotland in the Firth of Forth in the North Sea (56°19′N, 2°56′W; Figure 13) and is an important nesting colony for common guillemot and many other species of seabirds including Atlantic Puffin (*Fratercula arctica*), Black-legged Kittiwake (*Risa tridactyla*), Razorbill (*Alca torda*), European Shag (*Phalacrocorax aristotelis*), and Northern Fulmar (*Fulmarus glacialis*) (Burnell et al., 2023). The summer breeding colony of common guillemot on the Isle of May has been monitored since 1982 making this one of the more comprehensive seabird breeding and diet datasets in the world (Wanless et al., 2023). The number of breeding guillemots increased from 1990 to a peak of ~20,000 pairs in 2004, after which numbers declined to under 14,000 in 2013. They have started to increase again since 2014 and in 2020 there were estimated to be ~17,000 nesting pairs (Wanless et al., 2023). There has been significant variation in breeding success, measured as the number of fledglings per pair, over this period (Wanless et al., 2023).

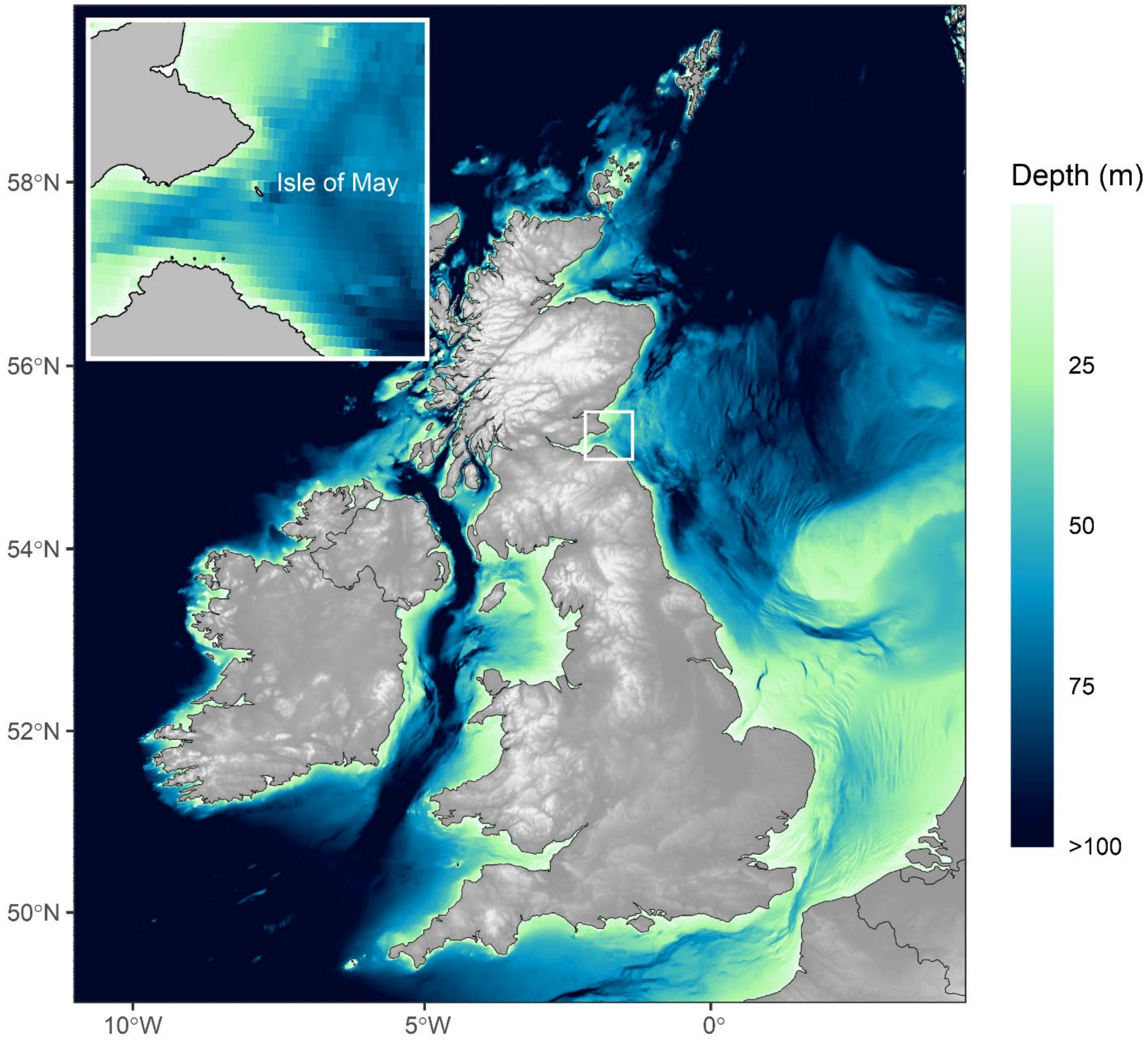


Figure 13. Map of the study area. Light colour represents shallow areas of the sea and blue to black areas represent deeper areas. Inset shows the Firth of Forth with the Isle of May inside the white box.

3.3.4 Guillemot Chick Diet

For the duration of the breeding season (April – July) guillemots on the Isle of May feed their chicks predominantly sprat and sandeel (Wanless et al., 2018). Guillemots carry only one fish at a time and nest in visually observable places which enables both the prey type (species or species group) and size to be visually observed, as well as the rate of delivery. To collect this diet data, fish brought to chicks are recorded visually over the course of full day watches during daylight hours per season. Three watches were conducted per season from 2000 to 2010, increasing to four and seven in 2004 and 2005, respectively, due to concerns of low prey availability. From 2010 to 2019 there were two annual watches, with no survey possible in 2020 due to the Covid-19 pandemic. As surveys are performed visually, length estimation is potentially subjective. The long-term monitoring protocol attempts to deal with this by assigning length categories a mean length for each season based on the observed length frequencies for that season and for each prey species. Length will therefore be listed as minute, small, medium, or large, but each year will have a mean length associated with the categories which will allow them to be converted to length estimates, i.e. a small sandeel in 2006 had a mean length of 7cm while a small sandeel in 2009 had a mean length of 11cm. It is impossible to identify young clupeids to species from distance, but 139 out of 151 (92%) Clupeids dropped by guillemots were identified as sprat (Wanless et al., 2023), thus for simplicity in this analysis we assume all clupeids are sprat. Gadoids constitute <5% of the chick diet and so we do not consider them further here. When chick feeding was inferred from adult behaviour, with no prey item identified, the ratio of sandeel, sprat and gadoid numbers per watch was used to partition unidentified feeds among the respective prey groups. To enable prey biomass values to be estimated, unknown feeds were assigned to the most common prey length category recorded for that species in the relevant watch. The number of chicks and the biomass per prey species was then summed across watches to give a yearly total, which was then converted into annual estimates of daily consumption rates of each prey species as grams per chick per day.

3.3.5 Prey availability

The predicted spatial distributions of sandeel biomass are taken from Chapter 2. Full details of the modelling methodology are provided there, but in brief, the predictions were generated by fitting Bayesian Tweedie GAMMs with R-INLA to scientific survey data across 21 years, to produce annual predictions of fish biomass for the month of July at a spatial scale of 10km across the North Sea. The sandeel model combined data from the Q1 and Q3 International Bottom Trawl Survey (IBTS), the Q3 Beam Trawl Survey (BTS) and the dedicated sandeel dredge survey into one dataset. Caveats and justifications of joining surveys from different seasons as well as dealing with catchability issues for sandeel are discussed further in Chapter 2. Preliminary investigations showed that the sprat predictions described in Chapter 2 did not produce a well parameterized prey consumption model, likely due to the high uncertainty from joining bottom trawl survey and acoustic survey data into a single spatial model. Model performance for sprat in relation to the joining of different datasets into a single model and future methods to improve the modelling methodology was discussed in chapter two. There are several possible reasons for the poor performance of the joint sprat model, such as larger discrepancies between the bottom trawl data and acoustic data in deeper water in the northern North Sea, where the former would be sampling a smaller proportion of the water column. However, we didn’t have the capacity in this thesis to further test the outputs across the full range of the North Sea sprat population. Therefore, for this analysis we re-ran the spatial modelling, creating a spatiotemporal model for sprat biomass using only the Q3 IBTS data, with other details of the model as described in Chapter 2.

Determining the biomass of prey available to guillemots breeding on the Isle of May requires an estimate of their typical foraging range. In general, the foraging range of seabirds is variable and can depend on interannual environmental conditions, competition from other birds, prey availability and coastal morphology (e.g. linear coasts on the mainland vs. island coastlines) (Patterson et al., 2022). Tracking work on the Isle of May suggests guillemots forage up to an average of 65km from the colony (Bogdanova et al., 2021) and we used this as the cut off for guillemot foraging range in our model, assuming that all foraging zones within this distance were potentially available to a foraging adult guillemot. It is necessary to create an index of available prey availability and not realised foraging locations, as this already encompasses predator decision which is likely influenced by prey availability. We tested the effect of this foraging range by running the model with a maximum foraging distance of 300km. There were some differences in the results, and we present them in the Supplementary Material; however, the general patterns were similar and had little effect on the overall conclusions, and the resulting model was not well supported (Figure S8 and S9). As there was no strong evidence to suggest a larger foraging radius was necessary, we selected the foraging radius of 65km which is quantitatively based on tracking data. Because breeding seabirds are central place foragers it is expected that foraging is more likely closer to the colony (Birt et al., 1987). To account for this, we used a 1/ sqrt (distance from colony) distance decay weighting function, adapted from Critchley et al., (2018), applied to the prey abundance indexes which upweights locations closer to the colony.

In order to account for uncertainty in our prey abundance predictions we sampled from the posterior distributions of the INLA prey models using the function inla.rmarginal from the INLA package (Rue et al., 2023), taking 1000 samples from the full distribution for every point within the Isle of May foraging region. We then summed the biomass predictions for every draw giving us 1000 estimates of total biomass for the foraging area per year and we calculated the annual mean and standard deviation values from this.

3.3.6 Prey energy content

As guillemots are single prey loaders the quality of individual fish is likely important to maximise provisioning efficiency. To account for this, we converted estimates of both seabird chick consumption and prey availability from biomass into calorific content (kJ). Our predictions of prey biomass do not include individual length data and we therefore modelled the average length of each prey species per year for the study region for use in predicting energy content (Figure S8). UKCEH has collected data on annual length stratified energy density values of sandeel and sprat using intact fish obtained from nesting puffins and guillemots, enabling energy values to be calculated using proximate composition organic analyses, as detailed by Wanless et al. (2005). This includes length-stratified energy density data for 2004-2015, but we excluded 2004 when building our model as it was an extreme outlier, with energy density values of about ¼ of that typical from other years for either sandeel or sprat, across length classes (Wanless et al., 2005; Wanless et al., 2018). Based on UKCEH prey energy data from the 1980s and 1990s which show similar prey energy values to the period 2005-2015, we made the assumption that in the years 2000-2003 and 2016-2019 the energy density relationship with length is in line with the long-term average, and not an outlier like 2004 (Wanless et al., 2018). The GAMs were fitted to the UKCEH energy density data with a gamma distribution to predict energy content using length with a smooth function, using thin plate regression splines and setting k=4 to avoid overfitting. The model was used to predict energy content from length for both the prey abundance data and for the chick diet consumption data. The predictions for 2004 were divided by a factor of 4 to account for the four-fold reduction in energy density compared to the long-term average in that year. Finally, for each species, prey abundance estimates (in energy content, kJ) were scaled from 0 to 100 of the historical maximum observed to assist model fitting.

3.3.7 Multi-Species Functional Response model parameterisation and fitting

Understanding the mechanistic relationship between a predator that consumes more than one type of prey, and prey populations requires accounting for alternative prey abundance, as a predator can switch between prey depending on availability (Holling, 1959). This can be achieved by parameterizing and fitting an MSFR model with abundance estimates of available prey species, which can realistically describe predator consumption by accounting for switching, preference and saturation as parameters in the model (Smout et al., 2013). The general MSFR model is defined as:

$$c_i = \frac{(a_i n_i)^m}{1 + t\sum_j (a_j n_j)^m}$$

Where *ci* is daily consumption of prey *i* in KJ, *Ni* is abundance index of prey *i* in KJ, *ai* is the attack rate for prey *i*, *m* is the shared shape parameter and *cmax* is the shared maximum consumption rate in KJ per day defined as 1/ the handling time *tt*. Based on the value of *m*, a type I, II or III functional response is observed (Holling, 1959).

Models were fitted in a Bayesian framework using Monte Carlo Markov Chain (MCMC) simulation implemented with Stan in R using 10,000 iterations with a burn-in phase of 1,000 which were discarded. Using a Bayesian framework allowed us to incorporate uncertainty in estimates of chick diet and also in estimates of prey abundance. We set wide moderately informative Gamma priors for the parameters *a* (shape = 1, rate = 1) and *m* (shape = 2, rate = 1) based on knowledge of other MSFR studies (Ransijn et al., 2021; Smout et al., 2014). The *cmax* prior (maximum consumption) was estimated quantitatively and set at the maximum observed total consumption across the time series as a gamma distribution (shape=560, rate=2).

To assess the identifiability of the parameters we calculated the prior posterior overlap, which is a percentage measure of the overlap between the prior distribution supplied to the model and the posterior distribution estimated by the model (Conn et al., 2018). This measures how much information the model is getting from the data versus relying on the provided prior. In cases where the prior is estimated a large overlap is expected as the prior is close to the true value, therefore in ecological models such as ours the degree of overlap deemed acceptable is case dependent (Gimenez et al., 2009) . The MSFR model has input of abundance data and diet for both prey species; however, the model also estimates each of these variables. For these four values we can compare the observed data versus predictions to measure goodness of fit. We assessed model convergence by visually inspecting the trace plots.

3.3.8 Predicting consumption and calculating critical prey thresholds

We used the parameterized model to predict consumption by guillemot chicks of each of the two prey species for varying prey abundance combinations, from 0 to the maximum observed values for both sandeel and sprat. Summing the consumption of each species allowed us to create a density surface of total daily chick consumption for every combination of sandeel and sprat abundances.

A key consideration that could improve seabird conservation and prey fish population management is the identification of thresholds of prey abundances that would lead to negative impacts on chick development or to chick mortality and breeding failure. To address this, we used estimates of chick energy requirements derived from doubly labelled water analysis of 20 guillemot chicks from Hornøya, Norway (Geir Gabrielsen, unpublished data). Given that Hornøya is approximately 12 degrees of latitude north of the Isle of May, and that seabird energy requirements increase with latitude (Dunn et al., 2018), we estimate that seabird energy requirements will be 20% lower at the Isle of May compared to Hornøya (Geir Gabrielsen, Pers. Comm. January 2024). Furthermore, because diet watches on the Isle of May are timed each year to observe chicks that are a mean of approximately 10 days old, we estimate our energy requirements for chicks 10 days old. These estimates represent typical chick consumption; however, as we are interested in critical minimum thresholds of consumption that will lead to negative impacts, we convert these healthy thresholds to critical negative thresholds. Guillemot chicks experience negative impacts on growth and metabolism at c. 80% of normal weight and will reach a high risk of mortality at 60-70% of normal weight (Geir Gabrielsen, unpublished data). In the absence of specific data on chick consumption rates related to negative health effects, we assume that a chick at 80% of normal weight will have a consumption rate of 80% normal consumption. We therefore set a moderate threshold at 80% of normal consumption and a critical threshold at 65% of normal consumption in KJ per chick per day. We plot these thresholds on top of the predicted consumption density surfaces from the MSFR model to estimate the prey abundance levels that will lead to consumption rates below the identified thresholds. We compare our estimated thresholds to the 'One-Third for the Birds' threshold (Cury et al., 2011).

3.3.9 Relationships of prey abundance and predicted consumption to breeding success

Breeding success data was obtained from the Isle of May long-term study (IMLOTS) seabird annual breeding success 1982-2021 dataset on the UK government Environment Information Data Centre web page (Newell et al., 2022). Breeding success is calculated as the mean number of chicks fledged per breeding pair. We used these data to test the direct effect of prey abundances and predicted energetic intake on the breeding success of guillemots, a key population metric. First to investigate the relationship between breeding success and prey abundance and how these align with both thresholds we fitted a GAM of the form:

$$\text{breeding success} \sim s(\text{prey abundance})$$

The GAM was built using a Gaussian distribution with an identity link. We tested several models, using smoothed terms for sprat abundance only, and smoothed terms for sprat and sandeel abundance. The sprat only model was chosen as guillemot chick diets are now dominated by sprat. We used AIC to select the best model. We calculated the inflection point of the estimated GAM curve, by calculating when the slope of the curve is statistically different from 0, to understand at what level of prey abundance that breeding success is estimated to start to decrease.

Secondly, to test the relationship between total predicted consumption and breeding success we used a linear model. To compare this relationship with the predicted critical energy threshold we separated the mean breeding success per year into "above" and "below" this threshold and used an independent t-test to compare the group means. Sprat fishing has not occurred in this region of the North Sea since 1981 and is therefore not relevant to seabirds on the Isle of May (Jennings et al., 2012).

Linking breeding success to our predicted energy thresholds, in the models above as well as visually on the predicted energy surfaces also acts as a method of validation for our predicted threshold, as we can compare whether the breeding success in years with consumption predicted below our minimum energy thresholds had a depressed breeding success or not, indicating if a true prey shortage was experienced that year.

3.3.10 Software

All spatial modelling was done using the INLA package (Rue et al., 2023). MSFR models were fitted using Stan through R with the rstan package (Stan Development Team, 2024). GAMs were fitted using mgcv in R (Wood, 2017). All data manipulation, model fitting, visualisation and analysis was conducted in R (v4.3.1).

3.4 Results

3.4.1 Multi-Species Functional Response Models

The final MSFR model configuration was selected based on comparison of the diagnostic plots. Sandeel consumption was well predicted while sprat consumption was generally well predicted but displayed more uncertainty (Figure 14). The model predicted sprat and sandeel abundance moderately well; however, there was higher uncertainty for sandeel abundance. This is likely due to the low sandeel consumption rates observed during the study period. The model estimated a higher attack rate, *a*, for sprat (0.188, CI 0.138 – 0.255) than for sandeel (0.078, CI 0.062 – 0.093). The estimated functional response curves are shown in Figure 15. The models estimated that seabird chick provision rates of sandeel was highly dependent on the availability of sprat, with high levels of sandeel consumption only seen at low levels of sprat availability and high levels of sandeel abundance. Conversely, sprat consumption remained high across all levels of sandeel availability with sprat being consumed whenever sprat was available (Figure 15). The shared *m* parameter was greater than 1 (4.265, CI 3.485 – 5.288) indicating a type III functional response.

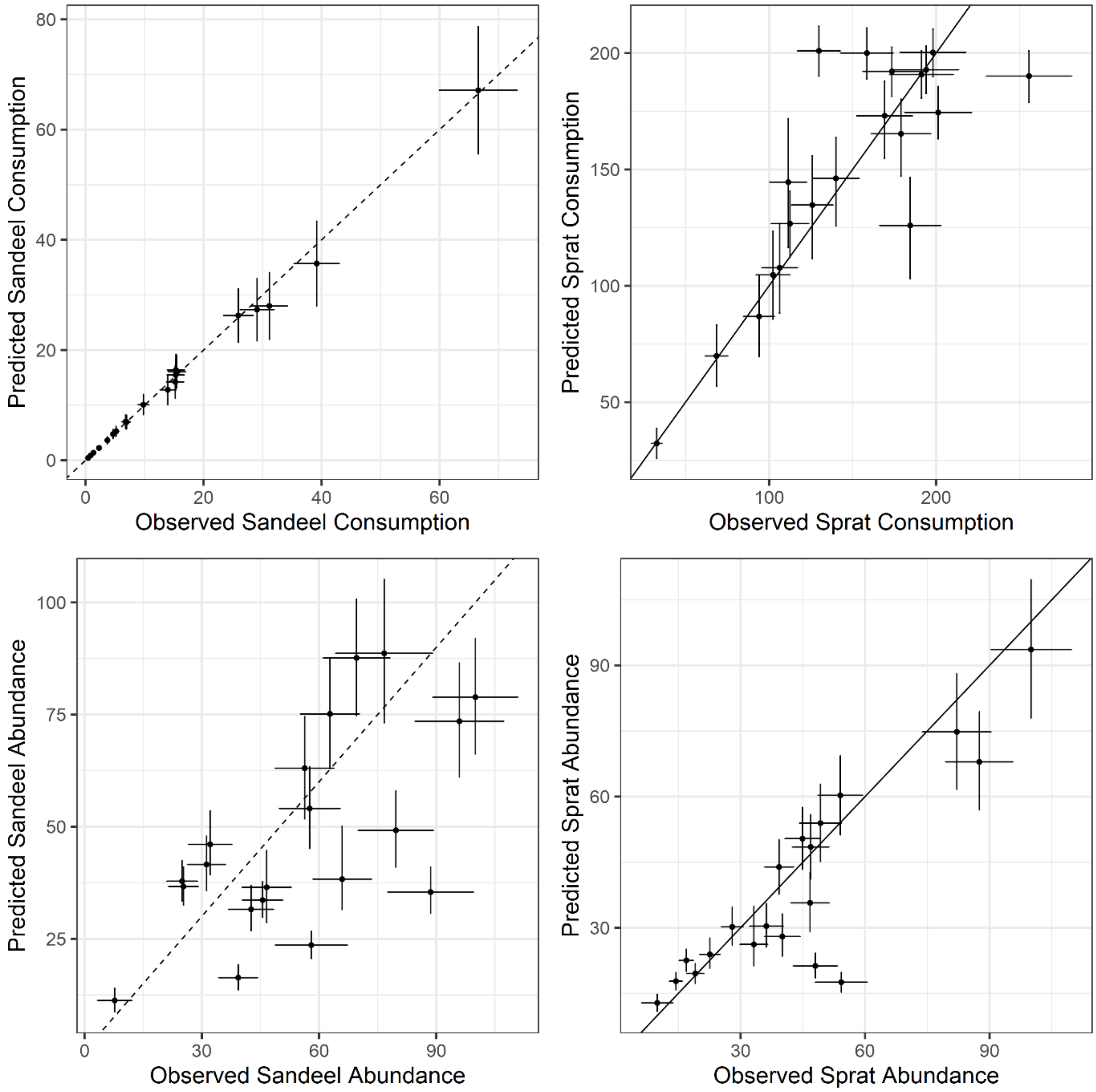


Figure 14. Plots of predictions against observations for sandeel (Left) and sprat (Right) and consumption (Top) and abundance (Bottom) used to evaluate the model fit.

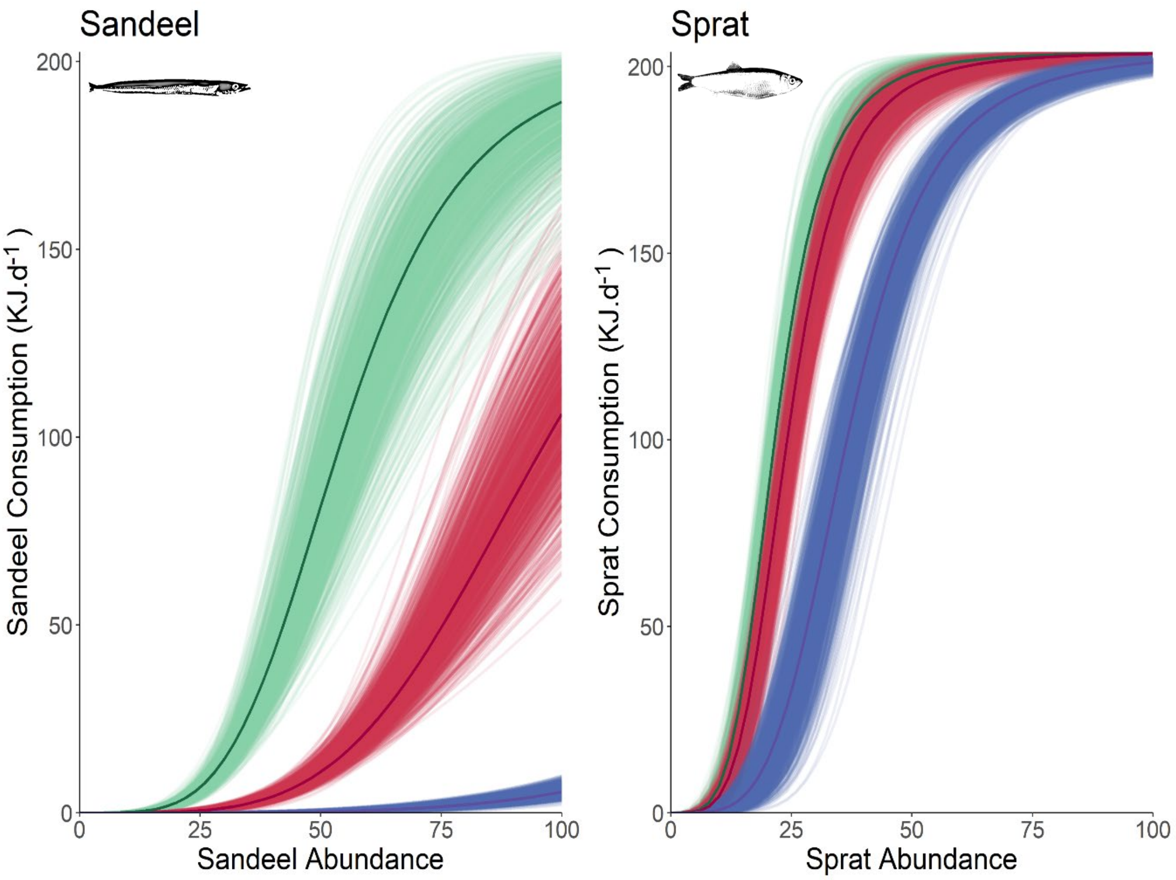


Figure 15. Multi-species functional response (MSFR) curves for guillemot foraging on sandeel and sprat. Each panel shows how the consumption of the focal prey species (y axis) varies with abundance of that species (x axis), and with abundance of the alternative species, with green, red and blue curves representing consumption when the abundance of the alternative prey abundance is set at the minimum, median and maximum of observed values in the data set, respectively.

3.4.2 Predicting consumption and calculating critical prey thresholds

The predicted total daily energy consumption (kJ) of guillemot chicks is shown in Figure 16. Predicted consumption was more influenced by the availability of sprat than sandeel. Based on chick energetics data we estimated the moderate provisioning threshold was 192 kJ/day and the extreme provisioning threshold was 156 kJ/day for a 10 day old chick. We saw no change in breeding success at the moderate threshold. Across the timeseries, reduced breeding success was only observed at prey abundances corresponding to consumption rates that fell below the critical provisioning threshold (Figure 16). Based on the critical threshold, guillemot provisioning was predicted to be sufficient at prey abundances above 29% of the historical maximum biomass for sprat and above 70% of the historical maximum biomass for sandeel. For low levels of sandeel the predicted critical threshold for sprat is close to the “One-Third for the Birds” threshold and guillemots can provision a chick from sprat alone above 29% of the historical maximum biomass for sprat abundance. However, as sandeel biomass increases, chick provisioning is compensated, and by 70% of the sandeel historical maximum biomass guillemots can successfully provision a chick from sandeel alone. From here on we will only discuss the critical minimum threshold.

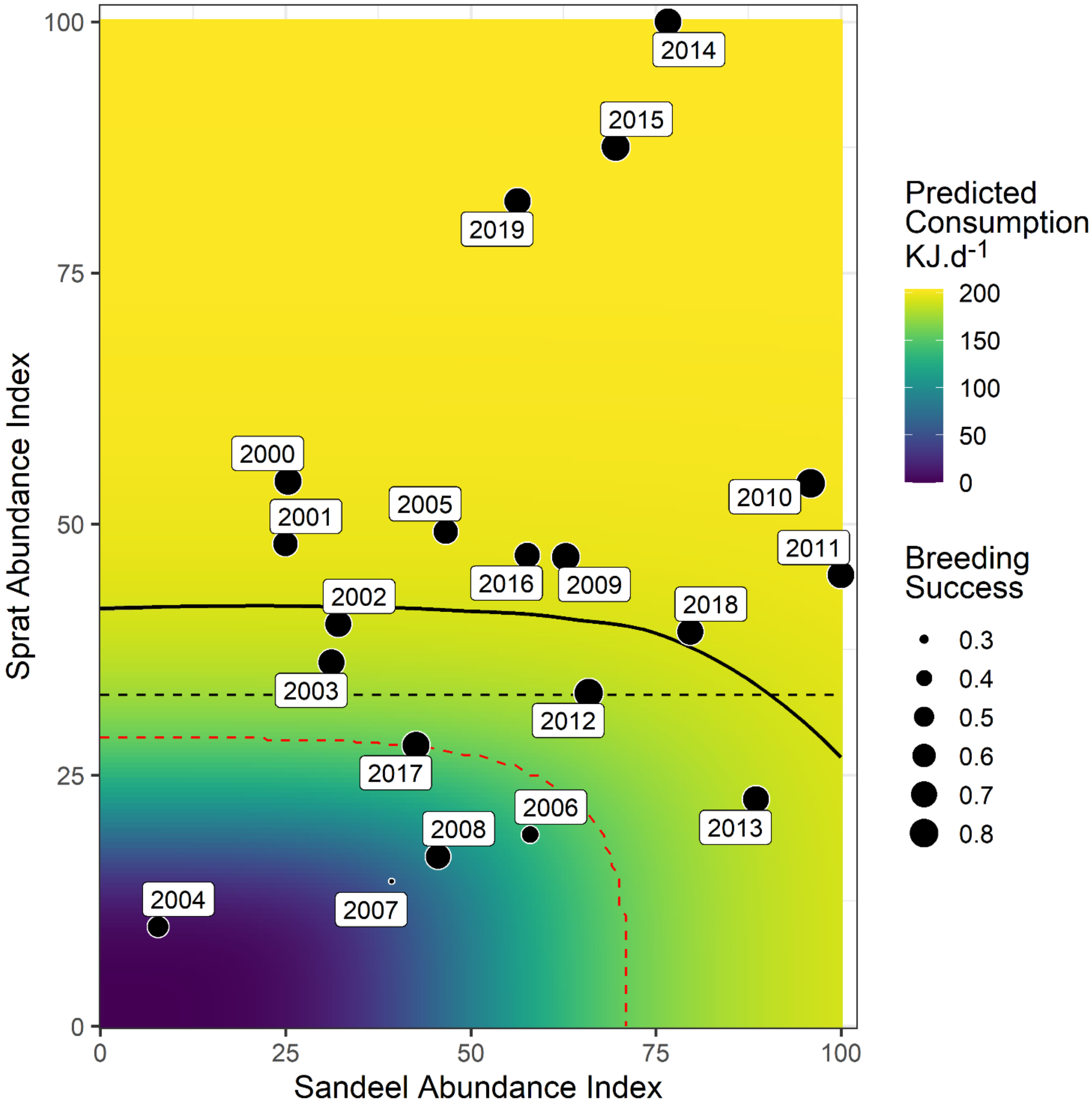


Figure 16. Predicted total consumption (kJ) 2d density surface with colour showing predicted consumption. Total consumption is the sum of sandeel and sprat consumption for every combination of sandeel and sprat abundance. Prey abundance is scaled to the respective historical maximum for each species where 100 is the maximum observed abundance in energy content. The points represent observed abundance of each prey species each year and the size of the points shows the breeding success for that year. The solid black line shows the moderate prey threshold, the dashed red line shows the critical prey threshold and the dashed black line shows the "one-third for the birds" threshold for sprat.

3.4.3 Relationships of prey abundance and predicted consumption to breeding success

Breeding success showed a non-linear relationship with sprat abundance (Figure 17). The final GAM model retained only the smoother for sprat abundance ($p < 0.001$). The deviance explained was 54.3%. The value of sprat abundance at which the slope of the curve is not statistically different from 0 (i.e. the inflection point when breeding success begins to decline) is 34.36, very close to the 'One-Third for the Birds' threshold. Our estimated threshold is non-linear as it varies with both sprat and sandeel abundance. For this analysis we selected the threshold for when sandeel is set at the mean value observed in the timeseries, which was a value of 55, which corresponded to a value of 26 for sprat. This is slightly lower than the "one-third for the birds" threshold and the GAM inflection point.

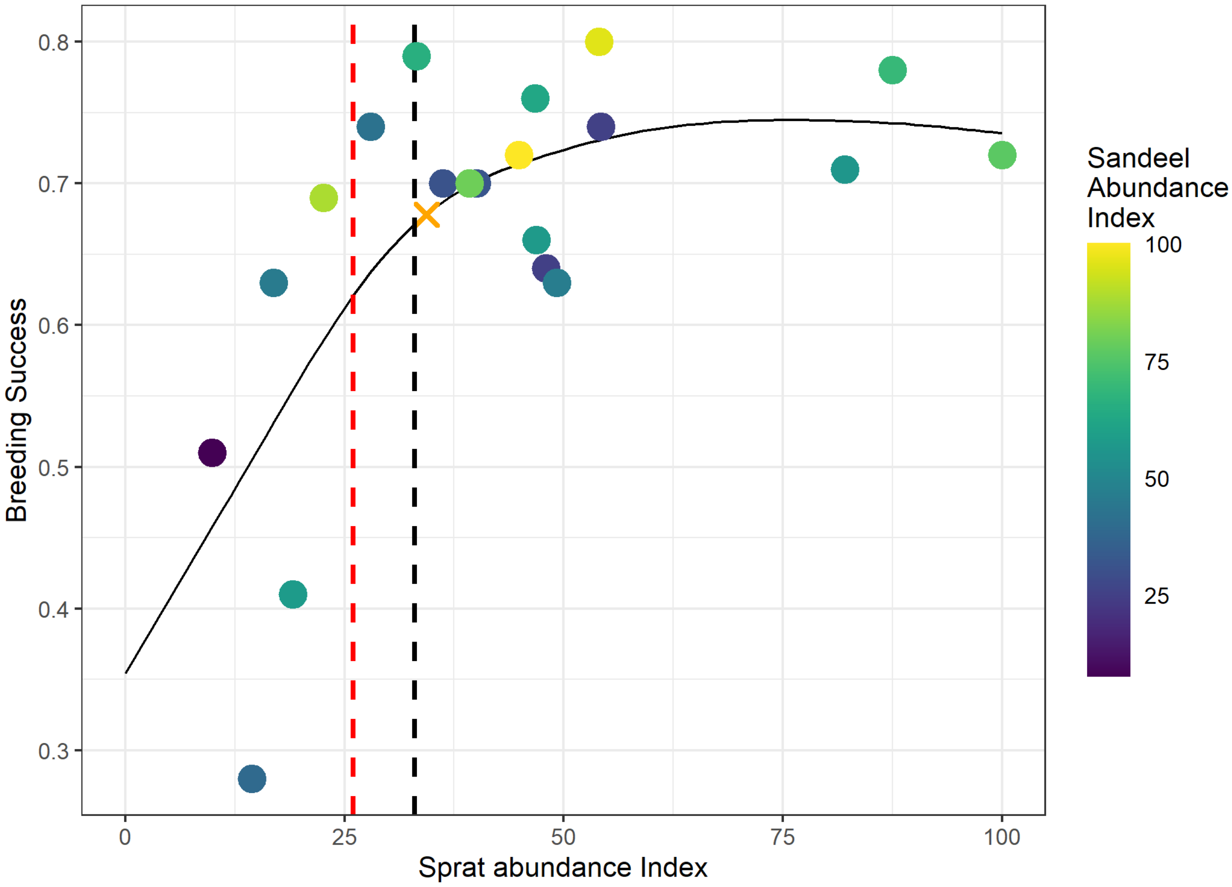


Figure 17. Relationship between sprat abundance and guillemot breeding success. Prey abundance is scaled to the respective historical maximum for each species where 100 is the maximum observed abundance in energy content. The colour of the points denotes sandeel abundance while the solid black line shows the fitted relationship from the GAM model that predicts breeding success based on the smoothed term of sprat abundance. The dashed red line denotes the abundance of sprat related to the critical minimum threshold; this is a non-linear threshold depending on the availability of sprat and sandeel and we show this threshold for when sandeel is set at 55, the mean of the timeseries. Note there are only small changes in this threshold until sandeel abundance is greater than 60. The dashed black line shows the "one-third for the birds" threshold. the orange X shows the estimated starting point of GAM inflection.

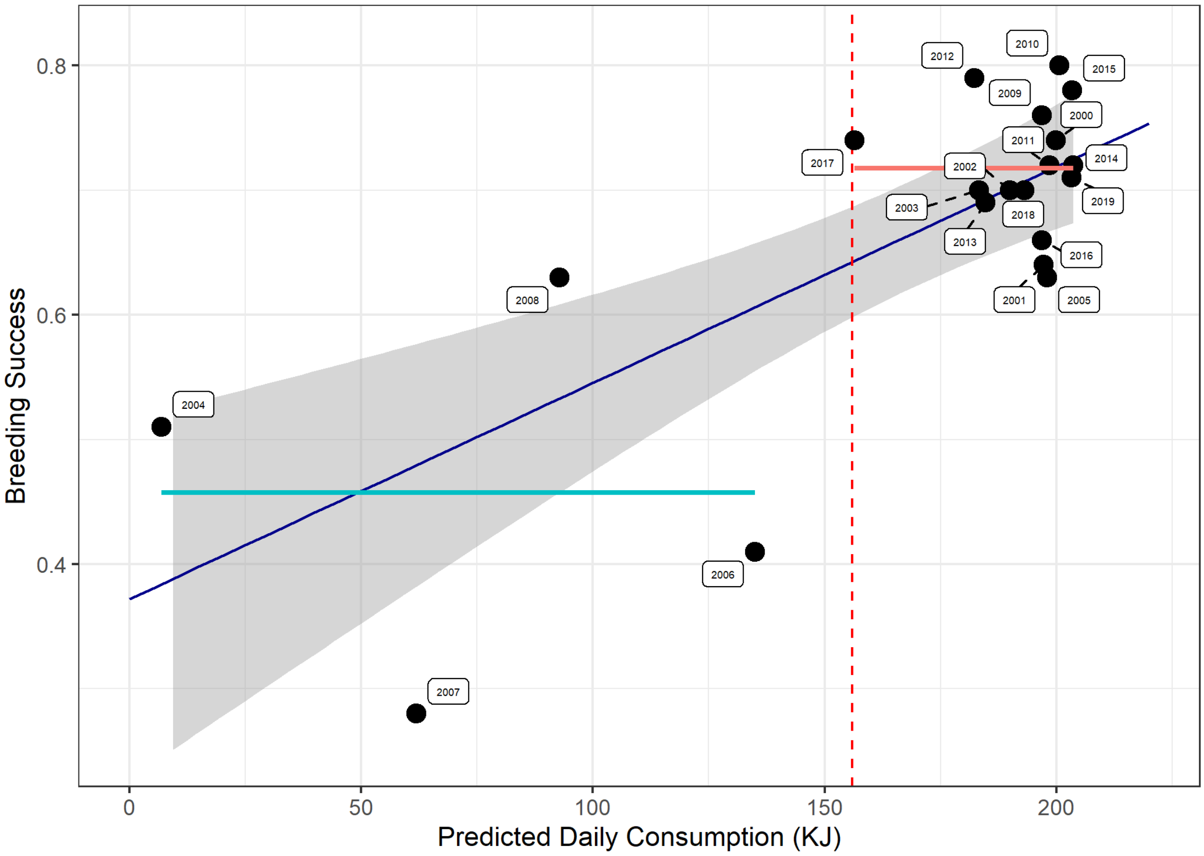


Figure 18. Relationship between guillemot breeding success and total predicted prey consumption by chicks. The dark blue line shows the fit from the linear model with the shaded area showing the 95% confidence interval. The dashed vertical dashed red line shows the critical minimum threshold for chick energy intake estimated from our model. The light blue and red horizontal lines show the means breeding success for years falling below and above the threshold value, estimated from the independent t-test. The black points show the observed breeding success and the predicted chick consumption for each year.

There was a significant positive relationship between guillemot breeding success and predicted daily prey consumption by chicks (Figure 18, dark blue line): for every 10 kJ increase in consumption breeding success increased by 0.017 ($p < 0.001$, CI 0.009 - 0.026). Breeding success was significantly lower in years where predicted daily consumption fell below the critical minimum consumption threshold than in years with higher consumption (t-test, t =3.45, $p < 0.0001$; Figure 18, horizontal light blue and red lines). The mean breeding success in years with consumption below the threshold was 0.458 (CI 0.376 – 0.541) compared to 0.718 (CI 0.68 – 0.756) in years with higher consumption.

3.5 Discussion

In this study we have successfully estimated guillemot chick provisioning rates on the Isle of May over a two-decade period by parameterising a multi-species functional response (MSFR) model with empirical field data. Using Bayesian methods, we accounted for significant variability and uncertainty in the abundance of key prey species. We found that guillemots are able to successfully feed their chicks over a wide range of prey abundances, in part due to their foraging flexibility and ability to switch to more abundant prey species confirmed by a type III functional response. Our study expands upon the previous work of Smout et al. (2013), adding more recent data and fundamentally different prey abundance indexes and model setup. We found a similar preference for sprat documented by Smout et al. (2013). In particular, the preference for sprat (a = 0.188) was over twice that for sandeel (a = 0.076). This is based on interpretation of the model attack rate parameter a, which in our model acts as a measure of relative prey preference as both of our prey abundance estimates are indexes and not absolute values of population size, therefore caution needs to be taken when interpreting these results as they only show relative preference. This is in line with observational evidence that guillemots on the Isle of May have switched to a sprat dominated diet since 1998 (Wanless et al., 2018). Only some bird species have been able to switch to sprat following sandeel declines and it would be highly informative to perform MSFR analyses on other seabirds in the region, such as black legged kittiwake and puffin, to understand how the shifting prey base has affected seabirds across different functional groups (e.g. diving vs surface feeding) and sandeel dependence.

Previous work on Isle of May guillemot functional responses predicted no prey switching, with a type II functional response preferred (Smout et al., 2013). In contrast, our model estimates switching, with the data best fitted by a type III functional response, with $m > 1$ ($m = 4.25$). The fine-scale fisheries independent predictions of sandeel and sprat abundance that we use in this study mean that our models likely better reflect the true foraging ecology of this guillemot population. However, because we only had these fine-scale prey abundance estimates available since 2000 (see Chapter 2), whereas Smout et al. (2013) included data covering the period in the 1990s when guillemot diets were more strongly dominated by sandeel (Wanless et al., 2018), it is possible that the functional response has genuinely shifted over time. Future work that can overcome data availability issues to model the functional response across a longer time series would be of benefit.

When attempting to link trophic levels it is important that the estimation of prey abundance index is matched to the ecology of the predator. This is tuned by the foraging radius in our model. We are not interested in the actual realised predator distribution as much as potential distribution the predator could target, as the former already contains information of predator choice which is linked to prey availability. We tested the effect of maximum foraging radius selection through a sensitivity analysis of 300km instead of the 65km limit used in our final model, which was based on telemetry data (Figures S8 and S9). Even with a large increase in potential foraging area there were only moderate changes in the model parameters and predictions highlighting the robustness of the modelling framework and data. As seabirds are central place foragers, we used an inverse distance weighting so that prey closer to the colony was given higher importance. These factors aim to ensure that our model accurately reflects guillemot predation ecology and leads to realistic estimates of the predator-prey relationship (Ransijn et al., 2021).

A major consideration for estimating a threshold based on a percentage of the maximum prey biomass is that it is relative to the available data. Our dataset covered the period 2000 to 2019 which follows major declines of local sandeel in the 1990s (ICES, 2023b) and sprat in the 1980s (Jennings et al., 2012). The sandeel population during our study period is likely lower than the maximum (ICES, 2023b). While ICES stock assessments predict that sprat across the North Sea have recovered to around half of the maximum level observed in the 1970s (ICES, 2022b), this is a North Sea wide assessment, and it is unclear whether this would vary on a local scale. Observational evidence of the decline of terns in the Firth of Forth following the sprat declines in the 1980s and recent recovery of terns to pre-crash levels following a local fishing ban on sprat may suggest that this region has shown an independent trend and may be close to population sizes similar to that before the population declines (Jennings et al., 2012). Thus, there is uncertainty around the recovery sprat on a localised scale, but this observational evidence may suggest our model is capturing close to the historical maximum of sprat biomass. However, it would be prudent in future work to attempt to extend the analysis as far back as possible to try to capture this pre-population crash stock size. In addition, if the analysis was to be extended to a seabird that has a diet more dominated by sandeel, it would likely be highly influential to have a prey dataset for sandeel that covers the 1990s, when sandeel began to decline in southern Scottish waters (ICES, 2023b).

We compared our results to those from the ‘One-Third for the Birds’ threshold proposed by Cury et al. (2011). That threshold was derived from global data on multiple seabird species, but did not account for alternative prey, which is important as most seabirds consume more than one type of prey. Secondly, the North Sea analysis in Cury et al. (2011) only considered the Shetland Islands, which is known to have different sandeel population dynamics to the rest of the North Sea (Poloczanska et al., 2004). Since the decline of sandeel since the 1980s, in Shetland low energy density gadoids have been the only alternate prey source instead of higher energy density clupeids (Anderson et al., 2014). These factors therefore make it unlikely for seabird-prey dynamics in the Shetland Islands to be representative of the entire North Sea region. Despite these differences both in overall spatial scale and in location-specific detail, we found the ‘One-Third for the Birds’ rule held approximately well for sprat, now the main prey of guillemots on the Isle of May. The GAM indicated that breeding success begins to decrease at around 34% of the maximum observed level of sprat biomass (Figure 17), which is remarkably close to the 'One-Third for the Birds' threshold. However, the ability of guillemots to prey switch adds an important caveat to such a simple rule. For instance, at high levels of sandeel abundance (~ 70% of historical maximum biomass), the provisioning guillemots can buffer against low sprat availability. The only year observed in the time series that had observed prey abundances in this combination of high sandeel with low sprat (i.e. below the "one-third" threshold but above our dynamic critical threshold) was 2013 (Figure 16). This year had a moderate breeding success value of 0.66, which would we expect would be much lower if seabirds that year were unable to successfully feed their chicks, suggesting that our varying threshold is more realistic than a flat constant threshold. Data for additional years, including those with this same combination of high sandeel and low sprat, would likely shed further light on which threshold is more accurate, and may modify the relationship estimated from the GAM model.

The relationship between prey consumption and breeding success indicated that breeding success was significantly lower when consumption was below the estimated critical threshold compared to above the threshold (Figure 18). Of note, 2013, which had prey abundance combinations above our estimated threshold but below the 'One-Third for the Birds' threshold, fell into the high consumption—high breeding success group. This indicates that for multi-prey predators such as many seabirds, a flat precautionary threshold based on a single prey species abundance index is inappropriate as trophic interactions are often more complex and multidimensional. In recent years the combination of low sprat and high sandeel biomass required for the flat threshold to fail has been rare but work on other seabird species with more generalist diets corroborates this view. For instance, the critical minimum threshold for maintaining productivity in Northern Gannets *Morus bassanus* was just 7.5% of maximum observed prey abundance of their preferred prey mackerel *Scomber scombrus* (Guillemette et al., 2018). This is potentially explained by the fact that gannets in the studied populations have a broad diet, in part due to their large size meaning a greater range of prey is available to them, and they are able to switch between several prey species (Guillemette et al., 2018). This again highlights that the complexity and regional flexibility of diet limits the ability of a single conservation threshold value to be applied globally to different species, populations and regions.

In response to increasing pressure on seabirds, sandeel fishing has now been banned inside English (https://www.gov.uk/government/consultations/consultation-on-spatial-management-measures-for-industrial-sandeel-fishing/outcome/government-response) and Scottish waters (https://www.gov.scot/publications/sandeel-prohibition-fishing-scotland-order-2024-final-business-regulatory-impact-assessment/), which together constitute the UK EEZ for the

North Sea. There is large uncertainty on the future of this policy as it is being challenged by the EU (https://www.euronews.com/green/2024/04/16/brussels-picks-fight-over-uk-ban-on-sand-eel-fishing). In addition, sprat fishing has not occurred in the northwest North Sea since the sprat population collapse in the 1980s. This means that the prey populations for seabirds in the region have one significant stressor removed and more resilience to deal with other pressures such as climate change (Sydeman et al., 2021). There have been calls to reopen sprat fishing in Scottish waters (Jennings et al., 2012), however, our analysis shows that for guillemots, sprat is now a vital prey resource for chick survival. Although we have shown guillemots are able to successfully provision their chicks over a wide range of prey abundances, and adults can also increase their foraging effort to maintain provisioning (Uttley et al., 1994), this has limits. Indeed, more recent work encompassing a period of significant change in forage fish populations has shown that guillemots have reached the limit of parental effort during chick rearing, such that future environmental change or prey declines would negatively impact productivity and adult survival (Wanless et al., 2023). Reopening the sprat fishery would therefore present significant risks to guillemots and other seabirds, given the other mounting pressures facing them (Sydeman et al., 2021) and the limited capacity adult guillemots have to buffer these stressors (Wanless et al., 2023).

Further north in the Shetland Islands guillemots have also shifted diet during the years 2000-2002. This is above the northern range of sprat (Chapter 2) and their diet has instead switched to gadoids (Heubeck, 2009). Gadoids have a lower energy density than clupeids, and guillemot chick fledging weight and breeding success in the Shetland Islands has declined since this diet shift. In contrast, breeding success on the Isle of May has stabilised at a moderate level after the low breeding success period of 2004-2008 (Searle et al., 2023b). Thus, the availability of sprat may have buffered the impact of sandeel declines for seabirds able to forage on them in Southern Scotland. However, in cases where alternative prey has lower energy density, such as in the Shetland Islands, there is a greater risk of chick mortality during years of low prey availability. The extreme seabird mortality that occurred in the Barents Sea following rapid decreases in capelin *Mallotus villosus* in the 1980s; however, subsequent capelin crashes did not result in the same effects on seabirds because of the availability of alternative prey (Gjøsæter et al., 2009). Similar effects have been observed for African penguins *Spheniscus demersus* in South Africa (Sherley et al., 2013) and Namibia (Ludynia et al., 2010). Thus, while the 'One-Third for the Birds' rule may be appropriate for guillemots on the Isle of May most of the time, it does not hold when alternative prey is not available to seabirds, in this case sandeel. We recommend that a region- and species- specific analysis of the multi-species predator-prey interactions is necessary for proper ecosystem management.

It is important to note that, although the initial impact of reductions in prey biomass may be on seabird breeding success, in extreme cases adult mortality is also possible. For instance, in South Africa prey availability below 25% of maximum prey biomass has been linked to an increase in adult seabird mortality (Robinson et al., 2015). This may be due to spatial variability in the key prey species in this region, sardines *Sardinops sagax and anchovy* Engraulis encrasicolus, which is more typical of an upwelling system and does not usually affect coastal shelf seas such as the North Sea. Thus, while prey shortages are currently affecting seabird productivity in the North Sea, there is a risk that increased prey declines could lead to adult mortality (wanless 2023). Seabirds are long-lived species that are adapted to weather short term prey variability; however, this life history strategy means that reduced adult survival can have large effects on population dynamics (Sandvik et al., 2005). Climate change is projected to increase significantly under current scenarios (Mathis & Pohlmann, 2014) and this may increase the current pressure on North Sea seabird populations through changes in the distribution and abundance of prey fish (D'Entremont et al., 2022) or heat waves (Olin et al., 2023). There is also the risk of carry-over effects with greater breeding season energy expenditure reducing adult energy budgets in the following winter (Bogdanova et al., 2017), thus there is concern about the future stability of seabirds in the region.

Because common guillemots are single prey loaders, their foraging efficiency is heavily influenced by prey quality as well as prey abundance (Bugge et al., 2011). We accounted for this in our models by using prey energy content (kJ) which improved the model by making a more realistic representation of foraging opportunities available to guillemots that influence provision rate (Smout et al., 2013). The year 2008 had a relatively higher breeding success than expected for the given prey availability and the predicted provisioning rate, as the only year below the estimated consumption threshold but with a moderately high breeding success (0.63), see Figure 16. 2008 was also the year with the largest difference between observed and modelled consumption with the model significantly underpredicting consumption (Figure S2). This might be explained by the fact that the mean length of sprat fed to chicks this year was 25% larger than the mean length for the remainder of the timeseries (the mean in 2008 was 12.7cm, the mean for the remainder of the time series was 10cm; Figure S10). The availability of larger more calorie dense sprat may have offset the effects of lower prey availability by increasing the provisioning efficiency of foraging guillemots. It would be informative to extend this analysis to multi-prey loaders as they are likely to be more directly linked to prey abundance metrics; however, the fact that we were able to produce well defined models for guillemots shows how robust the statistical framework is and the benefit of working with energy content.

Our estimation of the MSFR of a wild seabird population has only been possible because of the high-quality dataset available from the long-term seabird monitoring programme on the Isle of May. While there is some uncertainty about intra-annual variation in chick diet and how much monitoring effort is required to accurately capture that, chick diet monitoring could likely be improved with watches being spaced out across the breeding season (Harris et al., 2022). This highlights the importance of maintaining and updating such monitoring programmes which require long-term data to be able to address the kinds of questions we have investigated in this study.

Given the need we have highlighted for region- and species- specific analyses of trophic dynamics, the establishment of such monitoring programmes in regions where they are absent should be a top conservation priority, given the worsening effects of climate change (IPCC, 2023) and the rapid implementation of the offshore wind energy transition (Gușatu et al., 2021). In light of recent UK policy change, fishing pressure on sandeel and sprat for the time being is no longer a major stressor on Scottish seabird populations during the breeding season, however, this policy change is still under review and subject to objection from the EU. Therefore, given the rich availability of data for seabirds in the wider North Sea region, applying the models developed in this study for seabirds in the southern North Sea where both sandeel and sprat fishing still occurs at significant levels would likely be of great benefit. Guillemots are one of the few seabirds that have switched to a sprat dominated diet, and so studying the multi-species functional responses of other seabirds still predominantly reliant on sandeel, such as kittiwakes, would be highly informative to understand the functional relationship of the wider seabird community to ecosystem change.

3.6 Conclusion

Our multi-species functional response (MSFR) model was able to effectively quantify the relationship between provisioning guillemots and their fish prey on the Isle of May across different levels of prey abundance over the past two decades. We found that guillemots have a higher preference for sprat over sandeel and that they are able to successfully provision their chicks over a wide range of prey abundances. We identified 156 kJ as the critical daily threshold for chick consumption at 10 days of age, roughly the midpoint of chick rearing on the Isle of May, which corresponds to prey abundances of sprat above 29% of the historical maximum observed biomass or sandeel above 70% of the historical maximum observed biomass. Our results to some extent support the ‘One-Third for the Birds’ rule proposing that forage fish abundance needs to be at least a third of its historical maximum to maintain seabird productivity. However, we show that the predator-prey relationship of multi-prey seabirds is more complex with the availability of alternative prey being able to buffer the effects of low prey abundances of the preferred prey to a certain extent. Therefore, we do not deem a general rule to be globally applicable. Rather, species- and region- specific analyses are needed for effective ecosystem management, requiring ongoing support for intensive long-term monitoring programmes such as that on the Isle of May.

3.7 Chapter 3 Supplementary Material

3.7.1 Sensitivity testing model with foraging radius at 300km

Running the model with a larger foraging distance applied to estimate prey abundances lead to slightly different results (Figure S8 and S9). The main difference was a 13% lower attack parameter for sandeel (a_{300} = 0.066) which indicates a lower preference. This translates to lower consumption of sandeel and less buffering ability of sandeel in the case of low sprat abundance such that when sprat is low (<25) sandeel needs to be above 82% of the maximum observed value to have provisioning above the estimated threshold, which is relatively high. This also raised the threshold for sprat as well indicating that when sandeel was low sprat needed to be above ~32% of the maximum observed value. In the 300km foraging range model 2017 is now predicted to be below the estimated critical threshold, this is not congruent with the breeding success data which was high that year (0.75). A foraging range of 300km represents a large increase on that estimated from tracking data which is about 65km (Bogdanova et al., 2022), therefore, to observe only moderate changes in the parameters and predictions during the sensitivity analysis exemplifies the robustness of the model. We therefore conclude that a foraging range of 65km, based on telemetry data, is the best choice for the model.

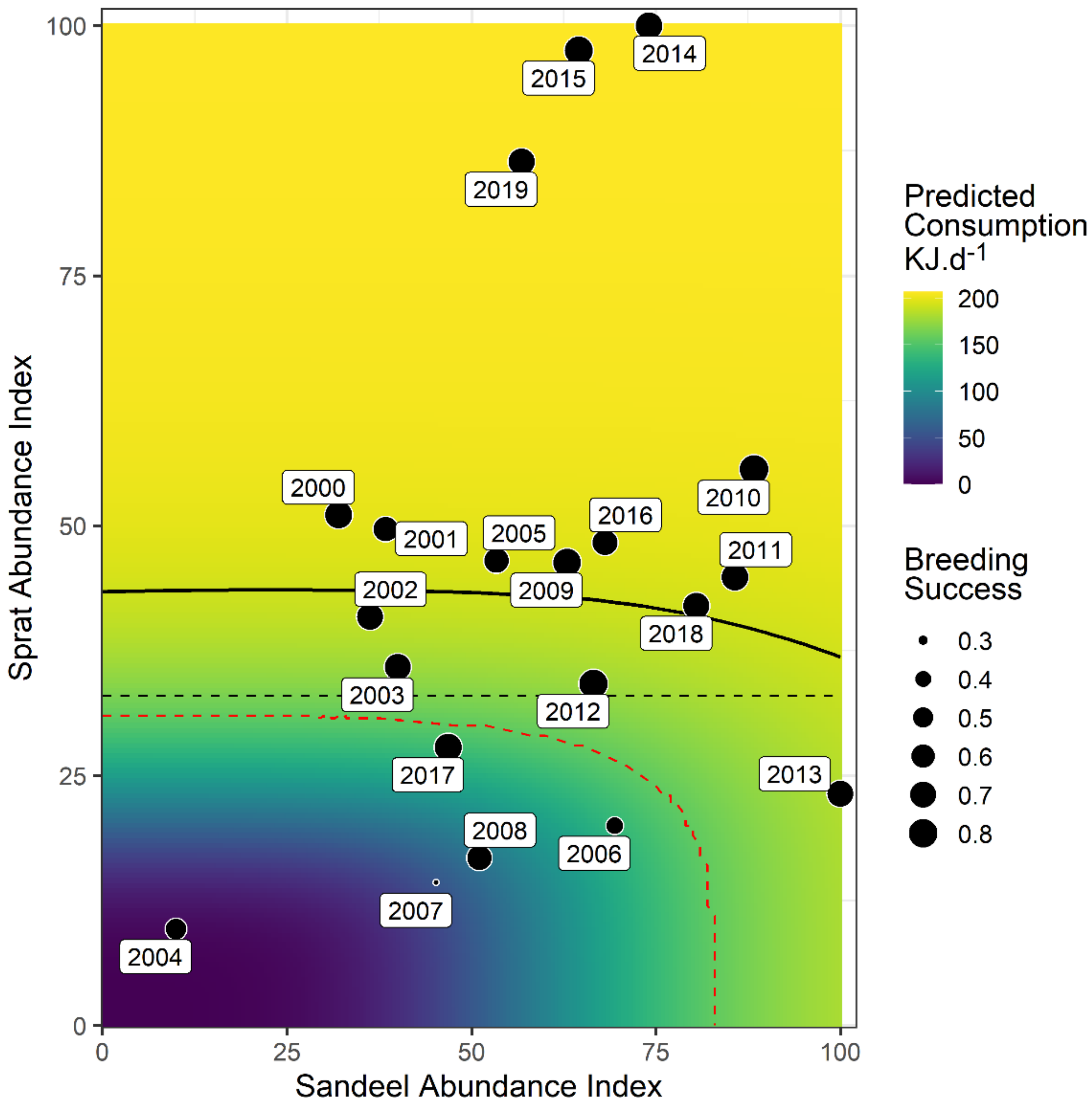


Figure S8. Predicted total consumption (KJ day^{-1}) 2d density surface for the model when parameterised with prey abundance from a 300km foraging radius. Total consumption is the sum of sandeel and sprat consumption for every combination of sandeel and sprat abundance and shown as the background colour from black (low) to yellow (high). Prey abundance is scaled to the respective historical maximum for each species where 100 is the maximum observed abundance in energy content. The points represent observed abundance of each prey species each year and the size of the points shows the breeding success for that year. The solid black line shows the moderate critical prey threshold, the dashed red line shows the extreme critical prey threshold.

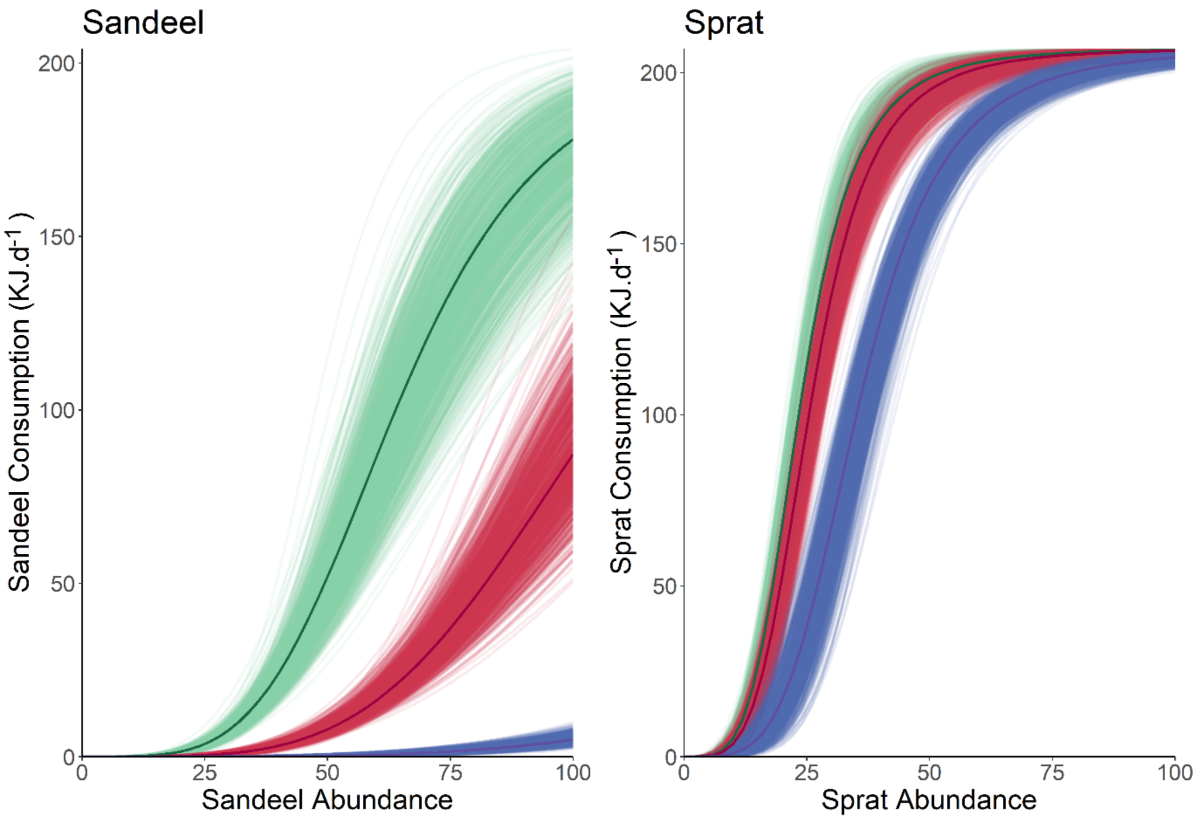


Figure S9. Multi-species functional response (MSFR) curves for guillemot foraging on sandeel and sprat with a 300km foraging radius. Each panel shows how the consumption of the focal prey species (y axis) varies with abundance of that species (x axis), and with abundance of the alternative species, with green, red and blue curves representing consumption when the abundance of the alternative prey abundance is set at the minimum, median and maximum of observed values in the data set, respectively.

3.7.2 Modelling mean prey size around the Isle of May

As our predictions of prey availability did not have information on length, we first calculated annual mean fish length around the Isle of May in order to predict energy content (Figure S10). For sandeel we modelled this with an INLA spatio-temporal model using Q3 IBTS, Q1 IBTS and sandeel dredge survey data using the mean length per trawl as the response variable, the model was based on data for the northwestern North Sea and used to make predictions for the Isle of May. The use of Q1 winter survey data was needed due to limited data coverage for the spatial extent, however as sandeel overwinter in the sediment there is likely very little growth from autumn until the following spring (Winslade, 1974). As our sandeel biomass predictions are based on data subsetted to 16cm and below (Chapter 2), we subsetted the IBTS data to this cut-off as well when modelling the mean length as this is the upper limit for sizes edible by guillemot chicks. The INLA model did not include environmental covariates, and only had a fixed effect accounting for survey. The continually indexed smoothed spatial random field was used as a spatial smoother to predict mean sandeel length (same as methods described in chapter 2 for spatial effect). Mean length predictions were made for 10km grid cells within 65km of the Isle of May (the foraging distance used in our MSFR model) and an annual mean was calculated from these points. For sprat we could not create a satisfactory model, so we took the mean length of Q3 IBTS trawls within 200km of the Isle of May. A 200km radius was required as there wasn't sufficient data coverage within the foraging range. Bottom trawls are known to have variable catchability for small pelagic fish so we applied length based catchability corrections for IBTS data for sandeel and sprat (Walker et al., 2017). For the sandeel dredge survey we applied a general 8% catchability correction as catchability does not vary by length in this survey (Johnsen & Harbitz, 2013).

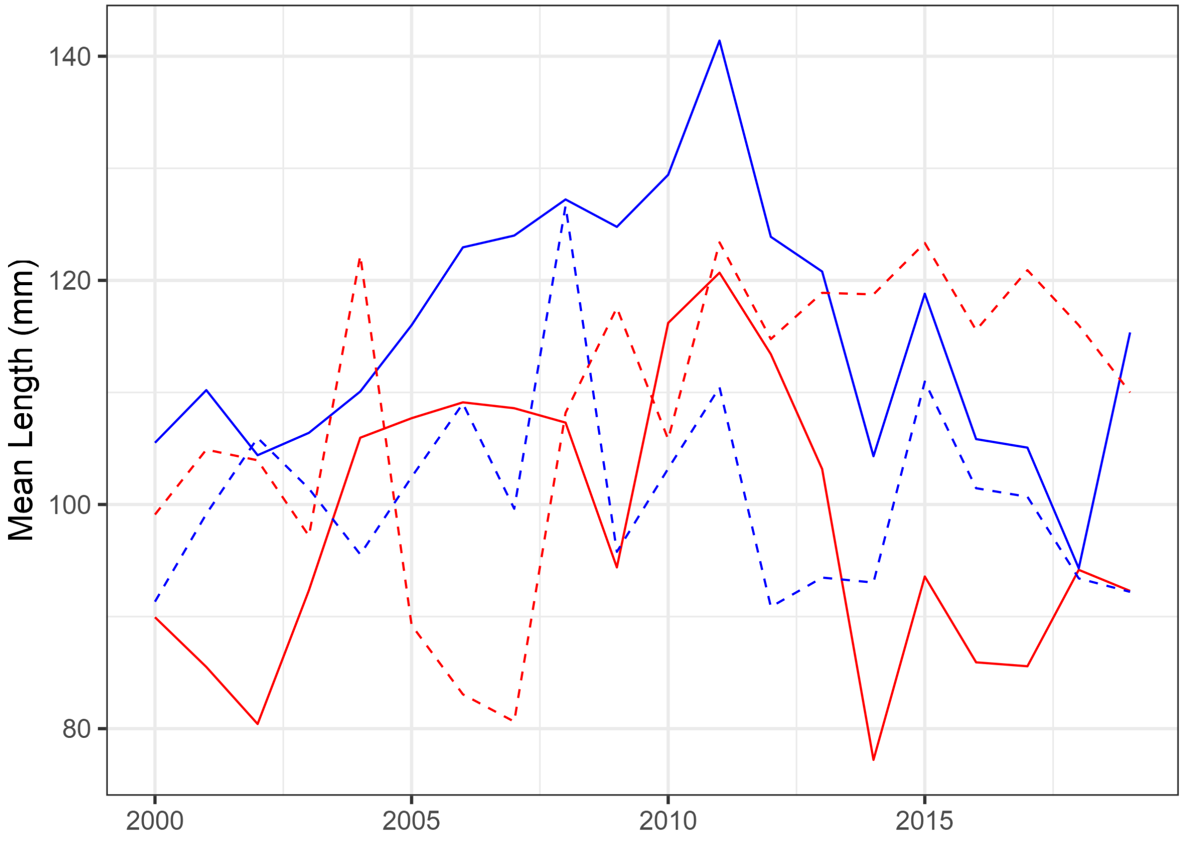


Figure S10. The annual mean length (mm) of sandeel (red) and sprat (blue) estimated from the fishery surveys timeseries around the Isle of May (solid line) and from chick diet data (dashed line).

3.7.3 Model validation

The best model configuration was selected using the fitted versus observed plots and the PPO plots. Diagnostic plots from the final model are shown in Figure 14. The PPO plots are shown in figure S11. All parameters had well defined posteriors and PPO values were all below 15. The observed versus fitted of total consumption is shown in Figure S12. Apart from 2000, there was slightly higher uncertainty in the model predictions from 2007. This uncertainty roughly coincides with the beginning of sandeel dredge survey in the model in 2008 and this is likely caused by uncertainty propagating from joining different surveys into the sandeel biomass model. The model moderately over predicted in the years 2000, 2008, 2012, 2013, 2014 and 2019 while the model moderately under predicted in 2008 and 2015, with 2008 having the largest difference between observed consumption and predicted consumption.

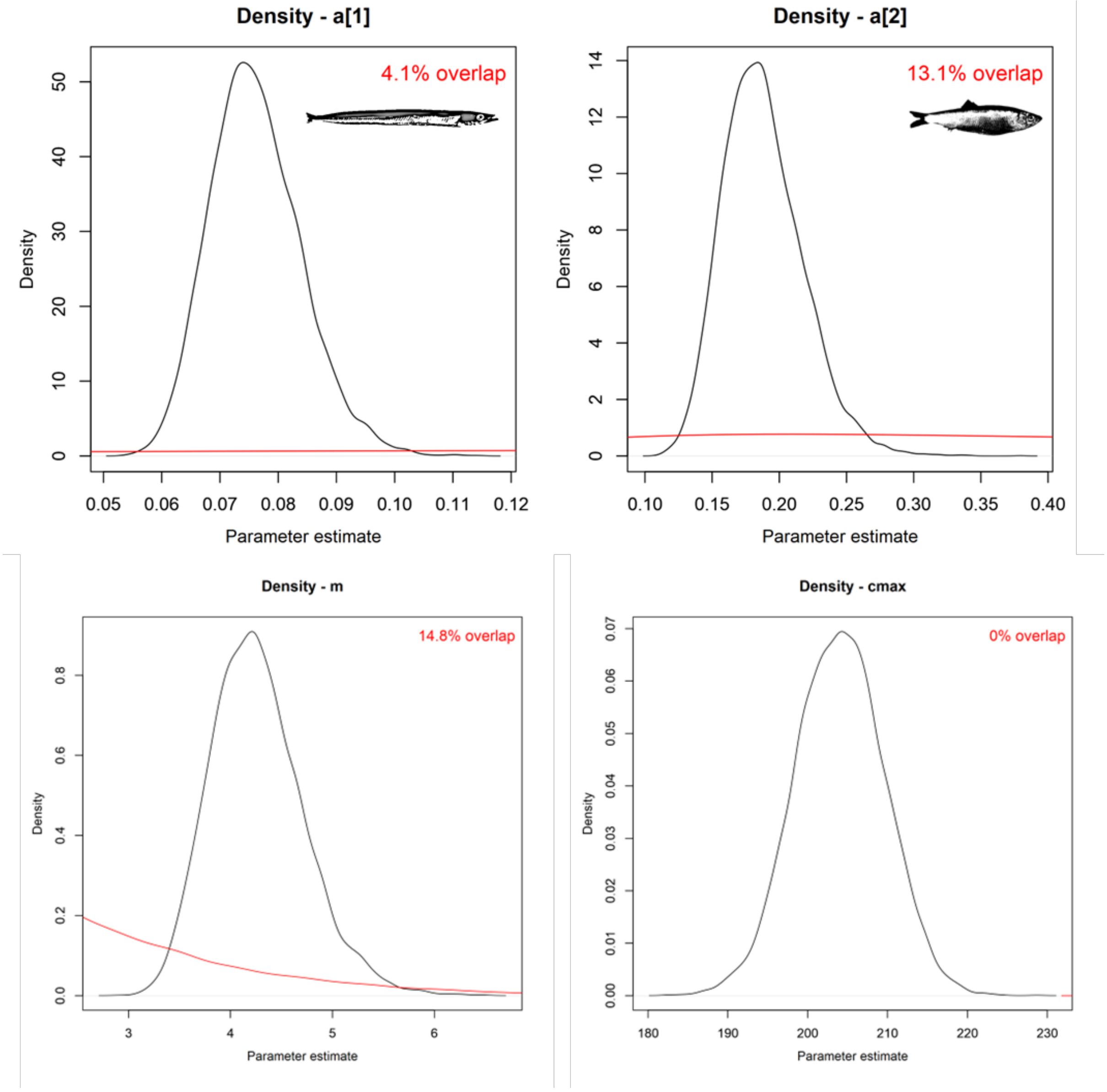


Figure S11. Prior posterior overlap plots showing the prior distributions (red) and the posterior distributions (black) of the estimated parameters from the model. the attack rate *a* is shown for sandeel (top left) and sprat (top right). The shared switching parameter *m* (bottom left) and the shared maximum consumption rate *cmax* (bottom right) are also shown The percentage overlap is shown in the top right.

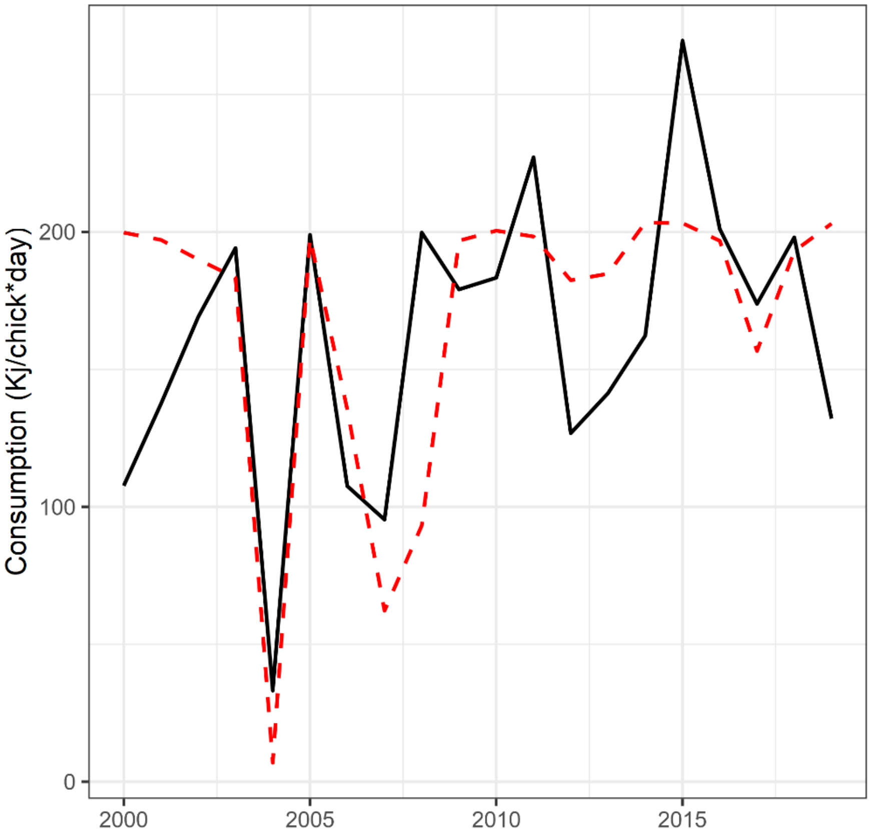


Figure 6

Figure S12. Comparison of the observed total consumption (black) and predicted total consumption (red).

4. Lower impact risk but higher spatial overlap of seabirds and anthropogenic stressors in a changing North Sea

4.1 Abstract

This study presents a cumulative stressor risk mapping analysis for seabirds and their key foraging zones in the Western North Sea, amidst increasing anthropogenic pressures. Using fine-scale distributions of sandeel and sprat, together with modelled at-sea distributions of three UK nesting seabird species: kittiwake, razorbill, and guillemot, we created a potential foraging habitat index by mapping the seabird-prey co-occurrence. We then examined foraging index overlap with current (2010-2014) and future scenarios, two based on planned and approve windfarms and no sandeel fishing (following the recent ban of sandeel fishing in the UK EEZ), and the third with the hypothetical continuation of sandeel fishing in the UK EEZ. Our findings indicate that the future windfarm scenarios, despite increasing the spatial overlap between seabird foraging areas and stressors, generally lead to a decrease in the intensity of cumulative stressor scores. This suggests a lower risk per affected area, with notable shifts in the location of high-risk overlap regions, especially within Marine Protected Areas (MPAs). Conversely, scenarios that maintain sandeel fishing show both increased spatial overlap and higher stressor index scores, indicating a potential for significantly greater impacts on seabird populations. The analysis underscores the ecological benefits of the UK's proposed sandeel fishing ban within its Exclusive Economic Zone (EEZ), highlighting the need for strengthened and standardized MPA protections to mitigate the multifaceted pressures seabirds face. Our work also calls for future research to refine the understanding of seabird-prey dynamics, the effectiveness of MPAs, and the implications of climate change, to better inform marine spatial planning and conservation strategies.

4.2 Introduction

Biodiversity is increasingly competing for space with a wide array of human activities (Jouffray et al., 2020). The use of marine space by human activities is growing drastically with the amount of global shipping increasing 4-fold since the 1990s (Tournadre, 2014), with global fishing capacity and effort peaking around 2010, but remaining at high levels (Bell et al., 2017). There are also several potentially conflicting targets being set for both marine protection and developing offshore wind to address both the biodiversity and climate crises. The Kunming-Montreal Global Biodiversity Framework has set a goal of protecting 30% of land and sea by 2030 (CBD, 2022) while COP28 agreed to triple global renewable energy capacity by 2030 (International Energy Agency, 2024). The cumulative effects of stressors are increasing worldwide (Halpern et al., 2015), but while studies have examined this on a coarse global scale (Halpern et al., 2008; O'Hara et al., 2024), finer-scale regional studies are required to study the particular species and issues of the area of concern (Brown et al., 2014).

The North Sea region is extremely developed with the legacy of offshore oil and gas platforms, an extensive fishing industry and some of the busiest shipping lanes in the world (Paolo et al., 2024). The region is an epicentre for existing and planned offshore wind production in the clean energy transition over the next several decades (Norrth Sea Governments, 2022). This dramatic increase in competition for space-use means there is a stark need for marine spatial planning to balance the needs of these economic activities with conserving biodiversity and de-carbonising targets in this region (Halpern et al., 2008).

The UK, and in particular Scotland, is host to internationally important seabird breeding colonies in summer months (Burnell et al., 2023). These colonies have been facing increasing pressure to successfully provision their chicks through reduced and variable prey availability (Fayet et al., 2021; Chapter 3) which is pushing adult energy budgets to their limits. The indirect trophic effects on seabirds are likely being driven from the bottom-up effects of climate change (Lindegren et al., 2018) and top-down pressure from industrial fisheries (Cook et al., 2014; Searle et al., 2023b), as well as extreme events (Frederiksen et al., 2008a) and disease (Lane et al., 2024). However, there are also anthropogenic stressors that can impact the adult birds directly such as offshore windfarms and commercial shipping. These may impact birds through direct collision, noise pollution, disturbance and avoidance of key habitat. Given the multitude of stressors, it is important to study the cumulative effects of these pressures to inform conservation management for seabird populations (Burthe et al., 2014).

Seabirds during the breeding season are central place foragers and thus are particularly sensitive to spatial pressures. In addition, many seabird species in the region rely on a key prey species, the lesser sandeel (*Ammodytes marinus*), which is patchily distributed, highly habitat specific, and relatively immobile as adults (Chapter 2). As a consequence, both predator and prey have very limited scope to relocate in response to the presence of a human pressure. The picture is complex however, as some species of bird in the region such as guillemot (*Uria aalge)* and razorbill (*Alca torda*) in the region have been able to switch to sprat (*Sprattus sprattus*) (Wanless et al., 2018), which is a more mobile species and thus potentially less sensitive to spatially static pressures. In addition, as sprat is a warm water species, sprat populations and bird species that can forage on them are likely to be less impacted by climate change (Lindegren et al., 2020). Given the importance of foraging for successful chick rearing (Chapter 3), the limited dispersal capacity of chick rearing seabirds and the possibility that these stressors can add to pressure that adult seabirds are already facing in adequately provisioning their chicks, it is vital for effective conservation management to consider how these cumulative effects overlap spatially with key seabird foraging areas during the breeding season (O'Hanlon et al., 2023).

Several studies have aimed to assess the spatial distribution of seabirds and the relevant stressors they face. However, a critical gap has been the accurate prediction of sandeel and sprat distributions, which are essential for understanding seabird foraging areas and their exposure to various stressors. Many spatial risk mapping studies in the North Sea have concentrated on direct impacts on seabirds themselves, particularly in relation to offshore wind farms (Bradbury et al., 2014; Fauchald et al., 2024; O'Hanlon et al., 2024) or combined wind farms and shipping (Leopold et al., 2015). More comprehensive multi-stressor studies either lack spatial specificity (Burthe et al., 2014) or are restricted to smaller areas within the region (Andersen et al., 2020). Attempts to identify seabird foraging areas using tracking data and hidden Markov models have faced significant uncertainty, highlighting the need for better predictive models (O'Hanlon et al., 2024). In Chapter 2, this gap was addressed by modelling the fine-scale spatio-temporal distribution of sandeel and sprat across the entire North Sea. By integrating these prey fish predictions with seabird density estimates at sea, it is possible to estimate key seabird foraging regions and assess how these overlap with anthropogenic stressors across the North Sea.

Seabirds have traditionally been assessed at sea using ship transect surveys, which then need to be appropriately modelled to give estimates of densities. This method has some uncertainty associated with the distance weighting functions applied to the seabird sightings and the assumptions of detectability proportional to distance. In addition, it is not possible to distinguish if the seabird is breeding or non-breeding. An alternative is to use tracking data to model colony foraging distributions. This approach is taken by Wakefield et al., (2017) which uses tracking data with estimates for maximum foraging ranges together with the assumptions that breeding foraging distributions are largely influenced by prey availability and competition from other foraging seabirds and other seabird colonies. We use this dataset for our analysis which models foraging distributions for common guillemots (*Uria aalge*), razorbills (*Alca torda*) and black-legged kittiwakes (*Risa trydactyla*). Data are based on tracking from the UK and Ireland and therefore the predictions are available only for the Western North Sea. This analysis is therefore limited to this region and focuses on UK breeding seabirds.

A second aim is to assess the extent to which key seabird foraging areas are contained within the current network of marine protected areas (MPAs), whether anthropogenic activities are continuing to occur within the MPA network, and whether regions of high stressor overlap are also covered by MPAs. The overlap of key seabird foraging areas and stressors within MPAs can be viewed as a positive, with minor adjustments to existing laws or management plans potentially sufficient to provide protection. On the other hand, a high degree of the high-risk zones being located inside these protected areas could signify a failure of the MPA network to offer protection to the seabirds, so called “paper parks” (Di Minin & Toivonen, 2015).

Two major changes to stressors affecting seabirds in the North Sea are expected in the near future. The first is a policy change where sandeel fishing has now been banned for inside English (https://www.gov.uk/government/consultations/consultation-on-spatial-management-measures-for-industrial-sandeel-fishing/outcome/government-response) and Scottish waters (https://www.gov.scot/publications/sandeel-prohibition-fishing-scotland-order-2024-final-business-regulatory-impact-assessment/). This is, however, being challenged by the EU and there remains significant uncertainty on the outcome of this decision. As sprat fishing only occurs in the Southern North Sea (Jennings et al., 2012), the seabird community that breed on the East coast of the UK, which primarily provision their chicks with sprat or sandeel, will potentially no longer be impacted from fishing. The second is the rapid energy transition, with a huge number of offshore windfarms planned for the North Sea as it has ideal shallow habitat (Norrth Sea Governments, 2022). We therefore investigate the effect that these two large-scale changes will have on the distribution of stressors and the degree of overlap with key seabird foraging areas. We also assess the overlap of this future scenario of stressors with MPAs to assess how effective current protected areas will be in future scenarios. We aim to identify hotspots of foraging habitat and hotspots of cumulative pressures and to quantify the impacts of sandeel fishing cessation and planned and approved windfarm designation on seabird foraging, to aid with future marine spatial planning in the region.

This study aims to address the critical knowledge gaps in seabird conservation within the North Sea by integrating prey distribution data into risk mapping and evaluating the effectiveness of Marine Protected Areas (MPAs). The research focuses on three key objectives:

1. **Risk Mapping**: Developing a comprehensive risk map for seabirds that incorporates the spatial distribution of their primary prey, sandeel and sprat, alongside anthropogenic stressors such as offshore wind farms and shipping lanes. This will help to identify key foraging areas and understand how they are impacted by human activities.
2. **Effectiveness of MPAs**: Assessing the current MPA network to determine its adequacy in protecting critical seabird foraging habitats. The study will evaluate whether existing MPAs cover high-risk areas where seabirds face significant stressors.
3. **Future Forecasting**: Projecting the future distribution of stressors, particularly in light of the anticipated increase in offshore wind farms and changes in fishing policies. This will involve forecasting how these developments might affect seabird foraging habitats and evaluating the future effectiveness of the current MPA network.

By addressing these aims, the research seeks to inform future marine spatial planning and enhance conservation efforts to protect seabird populations in the North Sea.

4.3 Methods

4.3.1 Study area

The North Sea is a semi enclosed relatively shallow shelf sea with a temperate climate, bounded on three sides in the Northwest of Europe. The surrounding coasts have very high population density with many commercial and industrial activities in the maritime area such as commercial fishing, renewable energy production, shipping, oil and gas extraction and sediment extraction (OSPAR, 2018). Due to available seabird data, we focus on the Western North Sea.

4.3.2 Data sources and processing

4.3.2.1 Seabird Distributions

Estimates of seabird density at sea during the breeding season were available for four species, common guillemot, razorbill and black legged kittiwake from the predictive modelling work of (Wakefield et al., 2017). Shags were excluded from this analysis due to their inshore foraging distribution, leaving three species of seabirds. The modelling framework uses poisson point process habitat use models that account for intra- and inter-species density-dependent competition and coastal morphology. The tracking data covers the period 2010-2014 and the predictions thus relate to this time period. Bird density predictions are available on a grid with a spatial scale of 0.027° × 0.021°; however, in order to match the scale of prey fish predictions the bird density data was rescaled to a resolution of 0.111° × 0.067°.

4.3.2.2 Prey Fish Distributions

Fine scale distributions of key prey fish in the North Sea, sandeel and sprat, were derived by using data from multiple surveys to model the distribution of fish biomass using Bayesian spatial GAMs with spatial random effects (Chapter 2). The model relates fish biomass to a suite of environmental covariates and accounts for spatial autocorrelation by approximating a smoothed Gaussian random field using a stochastic partial differential equation (SPDE) framework with a Mátern correlation. Temporal correlation in the data is accounted for by applying a random field for every year and linking them with an autoregressive order 1 (AR1) process.

The mean biomass of prey fish for the years 2010-2014 in a grid cell was weighted for each bird species by the mean proportion of the respective prey species in the diet provisioned to chicks at the Isle of May for the period 2010-2014 (Wanless et al., 2018)w (Table 2). This does not account for known spatial variability in seabird diets between colonies (Anderson 2014); however, data on the diet of kittiwake and razorbills are only available for the Isle of May from the long term UKCEH diet monitoring programme (Chapter 3). To maintain consistency with the other bird species we only used guillemot diet data from the Isle of May.

4.3.3 Foraging Index

We map the overlap of seabird density at sea with prey fish biomass to create an index of foraging habitat. This has the benefit of having data coverage in areas with no seabird tracking data. However, consideration needs to be taken that both sets of input data are modelled, and we do not have any ground truthing data to confirm if co-occurrence implies foraging and we keep this in mind when drawing conclusions from our results. The equation for the foraging index for each seabird was set as follows:

$$F_i = S_i \times \sum i\ (B_{sandeel}\ x\ D_{sandeel}) + (B_{sprat}\ x\ D_{sprat})$$

Where F_i the foraging index at location *i*, S_i is the seabird density at location *i* multiplied by the sum of $B_{sandeel}$ the sandeel biomass at location *i* weighted by $D_{sandeel}$ the proportion of sandeel in the diet plus B_{sprat} the sprat biomass at location *i* weighted by D_{sprat} the proportion of sprat in the diet. This is repeated for each seabird species.

4.3.4 Stressor Datasets

Following the methods of Halpern et al. (2008), all datasets were normalised using a log transformation and standardised between 0 and 1 to down weight extreme outliers and make the datasets comparable. Bird density predictions from Wakefield et al. (2017) were available for the time period 2010-2014 and all subsequent datasets of prey fish and stressors are therefore matched to, or as close as possible to, this time period.

For every stressor we had a corresponding vulnerability score to weight the potential impact of the stressor for each seabird species. This was either taken from other studies which quantitatively ranked species vulnerability to a stressor, or for the case of climate change we developed our own semi-quantitative ranking. For the weighting taken from quantitative studies the species vulnerability value was scaled by the maximum vulnerability score in the analysis giving a score of between 0 and 1. A schematic of the analysis components is shown in Figure 19.

4.3.4.1 Sandeel Fishing Pressure

Fishing pressure in the North Sea is of most concern for indirect resource competition effects. We consider only sandeel fishing, as sprat fishing occurs mostly in the Southern North Sea. Sandeel fishing pressure data was available from the Scientific, Technical and Economic Committee for Fisheries (STECF) website (https://stecf.jrc.ec.europa.eu/dd/fdi), which is a database of EU member state landings data. We used the biomass of sandeel landings as a measure of fishing pressure. Data closest to the study range was available for the years 2013-2016 and we took the sum of the landings per grid square across these years. Fisheries landings data is sensitive data and is published on a coarse scale of 1° × 0.5°, which represents the coarsest scale data in the analysis. We resampled the data onto a finer grid to match the other datasets with a spatial scale of 0.111° × 0.067°, where every smaller grid cell inside each larger coarse grid cell was assigned the value for the larger grid cell.

Weighting of seabird sensitivity to sandeel fishing was taken from (Furness & Tasker, 2000) which weights the vulnerability of seabird species to sandeel depletions by the industrial fishery based on biological traits (Table 2).

4.3.4.2 Windfarm Turbine Density

We used a recently published database of individual wind turbine spatial locations (Martins et al., 2023). This allowed calculation of windfarm density on a comparable scale to the other data. we used all of the windfarm data within this dataset which includes windfarms constructed up to and including 2021, this was not fully matched to the study period of 2010-2014 but as these structures have such a permanent position, we wanted to fully represent the current distribution, to compare the differences from the full current situation to future planned and approved windfarms. From this dataset we calculated the density of wind turbines per grid square with a spatial scale of 0.111° × 0.067°. This dataset only includes existing installations and does not include windfarms currently under construction.

Much focus and debate has taken place on the potential impact of windfarms on seabirds. It is generally recognised that two major impacts affect seabirds, collision and displacement (Searle et al., 2023a)s. As both of these are relevant to foraging seabirds, we included both in our analysis. Seabird vulnerability scores were taken from (Bradbury et al., 2014) and the scores for collision and displacement were combined into a single vulnerability weighting index (Table 2).

4.3.4.3 Shipping Density

Shipping traffic has the potential to disturb birds attempting to forage. Shipping occurs at a massive scale across the North Sea, and two of the largest shipping ports in the world, Rotterdam and Hamburg, are located on North Sea coasts (OSPAR, 2018). Shipping occurs in predefined shipping lanes and the density of boats in these areas can cause disturbance to foraging seabirds (Fliessbach et al., 2019). Shipping density data was taken from the EMODnet Human Activities Vessel Density dataset (https://emodnet.ec.europa.eu/en/human-activities) for the years 2017 to 2019, as this was the closest available data to the study period, taking the mean ship density per grid cell. The database contains all ship types and we decided to include them all as they all pose a disturbance risk to seabirds. The dataset has a spatial scale of 1km × 1km and we resampled the data by taking the sum of the finer grid cells onto a coarser grid to match the other datasets with a spatial scale of 0.111° × 0.067°. The vulnerability scores for shipping disturbance were taken from Fliessbach et al. (2019) and used as the weighting for the shipping stressor variable (Table 2).

4.3.4.4 Climate Change

There are many ways to spatially represent climate change. Here we use the linear change over time in sea surface temperature (SST) in degree Celsius. To calculate this metric we used the Copernicus Atlantic- European North West Shelf- Ocean Physics Reanalysis dataset (https://www.copernicus.eu/en) to extract SST mean monthly values for the years 1993 to 2020, we then took the mean value across the whole year giving an annual mean value per pixel with a spatial scale of 0.111° × 0.067°. We selected the whole year as we wanted to capture temperature change across the annual cycle, where seabird prey may be impacted by previous winter conditions. This gives a time series of 28 years to enable enough data to capture climatic trends. Using this data, we fitted a linear model of SST as a function of year for each grid cell, and we used the slope of this fitted model as the index of temperature change for that cell, multiplied by 10 to give change in SST per decade.

Climate change can impact seabirds through bottom-up effects on their prey (Frederiksen et al., 2013), and we therefore create a climate changing weighting by ranking seabird sensitivity by the proportion of sandeel in the diet for the years 2010-2014. This is because, as cold-water species, sandeel are expected to be more negatively impacted by climate change in the North Sea than the more southerly, warm-water sprat (Russell et al., 2015). Climate sensitivity is therefore defined as the proportion of sandeel in the diet of the seabird species: a species 60% by weight of sandeel in their diet will be assigned a climate sensitivity weighting of 0.6. Again, to maintain consistency between bird species, we only used diet data from the Isle of May when calculating the climate sensitivity weighting for the climate change index.

4.3.5 Cumulative Stressor Index

The cumulative stressor index is defined as the sum of the stressor values weighted by their respective vulnerability scores:

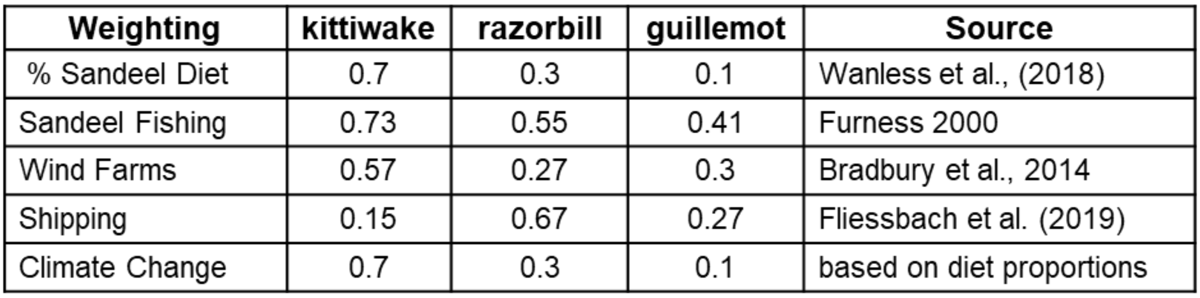
$$CS_i = \sum i \, (Str_{ship} \times W_{ship}) + (Str_{fishing} \times W_{fishing}) + (Str_{wind} \times W_{wind}) + (Str_{temp} \times W_{temp})$$

Where CS_i is the cumulative stressor index at location i which is defined as the sum of the stressor values Str_x multiplied by their respective weights W_x. This is repeated for each seabird species.

4.3.6 Identifying Hotspots and Quantifying Overlap

We identified the hotspots of the foraging and stressors for each seabird species as those grid cells at or above the 90th percentile for both the foraging index and the stressor index for each scenario. In this analysis we define four scenarios, the current based on data from, or as close as possible to 2010-2014, and three future scenarios which apply different levels of sandeel fishing and windfarm development, these are described in detail in the net section. The results grids were categorized as “none”, “Foraging” hotspot, “Stressor” hotspot, and if a grid cell was both a foraging and stressor hot spot the grid cell was categorized an “Overlap” hotspot. Hotspot and overlap maps were made for each species. While identifying stressor hotspots required us to have a relative threshold for each scenario, we were able to sum the total stressor index value for pixels that overlapped with foraging hotspots to give an estimate of absolute stressor pressure and the temporal trends into the future. The study area is defined by the dataset with the smallest spatial extent, which is the UK seabird density model outputs from Wakefield et al. (2017), which is larger for kittiwakes compared to the two auk species based on their foraging range.

Table 2. Sensitivity weighting scores for each species and associated stressor used in this study ranging from 0 to 1, listing the source of the data.



Weighting	kittiwake	razorbill	guillemot	Source
% Sandeel Diet	0.7	0.3	0.1	Wanless et al., (2018)
Sandeel Fishing	0.73	0.55	0.41	Furness 2000
Wind Farms	0.57	0.27	0.3	Bradbury et al., 2014
Shipping	0.15	0.67	0.27	Fliessbach et al. (2019)
Climate Change	0.7	0.3	0.1	based on diet proportions

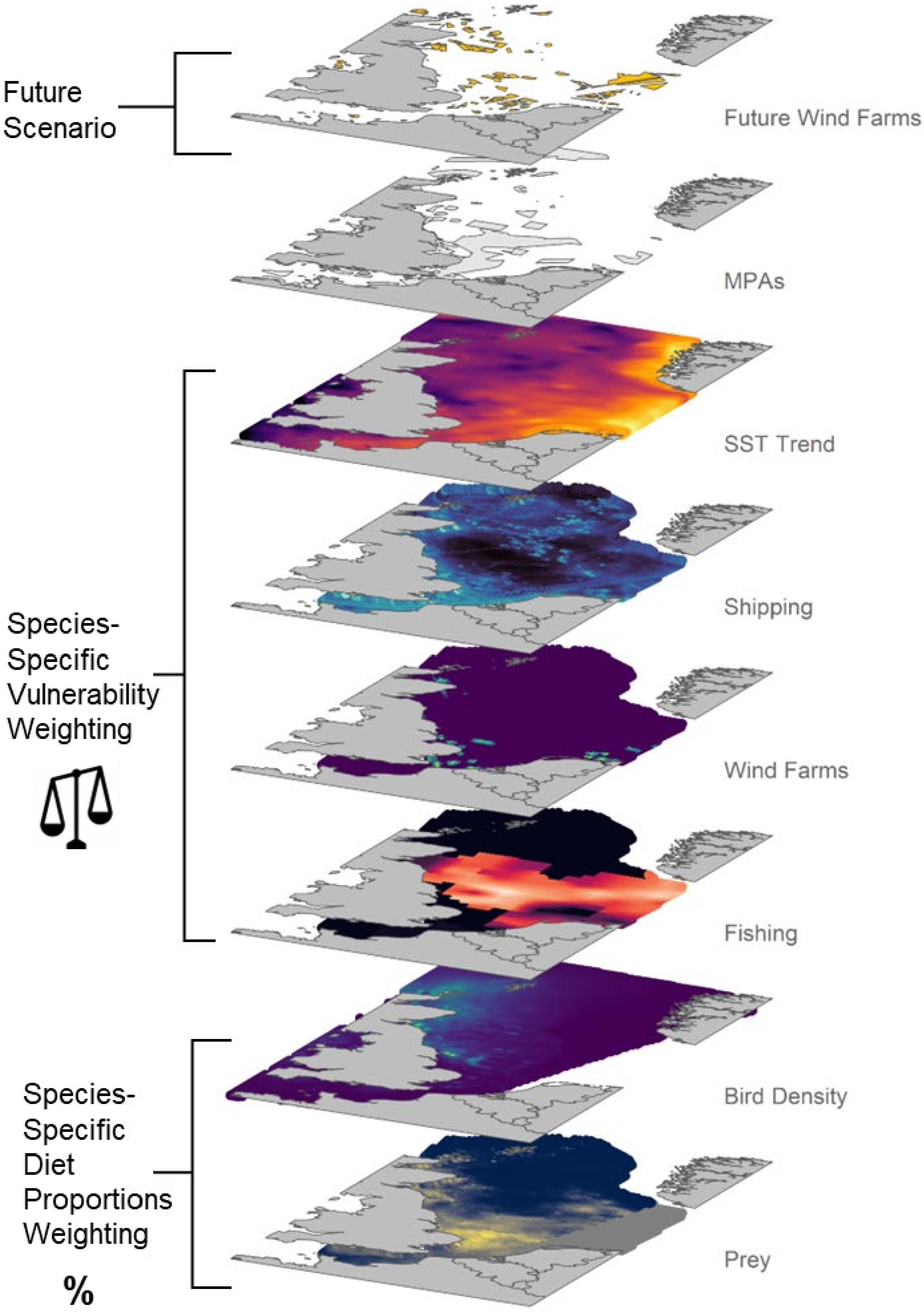


Figure 19. Schematic of the analysis. Prey weighting is the numerical proportion of each prey in the diet of seabirds breeding on the Isle of May for the years 2010-2014. Species vulnerability proportions are either quantitatively estimated in other studies, or in the case of SST we use a semi-quantitative weighting based on potential climate risk to prey species (i.e. cold-water sandeel vs warm-water sprat).

We quantified the extent to which these hotspots coincided with MPA coverage by calculating the percentage of grid cells from each hotspot category that fell within an MPA. Data on the spatial distribution of MPAs was obtained from the Protected Planet European region (https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas). MPAs have different protection status; however, to simplify the approach we were not able to account for this in our analysis, and all MPAs were treated the same, regardless of whether the particular protected area offered real benefit to a foraging seabird or their prey species.

4.3.7 Future Scenarios

We constructed three future scenarios to represent the two large changes to the Anthropogenic seascape planned for the North Sea. The first stressor change is the banning of sandeel fishing inside the UK exclusive economic zone (EEZ) from the 26th March 2024. For kittiwake, which have a greater maximum foraging distance than the other two species, extending beyond UK waters, some areas on the edge of the potential distribution for UK breeding birds may still overlap with fishing activity. However, the bird density predicted this far out to sea during the breeding season is very low, and a central-place foraging kittiwake would only rarely travel that far to provision a chick. For this reason, these peripheral sections were ignored, and fishing was totally removed from both windfarm only future scenarios.

The second large change is the rapid expansion of windfarm renewable energy infrastructure across the North Sea as part of the energy transition. Future windfarms can be divided into two categories: ‘Approved’, which are those approved and/or under construction, and ‘Planned’, which are those where planning has not yet been approved. There is uncertainty over which Planned windfarms will be approved, so this represents a “potential” scenario. The future windfarms dataset was obtained from the EMODnet Human Activities windfarm dataset (https://ows.emodnet-humanactivities.eu/geonetwork/srv/api/records/8201070b-4b0b-4d54-8910-abcea5dce57f). Some windfarm entries in the database had information on the number of turbines, and taking this with the total area of the future windfarm we calculated a turbine density. Some entries had no information on turbines but did have information on total power output in megawatts (MW). We therefore used the linear relationship between power output and number of turbines, where both figures were available, to estimate number of turbines from power output data alone. As turbines are increasing in size and efficiency, impacting the layout of modern windfarms, we used only data from 2016 onwards to model the turbine number-power relationship. The predicted number of turbines was then converted to turbine density using the proposed windfarm area. For the remaining data still missing information on density we used the mean turbine density within existing windfarms. For the future windfarm grid cells with recorded or predicted wind turbine density this was scaled to the area of the grid cells of the previous analysis which was 0.111° × 0.067°. The future windfarm polygons were then mapped onto the analysis grid, where every grid cell within a windfarm polygon was assigned either the recorded density, predicted density or the mean density of wind turbines.

With these future changes we constructed three future scenarios. The first ("Approved") scenario contained no sandeel fishing with approved and under-construction windfarms added to the stressor index. The second ("Planned") scenario contained no sandeel fishing with approved, under-construction and planned windfarms added to the stressor index. The Third ("Fishing") scenario contained the full windfarm scenario together with the continuation of current sandeel fishing. This will allow us to test the possible impacts of sandeel fishing cessation in the UK EEZ, compared to a scenario without the fishing ban. The remaining data, namely, seabird and prey fish distributions and shipping are assumed to remain constant for the future scenarios. Shipping is unlikely to change drastically as it follows predetermined shipping routes, while the linear trend in SST representing climate change already contains information on the temporal trend and thus should have some relationship to future climate change, at least over the short term. There is a high probability that seabird foraging, and prey fish distributions will change, but in the absence of future modelled datasets, and the uncertainty that would come from forecasting biological populations, we make the assumption for this analysis that they will remain the same. The full analysis was run for all three future scenarios, calculating and mapping hotspots as well as quantifying MPA overlap.

4.3.8 Overall Stressor Index Score

While the identification of hotspots required relative thresholds for each species and scenario, thus making it inappropriate to compare between species or scenarios, we could separately quantify the absolute stressor index scores to enable comparison. We did this by summing the stressor index scores for every pixel identified as important seabird foraging habitat, i.e. the "Foraging" and "Overlap" hotspot categories identified above. We repeated this for every species for each scenario. The results were plotted in a grouped bar chart. For the current scenario, which does not involve assumptions of stressors, we also quantified the relative contribution of each stressor (weighted by sensitivity score) to the total summed stressor index for each species, standardised between 0 and 100 for each species.

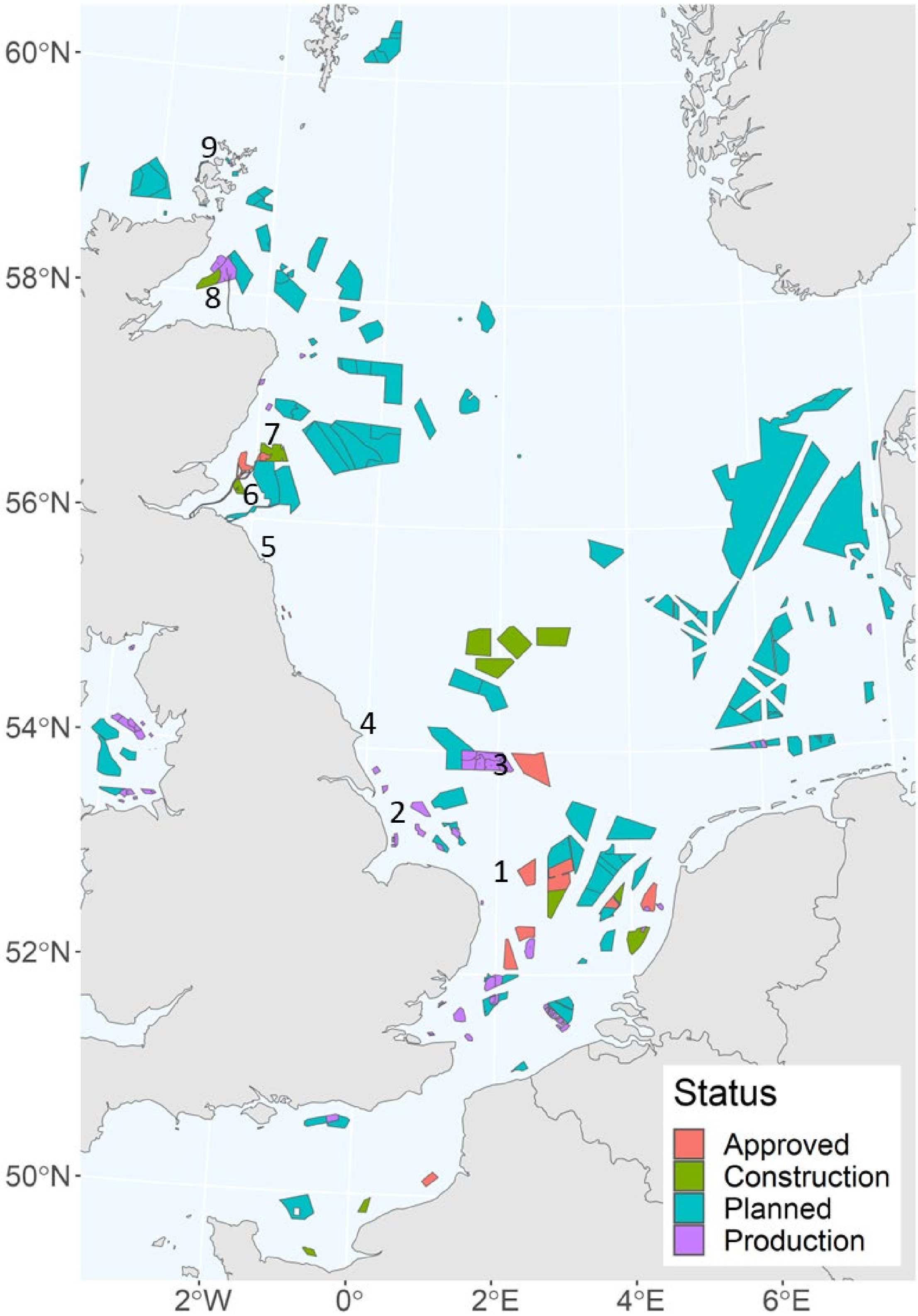


Figure 20. Map of current and future windfarms across the greater North Sea with the colour of the polygon signifying the status of the project. Data is from the EMODnet Human Activities windfarm dataset. The current situation is composed of the "Production" windfarm category, the future approved scenario is composed of the "Approved" and "Construction" categories and the future planned scenario is composed of the "Approved", "Construction" and "Planned" categories. 1 – Norfolk Banks, 2 – Inner Silver Pit, 3 – Outer Silver Pit & Hornsea windfarm, 4 – Flamborough Head, 5 – Farne Islands, 6 – Firth of Forth, 7- Greensea windfarm, 8 – Moray East and West windfarms, 9 – Orkney Islands

4.4 Results

4.4.1 Identifying hotspots and Quantifying Overlap

4.4.1.1 Current Situation

Seabird density was broadly similar for all three species, along the East coast of Scotland from the Orkney Islands to the East Anglian coast, with kittiwake having a more pelagic distribution and the auk species a relatively more coastal distribution (Figure 21). In the current situation kittiwake overlap with hot spots of stressors occurred between the Norfolk Banks and the Outer Silver Pit (Figure 21; see Figure 20 for locations), known sandeel fishing grounds in the southwestern North Sea (Jensen et al., 2011) as well as the Hornsea 1 windfarm (Figure 20; see Figure 20 for locations). The auk species both displayed a similar foraging distribution with razorbills slightly more coastal than guillemots. They both however had the same hotspots of stressor overlap, occurring in a coastal zone surrounding the Farne Islands stretching along the northeastern English coast and in a more offshore zone adjacent to Flamborough Head on the central eastern English coast (Figure 21; see Figure 20 for locations). Small, localized pixels of overlap were identified for kittiwakes in the southwestern Dogger bank and for the auk species in the northern Moray firth and on the coast near Aberdeen.

In general seabird foraging hotspots had a low spatial overlap with stressor hotspots, occurring at <5% of identified foraging hotspots (Table 3). The highest was for guillemots (4.89%), followed by razorbills (3.71%) and then slightly lower for kittiwakes (3.43%). Of the three bird species, kittiwakes consistently had the highest overlap between MPAs and both foraging hotspots and overlapping foraging and stressor hotspots. In the current situation the prevalence of stressor hotspots within MPAs was highest for guillemots, followed by razorbills and then kittiwakes (Table 3).

4.4.1.2 Future Scenarios

In both of the windfarm only future scenarios overlap locations were generally similar, with slightly more sites in the planned windfarms overlapping with foraging hotspots such as the Seagreen 2 and 3 windfarms (Figure 21; see Figure 20 for locations). All seabird species had considerable future overlap in the northern Moray Firth with the Moray West and Moray East windfarm sites, as well as the Firth of Forth region (Figure 21; see Figure 20 for locations). Kittiwakes also had future overlap hotspots around the inner silver pit which contains operational windfarms; however, with the removal of sandeel fishing, these windfarms have now been upweighted and included as stressor hotspots, which was not the case in the current situation analysis (Figure 21; see Figure 20 for locations). Both auk species saw decreases in overlap areas occurring on the English coasts with only small, scattered overlap locations along the coast.

Future windfarm only scenarios generally saw a 2- to 3- fold increase in the overlap of seabird foraging and stressor hotspots ('% stressor overlap', Table 3). For kittiwakes this was markedly higher for the future scenario including planned windfarms than for the scenario of only approved windfarms. For guillemots there was a slightly higher overlap in the future planned scenario, while for razorbills both future scenarios lead to similar levels of stressor overlap. All species saw a large decline in the stressors overlap occurring within marine protected areas ('% overlap MPA coverage', Table 3). Coverage was lowest in the future planned scenario, except for kittiwakes that had lowest overlap MPA coverage in the future approved scenario. The prevalence of stressor hotspots within MPAs was predicted to decrease in future scenarios for all species. In the future windfarm only scenarios the prevalence of stressor hotspots within MPAs was reversed, and it was predicted to be highest for kittiwakes, by a small margin.

The future fishing scenario spatial overlap percentages generally displayed a average situation between the current scenario and future windfarm only scenarios for all three species. There was higher stressor overlap percentages, but not as high as the windfarm only scenarios, and lower overlap hotspots and stressor only hotspots occurring inside MPAs, but with only modest decreases compared to the windfarm only scenarios (Table 3).

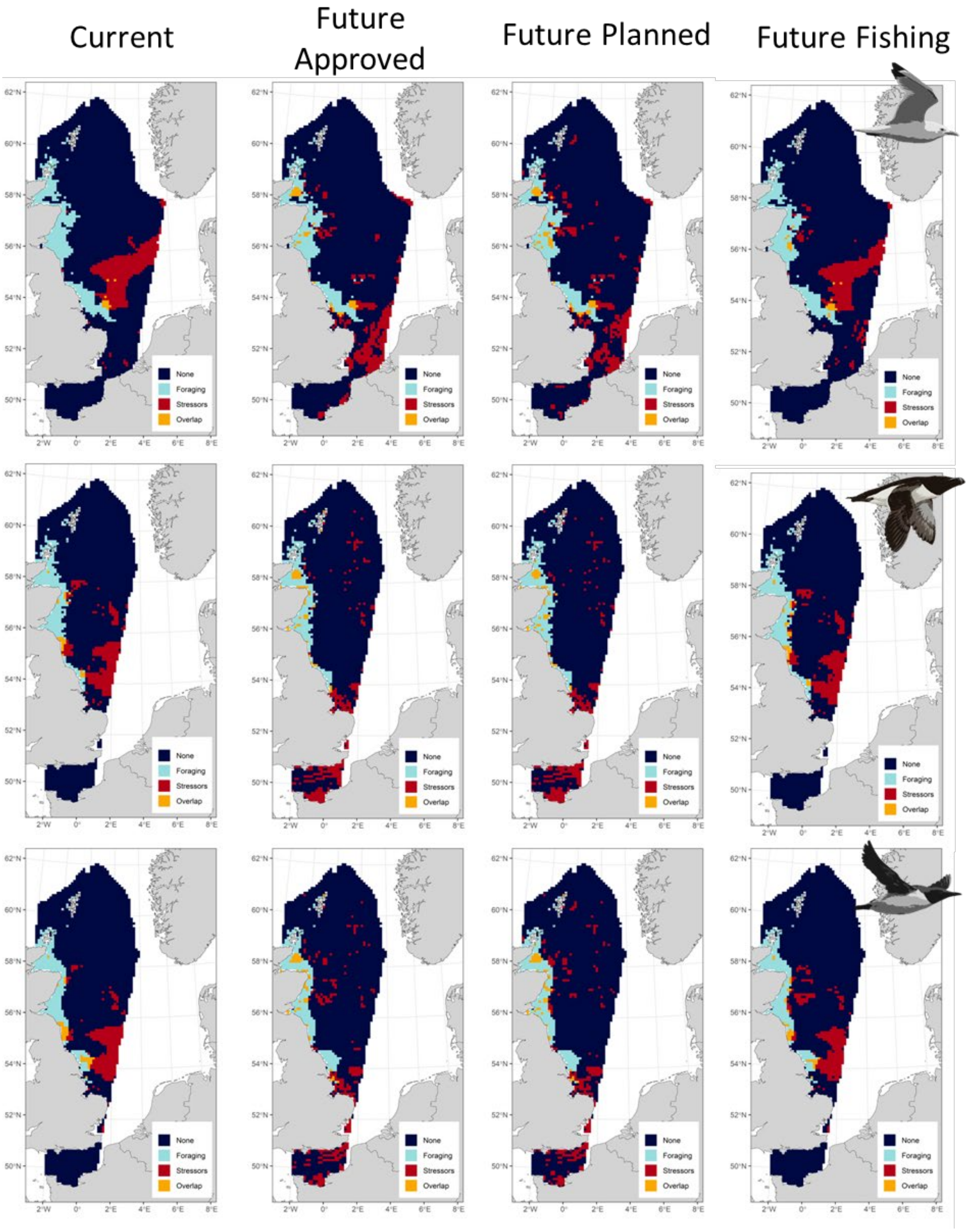


Figure 21. Stressor index overlap hotspots maps for kittiwake (top), razorbill (middle) and guillemot (bottom) across the current situation and future scenarios. Navy blue areas have neither hotspots present, light blue areas indicate foraging hotspots, red areas indicate stressor hotspots and orange areas denote overlapping stressor and foraging hotspots. Hotspots are identified for each scenario and indicate what areas are of concern for that moment in time.

Table 3. Percentage overlap of foraging hotspots and stressor hotspots, the prevalence of these overlap locations within MPAs and the prevalence of stressor hotspots that do not overlap with foraging hotspots within MPAs. Values are shown for all 3 species, each across the current state and future scenarios.

	Kittiwake				Razorbill				Guillemot			
	Current	**Future Approved**	**Future Planned**	**Future Fishing**	**Current**	**Future Approved**	**Future Planned**	**Future Fishing**	**Current**	**Future Approved**	**Future Planned**	**Future Fishing**
% stressor overlap	3.43	11.77 (+243%)	14.95 (+336%)	6.37 (+86%)	3.71	15.54 (+319%)	15.2 (+310%)	11.49 (+210%)	4.89	15.31 (+213%)	16.61 (+240%)	11.73 (+140%)
% overlap MPA coverage	71.43	22.92 (-68%)	27.87 (-61%)	61.54 (-14%)	44	15.22 (-65%)	13.33 (-70%)	41.18 (-6%)	34.88	17 (-51%)	15.69 (-55%)	30.56 (-12%)
% stress MPA coverage	50	38.33 (-23%)	34.58 (-31%)	47.38 (-5%)	54.61	34.4 (-37%)	33.86 (-38%)	54.58	60.99	31.92 (-48%)	32.42 (-47%)	56.83 (-7%)

4.4.2 Overall Stressor Index Score

In the current situation kittiwakes had a substantially higher index of stressor overlap, followed by razorbills and guillemots having considerably lower stressor index values (Figure 22). All species were projected to have lower overall values of the stressor index in the Future Approved and Future Planned scenarios, with the decline particularly marked in kittiwakes, where the stressor index becomes much closer to that of razorbills in both future windfarm only scenarios. Both of these scenarios had the same stressor index value for guillemots and razorbills, while kittiwakes had a slighly higher stressor index in the full future planned scenario over the future approved scenario. The Future Fishing scenario had a greatly higher total stressor index score, especially for kittiwake which has the highest estimated sensitivity to sandeel fishing. This shows that for all three bird species sandeel fishing had the largest impact on the future scenario changes stressor index scores.

Looking at the breakdown for the current scenario, we see that for kittiwakes sandeel fishing and climate change are the two biggest components of the total stressor index, followed by shipping and then windfarms (Figure 23). Razorbills were most exposed to shipping, followed by climate change, sandeel fishing and then windfarms. The stressor index for guillemots had the largest influence from shipping, followed closely by sandeel fishing, then climate change and windfarms.

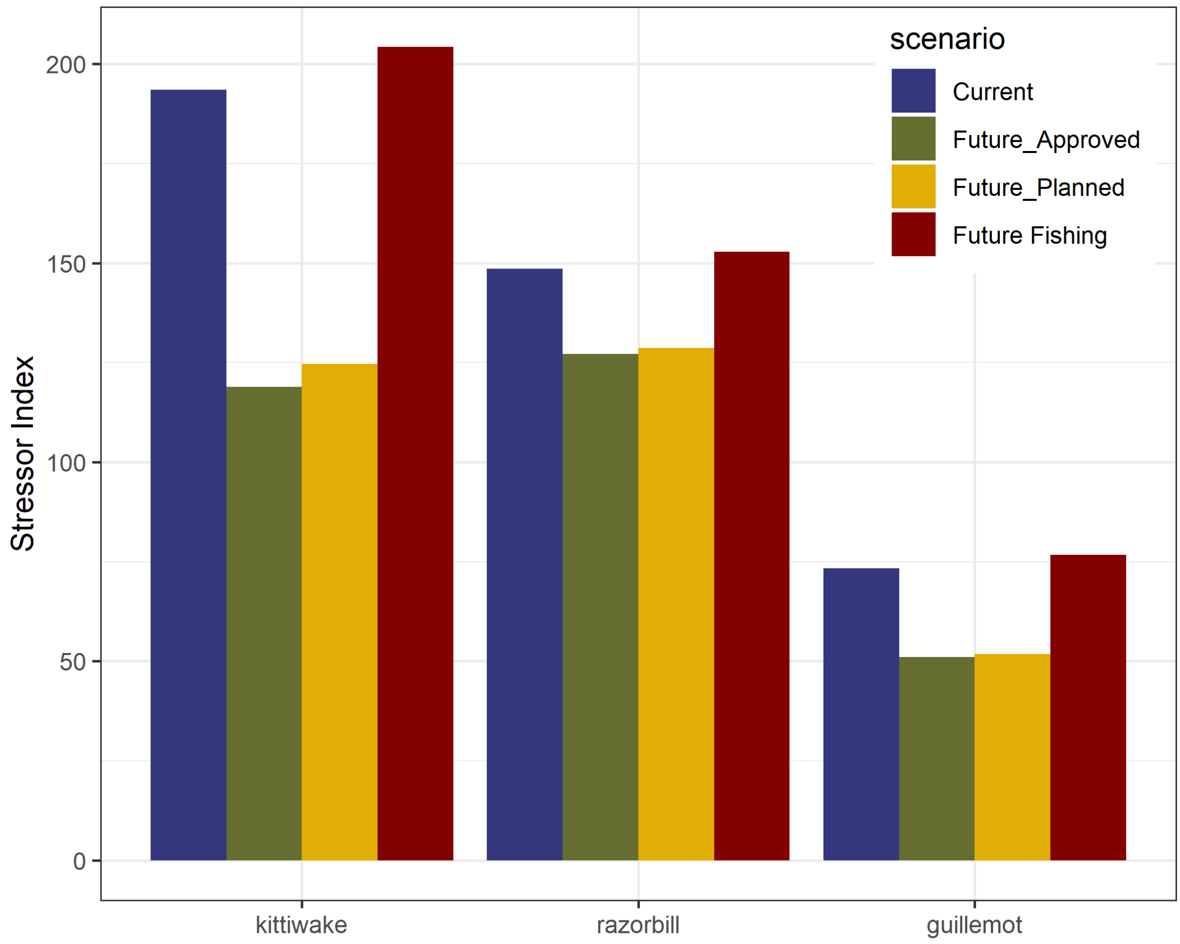


Figure 22. Total summed stressor index values for all pixels identified as key seabird foraging habitat ("Foraging" and "Overlap" categories) for the three species and four scenarios. These indexes are not relative and allow comparison between scenarios and species.

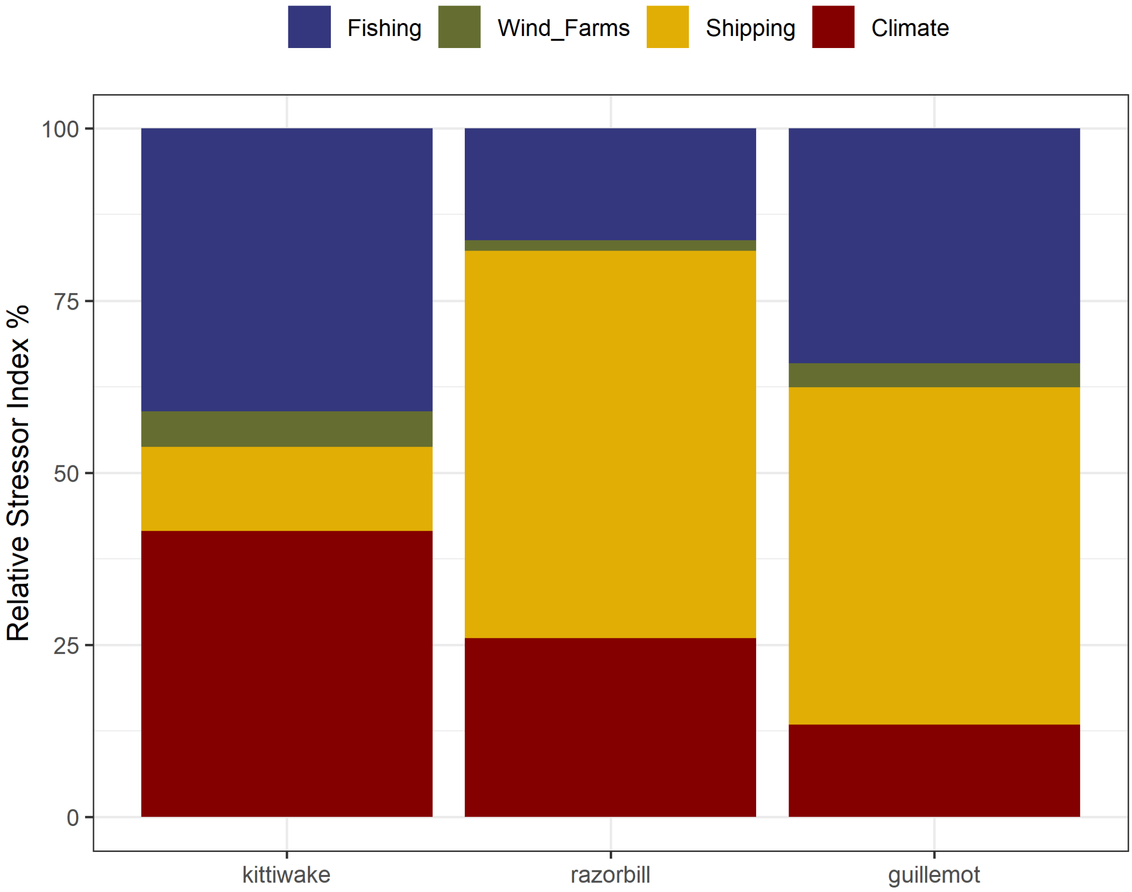


Figure 23. Relative contribution (%) of each weighted stressor to the total summed stressor index in the Current scenario for all pixels identified as a foraging hotspot ("Foraging" and "Overlap" categories), for each bird species.

4.5 Discussion

Here we provide the most comprehensive cumulative stressor risk mapping analysis for seabird and their key foraging zones in the North Sea to date. Given the major concerns for the impacts of breeding season prey shortages, our analysis has focused on potential foraging hotspots, and not only the distribution of the foraging seabirds themselves. This has been enabled by the availability of fine-scale distributions of sandeel and sprat. In the future windfarm only scenarios, despite a 3-to-4-fold increase in spatial overlap of seabirds and their relative stressors, there was a decrease in the intensity of the stressor index scores across the overlap regions, indicating a lower risk for impact. The regions where these high-risk overlap areas occur is predicted to change with a significant decrease of occurrence within MPAs. This is likely driven by the fact that fishing, which dominated the current scenario, is more prevalent inside MPAs in the region as they only restrict very specific anthropogenic activities, while windfarm designation has a lower co-occurrence with MPAs.

Given the current policy situation, the UK EEZ sandeel fishing ban, while being contested by the EU, is expected to come into effect and seabird stressors will transition from a fishing-dominated to a wind-dominated environment. This was represented by our two future wind farm only scenarios (“Approved” and “Planned” scenarios), which generally resulted in a larger spatial overlap but lower total risk score, giving a lower impact per pixel as well as a lower impact for the region as a whole. There were some species-specific patterns to this based on species-specific foraging range and sensitivities to certain stressor, however, broadly they followed the same trend. In our hypothetical future fishing situation, which contained both all potential windfarm developments and the continuation of sandeel fishing within the UK EEZ, there was both an increase in spatial overlap and total stressor index score for all species. This suggests a double impact of both increased overlap and severity, and thus the potential for greatly increased impact on the seabird populations. This analysis provides evidence for the benefit of the sandeel fishing ban in the UK EEZ, as a means to greatly reduce anthropogenic impact on seabirds that are facing a multitude of increasing pressures.

Identifying key foraging areas for predators is a key concern for conservation, yet this has remained difficult in practise, likely due to a number of factors influencing predator distribution and decision making. Previous methods have explored hidden Markov models using telemetry data but this had high uncertainty (O’Hanlon et al., 2024). Here we take another approach by applying modelled distributions of seabirds at sea and combining them with modelled distribution of prey biomass. However, prey distribution might not be directly related to seabird distribution, it is also related to prey availability, which is influenced by stratification, depth and shoal size (Cox et al., 2013; Waggitt et al., 2018). Despite this, other studies have shown prey abundance to be the best predictor of seabird density (De La Cruz et al., 2022). Thus, there remains uncertainty in the relationship between seabird distribution and prey density, and the ability to weight the prey distribution by some spatial estimates of availability would be key future work.

The hotspot analysis required using relative thresholds, therefore for each time period the overlap hotspots indicate the areas of high stress relative to the specific time period, thus only the distribution is comparable, and the absolute values are not. We also performed a separate non-spatial comparison of total stressor index. In all instances the stressor index was lower in the future scenarios with the cessation of sandeel fishing, even with the projected increase in windfarms (Figure 22). This is evident with the English Channel shipping lanes identified as stressor hotspots for both auks only in the future scenarios in the absence sandeel fishing (Figure 21). This is due to the high impact that sandeel fishing is estimated to have on sandeel dependent seabirds, with greatly increased stressor index scores for the future fishing scenario. However, we can't rule out the bias introduced by the coarse scale of the sandeel landings data, available only at a half a degree scale. This likely inflates the spatial distribution of the sandeel fishing activity which likely acts at a more confined locality (Jensen et al., 2011). Therefore, future work with access to Danish VMS data (as Denmark has the majority of sandeel quota in the North Sea) would greatly improve the analysis of sandeel fishing spatial impact on seabirds. Despite this we are still able to identify the relative distribution of the seabird foraging stressors and their hotspots which is available to inform future marine spatial planning decisions.

A key consideration in our work is the fact that only kittiwake in the western North Sea have been shown to be directly impacted by sandeel fishing (Cook et al., 2014; Searle et al., 2023b), while auks, through behavioural changes or diet switching to sprat, have been able to buffer declines in breeding success (Searle et al., 2023b). This was explicitly shown for guillemots in chapter 2 with dynamic functional responses being able to buffer declines in a single prey species. The seminal work of Furness and Tasker (2000) which quantified seabird sensitivity to reductions in sandeel abundance is relatively old at this stage and was conducted before the diet transitions of guillemots and razorbills to sprat dominated diets. Daunt et al. (2008) recalculated this sensitivity score based on more recent diet proportions of sandeel, but at this stage there had only been a few years of high sprat consumption rates and taking a mean diet proportion they still calculated 84% of guillemot chick diet to be composed of sandeel. Guillemot chick diets on the Isle of May from 2010 to 2014 had a mean portion of 10% sandeel, while razorbills have fluctuated with much greater but had a mean proportion of 30% sandeel (Table 2). Thus, if the sensitivity scores were recalculated, they would likely significantly reduce the impact of sandeel fishing calculated here within the stressor index, especially for guillemot. Future work should focus on updating this sensitivity index to have a more accurate estimation of sandeel fishing impact.

While we looked at the direct spatial overlap of sandeel fishing and potential seabird foraging areas, it is possible that fishing could be a more diffuse effect impacting the local sandeel population dynamics. Sandeel are relatively immobile as post-settlement (Johnsen & Harbitz, 2013) and this is illustrated by the fact that Norway currently manages its sandeel fishery on a sub-regional sandbank-complex basis (Johannessen & Johnsen, 2015). This would suggest a direct spatial footprint of sandeel fishing impact. However, sandeel larvae are capable of greater dispersal by ocean currents, and it's possible some sandbanks could be source populations of productivity for surrounding habitat (Allgayer et al., 2024). Therefore, fishing on high productivity sandbanks may have farther reaching impacts. Thus, there is still large uncertainty in sandeel recruitment and spatial dynamics, where greater understanding of the elusive details of these processes will improve the required understanding of sandeel ecology needed for effective conservation measures.

All MPAs were included here, but there is a wide variety of MPA protection categories and MPAs may be designated to protect different priority features, thus only activities deemed to impact the specific priority feature would be prohibited (Dudley, 2008). This is a limitation of our study as we were not able to account for protection status of the MPAs included in the analyses. Future work focusing on delineating the MPAs that would afford protection to seabird and their key foraging areas would be of great benefit. Our work does however highlight the need to strengthen and standardise protection afforded by an area designated as an MPA. In fact, the UK seabird census has shown that seabirds have been declining in SPAs as well as outside them, therefore current seabird protection measures have not been fully successful (Burnell et al., 2023). As we strive towards international biodiversity targets of 30% of land and sea protection (CBD, 2022), there may need to be a shift to a more holistic focus on MPAs as areas of total protection with the prohibition of all potentially damaging or extractive activities.

The future scenario analysis only contains updated data for fishing and windfarms, and we had to make assumptions on the stability of other distributions such as prey fish, seabirds and shipping for this analysis. However, these elements, especially the biological component are variable in relation to a constantly changing environment and the inclusion of future predictions would be of great benefit for informing marine spatial planning decisions. Ecological forecasting is difficult (Payne et al., 2017) due to the uncertainty in predicting complex physical systems how animals might respond to those changes. This represents an exciting frontier for ecological modelling work. Recent work has predicted that seabird foraging ranges will increase with changing prey availability, impacting energy budgets and with greater potential to interact with anthropogenic activities (Searle et al., 2022). Work modelling the effect of future climate change under the RCP8.5 scenario has predicted large declines for many breeding seabird species in the UK and Ireland (Davies et al., 2023). While the most dramatic decreases and even total extirpations were predicted for SW Ireland and the SW UK, significant declines were also predicted for the North Sea for all three species included in this analysis. Our linear models were constructed with 28 years of data and therefore capture the long-term trend of SST over the past 3 decades. As this captures the current trend it should be related to the future trend, i.e. hotspots of increasing SST over the past 3 decades are likely to be hotspots of SST in the near future, however, this is only an assumption and incorporation of robust future modelling would benefit a future spatial risk mapping analysis. We only employed simple linear models with a fixed effect for year to capture the linear SST trend, as complex climate modelling was out of the scope of this analysis. Incorporation of more complex models to capture the climate signal would be of great benefit to future work. In addition, heatwaves are likely to have significant impacts on seabirds in the future (Cannell et al., 2024), and inclusion of absolute temperatures would greatly improve future work. While shipping lanes are strictly regulated in designated lanes and thus not variable across space, the intensity may increase in line with the economic activity of the surrounding nations, given the potential impact for disturbance that we have identified for the auk species here, the impacts of shipping should be fully considered in future management decisions.

Our work focused on the UK EEZ portion of the North Sea due to spatial extent of available modelled seabird density layers. The southern North Sea should also be considered in future work, as this is the region where both sandeel and sprat fishing still occur. In addition, in our future scenarios without sandeel fishing, the relative stressor hotspots were centred towards the southern North Sea for all three species. Future work to quantify the different MPA protection categories would be a significant improvement on this study. As stated previously global stressor assessments have been conducted (Halpern et al., 2008) but region-specific analyses are required to inform local marine spatial planning policy. While the North Sea is projected to be an offshore windfarm hotspot, there are likely many others around this world where these stressor overlap methods would be highly applicable to provide scientific advice for the global energy transition (Hu et al., 2022). The methods developed in this chapter have the potential to be applied to any predator where distribution and prey data are available. In addition, there are currently significant disparities in achieving global marine protected area coverage with many areas identified as having high biodiversity but low MPA coverage (Briscoe et al., 2016; Davidson & Dulvy, 2017; Lascelles et al., 2012). This disparity may be due to MPAs designated for political or social reasons (Fox et al., 2012), and might indicate a need for data-driven approaches in MPA marine spatial planning based on overlaps between habitats and significant pressures, such as the methods used in this study.

4.6 Conclusion

Our work presents a novel estimation of important seabird foraging habitat in the North Sea, by combining modelled estimates of concurrent seabird and prey fish distributions. We mapped how these are overlapping with the most pressing anthropogenic stressors. With these methods this study provides critical insights into the cumulative impacts of multiple anthropogenic stressors on seabird populations in the North Sea, with a particular focus on key foraging areas. Our analysis demonstrates that the cessation of sandeel fishing, coupled with the expansion of windfarms, is likely to alter the spatial overlap and intensity of stressor impacts on seabirds. While windfarm expansion increases the spatial overlap between seabird foraging areas and stressors, it generally results in a lower overall risk compared to scenarios where sandeel fishing continues. This suggests that the proposed sandeel fishing ban within the UK EEZ could significantly reduce the cumulative stress on seabirds, particularly for species with high sensitivity to fishing impacts, like kittiwake.

The findings also highlight the shifting nature of stressor hotspots, with a predicted decline in their occurrence within Marine Protected Areas (MPAs) under future scenarios. However, this also underscores the need to standardise MPA protections, where current protection for a given community, such as seabirds, depends on the target species and target anthropogenic activities in the MPA management plan and on enforcement of this plan. Improving the understanding of seabird-prey dynamics in the southern North Sea and incorporating robust climate change and predator-prey projections, are crucial for future effective conservation planning. Overall, this study emphasizes the importance of considering the dynamic nature of marine ecosystems and the cumulative impacts of human activities. By refining our understanding of these interactions and improving spatial risk assessments, we can better inform marine spatial planning and policy decisions aimed at conserving seabird populations and maintaining the ecological integrity of the North Sea.

5. General Discussion

Throughout this thesis I have explored the spatial, temporal and quantitative mechanics of seabird foraging ecology in the Western North Sea and examined how this aligns with the distribution of anthropogenic pressures and marine protected areas in the region. In this general discussion I will lay out the important findings of the three data chapters, their implications and how they have improved my knowledge of the gaps identified in the introduction of the thesis. I will then discuss future directions for continued research in this area.

5.1 Seabird prey in space and time: Joining multiple datasets to model the distribution of sandeel (*Ammodytes marinus*) and sprat (*Sprattus sprattus*) in the North Sea

Despite their economic and ecological importance there is limited data available on the fine-scale distributions of sandeel and sprat, key mid trophic small pelagic fish in the North Sea. For sandeel this is partly due to the difficulty in their sampling, which means standardised bottom trawl surveys such as the international bottom trawl survey have been considered inappropriate due to uncertainty in catchability. For both species in general this is likely also because stock assessments, the main end point for much of the data collected on their abundance, are conducted based on regionally delimited stocks and do not require spatially explicit information beyond being categorized within a large-scale management area.

I filled this gap by modelling the spatial and temporal distribution of sandeel and sprat across the North Sea for the past two decades, providing to the best of my knowledge the first spatiotemporal model of sandeel distribution at this scale, and the most fine-scale and comprehensive model of sprat distribution for the North Sea region. Doing this required several quantitative steps and can be considered rather experimental because the data have never been combined in such a way.

For sandeel this required exploring the utility of bottom trawl surveys (IBTS and BTS), attempting to account for issues with catchability by applying catchability efficiency estimates from Walker et al. (2017) and combining them with the dedicated sandeel dredge survey and the winter IBTS. For most fish species the inclusion of data from different seasons would not be a good choice, however, sandeel are highly immobile and remain buried in the sediment during the winter, suggesting their winter distribution should be strongly related to their distribution at the end of the summer before recruiting to the benthos for winter. By combining the highly specific but spatially and temporally restricted sandeel dredge survey data with the widespread but higher uncertainty bottom trawl data I created a novel dataset for sandeel that was the foundation for the analysis. Sprat are considered to be more reliably caught in bottom trawl surveys, however, given they are a pelagic species and are also well sampled by the herring acoustic survey, I combined both data sources to increase the statistical power of the analysis, again to the best of my knowledge creating a novel data set for sprat.

I applied the cutting-edge Bayesian spatial modelling technique INLA to the prey fish data. This method robustly quantifies uncertainty, is less sensitive to data sparsity and can account for spatio-temporal autocorrelation by applying smoothed spatial random fields fitted as spatial random effects. Spatial autocorrelation is a major consideration in ecological data and its presence in the residuals of a model often indicates an over-simplified model that is not fully capturing the population drivers. Sandeel are highly habitat specific, which should lead to well-defined spatial models. However, the inclusion of a spatial random effect greatly improved the models of both sprat and sandeel. Interestingly, I found that the spatial random effect was negatively correlated with fishing pressure in sandeel area 4 off the coast of Scotland. This was, however, only a simple correlation and caution must be taken drawing conclusions, but it certainly warrants further research into the direct impacts of fishing on sandeel abundance and availability to predators (Searle et al., 2023b).

Sprat are known to tolerate wide ranges of environmental conditions, which can make it difficult to accurately model their distribution based on environmental covariates. This was reflected in my results, with the sprat model having a strong spatial random effect with a distinct north south divide which incrementally moved North, corresponding to the northern range limit for this species. I hypothesize this could be either due to climate change and slow poleward migration as changing temperature might be spreading the optimum temperature range for sprat further North (Lindegren et al., 2020; Peck et al., 2012), or density-dependent effects with an increasing population and competition for food resources, with some fish forced to occupy sub-prime habitat at the edge of the population distribution (Olafsdottir et al., 2016). A similar expansion has been observed for mackerel in the North-East Atlantic and both mechanisms listed above have been proposed for the drivers of the mackerel expansion (van der Kooij et al., 2016).

5.2 Identifying critical prey thresholds for successful guillemot chick survival in the face of a shifting prey base

A key necessity to transition to ecosystem-based fisheries management that broadens the scope of sustainability from solely the target fish species, is having quantified thresholds for predators to include in the stock assessment as evidence for quantitative reference points when setting catch quotas (Hill et al., 2020). This can be hard to quantify due to the complexities in observing predator-prey relationships. Multi-species functional response models allow us to estimate this relationship by making realistic models of predation that allow for prey switching.

I estimated that guillemots provisioning chicks on the Isle of May are far more sensitive to changes to sprat availability, which aligns with the fact that guillemots have largely switched to sprat dominated diets over recent decades (Wanless et al., 2018). My models did predict that sandeel would be consumed when it is at high levels, however, this has been a rare occurrence during the past two decades. Guillemots have been the seabird species that has exhibited the strongest switch from sandeel to sprat, and this is likely also influenced by the species being single-prey loaders when provisioning chicks, as they would need to maximise energy density per foraging trip. While both sprat and sandeel have declined in size over recent decades (Burthe et al., 2012), a given sprat 10cm long would have a mean energy content of ~ 44 Kj while a sandeel of the same length would have a mean energy content of ~ 17 Kj, representing a 2.6 times higher energy value, due to their wider shape and higher weight. Perhaps given this difference in energy content and the need to maximise foraging efficiency it was only the decline of sprat populations in the 1980s that led to a switch to sandeel diets in subsequent decades, and a switch to sprat dominated diets has been driven by a return to increasing sprat abundance as much as decreasing sandeel abundance.

Taking unpublished data from Norway on chick energetic requirements, I used functional response curves to estimate what levels of prey availability would be associated with the onset of impacts on chick survival, so-called “critical prey thresholds”. I found this was largely influenced by sprat abundance, occurring at 29-26% of historical maximum of sprat biomass. This aligns with the “One-Third for the Birds” estimate of 34% (Cury et al., 2011). However, above 70 % of the historical maximum of sandeel biomass, adult guillemots were able to successfully provision their chicks regardless of sprat biomass, suggesting a buffering capacity at high enough sandeel levels which is not captured in the single-species the “One-Third for the Birds” threshold.

Adult breeding success was found to decline around 34% of sprat biomass, which is strikingly close to the “One-Third for the Birds” threshold, providing more evidence agreeing with this estimate. However, the combination of high sandeel and low sprat that was predicted to buffer against low chick consumption, which in the single prey analysis of the “One-Third for the Birds” threshold is not accounted for. However, this prey abundance combination was exceedingly rare in my timeseries, occurring only once in 2013. Interestingly this year had comparable breeding success with other high consumption years. While this provides initial support for my dynamic threshold, more years of data covering this combination of prey availabilities would be needed to further confirm this.

5.3 Lower impact risk but higher spatial overlap of seabirds and anthropogenic stressors in a changing North Sea

The North Sea is a rapidly changing environment, heavily modified and used by anthropogenic activities (OSPAR, 2018), and there are a multitude of stressors that may impact seabirds. There have been many studies assessing the impact of these stressors (Andersen et al., 2020; Bradbury et al., 2014; Burthe et al., 2014), however, a holistic analysis that takes into account multiple stressors and their cumulative risk of impact and how this risk is distributed across space is particularly lacking for seabirds in the western North Sea. I aimed to fill this gap by assembling a dataset of stressors and mapping their distributions. Given the importance of successful chick rearing to population dynamics, and the critical energy requirements needed during this period that I have demonstrated in the previous chapters, it would be highly informative to examine the interaction of stressors in relation to seabird foraging.

When examining impacts on seabirds much of the previous studies have looked at direct collision mortality risk or disturbance (Bradbury et al., 2014; Gușatu et al., 2021). However, of prime interesting to chick rearing seabirds is examining stressor impacts on foraging, which has been difficult in the past due to the complexities of determining key seabird foraging areas at sea. Recent work has identified oceanographic features that are targeted by seabirds because of enhanced prey accessibility, and these may be used to predict foraging areas, however, there was large variability and the trade-off between prey accessibility, predictability and abundance seems to be a complex dynamic for seabirds (Scales et al., 2014; Waggitt et al., 2018). In addition, this is likely to be species specific as the importance of prey accessibility would vary depending on foraging guild (e.g., high for surface feeding birds such as kittiwake). There also remains the issue of spatial scale, at what distance are seabirds following cues, to locate a prey patch on smaller local scales within an area or to identify large-scale foraging grounds? (Fauchald et al., 2000; Lieber et al., 2021; Weimerskirch, 2007). Recent work has attempted to employ hidden Markov models to analyse tracking data and determine foraging locations, however, this led to large uncertainty and the methods likely still need to be refined for large scale foraging trips that seabirds perform (O'Hanlon et al., 2024). Thus, I present an alternative method for identifying key foraging areas, mapping the co-occurrence of modelled seabird and prey densities that has the potentially to be applicable over large spatial scales, without the need for high density and costly boat surveying and with the ability to make predictions for colonies without tracking data, combining the modelled distributions of both seabird and prey fish and quantified the overlap hotspots.

I found that kittiwake, followed by razorbill and then guillemot had the highest total stressor overlap index, measured as the sum of the stressor index across all pixels identified as foraging hotspots, respectively. This is likely influenced by the fact that kittiwake have greater potential maximum foraging ranges and are thus more likely to overlap with a stressor. This is also seen where kittiwake had a slightly lower percentage of foraging habitat overlapping with stressors hotspots, yet this still led to an overall larger absolute index of stressor risk. Of course, the seabird density predictions of Wakefield et al. (2017) are based on distance, competition and environmental variables and so do not take into account behaviour, such as avoidance of windfarms (Peschko et al., 2020). Taking into account the effects on anthropogenic activities on top predator movements and behaviour would likely greatly benefit our understanding of the potential impacts on these populations.

Kittiwake overlap hotspots were centred on the southwestern Dogger Bank, where there is considerable windfarm development and sandeel fishing. This is possibly affected by the coarseness of the available sandeel fishing data (0.5° scale) which is giving the false impression of an overlap, where it is unlikely fishing is permitted within the bounds of the windfarm. However, fishing is likely a diffuse and not direct impact, and kittiwake foraging in this area have been shown to be negatively impacted by industrial sandeel fishing when the sandeel stocks are low (Cook et al., 2014). The two auk species displayed similar distributions, and both had overlap hotspots along the English coast, roughly from the Scottish border down to the Humber estuary.

Looking at the future scenarios there was only a small difference in the absolute stressor index for all 3 species between the “Approved” and “Planned” windfarm scenarios, suggesting the approval of windfarm applications still in the planning stage would have only a small impact on seabird populations. This is a positive finding given the rapid urgency needed for the clean energy transition. However, all three species had significantly higher proportions of foraging habitat that overlapped with stressor hotspots. This suggests a future scenario with a lower impact but greater stressor overlap for foraging seabirds. This is likely driven by the switch from a fishing dominated stressor index, which occurs in more offshore pelagic regions, to a more wind-dominated scenario which has more hotspots in nearshore regions along the Scottish coast. It is difficult to make conclusions on what is likely to be less impactful on seabird foraging, lower spatial overlap or lower stressor intensity. A tentative hypothesis would be that lower intensity but more disperse stressors would be less impactful on seabirds as they may be able to adapt to moderate pressure. One key aspect which needs to be monitored in the years following the sandeel fishing ban, is the impact of effort displacement, as the regions with sandeel fishing still open may receive much greater fishing effort as the fishing fleet redistributes (Püts et al., 2023).

Given the increased prevalence of stressor overlap for seabirds in the future windfarm scenarios, it would be of great benefit if the MPA network could provide spatial areas of refuge, and indeed this was the case with overlap hotspots occurring within current MPAs greatly reducing for all three species. Again, this is related to the spatial distribution of stressors and the switch in dominant stressor within the index. It is important to remember that the identified overlap hotspots are relative for each species and scenario, so the methodology will always identify the hotspots for the given data in a scenario, however, the magnitude of these between species and scenarios may be vastly different, as we have seen in Figure 22. While we observed a decrease of seabirds overlapping with stressors with MPAs, across large scales seabirds, especially pelagic species, have a low overlap with MPAs in Britain and Ireland (Critchley et al., 2018). This suggests that the current conservation measures in the North Sea have not been planned to maximise efficiency for seabirds and more explicit analyses of trade-offs to improve this should be conducted (Püts et al., 2023).

In the final scenario, which contains both the full planned windfarm dataset and sandeel fishing as usual, there is both an increase in spatial overlap and increase in stressor intensity at the overlap hotspots. This essentially represents a “worst of both worlds” scenario and is likely to have serious negative impacts on seabird populations. The UK sandeel fishing ban has already been implemented but given the legal challenge by the EU there is large uncertainty to its future. Given my analysis I believe there is strong evidence for the need to reduce pressures on these seabird populations that have been facing a multitude of stressors over the past two decades. However, with the closure of a large portion of the North Sea and major sandeel fishing grounds, there is the potential for the fishing capacity to now be displaced to the remaining open fishing grounds, greatly increasing the pressure on the sandeel and dependent predators in these regions. While the closure of sandeel fishing grounds by the UK is likely to be beneficial for seabirds breeding in the UK, the extension of an analysis similar to chapter 4 in this thesis to the entire North Sea would therefore be greatly beneficial to ensure the shifted fishing pressure does not become highly concentrated across another local ecosystem.

5.4 Future Work

The work conducted in this thesis has been novel in many aspects. In particular, in Chapter 2 the creation of a dataset of sandeel data that tests the utility of combining different surveys into the first spatio-temporal model of sandeel across the entire North Sea. This a foundational step in North Sea ecological research as knowledge of this centrally important species is beneficial to the study of many other aspects of the ecosystem. However, the methods can certainly be improved and focusing on more complex methods to integrate the different survey datasets into a single model would greatly improve the performance of the model. In this work I have pooled the data together, using estimated efficiency rates to adjust for biases in the bottom trawl data (Walker et al., 2017), joined together with the sandeel dredge survey and used fixed effect factors to account for difference between the data sources. Likewise, the sprat model was based on the combined datasets of the IBTS and herring acoustic survey. The sprat model displayed large variability, and this is likely due to the variance displayed between the two datasets with often conflicting trends observed in the sprat biomass for given years. One way to explain this is that the surveys are only targeting potentially partially overlapping sections of the vertical water column and may be detecting different parts of the population. Indeed, older sprat tend to recruit closer to the seabed (Van Der Kooij, Pers comm 17th October 2022) and therefore there may be the possibility for an age bias in the detection for the two surveys. These models would be improved by more sophisticated data integration techniques that have recently been developed for modelling species' distributions (Isaac et al., 2020; Paradinas et al., 2023). However, given the uncertainty and methodological differences, I advise that work is carried out into more advanced statistical models that develop methods for specifically joining acoustic and bottom trawl data that accounts for the biases in each dataset, such as Integrated Species Distribution Models (ISDMs) before they are joined in a single analysis.

Chapter 3 was concerned with modelling the critical prey thresholds of provisioning seabirds, and this work built upon that of Smout et al. (2013). My analysis had quite different results and this is likely due to the more recently available data and more complex modelling methods. A benefit for future work would be to extend this analysis beyond guillemots to other seabirds, in particular those that have a higher proportion of sandeel in their diet such as kittiwake, puffin and razorbill. Kittiwake have been shown to be particularly sensitive to sandeel availability (Cook et al., 2014; Searle et al., 2023b) and investigations on their functional relationship with their prey would be of key importance to their conservation, these datasets of diet on the Isle of May are already collected by UKCEH. Likewise, with the UK ban on sandeel fishing, seabird populations in the southern North Sea are likely to be facing higher anthropogenic pressures than those off the coast of Scotland, and the extension of the multispecies functional response modelling framework to populations in the region of the North Sea would also likely be of prime interest to their conservation. Given the effort required to study seabird diets on selected index colonies, the application of non-conventional techniques such as molecular analysis would likely greatly expand the temporal and spatial coverage possible for seabird diet monitoring (Oehm et al., 2017).

5.5 Concluding Remarks

The work I have presented in this thesis has provided a holistic assessment of the different aspects of seabird foraging ecology in the western North Sea. It fills foundational knowledge gaps and acts as a springboard for future ecological work that might use and build upon the quantitative work conducted during this PhD. Using cutting edge Bayesian spatial modelling techniques, I created the first fine-scale spatio-temporal model of sandeel biomass across the entire North Sea that covered two decades, providing a thorough assessment of the dynamics of sandeel populations across ecologically relevant spatial and temporal scales. In addition, I created a fine-scale, complex model of sprat that covered the summer months by combining for the first time, to the best of my knowledge, the international bottom trawl survey with the herring acoustic survey. Both of these models can be regarded as quite experimental in nature and demonstrate the ambition and strong innovative outlook of this work. Chapter 2 quantified the predator-prey interactions of chick-rearing guillemots on the Isle of May providing important information on the ecology of the species. I identified that ~ 29% of historical maximum sprat biomass was the critical minimum prey threshold to maintain productivity. This was very similar to other studies on seabird minimum prey thresholds. However, my work identified that sandeel biomass over 70% of the historical maximum could buffer chick provisioning in the event of low sprat (i.e. below the 29% sprat threshold). This is in contrast to the “One Third for the Birds” threshold which is static and based on a single prey species, thus the use of dynamic multi-species thresholds is an improvement towards more ecologically realistic modelling of seabird foraging. Finally, I assessed the cumulative stressor overlap with seabird foraging for the western North Sea. I identified overlap hotspots as potential sites of concern to focus management measures and I found that in the likely future scenario, with the cessation of Sandeel fishing in the UK EEZ and the large deployment of offshore windfarms as part of the clean energy transition seabirds would be facing lower intensity but higher spatial overlap of anthropogenic stressors. As a result of the work conducted in this thesis, we now have a estimates of fine-scale sea bird prey distributions across the North Sea. These data were a key knowledge gap in the scientific study of the North Sea ecosystem, and as well as being the foundation for the quantitative analysis in chapters 3 and 4, they will also be freely available to other researchers, greatly expanding the scope of ecological research that can be carried out in this region. This is vital for seabird research as there are many other aspects of seabird ecology that were outside of the scope of this thesis that can now be informed with this new data. looking back to the initial aims set out in the introduction of this thesis, I can conclude that all of the goals were achieved and that the scientific understanding of the spatial and trophic ecology of seabirds on the East coast of the UK is greatly improved following this work. The work presented in this thesis has had a strong real-world focus and the outputs from chapter 3 and 4 have the aim to improve sustainable fisheries management and marine spatial planning, respectively. This is a great benefit, for both the environment and society, as it extends the impact of this body of work and aims to have tangible beneficial impacts on a changing North Sea, which I believe are key roles as publicly funded scientist. Extending the results of my research from scientific journals into the awareness of policy makers is vital now more than ever, as the anthropogenic political environment - how we manage and protect nature following on from Brexit, the rapid clean energy transition in response to climate change and which has been sped up by the Russian invasion of Ukraine, and the move to increase protected area coverage and habitat restoration - is changing alongside the ecological environment.

6. References

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