MARINE MAMMAL PREDATOR-PREY INTERACTIONS IN THE NORTH SEA

Janneke Ransijn

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University of
St Andrews

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May 2022

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ABSTRACT

Trophic levels within an ecosystem are linked by the functional response which describes how the consumption rate of a predator varies in relation to prey density. Knowledge of functional responses is key to understanding predator-prey interactions, population dynamics, predation pressure, prey preference, and the ecosystem. This thesis explores multi-species functional responses (MSFR) of key marine mammal predators in the North Sea, and the prey energy available to them. Spatiotemporal variation in prey energy available to harbour porpoises (*Phocoena phocoena*) was modelled, using species distribution models, and showed that large amounts of energy were available both within and outside the Southern North Sea (SAC). Sandeels are energy-rich, their patchy restricted distribution drove the observed patterns of the spatiotemporal distribution of all porpoise prey energy. The MSFR of three predator species (harbour porpoise, grey (*Halichoerus grypus*) and harbour seal (*Phoca vitulina*)) were modelled using Bayesian methodology. Fitted responses indicated that all predators exhibit a type III functional response, and that sandeels are important and more strongly preferred by grey seals and harbour porpoise compared to harbour seals. They may be preferred as they are probably easy to catch due to their immobility and predictable occurrence, as inferred from their restricted modelled distribution. Harbour seals have more diverse diets than grey seals and seem to show a more sigmoidal response which may indicate a greater tendency to switch between prey types. Of the predators, harbour porpoise had the highest consumption estimates, mainly due to the larger number of animals in the area. Generally, marine mammal consumption was low compared to fisheries landings (≤ 20%). Overall, this thesis shows the benefit of MSFR modelling to improve ecological understanding of important marine predators and the results allow future integration of the MSFRs into ecosystem models to explore the consequences of predation on various fish stocks.

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CHAPTER 1
General introduction

Ecosystems are complex adaptive systems in which trophic structure and patterns in biomass flow arise from interactions among compartments (i.e. group of species that interact but have weak interactions between them and exploit similar resources) (Levin, 1998), the environment, and anthropogenic pressures. Ecological communities are characterised by nonlinearity resulting in multiple possible outcomes for dynamics (Levin, 1998). Alterations in food webs have consequences for biodiversity, ecosystem state, predator-prey dynamics, and fisheries (Cheung et al., 2008; Elmqvist et al., 2003; Kennedy et al., 2002). For instance, the loss of top predators can result in major alterations for the system (Estes et al., 1998; Estes & Duggins, 1995; Myers et al., 2007) because predation can have a large impact on prey populations and community structure (Fortin et al., 2005). However, the effects of predation differ considerably among species and systems (Ferretti et al., 2010). In extreme cases, food web variations could even result in delayed population growth, large population fluctuations, regime shifts, alternative states, or trophic cascades which have major consequences for ecosystem function (Estes & Duggins, 1995; Frank et al., 2005) and ecosystem services (Elmqvist et al., 2003). For example, one of the best known trophic cascade studies in the marine environment showed that the sea otter population decline in Alaska led to an explosion in one of their prey species, sea urchins, which destroyed large quantities of kelp forest by overgrazing (Estes & Palmisano, 1974).

Climate change is likely to have a strong influence on the future distribution of biodiversity and has been linked to changes in the composition of communities, phenology, habitat choice, species abundance and distribution (Davies et al., 2006; Parmesan & Yohe, 2003; Pounds et al., 1999; Root et al., 2003; Walther et al., 2002) which can cascade through the food chain (Berg et al., 2010). Temperature rise might exceed species thresholds which could cause species to shift their range in latitude (Devictor et al., 2012; Perry et al., 2005), altitude, or depth (Dulvy et al., 2008). As a result of fewer barriers, species migration rates within an oceanic environment are higher than on land (Cheung et al., 2008). Some species cannot keep up with climate change and might come into “climatic debt” (Devictor et al., 2012). How well species are able to cope with change is dependent on attributes including diet, dispersal rate, and habitat (Jenni & Kéry, 2003; Jiguet et al., 2007; Munday, 2004; Perry et al., 2005). Therefore, the responses of predators can either be quite effective (Charmantier et al., 2008) or lead to mismatches both spatially and temporally with their prey (Visser et al., 1998). Exactly these mismatches between species that are linked through the food web may destabilize community composition (Berg et al., 2010). Furthermore, this might have consequences at a community level through trophic interactions (Brown et al., 1997; Schweiger et al., 2008) and invasions of non-native and loss of established species (Hiddink

& ter Hofstede, 2008). However, predicting the impact of climate change is a major challenge because we are still unsure of the responses of populations let alone the influence on an ecosystem level (Brown et al., 2011).

Ecosystem models might offer a solution to improve understanding because they can predict how different realistic enviromental (*e.g.* rising temperature, ocean accidification) and human use scenarios affect the entire ecosystem and its components. However, it appears to be more difficult than anticipated within oceanic environments to incorporate both anthropogenic changes and biological outcomes in ecosystem models (Francis et al., 2007). Advances in computational power and ecological methods mean that it is now possible to explore these topics at an ecosystem level (Cury et al., 2008). These kind of explorations should allow for more strategic decisions to be made regarding resource management and protection.

Fish assemblages and fishing in the North East Atlantic and the North Sea

Fisheries pressure, climatic and environmental changes have substantially altered the fish assemblages in waters around the United Kingdom during the last fifty years (Engelhard et al., 2011; Heath, 2005; Perry et al., 2005). The fish assemblage in the North Sea (Figure 1.1) is quite diverse and fisheries used to remove between thirty to forty percent of the biomass of targeted fish species each year (Gislason, 1994). Although, over the last thirty years landings have gradually declined, many targeted stocks are still outside safe biological limits with poor recruitment estimates (ICES, 2017). Increased temperatures in the North Atlantic Ocean have been linked to some of the globally most rapid distributional shifts for fish and zooplankton (Beaugrand et al., 2009; Dulvy et al., 2008). Increasing water temperatures are correlated with a decrease in species richness in the area of the North Atlantic that is located near the west coast of Scotland while species richness within the North Sea has increased

(Ter Hofstede et al., 2010). The mean trophic level has been in decline (Heath, 2005; Jennings et al., 2002) and it has been proposed that a shift from a demersal- to a pelagic-dominated fish community in the North Sea has occurred (Engelhard et al., 2011). The status of fish stocks differs among species, overall many stocks in the North Sea are/were below sustainable biological limits and the situation is even worse on the west coast of Scotland. However, within complex ecosystems, the result of changes in fisheries pressure on fish stocks is not straightforward, sometimes even counter-intuitive, because fisheries do not only alter the abundance of targeted species, but they also influence their prey, competitors, and predators (Moullec et al., 2017; Österblom et al., 2007). The same is true for other multi-species interactions (e.g. among seabirds and their prey) within an ecosystem that may result in unexpected outcomes for prey and predators (Hilborn et al., 2017; Yodzis, 2001).

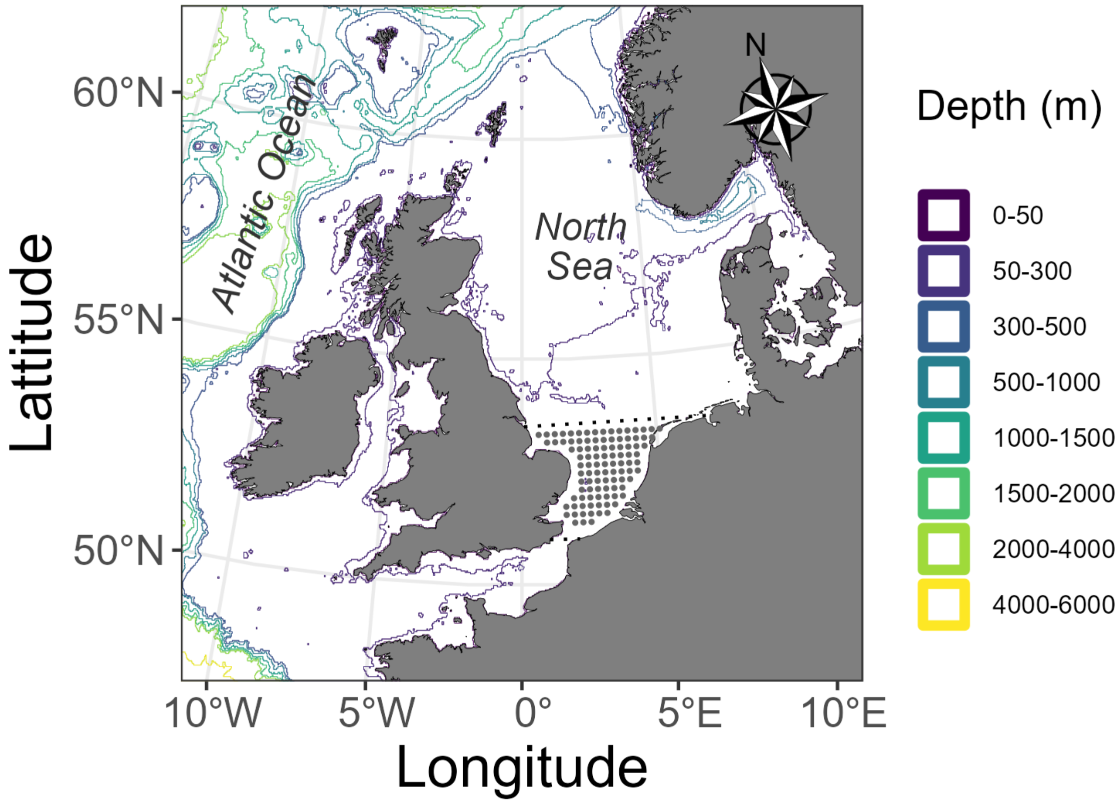

Figure 1.1 The North Sea and part of the North Atlantic Ocean, grey dotted area is defined as the southern North Sea and the area of interest for Chapter 3.

To include these important trophic interactions into fisheries management analysis there is a need for multi-species models. However, fisheries management has been dominated by single-species assessments to determine fish stock sizes and catch quotas. This approach entirely ignores species interactions within the ecosystem and might be rather misleading for management purposes, because decisions regarding one species are affected by others (Pauly et al., 1998). Single-species assessments may prioritize short-term economic and social profits over sustainable long-term benefits (Mackinson & Daskalov, 2007). Thus, there is currently a need for a wider focus for fisheries management (Smith et al., 2007). Until now, fisheries management in the North Sea has mainly focussed on single-stock assessments (ICES, 2022) and it has been generally accepted that this approach together with the unsatisfactory level of compliance on set quotas has failed to keep fish stocks within sustainable biological limits. However, single-species assessments have developed quite extensively over the last couple of decades by for instance increasing complexity and adding in multiple sources of uncertainty (Mace, 2001; Probst et al., 2021). Progress towards adopting a broader ecosystem approach (Garcia & Cochrane, 2005; Greenstreet & Rogers, 2006) is fundamental to our understanding of the regulation of biodiversity and for decision-making regarding conservation and management of natural resources**.**

Bottom-up (*i.e.* environmental factors/prey driven) and top-down (*i.e.* predator dominated) control can influence populations by acting simultaneously in synergy, or sometimes the control within a food web switches between bottom-up and top-down control (Frank et al., 2007). Predation has the potential to regulate the dynamics of both predator and prey populations. Fluctuations in prey abundance have implications for predators which will depend on the predator’s strategy (*e.g.* generalist or specialist). Consequences could entail alterations in predator diet, feeding grounds, fitness, or abundance (Bjørge, 2003; Lewis et al., 2001; Rosen & Trites, 2000; Roth, 2003). For example, occasional breeding failure of the abundant common guillemots (*Uria aalge*) in the North Sea was probably caused by a reduction in sandeels (Ammodytidae) (Wanless et al., 2005). Sandeels are also an important prey for many other species within the North Sea such as other fish (Daan et al., 1990; Engelhard et al., 2014) other seabirds (Rindorf et al., 2000), harbour porpoises (*Phocoena phocoena*) (Gilles et al., 2016; Leopold, 2015; Santos & Pierce, 2003) and both grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) (Hammond & Grellier, 2006; Thompson et al., 1996; Wilson & Hammond, 2019).

Marine mammals in the North Sea and West coast of Scotland

Marine mammal populations, whose consumption of commercial and forage fish is substantial, have shown important changes in the North Sea (Engelhard et al., 2014). Population trends of grey and harbour seals are quite different. Generally, grey seals are increasing in the North Sea and stable around the Northern and Western Isles while harbour seals are declining along the north-east coast of Scotland, in the Northern Isles and recently in the southern North Sea but stable or increasing in the Western Isles (Morris et al., 2021; Russell et al., 2019; SCOS, 2022; Thomas et al., 2019; Thompson et al., 2019).

The most abundant cetacean species in the North Sea is the harbour porpoise with an estimated abundance of 345,373 in 2016 (Hammond et al., 2021) and two species of seal are considered native to the area (i.e. harbour and grey seals). Of these, grey seals are the largest and have a high level of sexual dimorphism compared to the other species. The annual breeding and moulting cycles of harbour and grey seals are asynchronous (SCOS, 2021). Around the UK, grey seals moult between December and April and pupping follows a clockwise cline starting in August in southwest Britain while pups in Scotland are mainly born between September-November (SCOS, 2021). Harbour seals in the UK moult in August and their pupping season occurs between June and July (SCOS, 2021). Grey seal mothers, fast during the lactation period, and can lose ~40% of their mass in contrast to harbour seal mothers that continue to forage and may leave their pup for several hours (Brasseur, 2017; Fedak & Anderson, 1982; Pomeroy et al., 1999). In the North Sea, harbour porpoise calves are born mainly during June-August, followed by a lactation period of up to 10 months (Kesselring et al., 2017; Lockyer, 2003).

Temporal variation in individual body mass is dependent on various factors including seasonal changes in prey availability and life history stage (e.g. moult for seal and bird species, parental care, reproduction, and growth). Individuals need to obtain sufficient energy to balance the costs of survival and reproduction. Energetic costs include acquiring, handling and processing prey, movement, and maintaining body functions while benefits encompass food energy used for growth and reproduction (Costa, 2009). Reproduction is energetically expensive (i.e. associated with rearing off-spring, fasting during parental care, mate acquisition, and resource defence). Energetic balance results when an individual's energetic costs equate to the energy they can extract from their environment (Schneider, 2004) which differs between species and environments (Costa, 2009). Among capital-breeders, for instance the grey seal, dramatic seasonal changes in body mass are related to alternate periods of fasting and foraging related to reproduction with higher cost higher magnitude of energetic expenditure and mass changes for females related to parental care (Beck et al., 2003). In contrast, income breeders like the harbour porpoise need to feed more continuously (Bjørge, 2003; Spitz et al., 2012b; Wisniewska et al., 2016).

The summer distribution of harbour porpoises has shown a major shift from the northern areas to the south-western areas of the North Sea from 1994 to 2005 and was maintained through 2016 (Hammond et al., 2002, 2013, 2021).

The drivers of the distributional shift of harbour porpoises and causes for the different observed population trends for seals are not yet understood. The distribution of porpoises is likely to be linked to changes in prey distribution (Hammond et al., 2013; Sveegaard et al., 2012). One of the possible causes of declines in harbour seal numbers could be reduced prey availability and/or interspecific competition with grey seals (Bowen et al., 2003a; Svensson, 2012; Wilson & Hammond, 2019). Another/additional possible cause may be the presence of killer whales (*Orcinus orca*). In the North-east Atlantic killer whale occurrence has been associated with the distribution of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) but killer whales are also observed to predate on pinnipeds (e.g. harbour and grey seals) (Bolt et al., 2009; Jourdain et al., 2017; Luque et al., 2006; Similä et al., 1996). The minimum estimated killer whale population size in UK waters in 2019 was 124 (JNCC, 2019) with around 50 individuals utilising the waters around the Northern Isles (i.e. Orkney and Shetland) (Foote et al., 2010). Killer whale prey preference around the Northern Isles is largely unknown, but they have been observed to feed on both fish and marine mammals (i.e. seals and harbour porpoise) (Bolt et al., 2009; Deecke et al., 2011; personal observation, Julia Sutherland,2022) and killer whale sightings around Shetland coincide with harbour seal pupping season (Bolt et al., 2009). However, according to bioenergetic modelling around Shetland it seems unlikely that killer whale predation alone has imposed the change in harbour seal population trends around Shetland (Arso Civil et al., 2018). Currently, the

ECOPredS[1] (Ecological Consequences of Orca Predation on Seals; 2019-2024) project has commenced that will investigate predator-prey interaction between killer whales and seals around Scotland to better understand both predation mortality and any behavioural consequences (i.e. landscape of fear (Jorgensen et al., 2019; Laundre et al., 2010)).

A recent study found that there is spatial partitioning between these species, generally, harbour seals stay closer to the coast than grey seals (Jones et al., 2015). These predator species are highly mobile (Cunningham et al., 2009; McConnell et al., 1999; Read & Westgate, 1997; Russell et al., 2015) and it is usually assumed that they are adaptable foragers that take advantage of prey that is locally available, which is also reflected in the inter-annual and seasonal variation in diet (Hall et al., 1998). However, inter-specific competition might still occur as generally similar prey species are consumed by both seal species (Wilson & Hammond, 2019).

Predation and prey availability

To target the most abundant and/or profitable prey, predators might switch between prey species, foraging tactics, or feeding grounds (Schenk & Bacher, 2002). This could imply that their diet or feeding areas could alter when the availability of their prey changes. Seals that are central place foragers might have to adjust more frequently as they are probably more likely to deplete prey resources close to haul-out sites, which might entail that over time animals have to travel further to find other feeding grounds (Aarts et al., 2016). So, the spatial accessibility of prey may also be very different between predator species and therefore their food availability can be quite unalike (Hilborn et al., 2017).

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[1] https://ecopreds.com/

If top predator populations decline, this may have considerable cascading effects on their ecosystem. It can lead to a reduction in top-down control mechanisms and reduce food chain length. These changes to the food web might be difficult to reverse (Estes et al., 2011). However, the impact of reduced predation is often only noticeable when predators are completely lost from a system (Estes et al., 2011). As long-lived animals and with some species are distributed globally, and a few roaming large geographical distances, marine mammals are considered prime sentinels of their ecosystem and their population status is often thought to be indicative of the health of their environment (Bestley et al., 2020). Their diets and body condition can provide information on long term food web changes (Moore, 2008). However, they may be able to adapt to compensate for changes within the ecosystem by buffering for temporal variation (*e.g.* blubber reserves) or by altering their diet, or foraging activities (Croxall et al., 1999). Additionally, marine mammals can counter decreased food availability to some extent by being more flexible in their time budgets (e.g. spending more time foraging) (Burger & Piatt, 1990). This suggests that marine mammal populations might not deliver the fastest signs of change. However, this is dependent on the sensitivity of species, for instance animals that are reliant on sea ice for foraging or breeding such as the ringed seal (*Phoca hispida*) may provide faster signs of change to climatic variations (e.g. reduced productivity) (Stirling, 2002).

Probably, there is a link between the decline in abundance and/or body condition of marine mammals and prey availability (Øigård et al., 2013; Rosen & Trites, 2000, 2005; Trites & Donnelly, 2003) and food quality (Österblom et al., 2008). For instance, harbour seals in the Moray Firth had a better body condition during years of higher clupeid ("fatty fish") abundance which might be due to lower foraging costs (Tollit & Thompson, 1996). Furthermore, a Dutch dietary study revealed that porpoises with a good body condition were more likely to have higher amounts of energy-rich fish in their diet than emaciated porpoises (Leopold, 2015) suggesting that to meet their high energy needs porpoises may need to consume energy-rich prey (Spitz et al., 2012a). This could be related to the idea that harbour porpoise might be attracted to areas with high sandeel abundance as it was found that porpoise's densities increased with decreasing distance to sandeel grounds (Gilles et al., 2016).

Harbour porpoises feed at high rates, foraging almost continuously (*i.e.* pursuing up to 550 prey items an hour with high capture success rates) (Wisniewska et al., 2016) suggesting that they need a relatively continuous availability of prey. But, it has been suggested that this study might show an extreme view of porpoise biology (e.g. biased age structure of tagged animals and short duration of monitoring just after release from pound nets) (Hoekendijk et al., 2018). Still, harbour porpoises have a high metabolic rate and only a limited energy storage capacity (Bjørge, 2003). Consequently, this makes them quite susceptible to starvation (Bjørge, 2003; Kastelein et al., 1997) and less able to buffer against diminished food availability/quality (Leopold, 2015; Spitz et al., 2012a) if they fail to meet their high metabolic needs (MacLeod et al., 2007; Spitz et al., 2012a). Although, marine mammals in general are probably not the preferred indicator species to infer bottom-up variation, porpoises might be the most suitable species. On the other hand, seals have to regularly return to locations on land enabling us to obtain data on movement and diet. Therefore, they could be seen as a relatively easy and cost-efficient subject in comparison to other marine top-predators.

Marine mammals and fisheries interactions

Foraging behaviour should eventually, according to optimal foraging theory, result in individuals maximizing their fitness (Pyke, 1984) by maximizing the energy obtained per unit of energy spent. Predator diet is the result of the predator's response to variability in prey availability, including the predator's feeding strategy and capabilities, and on prey density which will depend on predator-prey spatial and temporal overlap. Harbour porpoise and seal diet consists of a wide variety of both commercial and non-commercial prey species which varies spatially and temporally; however only a few prey types dominate the diet in any one area (Hammond & Wilson, 2016; Leopold, 2015; Santos et al., 2004; Santos & Pierce, 2003; Wilson & Hammond, 2016). Overall, sandeels and gadoids are dominant prey species in grey seal and harbour seal diet around the United Kingdom and within the North Sea (Brown et al., 2012; Hammond & Wilson, 2016; Wilson & Hammond, 2016, 2019). However, sandeels are less important for seals west of Scotland which have more varied diets (Hammond & Wilson, 2016; Wilson & Hammond, 2016, 2019). Differences in supplementary important prey species are observed, most likely according to habitat differences (Tollit & Thompson, 1996a), including higher contributions of pelagic, flatfish and/or benthic species (Wilson & Hammond, 2019). In Scottish waters, whiting (*Merlangius merlangus*) and sandeels also dominate the diet of porpoises (Santos et al., 2004; Santos & Pierce, 2003). Further south in Dutch coastal waters, their diet is diversified with relatively high proportions of gobies (Gobiidae) and clupeids (Clupeidae) (Leopold, 2015).

To what extent there are 'competitive' interactions between marine mammals and fisheries has been a topic of ongoing debate (DeMaster et al., 2001). In a number of marine systems, grey seals are considered as an important predator for commercially exploited fish species such as cod (Bundy & Fanning, 2005; Chouinard et al., 2005). They can consume a considerable amount of fish, for instance it was estimated that an adult grey seal consumes between 4-7 kg a day (SCOS, 2017) and annual grey seal consumption estimates in relation to fish stock size are probably small (highest for cod, 5.1%) in the North Sea while west of Scotland consumption is estimated to be around 10% for whiting and over 100% for cod (Hammond & Wilson, 2016). This impossible estimation of cod consumption could be due to the low fish assessment coverage in the area west of Scotland (Hammond & Wilson, 2016). However, the broader issue of concern relates to top-down control (Myers & Worm, 2003) and would need a more holistic approach than solely looking at consumption quantities. Predation by grey seals may possibly be insignificant (Lundström et al., 2007) and their removal of fish from the system is typically far less than fisheries removals (Smout et al., 2014). Nevertheless, in the Northwest Atlantic around Newfoundland and Labrador it is suggested that grey seal predation is a factor that limits the recovery of Atlantic cod (*Gadus morhua*) (Bundy et al., 2009). Most studies agree that grey seals are probably not the cause of the currently low levels of some fish stocks, but, that their predation pressure might contribute in keeping them at low abundance and preventing stock recovery of overexploited species (Cook et al., 2015; Serpetti et al., 2017; Smout et al., 2014; Trzcinski et al., 2006). However, quantifying interactions between fisheries and predators is difficult (Yodzis, 2001) especially within a complex food web with many trophic links. This may cause difficulties in deciding on management measures for marine systems, such as setting fishing quotas, that balance conservation and will effectively support sustainable fisheries objectives.

Multi-species modelling

Examining the interaction between marine mammals and fisheries is, according to Butterworth & Punt (2003), a good first step to assess multi-species models. Recently, even whole ecosystem models have been used to explore these kind of interactions and top-down control by marine mammalian predators on their prey (Lassalle et al., 2012; MacKenzie et al., 2011). Nevertheless, current predictions of the consequences of marine mammal predation remain uncertain and diet flexibility should be included in ecosystem models to evaluate their likely influence on the food web (Smout et al., 2014). Illustrating a previously mentioned point about counter-intuitive outcomes for fisheries management due to trophic interactions, a fairly recent study found that the capelin (*Mallotus villosus*) stock in the Barents Sea was more affected by the fishery on polar cod (*Boreogadus saida*) than the fishery on capelin itself due to indirect effects of trophic interactions (Lindstrøm et al., 2009). Furthermore, it was suggested that minke whale (*Balaenoptera acutorostrata*) consumption of cod was more dependent on the abundance of capelin than on cod abundance, possibly due to prey switching (Lindstrøm et al., 2009). These results highlight that multi-species approaches are crucial for adopting appropriate management and that solely basing quotas on single-species assessment that do not take trophic interactions into account can be highly misleading.

Assuming 'fixed' diets for generalist predators is very unrealistic and to gain insight into diet adaptability a multi-species functional response (MSFR) has to be modelled. This is because the consumption of a particular prey species is expected to change, particularly preferred prey, according to overall prey availability. Strong prey preference is reflected by little to no change in diet (*i.e.* specialist) when that prey availability drops, while switching behaviour of the predator reveals weaker prey preferences (*i.e.* more generalist diet) (Holling, 1959; Murdoch, William, 1969). The shape of the functional response leads to different implications for system function (Smout et al., 2010) and the coexistence of species (Vincent et al., 1996). Even small changes in predation thresholds can alter food web oscillations (Murdoch & Oaten, 1975; Van Baalen et al., 2001). For instance, a sigmoidal form (*i.e.* Type III functional response) is indicative of prey switching when prey is at low abundance.

Furthermore, this type of functional response may result in persistence and/or stabilizing effects on predator-prey dynamics (Murdoch & Oaten, 1975) because it may prevent one prey species from outcompeting others (Roughgarden & Feldman, 1975). The presence of ‘alternative’ prey can be very important in stimulating the persistence of predator-prey systems (Van Baalen et al., 2001). However, this type of functional response could also mean that the predator population can keep a prey species at low levels, trapping the prey in a ‘predator pit’ because the mortality inflicted by the predator increases with prey abundance (see Figure 1.2). So, changing the type of functional response can significantly alter the implications for the stability of predator-prey interactions.

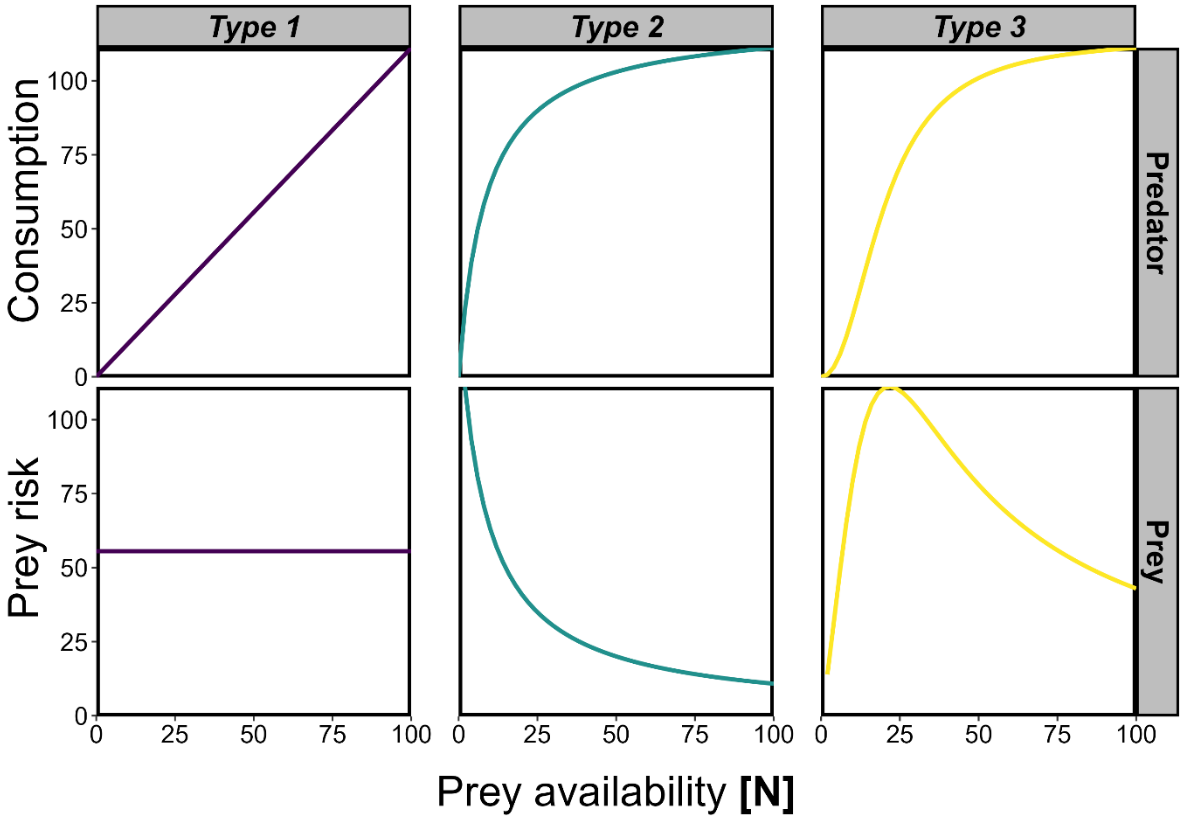


Figure 1.2 Single species functional response curves. The top row illustrates the relationship between prey availability and food consumption from a predator’s perspective defined by different Holling types. Bottom row represents the functional response relationships from the prey’s perspective. Left panels represent the Holling type 1 functional response, middle panels type 2, and the right panel a type 3 functional response.

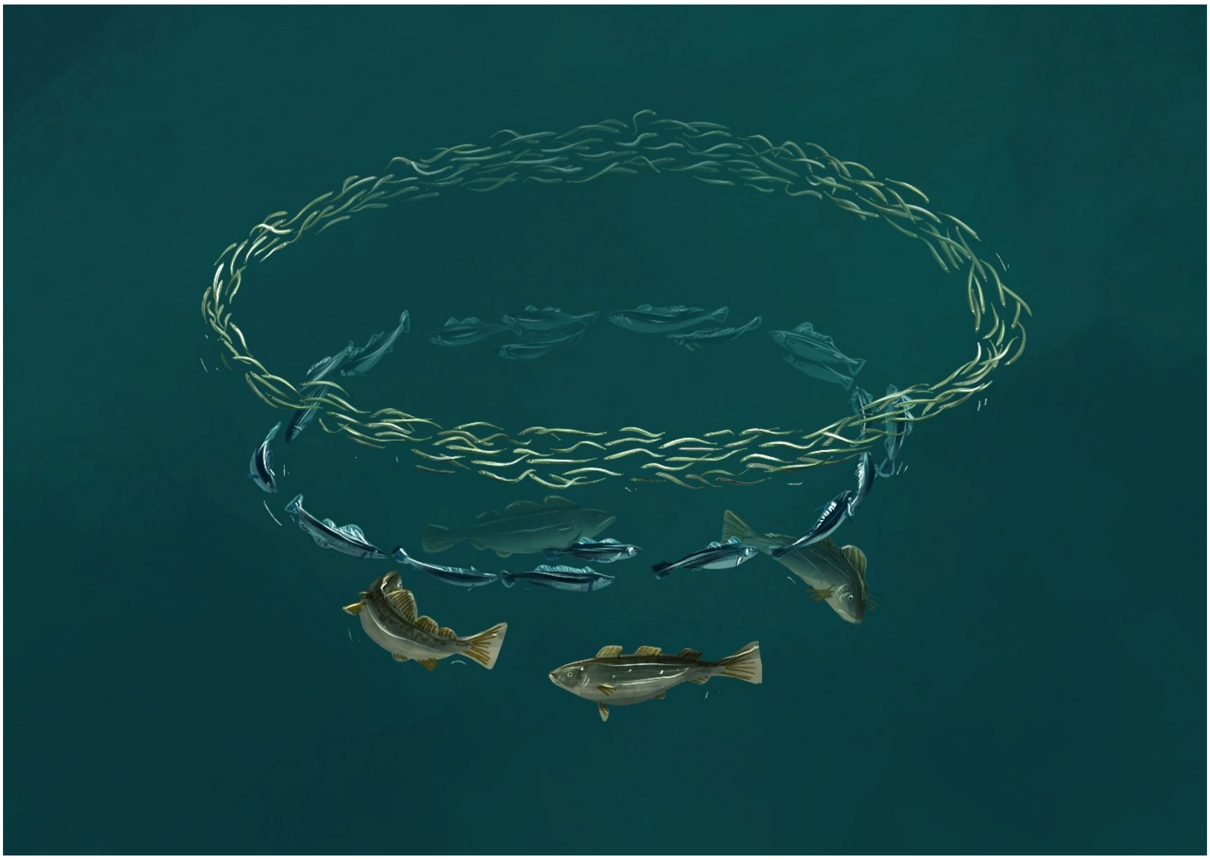
Modelling functional responses is challenging for wild animals because observing both consumption and prey availability outside a controlled environment is difficult. Therefore, parametrising a MSFR requires substantial datasets on predator diet and the availability of multiple prey species. Additionally, the data should cover a wide range of prey densities and should overlap spatially and temporally. Therefore, it is not strange that most studies on the role of predation concern controlled experiments or describe it for either small-bodied or specialist predators in few-species (less than three prey species) systems (Morozov & Petrovskii, 2013). Unfortunately, we therefore have an incomplete picture of the effects of top-predators in many ecosystems (Estes et al., 2011). However, Bayesian methods that support the use of prior information have recently been employed to overcome the problem of data sparsity, allowing for MSFR models to be fitted for marine (Smout et al., 2014; Smout & Lindstrøm, 2007) and terrestrial (Smout et al., 2010; Suryawanshi et al., 2017) top-predators. Furthermore, Bayesian inference enables incorporating uncertainty into data estimates and independent variables in a more a more convenient framework.

Currently, we are lacking information on the dynamic relationships between many marine mammals and their prey. Consequently, it is uncertain how changes in prey may have influenced the observed changes in marine mammal populations. This limits our understanding and ability to predict the consequences of (i) prey driven bottom-up processes for these predators, and (ii) the top-down impact of these predators on the rest of the ecosystem and the fisheries that depend on it.

This thesis examines predator-prey interactions in the North Sea by 1) improving our understanding of the spatio-temporal variation in prey abundance, 2) parameterising the MSFR for three marine mammal species (*i.e.* grey seals, harbour seals and harbour porpoises), and 3) comparing consumption estimates of these three predators to fisheries landings.

CHAPTER 2

A calorific map of harbour porpoise prey in the North Sea



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<u>Authors' Contributions</u>
Janneke Ransijn: Conceptualization (Equal); Formal analysis (Lead); Methodology (Equal); Visualization (Lead); Writing-original draft (Lead); Writing-review & editing (Equal). **Cormac Booth:** Conceptualization (Equal); Project management (Lead); Supervision (Equal); Writing-review & editing (Equal). **Sophie Smout:** Conceptualization (Equal); Methodology (Equal); Supervision (Equal); Writing-review & editing (Equal).

2.1 Abstract

This project provides a first attempt to describe the spatiotemporal energetic availability of different prey species to harbour porpoises (*Phocoena phocoena*) in the North Sea. Harbour porpoises are very abundant in the North Sea and their diet consists of a variety of prey species. Harbour porpoises are listed on Annex II of the EU Habitats Directive and accordingly Special Areas of Conservation (SAC) are designated for this species, one of them being in the southern North Sea. The distribution of porpoises is thought to be prey driven but our understanding of prey availability, particularly in the context of the Southern North Sea SAC, is currently limited. The need to assess and potentially manage activities within the SAC is the context for initiating this work.

To compare the prey estimates with knowledge of porpoise distribution, prey availability was predicted for the most recent two years that North Sea-wide cetacean surveys were carried out (2005 and 2016). A cleaned dataset of the International Bottom Trawl Survey (NS-IBTS) was used to create density surface models using generalised additive models for the different prey species. Soap filters were used to avoid smoothing across boundary features. Relative gear efficiency factors per prey species and size class data were used to correct for catchability and biomass values were converted to energetic content using energy density values from the literature. Energy maps were produced for Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), European sprat (*Sprattus sprattus*), Atlantic herring (*Clupea harengus)* and sandeels (Family *Ammodytidae*).

The modelled prey distribution maps fit well with previously described spatial patterns for the fish species. Overall, it appears that the energy available was higher in summer and was also higher in 2016 in comparison to 2005, especially in the southern and north-western

North Sea. For both the Southern North Sea SAC and in the wider North Sea, the main energetic contributions to the overall energy density were from whiting and sandeels. During the winter, European sprat also added considerably to the overall energy density while in summer, Atlantic herring added a substantial amount of energy.

Overall, large amounts of prey energy are predicted to be available both within and outside the SAC boundary. Based on five of the reported main prey species of harbour porpoise overall mean estimates of total energy available in the North Sea ranged between 21,610 (winter) - 30,764 megajoule (MJ) per km^2 (summer) in 2005 and 34,661 (winter) - 76,938 MJ per km^2 (summer) in 2016. Reviews of harbour porpoise daily energy requirements varied between 9 - 31 MJ per day. However, the energy predicted may not correlate to the actual available energy for porpoises given the role of other marine predators and the fishing industry present in the North Sea.

2.2 Introduction

Harbour porpoises are wide-ranging highly mobile animals (Read & Westgate, 1997) and the most abundant cetacean species in the North Sea (Hammond et al., 2002, 2013, 2021). The diet of harbour porpoises consists of a wide variety of fish and cephalopod species and varies regionally; however only a few prey types dominate the diet in any one area (Santos et al., 2004; Santos & Pierce, 2003). In Scottish waters, historical studies have indicated whiting and sandeels dominate porpoise diets (Santos & Pierce, 2003). In Dutch coastal waters, porpoises tend to consume predominantly gadoids such as cod and whiting, gobies (Family *Gobiidae*), sandeels, and clupeids like European sprat and Atlantic herring (Leopold, 2015).

Harbour porpoises are considered to feed at high rates, (*e.g.* pursuing up to 200-550 prey items an hour at peak times with high capture success rates) (Wisniewska et al., 2016, 2018). It has been suggested that Wisniewska et al. (2016) might show an extreme view of porpoise biology (Hoekendijk et al., 2018). Still, harbour porpoises have a high metabolic rate and only a limited energy storage capacity (Bjørge, 2003). Consequently, there is concern porpoises could be vulnerable to starvation due to their limited ability to buffer against diminished food availability.

Different prey types have a range of energy densities and therefore represent different values to the predator (Booth, 2020). Given that there are estimates of foraging effort (Wisniewska et al., 2016, 2018) and energy requirements (for the same individuals) (Rojano-Doñate et al., 2018), it is now possible to assess the potential for porpoises to meet their energy demands. Estimates from Booth (2020) indicate a broad range of energy intake rates for tagged harbour porpoises between 0.57 - 0.99 MJ per hour for juveniles and 0.92 - 2.45 MJ per hour for adults (prey type and prey target size were key drivers of energy intake estimates). The energy requirements for the same tagged individuals ranged from 0.39 - 1.29 MJ per hour (Rojano-Doñate et al., 2018) (these correspond well to estimates of the daily energy intake for captive porpoises ranges between 8 - 35.5 MJ per day (Kastelein et al., 1997; Lockyer, 2003)). From a model developed for wild adult harbour porpoises, Gallagher et al. (2018) estimated minimum daily energy intake requirements to range from 6.7 (± 2.1 SD) MJ per day for males and 16 (± 5.3 SD) MJ per day for pregnant and lactating females.

Harbour porpoise limited energy storage, high foraging and metabolic rate, may mean that porpoise distribution is more tightly linked to higher prey abundance and/or prey quality than for other marine mammal species (*e.g.* bottlenose dolphins and seals which have larger energy stores (Spitz et al., 2012a) and therefore are more likely to be able to cope with periods with limited prey availability). For harbour porpoises, this highlights that understanding prey quality and considering the energetic content of prey is critical to our understanding of porpoise ecology.

Results from dedicated North Sea-wide surveys showed a major north to south shift in the summer distribution of harbour porpoises from 1994 to 2005, maintained through 2016 (Hammond et al., 2002, 2013, 2021). The drivers of this distributional shift are not yet identified but are likely to be linked to changes in prey distribution (Hammond et al., 2013; Ransijn et al., 2021; Sveegaard et al., 2012). However, the spatiotemporal relationship between these predators and their prey is poorly understood. Defining important areas for harbour porpoises is therefore difficult due to their high mobility and probable prey-driven distribution.

The identification and designation of Special Areas of Conservation (SAC) in the UK under the Habitat's Directive has used environmental variables as proxies for prey distribution. One of these SACs lies within the southern North Sea. The selection process for this site was based on predictions of persistent high-density areas of harbour porpoise (Heinänen & Skov, 2015). The resulting Southern North Sea SAC is located off the east coast of England covering an area of 36,951 km^2 and includes distinct key winter (October-March) and summer (April-September) areas thought to be preferred due to prey availability (JNCC, 2017). The majority of the northern part of the site represents the summer area while the southern part is considered an important winter region (Figure 2.1).

To more fully understand the extent to which the SAC contributes to achievement of the Favourable Conservation Status (FCS) for harbour porpoises within UK waters it is crucial to better understand the relationship between porpoises and their prey.

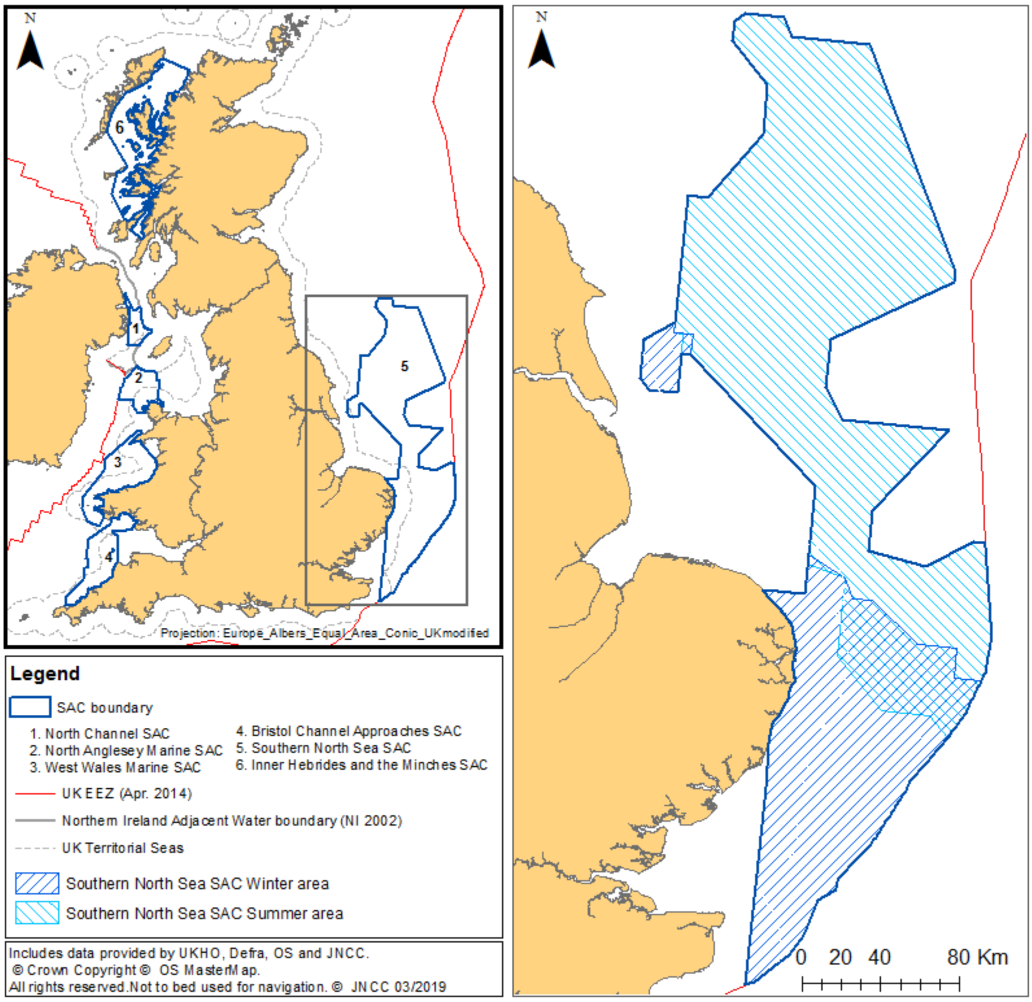

Figure 2.1 Sites designated for harbour porpoise in UK waters. Site 6 (six) is the Southern North Sea SAC and is the primary focus of this project.

Project objectives

The overall goal of this project was to better understand the spatial and temporal variations in prey abundance and to map the calorific value of prey that might impact porpoise distribution. The project can be broken down into the following specific objectives:

- Review published literature to summarize harbour porpoise diet and identify ‘main’ prey species along with a range of energy density values for the ‘main’ prey species (by season and size class where available).

- Generate seasonal maps of the energetic value of the 'main' prey species in the North Sea and seasonal maps showing the total calorific value of all the 'main' prey species combined.

2.3 Material and methods

Identification of important prey species

The importance of prey species for harbour porpoises was assessed through the estimated proportion (by reconstructed biomass) that prey species contributed to the diet. This was done by examining different studies that used stomach content analysis to determine the diet of harbour porpoises in the western North Sea (see the overview in section 2.2 and below). This method derives the estimated diet composition of undigested hard prey remains (*e.g.* otoliths) in stomach contents of stranded and bycaught individuals. Prey species that contributed ≥ 5% of the total prey weight (regardless of season or year) were selected as main prey species.

Important prey species for harbour porpoises in the western North Sea included: gobies, whiting, Atlantic herring, sandeels and European sprat (Table 2.1). In Scottish waters; the north-western North Sea, whiting and sandeels dominated the diet (Santos et al., 2004; Santos Vázquez, 1998). In Dutch waters in the southwestern North Sea, the most important prey species included six different types of fish: gobies, whiting, sandeels, European sprat, Atlantic herring, and Atlantic cod (Jansen, 2013; Leopold, 2015; Leopold et al., 2011; Santos Vázquez, 1998). The same species groups were also identified as most important for harbour porpoises that stranded along the Dutch coastline by (Leopold, 2015) according to an Index of Relative Importance (IRI). However, the recovery rate of large otoliths is higher due to longer digestion times compared to smaller ones (Ross et al., 2016). This may introduce bias as the contribution of larger fish species (*i.e.* cod, whiting) in the diet could be overestimated, while smaller species are underestimated (*i.e.* Atlantic herring, European sprat, gobies, sandeels).

Table 2.1 The main diet composition of harbour porpoises in different areas of the North Sea. Calculated according to the estimated proportion (by reconstructed biomass) that each prey contributed to the diet. The sample size of each study is reported as n. Numbers are not always reported to species level, in such instances, values are reported by species group. Grey highlighted numbers represent prey groups and species that contributed more than 5% of the total prey weight.

Species group and species	Dutch North Sea				Scottish North Sea	
	1989-1995[1] n=62	2003-2010[2] n=76	2003-2010[3] n=229	2006-2014[4] n=826	1992-1996[1] n=72	1992-2003[5] n=188
Gobies	6.4%	36.6%	22.1%	20.5%		
Gadidae	85.9%			36.5%	54.2%	
whiting	78.7%	25.4%	42.3%		43.6%	53.0%
haddock						5.6%
saithe						
pollock						
Atlantic cod	3.3%	5.2%	4.4%			3.8%
Clupeidae	1.9%			10.9%		
Atlantic herring		5.9%	4.6%		3.0%	1.3%
European sprat		4.1%	5.8%			
Sandeels	2.8%		11.1%	18.1%	41.1%	25.6%
Lesser sandeel		13.2%				

[1] (Santos Vázquez, 1998) [2] (Jansen, 2013) [3] (Leopold et al., 2011) [4] (Leopold, 2015) [5] (Santos et al., 2004)

2.3.1 Fish biomass estimation

2.3.1.1 Trawl survey data

The generation of calorific maps for harbour porpoise, prey species in the North Sea were based on fish survey data. Within the North Sea, the International Council for the Exploration of the Sea (ICES) coordinates the International Bottom Trawl Survey (NS-IBTS). This survey aims to monitor the abundances of commercial and non-commercial fish species. The NS-IBTS started in the 1960s but in 1983 surveying expanded to the entire North Sea within the 200 m depth contour from January-March. From 1991 these surveys were carried out in each season (known as quarters) to provide information on the seasonal distribution of stocks sampled. However, it was impossible to maintain such high levels of research vessel effort (ICES, 2012) and therefore, since 1996 most countries carry out surveys only twice a year, in quarter one (January-March) and quarter three (July-September). This therefore dictates the resolution available for exploring seasonality in prey availability for harbour porpoises.

Data from these surveys are reported as Catch Per Unit Effort (CPUE), measured as the number of individuals caught per half an hour trawling. However, here estimates of fish density per unit area are desired and thus there is a need to correct for the area swept during the trawl. This also reduces the high variation in CPUE that is due to differences in area swept (largely linked to trawl duration and tow speed but also related to door- and wing-spread). Furthermore, although the data that are available from ICES[ii] have passed quality control routines there are still quality issues (Daan, 2001; ICES, 2018). Fortunately, Marine Scotland Science has produced publicly available quality assured monitoring and assessment datasets that are derived from the NS-IBTS (Moriarty et al., 2017) and these have been used for this project. The catch data for all species are expressed as biomass per km^2 at length classes (cm). Biomass per km^2 was calculated as:

$$\boldsymbol{D_{biomass,S,L,H}} = \frac{(\boldsymbol{N_{S,L,H}} * \boldsymbol{W_{S,L}})}{\boldsymbol{A_{H,Wing}}} \qquad \text{(eqn 2.1)}$$

Where $D_{biomass,S,L,H}$ is the biomass of fish of species (S) and length (L) per km^2 estimated at the spatial location of trawl sample (H), $N_{S,L,H}$ is the total number of fish of specified species and length in the catch at a location, $W_{S,L}$ is the estimated weight of individual fish of specified species and length, and $A_{H, Wing}$ is the area of seabed swept by the net.

[ii] datras.ices.dk

2.3.1.2 Data selection

Data from 2003-2017 were used to make predictions for the years (2005 and 2016) for which estimates of harbour porpoise abundance in the North Sea are available (Hammond et al., 2013, 2021). Survey coverage across the North Sea for the NS-IBTS is displayed in Appendix 2.1. For this project both the quarter 1 (January-March) and quarter 3 (July-September) datasets were used (Moriarty et al., 2017; Moriarty & Greenstreet, 2017b, 2017a). These quarters were taken to represent the winter (October-March) and summer (April-September) seasons identified within the SAC. Only size classes determined to be readily consumable by harbour porpoises (< 40 cm - Aarefjord et al., 1995) were selected.

2.3.1.3 Catchability

As bottom trawl gear does not catch all fish in the path of the net, survey catches do not represent true amounts of fish in the area surveyed. To account for this relative gear efficiency factors per species and size class from (Walker et al., 2017) were used. These factors were estimated by Walker et al. (2017) using a method that firstly estimated catch-ratios between different gear types that were then rescaled to estimate gear efficiency by comparing abundance estimates with the estimates from stock assessments (Fraser et al., 2007; Walker et al., 2017).

2.3.1.4 Sandeels and gobies

Due to catchability issues and the vertical distribution pattern of sandeels the NS-IBTS data are not representative for this species and therefore another approach had to be adopted. Annual total stock biomass (TSB) estimates from ICES for sandeel area 1-4 (excluding the northern North Sea Figure 2.5) and sandeel habitat areas were used (ICES, 2016; Jensen et al., 2011). Various studies have indicated differences (i.e. in larval drift, recruitment, and growth) among geographical locations and therefore sandeels are not assessed as a single North Sea stock but on an area basis (ICES, 2016). Currently, analytical assessments are available for 4 sandeel areas in the North Sea and assessment are based on SMS-effort model that incorporates several data sources (i.e. dedicated sandeel survey dredge data, other fish survey data, and commercial catches) (ICES, 2021b). Annual TSB per sandeel area was converted to energetic content using the energy density from Table 2.2. The estimated energetic content was then divided by the total area of the sandeel habitat in the ICES area resulting in an energy per km^2 for each sandeel area.

Gobies are also not well represented in the NS-IBTS data due to their small size and occurrence in untrawlable areas close to the coast (Knijn et al., 1993). Therefore, gobies had to be excluded from the analysis.

2.3.1.5 Energy conversion

Estimates of biomass for each prey species were converted to energetic content using energy density values from the literature. Where available, energy densities per season and length class for the study area were used. However, there are only limited published data records and therefore this could only be done for Atlantic herring and whiting. When data for a given size class was missing, the value of the closest size class was assigned. When such data were not available, a single energy density value was used for all size classes (*i.e.* cod, European sprat and sandeels). The energetic conversion factors are shown in Table 2.2.

2.3.2 Estimation of spatial distribution of energy

The spatial energy distribution represented by each prey species and season (quarter 1 and 3) over the entire North Sea was modelled as a function of a number of covariates using a generalised additive modelling (GAM) framework. Covariates considered included depth, year, latitude, and longitude. All analysis was performed in R version 3.5.1 (R Development Core Team, 2018).

Table 2.2 Prey species energy content.

Species	Size class (cm)	Quarter	Energy Density (kJ per g)	Reference
Cod	all	all	4.2	1
Whiting	1.0-11.9	1	4.1	2
	12.0-14.9	1	4.0	2
	15.0-19.9	1	4.3	2
	20.0-24.9	1	4.8	2
	25.0-39.9	1	5.0	2
	1.0-5.9	3	3.8	2
	6.0-7.9	3	3.7	2
	8.0-9.9	3	3.6	2
	10.0-11.9	3	3.8	2
	12.0-14.9	3	3.9	2
	15.0-19.9	3	4.7	2
	20.0-24.9	3	5.3	2
	25.0-39.9	3	5.4	2
Atlantic herring	1.0-9.9	1	4.6	3
	10.0-11.9	1	4.7	2
	12.0-14.9	1	4.4	2
	15.0-19.9	1	4.4	2
	20.0-24.9	1	6.5	2
	25.0-39.9	1	8.5	3
	1.0-4.9	3	4.1	2
	5.0-5.9	3	4.2	2
	6.0-7.9	3	3.9	2
	8.0-9.9	3	4.5	2
	10.0-11.9	3	4.4	2
	12.0-14.9	3	5.2	2
	15.0-19.9	3	10.1	2
	20.0-24.9	3	11	2
	25.0-39.9	3	11.9	2
Sandeel	all	all	5.8	3
European sprat	all	all	7.6	3

[1](Lawson et al., 1997) [2](Pedersen & Hislop, 2001) [3] (Wanless et al., 2005)

The GAMs included a three-dimensional tensor product smooth for space (longitude, latitude) and time (year). Furthermore, to increase confidence in predictions close to land and to avoid smoothing across boundary features, soap film smoothers were used (Wood et al., 2008). This approach avoids the assumption that densities are similar in neighbouring areas that are separated by land. In generating the soap film, knots were placed over the data and land was set to zero which ensured smoothing towards data points and avoided predicting over the land boundary.

In preliminary analyses, a variety of error distributions were considered for the response variable (energy density (in MJ) per km^2): Gaussian, negative binomial, quasi-Poisson, and Tweedie distribution. Additionally, a log-transformation of the response variable was considered for all error distributions. The appropriate distribution and/or transformation was selected by visual inspection of Normal Q-Q plots and Residuals vs Fitted plots.

Smoothing parameter selection was performed by restricted maximum likelihood (REML) (Wood, 2011). Model selection was based on a mixture of measures (*i.e.* Akaike information criterion (AIC), REML, percentage deviance explained) and a visual inspection of predicted versus observed spatial distributions. Additionally, the need of the complex full soap model with a smooth interaction of space and time was checked. The full soap 3D model (equation 2) was compared with a soap 2D model that replaced the three-dimensional space-time effect by an additive space-time effect. Furthermore, the three-dimensional space-time model with the soap filter was compared against fitting the model with a conventionally used thin-plate regression spline (TPRS) basis. Year was included as a cubic regression spline (CRS) and depth was modelled as a smoothing spline.

Three-dimensional space-time effect model:

$$\left(\text{Energy}_{it}\right) = s\left(\text{depth}_{it}\right) + te\left(\text{longitude}_{i},\ \text{lattitude}_{i},\ \text{year}_{t}\right) \qquad \text{(eqn 2.2)}$$

Additive space-time effect model:

$$(\mathrm{Energy}_{it}) = \mathrm{s}(\mathrm{depth}_{it}) + \mathrm{te}(\mathrm{longitude}_i, \mathrm{lattitude}_i) + \mathrm{s}(\mathrm{year}_t) \quad \text{(eqn 2.3)}$$

For a given haul the energy per unit area is represented by $\mathrm{Energy}_{i,t}$ having space coordinates i and a date/time t.

Within the three-dimensional space-time effect model the spatial pattern could change with time. In the additive space-time effect model the spatial pattern was fixed, but the intensity could change with time.

Temporal autocorrelation of the residuals was checked using autocorrelation function (ACF) plots and spatial autocorrelation was investigated using variograms and bubble plots.

2.3.3 Prediction maps

Prediction surfaces showing the spatial variation in energy represented by each prey species were generated over a regular bathymetry grid available from the European Marine Observation Data Network (EMODnet) Seabed Habitats project[iii]. This raster with a resolution of 115 m * 115 m was re-gridded to a resolution of 1 km^2.

The prediction grid was restricted to the area that was covered by the data for each season. The prediction grid for winter covered an area of 469,145 km^2 and in summer the grid was slightly smaller (463,010 km^2).

First, a distribution map for each prey species per year (2005, 2016) and season (winter – January-March, summer – July-September) was generated. Second, surfaces for each species

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[iii] emodnet-seabedhabitats.eu

were summed to produce a map of combined energy represented by all prey species combined (maps separated by season and year). This process was done with and without the inclusion of sandeels because the approach to generate the energy surfaces for sandeels was different from the other species.

Third, the total energy represented by each species over the entire North Sea was calculated by summing energy values over all grid cells in the prediction grid. The mean energy density was estimated, as well as the % of the total energy that lay within the entire SAC and the seasonal component of the SAC that matched the season of the distribution map. Furthermore, the interquartile range (IQR) and median values for energy surfaces for each species by year and season for the entire North Sea were calculated. To compare the amount of energy in the SAC in comparison to the North Sea relative to the area size, a Ratio Energy SAC (RES) score was calculated per species. RES values of 1 would indicate that the SAC has similar average energy (MJ per km^2) to the wider North Sea while values >1 would suggest that the SAC has higher average energy values. RES was calculated both for the entire SAC and for the seasonal component of the SAC as:

$$RES = \frac{(total\ energy\ SAC{:}total\ energy\ North\ Sea)}{(total\ area\ size\ SAC{:}total\ area\ size\ North\ Sea)} \qquad \text{(eqn 2.4)}$$

2.4 Results

2.4.1 Model

The assumption of normality and homogeneity of variances was most appropriately satisfied by a log-transformation and Gaussian distribution of the response variable. The log-transformation reduces the effects of relatively high/low catches. Correlograms, variograms, and bubble plots of the final models indicated very weak autocorrelation and deviance residuals were evenly spread.

The most adequate model for all prey species was the full soap 3D model explaining between approximately 26% to 79% of the total observed variation in the data (Table 2.3). Although, the TPRS model always (except for sprat in winter) had a better fit in terms of AIC and other measure (Table 2.3) the full soap 3D model improved the performance of the model by avoiding leakage across land. Furthermore, the soap filter seemed to perform better in the visual comparison between predicted and observed distributions and used considerably fewer degrees of freedom. The variation explained was considerably higher for European sprat probably due to the distinct distributional pattern.

2.4.1.1 Depth

For each prey species, energy increased with increasing depth until reaching a maximum after which the trend either plateaued or decreased (Figure 2.2).

The density of Atlantic herring reached an optimum around 145m depth in winter and 105m depth in summer. The optimum density distribution, for cod seemed to lie around 100m depth in both seasons. In winter the trend plateaued while in summer the trend declined sharply at depths greater than 100m. Regardless of season, the optimum density distribution of European sprat was around 60m. The optimum density distribution of whiting lay between 75m and 150m depth.

Table 2.3 For all models (i.e. full soap 3D (three-dimensional space-time effect model with soap filter) TPRS (three-dimensional space-time effect model with a TPRS base) and the soap 2D (additive space-time effect model with soap filter)) the AIC score, REML score, percentage deviance explained (% DE), and degrees of freedom (DF) per prey species and season. Winter represents January-March and summer represents July-September.

Species	Season	Model	AIC	REML	% DE	DF
Cod	*Winter*	**full soap 3D**	**18525**	**9325**	**26.1**	**109**
		TPRS	18482	9312	29.3	198
		soap 2D	18644	9367	21.9	57
	Summer	**full soap 3D**	**14926**	**7540**	**41.5**	**111**
		TPRS	14858	9321	45.7	198
		soap 2D	15000	7553	38.4	62
Atlantic Herring	*Winter*	**full soap 3D**	**19721**	**9972**	**41.5**	**159**
		TPRS	19596	7528	42.8	278
		soap 2D	19983	10053	29.9	62
	Summer	**full soap 3D**	**17638**	**8879**	**40.2**	**106**
		TPRS	17578	9943	43.9	182
		soap 2D	17689	8894	37.5	59
European Sprat	*Winter*	**full soap 3D**	**17461**	**8851**	**78.8**	**172**
		TPRS	17762	8868	81.0	297
		soap 2D	17770	8958	75.8	64
	Summer	**full soap 3D**	**16021**	**8134**	**60.9**	**144**
		TPRS	15854	8793	65.8	279
		soap 2D	16059	8125	58.7	73
Whiting	*Winter*	**full soap 3D**	**16042**	**8156**	**50.1**	**151**
		TPRS	15907	8090	54.3	267
		soap 2D	16212	8189	45.6	67
	Summer	**full soap 3D**	**14235**	**7265**	**49.9**	**161**
		TPRS	14009	8101	55.1	230
		soap 2D	14212	7232	47.7	81

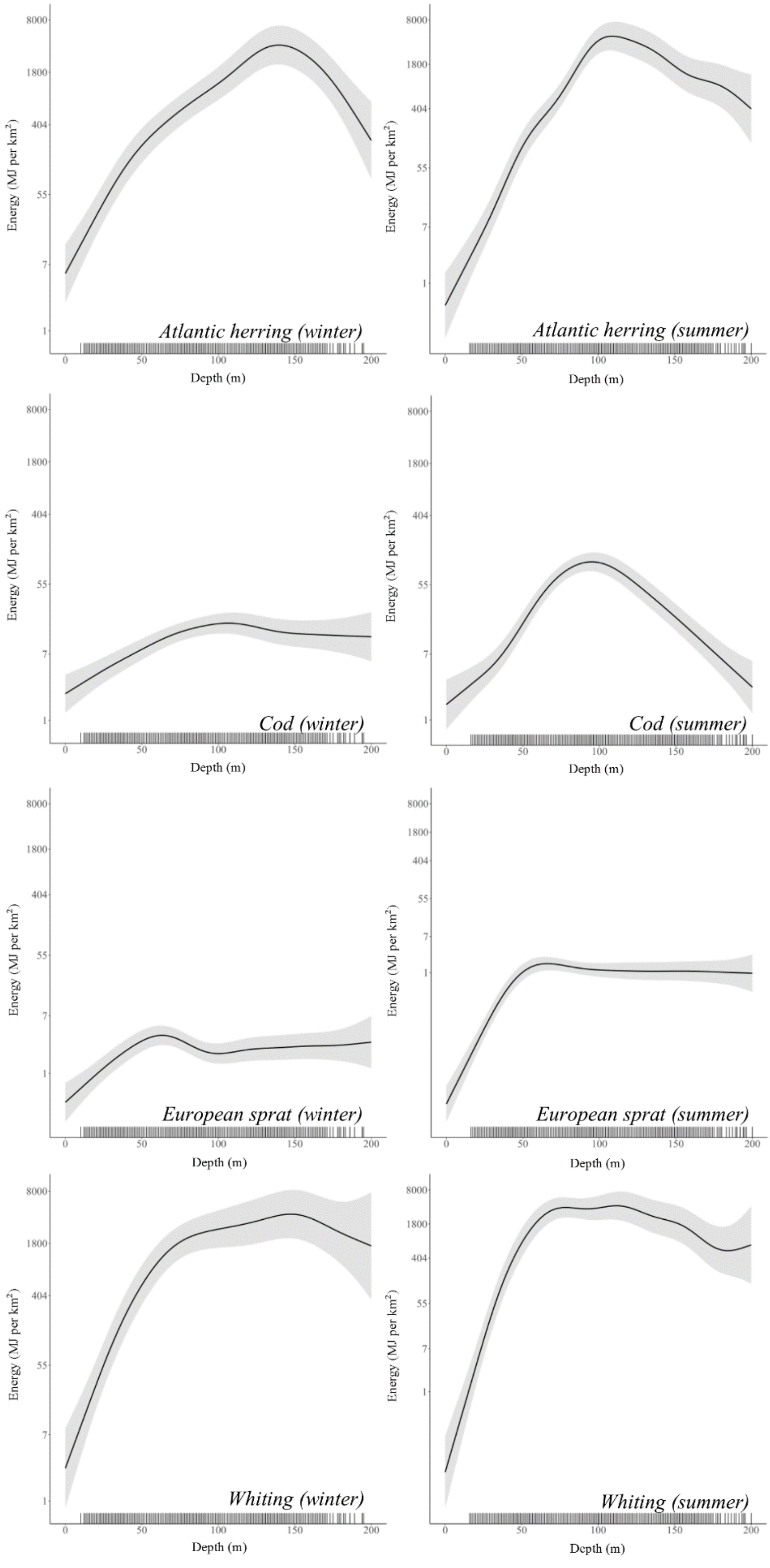

Figure 2.2 Effect of depth (m) on the energy (MJ) per km2 according to final generalised additive models. Created by fixing all other parameters in the model (i.e. x, y, year) to median values. Note y-axis is at similar scale but plots are not aligned.

Distribution maps of energy represented by each prey species (except sandeels) are shown in Figure 2.3 for winter and Figure 2.4 for summer. Predicted energy availability was greater in 2016 than in 2005 for all species except cod. The annual distribution of energy represented by sandeels in 2005 and 2016 is shown in Figure 2.5. Median energy values along with the IQR for each species and overall are summarized in Table 2.4.

2.4.1.2 Atlantic herring

Atlantic herring energy was mainly distributed in the south-eastern and north-eastern North Sea in winter and in the north-western North Sea during summer. During both seasons, high energy density areas shifted southwards from 2005 to 2016. The lowest overall amount of energy was observed in the summer of 2005 with median energy values of 601.8 MJ per km^2 (IQR = 54.6 - 4914.8) and the highest in the summer of 2016 (median = 812.4 MJ per km^2 (IQR = 134.3 - 6634.2)).

2.4.1.3 Cod

The available energy represented by cod (<40 cm - see methods) was relatively low in comparison to the other prey species and was especially low in the summer of 2016 (median (IQR) = 7.4 (1.1 - 54.6) MJ per km^2). Median energy in winter 2016 was estimated to be 13.5 (IQR = 5.0 - 73.7) MJ per km^2. Energy available was higher in 2005 in both summer and winter (medians of 30.0 and 18.2 MJ per km^2 respectively). The available energy from cod was mainly distributed in the northern part of the North Sea with high values on the north-eastern edge of the predicted surface (close to the Norwegian trench). In winter, cod energy values were greater in 2016 than in 2005, especially in the northern North Sea. In the northern North Sea, energy represented by cod in summer was higher in 2016 than 2005.

However, in winter energy was lower in 2016 compared to 2005 and shifted more to the north.

2.4.1.4 European sprat

Energy represented by European sprat was mainly distributed in the southern and north-western part of the North Sea. Relatively low values were observed in the north-eastern North Sea. In summer, energy was concentrated south of the Dogger Bank and north of the Southern Bight. The entire spatial pattern shifted slightly more north in 2016 in comparison to 2005. Energy estimates were higher in 2016 than 2005 in both the winter (medians: 2005 - 37 MJ per km^2; 2016 - 224 MJ per km^2) and summer (medians: 2005 - 109 MJ per km^2; 2016 - 543 MJ per km^2).

2.4.1.5 Whiting

Whiting energy was widely distributed throughout the North Sea except over the Dogger Bank and in the eastern part of the German Bight. These lower energy areas were more profound in 2005 than in 2016. In summer and in 2016 the energy was higher in the Southern Bight. Overall, the energy from whiting was the highest among all species modelled in this study (Figure 2.3, Figure 2.4 and Table 2.4). As with other species, the energy available was higher in 2016 than 2005 in both winter (medians: 2005 - 1339 MJ per km^2; 2016 - 2441 MJ per km^2) and summer (medians: 2005 - 4447 MJ per km^2; 2016 - 8955 MJ per km^2).

2.4.1.6 Sandeels

Sandeel energy values (for the whole year) were higher in the north-western North Sea and relatively very low in the eastern part. Overall, the energy represented by sandeels was higher in 2016 than 2005 and the difference between low and high values was amplified in 2016.

The IQR and median values of sandeels are zero (Table 2.4) indicating that the distribution of sandeels is patchy. But the mean energy estimates (Table 2.4) indicate that where they are present, large amounts of energy are available (mean 2005: winter - 9,577 MJ per km^2; summer - 9,452 MJ per km^2), especially so in 2016 (mean 2016: winter - 16,772 MJ per km^2; summer - 16,553 MJ per km^2).

2.4.1.7 Overall energy maps by season and year

Maps of the energy across all species analysed for each year (2005, 2016) and season (winter, summer) are shown in Figure 2.6. Energy contribution by species is shown in Table 2.4.

In Appendix 2.2 there are also combined maps for all species that could be modelled using GAMs, thus excluding sandeels. Appendix 2.3 shows maps of available energy resolved to the scale of the SAC boundary.

Overall, there are extremely high levels of energy available to harbour porpoises (and other predators) (relative to the population density and daily energy requirements of harbour porpoises in the North Sea). Total estimates (including sandeels) indicate mean energy available per unit area between 21,610 - 34,661 MJ per km^2 in 2005 and 30,763 - 76,937 MJ per km^2 in 2016 (Table 2.4). The higher values in 2016 are mainly in the southern and north-western North Sea. Of the five prey species considered here over the predicted two years, whiting and sandeels were the main contributors in terms of energy over the entire North Sea (Table 2.4). During winter, the contribution of European sprat to the overall pattern was also considerable. Atlantic herring is a main contributor in summer.

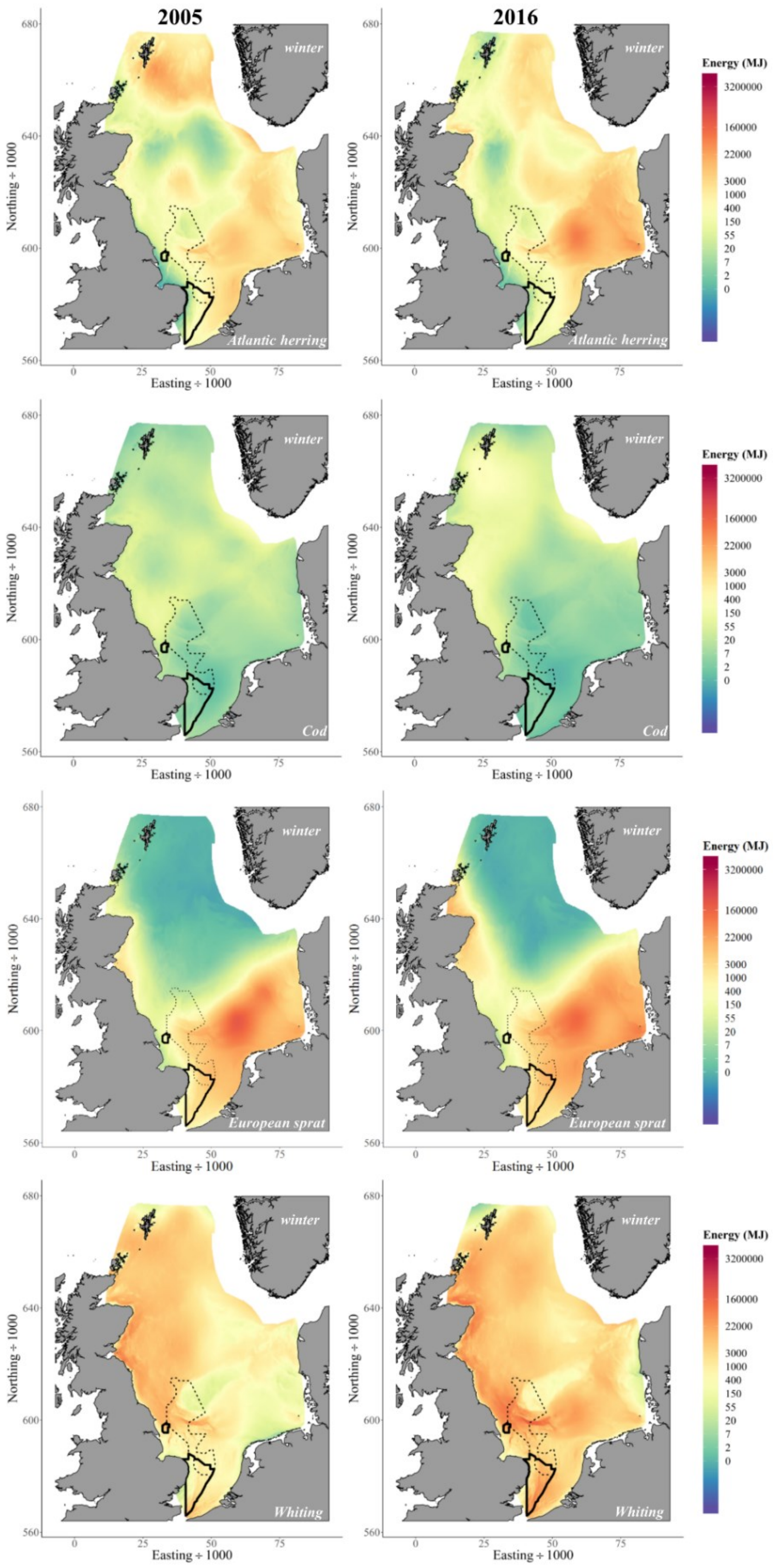

Figure 2.3 Spatiotemporal winter distribution (January-March) of porpoise prey species energy per km2 for the North Sea, illustrated for 2005 in left panels and 2016 in right panels. Bold outlines represent the winter part of the SAC and the dotted lines represent the summer part of the SAC.

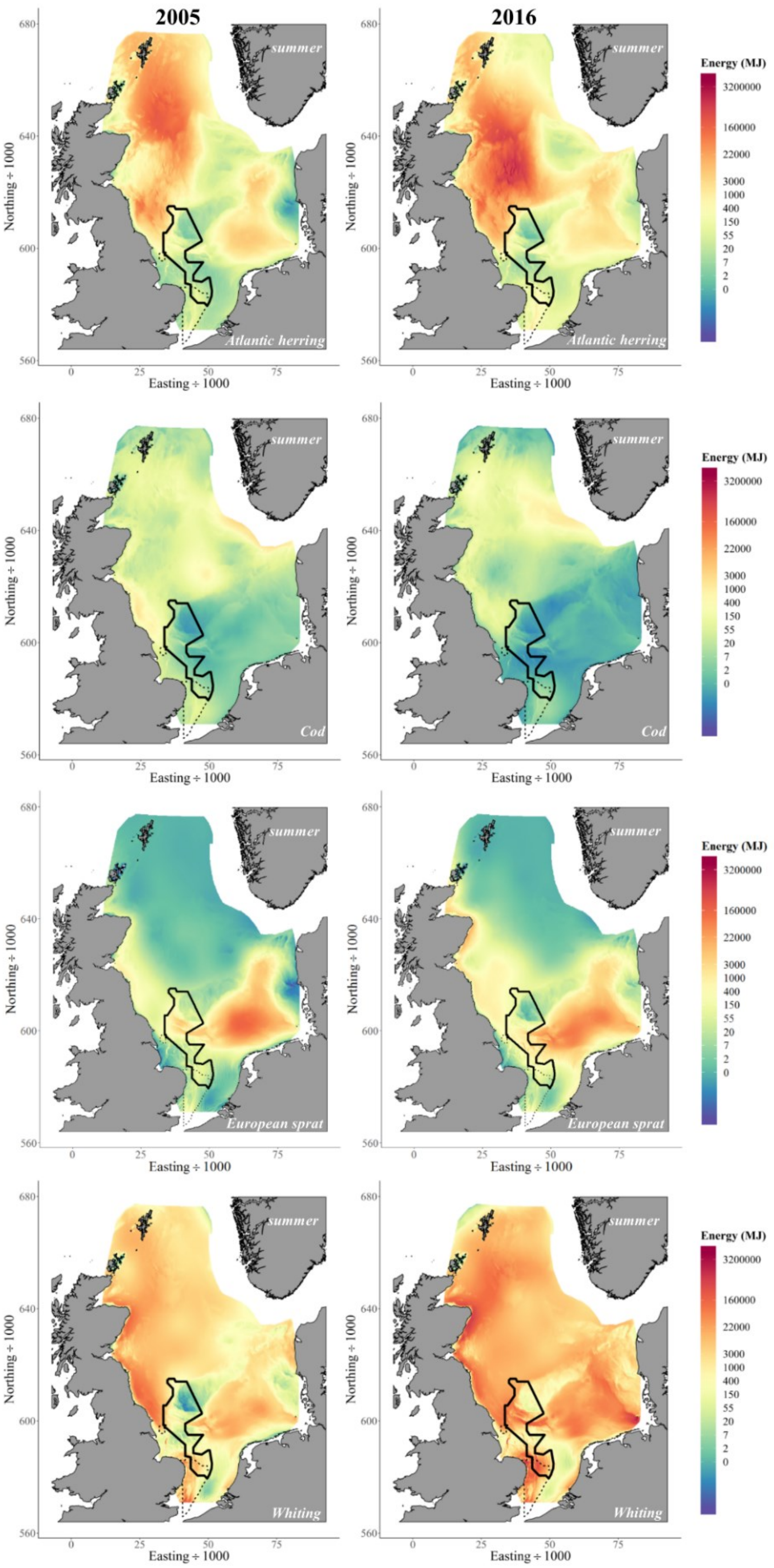

Figure 2.4 Spatiotemporal summer (July-September) distribution of porpoise prey species energy per km2 for the North Sea, illustrated for 2005 in left panels and 2016 in right panels. Bold outlines represent the summer part of the SAC and the dotted lines represent the winter part of the SAC.

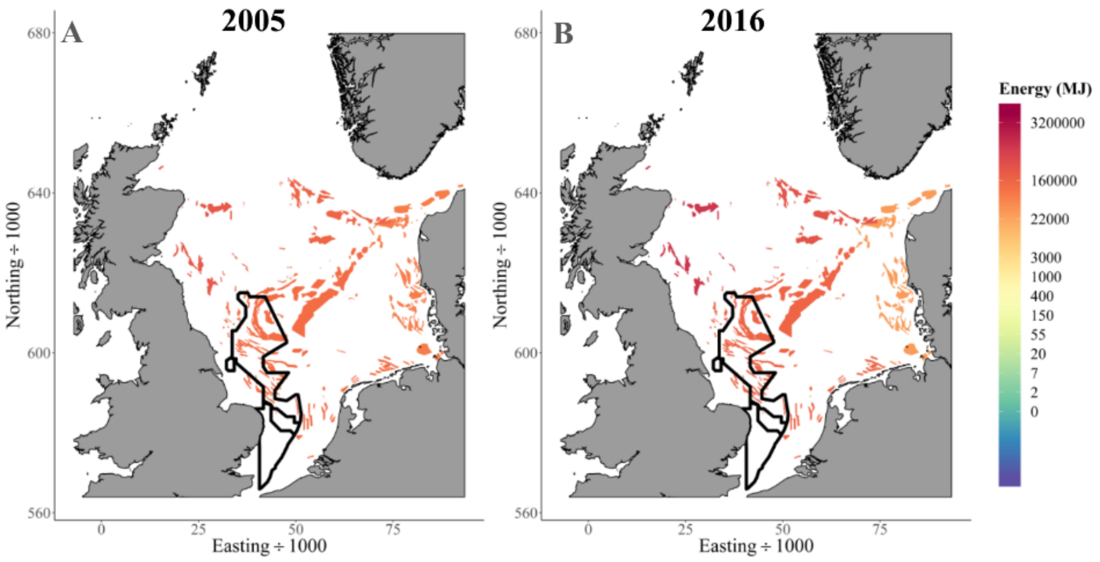

Figure 2.5 Distribution of sandeels per km2 for the North Sea in 2005 (left) and 2016 (right). Energetic values are based on ICES sandeel stock assessments and locations are based on sandeel fishing grounds. The bold outlines represent the entire extent of the SAC.

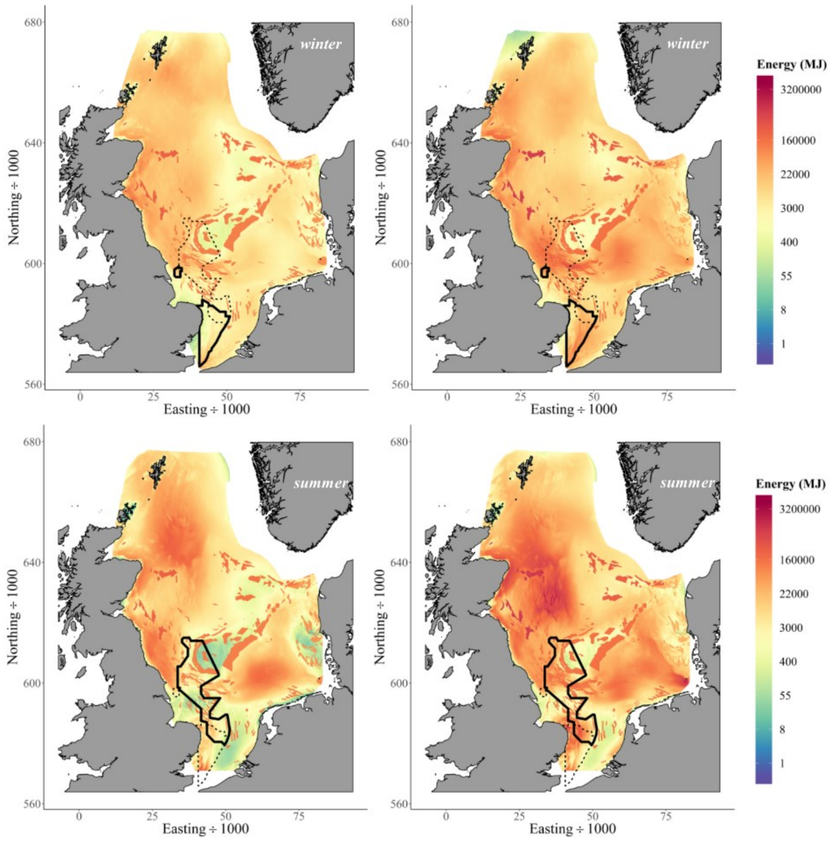

Figure 2.6 Spatiotemporal winter (January-March) and summer (July-September) distribution of all porpoise prey species energy per km2 for the North Sea, illustrated for 2005 on the left and 2016 on the right. Bold outlines represent the corresponding seasonal part of the SAC while the dotted lines represent the other part of the SAC.

Table 2.4 Mean, median, and Interquartile range (IQR) values for energy (MJ per km2) surfaces for each species and all species combined by year and season for the entire North Sea. Species contribution illustrates each species contribution to the energy in the North Sea. Note that the area of the North Sea that was predicted over is different by season, slightly smaller in summer (winter = 469,145 km2 and summer = 463,010 km2). To compare the amount of energy in the SAC in comparison to the North Sea relative to the area size a Ratio Energy SAC (RES) was calculated. RES SAC season represents the RES score using the seasonal SAC boundary and RES SAC total represents the RES score using the full SAC boundary. RES values >1 would suggest that the SAC has higher average energy values (MJ per km2) than the wider North Sea.

Species	Year	Season	Mean energy (MJ per km^2)	Median (MJ per km^2)	IQR (MJ per km^2)	Species contribution	RES SAC season	RES SAC total
Cod	2005	*Winter*	26	18	9 - 33	0.1	0.22	0.40
		Summer	93	30	6 - 90	0.3	0.10	0.19
	2016	*Winter*	54	14	5 - 74	0.2	0.07	0.08
		Summer	65	7	1 - 55	0.1	0.07	0.07
Atlantic herring	2005	*Winter*	1,668	602	148 - 2,208	7.7	0.19	0.23
		Summer	11,035	625	55 - 4,915	35.8	0.02	0.01
	2016	*Winter*	3,060	665	164 - 2,441	8.8	0.04	0.10
		Summer	31,409	812	134 - 6,634	40.8	0.02	0.01
European sprat	2005	*Winter*	6,668	37	2 - 2,981	30.8	0.41	0.40
		Summer	3,023	5	1 - 110	9.8	0.16	0.12
	2016	*Winter*	6,929	221	1 - 6,003	20.0	0.63	0.58
		Summer	2,617	33	2 - 545	3.4	0.17	0.13
Whiting	2005	*Winter*	3,797	1,339	493 - 6,003	17.5	0.44	0.65
		Summer	7,037	2,441	602 - 6,634	22.8	0.16	0.69
	2016	*Winter*	8,065	4,447	1,998 - 8,103	23.3	**1.81**	**1.94**
		Summer	26,073	8,955	3,641 - 24,343	33.9	**1.10**	**1.60**
Overall without sandeel	**2005**	***Winter***	**12,159**	**4,915**	**2,208 - 13,360**		0.30	0.44
		Summer	**21,187**	**4,447**	**1,097 - 19,930**		0.09	0.25
	2016	***Winter***	**18,108**	**9,897**	**5,432 - 22,027**		**1.63**	**1.74**
		Summer	**60,165**	**14,765**	**4,447 - 59,874**		0.50	0.71
Sandeel	2005	*Winter*	9,577	0	0-0	43.8	0.04	**1.88**
		Summer	9,452	0	0-0	31.2	**2.71**	**1.90**
	2016	*Winter*	16,772	0	0-0	47.8	0.04	**1.43**
		Summer	16,553	0	0-0	21.8	**2.05**	**1.45**
Overall with sandeel	**2005**	***Winter***	**21,611**	**6,634**	**2,697 - 16,318**		0.19	**1.07**
		Summer	**34,661**	**6,634**	**1,636 - 36,316**		1.00	0.83
	2016	***Winter***	**30,764**	**13,360**	**6,634 - 26,903**		0.85	**1.60**
		Summer	**76,937**	**22,027**	**5,432 - 80,822**		0.88	0.90

2.4.1.8 The SAC region relative to the wider North Sea

To assess the value of the SAC area relative to the North Sea, RES scores were calculated. In general, with the inclusion of sandeels to the energy surfaces, the RES values were close to 1 indicating the SAC area was as, or slightly less 'valuable' compared to the wider North Sea region on average. In winter 2005, the seasonal SAC region appeared to be below average (RES = 0.19) but the full SAC boundary had a score of 1.07 indicating the area was slightly above average overall. In general in 2016, the RES scores indicated the SNS SAC was very slightly below average (RES = 0.85 - 0.88 for the seasonal SAC regions) and above average during the winter period (for the full SAC boundary; RES = 1.60)

These results also demonstrate the importance of the role of sandeels in the SAC region as the species was a key driver of the RES scores (see 'Overall without sandeel' in Table 2.4). Without the inclusion of the sandeel data, the value of the SAC relative to the wider North Sea is greatly diminished with RES scores ranging from 0.30-0.71. The exception is winter 2016 where the distribution of whiting is important to the overall energy in the SAC.

As noted above, while there are relative spatial variations in energy available, the absolute values mean and median energy (MJ per km^2) indicate there are very high levels (relative to porpoise densities and known energy requirements in the North Sea) of energy available to porpoises via the five prey species considered here.

2.5 **Discussion**

This project provides a first attempt to describe the spatiotemporal distribution of energetic availability of harbour porpoise prey species in the North Sea.

2.5.1 Model evaluation

The results of the GAM-based spatiotemporal modelling indicate that this approach was capable of creating realistic distribution maps of energy density of prey species. The inclusion of a three-dimensional tensor product and the use of soap film smoothers allowed the spatial distribution pattern to change with time and avoided smoothing across boundary features. The final models captured an adequate amount of the variation in the data (Table 2.3) suggesting a good model fit.

The spatial covariates (longitude and latitude) did well in modelling the distributional pattern. However, biologically these variables are hard to interpret and are proxies for environmental covariates. To better understand why prey species are distributed in certain places the spatial covariates should be substituted or accompanied by more biologically meaningful parameters (*e.g.* temperature, salinity, primary productivity, and vertical mixing (Munk et al., 1995)). Covariate data could for instance be obtained from The Copernicus Marine Environment Monitoring Service[iv]. This could provide insight into how prey availability might alter due to environmental change and might be particularly interesting to explore in the North Sea as it is an area were temperature rise is faster than the global average (Dulvy et al., 2008).

2.5.2 Implications of the results

2.5.2.1 Distribution maps

Although there are species specific spatiotemporal variations there are several overall patterns that can be drawn from the results. The modelled distributional maps and overall trends of the prey species fit well with previously described spatial patterns and population trends from ICES stock assessment and other sources (*e.g.* (Heessen et al., 2015; ICES, 2017,

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[iv] marine.copernicus.eu

2018; Teal et al., 2009). However, there might be some discrepancies due to recent alterations in distribution or due to the size class restriction in this study (only selected fish < 40cm) which would only really affect cod and to a lesser extent whiting.

Overall, the predicted energy density was higher in summer and in 2016 compared to 2005 especially in the southern and north-western North Sea. During winter the highest energy values were observed in the southern North Sea an additional high area in the north-western North Sea was apparent in summer. The contribution of Atlantic herring and European sprat to the overall energy availability was distinct by season. It should be noted that there are likely to be variations in fish biomass and recruitment across different fish species, regions and years. It is unclear how porpoises would respond to such variations in prey density.

In general, the SAC region does not seem to cover the very highest energy areas identified by the spatial models in the North Sea, but nonetheless comprises a significant energy resource. Whiting and sandeels increase the relative average energy availability within the overall SAC to above the average of the North Sea in winter (RES score Table 2.4). The RES score for whiting is indicative of the value of the species in the SAC region. For sandeels, their patchy distribution in the North Sea drives the patterns observed and the SAC covers a couple of sandeel grounds. Furthermore, the results indicate that the summer component of the SAC encompasses an area with relative high amounts of sandeel energy. It is important to note, that although the energy values in some areas in the North Sea, including the SAC, are relatively low compared to very high energy areas, these ‘colder spots’ might not necessarily represent “bad” foraging areas. Overall, large amounts of energy are predicted to be available both within and outside the SAC region. Overall mean estimates of total energy available ranged between 21,610 (winter) - 30,764 MJ per km^2 (summer) in 2005 and 34,661 (winter) -

76,938 MJ per km^2 (summer) in 2016 (for five of the main harbour porpoise prey species). Wild harbour porpoise daily energy requirements vary between 9 - 31 MJ (Rojano-Doñate et al., 2018). This suggests that within "low" energy areas there would still be plenty of energy available to sustain porpoises in the area.

However, this estimation is overlooking the fact that there are other sources of energy "loss" such as competition with other predators (*i.e.* sea birds, other marine mammals, foraging fish as well as fisheries). Therefore, the energy predicted here may not correlate to the actual available energy for porpoises given the role of other predators and fishing industry present in the North Sea. This may vary significantly across the North Sea region and without this it is difficult to assess whether areas mapped as "high" energy represent high energy available to porpoises. This highlights the difficulty in assessing predator-prey relationships within a complex ecosystem with many different trophic interactions. Furthermore, by not considering these multi-species interactions the results might become counterintuitive.

2.5.2.2 Diet and prey quality

Given the relative importance of whiting and sandeels in the diet of harbour porpoises (Table 2.1) it was tentatively postulated that these species might be more abundant than other prey species. Correspondingly, the energy availability of these species is higher compared to the other species. Logically, given that other prey remains at constant abundance, regardless of prey preference one would assume that when a prey species is more abundant it would also be more consumed. However, this might be very dependent on the availability of other prey within the system. Furthermore, this result does not indicate if these species might be important for harbour porpoise distribution or if porpoises might prefer certain prey. Prey preference might be dependent on multiple factors such as predictability and catchability. To get a better idea what porpoises prefer the relationship between prey availability and consumption, a multi-species functional response, could be modelled (Chapter 3; Ransijn et al., 2021).

The energetic balance for any species is governed by the effort expended to acquire resources, the energy available in resources acquired and how the energy acquired is allocated. Marine mammals exhibit a wide range of life history strategies, from large, long lived species with long inter-birth intervals, to smaller species, like the harbour porpoise which reach sexual maturity quickly and reproduce frequently. For harbour porpoises, efficient foraging (maximising intake whilst minimising expenditure) is therefore an essential element in such organism's survival and reproduction. Therefore, understanding the energy available in an ecosystem is critical to understand the ecology of the species, identifying important areas and in understanding the potential drivers of change for populations. Foraging behaviour should eventually, according to optimal foraging theory, maximize the fitness of individuals (Pyke, 1984) by maximizing the energy obtained per unit of energy spent. To target the most abundant and/or profitable prey, predators might switch between prey species, foraging tactics, or feeding grounds (Schenk & Bacher, 2002). For a species like the harbour porpoise that feeds on multiple prey species, this could imply that the diet of harbour porpoises or their feeding areas may change as the availability of their prey changes.

Another consideration in the interpretation of the energy available maps is that porpoises will not be able to assimilate 100% of the energy available in any prey item. There are limited data on the assimilation efficiency (*i.e.* the percentage of energy from an item that is usable by the animal) in porpoises, but published estimates range from 0.74 (Yasui & Gaskin, 1986) to 0.95 (Lockyer, 2007) (*i.e.* 74%-95%). There are likely to be prey-specific assimilation rates as observed in studies with captive seals (Lawson et al., 1997).

Harbour porpoise life history suggests that proximity to suitable prey species is important for their survival. As a generalist species, this study suggests that the North Sea represents a suitable habitat for harbour porpoises with a range of energy sources available which might inform species distribution. However, it is important to consider that a number of other drivers affect a species distribution: including (real or perceived) risk of predation or injury from marine mammal interactions (*e.g.* grey seals, bottlenose dolphins or killer whales), competition, and potentially exposure to anthropogenic stressors.

2.5.3 Assumptions and uncertainty

In this Chapter the bias of the estimates and the uncertainty in the results were not explored but the three main sources that were explored in Ransijn et al. (2020) were catchability, energetic content, and spatiotemporal model predictions. It is not trivial to robustly estimate the uncertainty that results from combining these different sources of error.

2.5.3.1 Explorable uncertainty

To estimate absolute fish abundance the survey densities were scaled using relative gear efficiency correction factors from Walker et al. (2017). However, the uncertainty associated with these estimates were not incorporated here (but see Ransijn et al. (2020) and in section 4.3.3.7 of Chapter 4). The catchability uncertainty is probably the largest source of error; both the extent to which main prey species are represented in survey trawls (*e.g.* gobies, and depth distribution of different prey species) and because different assumptions could lead to quite significant alterations in the estimated numbers of fish (Aarts et al., 2019). Nevertheless, the spatial pattern is not believed to change considerably unless catchability also varies on quite a high spatial resolution scale and/or the size classes of a particular species are distinct in their spatial distribution.

Where possible, biomass was transformed to energy density according to fish length and season. However, for some species this information is not available and therefore a single conversion estimate was used that thus ignored the variation according to length and season. Furthermore, uncertainty in these estimates due to sampling error was not accounted for. Therefore, the energy available to porpoises might have been over or underestimated.

Uncertainty in the of the spatiotemporal predictions due three different sources of uncertainty (i.e. relative gear efficiency factors, energy conversion factors and model predictions) can be explored using different methods such as parametric or nonparametric re-sampling, jackknife, and others. An applications of such an approach to propagate uncertainty is described in section 4.3.3.7 and Ransijn et al. (2020).

2.5.3.2 Assumptions

The selection of "important" prey species for harbour porpoises was based on studies that used data from stranded and bycaught animals. There was no data from the UK for the southern North Sea region and the studies that were carried out in the UK (Scotland) span 1992-2003 and there may have been changes in the importance of prey species since then. As such, important prey species for porpoises within the SAC area could have been missed. However, when comparing studies from the North Sea, the proportion of prey species might change but it is believed that the "main" species were covered with the exception of gobies. While there is no published energy density value for a goby species, Booth (2020) indicates that the energy content of Family Gobiidae species is likely to be similar to grey gurnard and red mullet (estimated as 4.4 kJ per gram following Plimmer (1921)).

Biases due to stomach content methodology could have led to an underestimation of potential “important” prey species as it only provides information on the most recent meal (Jansen, 2013; Leopold, 2015). Although, as previously mentioned the importance of cod could have been overestimated their inclusion is unlikely to considerably alter the overall conclusions of this study as their energy availability is relatively low. Biases could also have been induced by variation in sample size and composition according to sex, age and origin of the sample (bycaught or stranded). Despite these limitations, stomach contents analysis gives valuable information on the harbour porpoise prey-spectrum and the contribution of prey to the diet.

As previously mentioned, the data used does not allow for a similar approach for other “important” prey species (sandeels and gobies) due to catchability issues in the survey design. Gobies had to be excluded and therefore the results underestimate the energy available to porpoises (because this and other foraged prey species are not accounted for in this five species analysis). This is especially the case in the southern North Sea were gobies are more abundant (Knijn et al., 1993; Tulp et al., 2008).

For sandeels another approach was applied. The coarse analysis for sandeels that precluded seasonal variations and only rough spatial variation to be modelled could have led to error in the availability estimates. This might have crucial implications as sandeels are an important prey species for harbour porpoises and contribute markedly to the energy available (Gilles et al., 2016; Leopold, 2015). In Chapter 4 section 4.3.3.6 a new approach is applied using a distribution model by Langton et al. (2021).

By selecting size classes that are smaller than 40cm the results show estimation for consumable prey. However, porpoises might have a particular preference for certain lengths. Therefore, it would be interesting to compare the length distribution of different prey types in the trawl data with the distribution that are consumed by porpoises from stomach content analysis.

The work from this Chapter has been used to explore the relationship between the density of harbour porpoise and some of its major North Sea prey species (Ransijn et al., 2020). That project investigated whether different prey distribution surfaces could explain the drivers of harbour porpoise distribution (see Figure A2.4) and shifts in porpoise density. Different prey species availabilities were used as covariates in porpoise distribution models (fitted by Claire Lacey see Lacey (in prep)) based on SCANS II (2005) and III (2016) survey data (Ransijn et al., 2020). This allowed exploration of a more detailed and direct overlap between the distribution of porpoise and their prey. For the SCANS-II survey (summer 2005), the best fitting model included distance to sandeel grounds, slope and aspect. For the SCANS-III (summer 2016), the best model retained information from two fish species energy distributions: mean sprat and distance to sandeel grounds, along with slope. However, it was established that the porpoise prey energy layers were inadequate in explaining harbour porpoise distribution observed during the SCANS-II and III surveys. The best fitting models explained low percentage deviance (2005: 13.8%; 2016: 5.7%) and therefore can be considered relatively poor fits and so do not provide a good description of summer harbour porpoise distribution.

2.6 Recommendations

In this study, available energy maps for harbour porpoises were generated based on modelling approaches notes on interpretation and the assumptions made in deriving the outputs have been outlined. Below recommendations for future work are presented, both to extend this effort to better understand the role of the Southern North Sea SAC in harbour porpoise ecology, but also to improve and refine predictions of energy available.

- **Gobies**

  Explore other data or approaches (*e.g.* habitat-based modelling) to model gobies an important prey that had to be excluded for this analysis.

- **Porpoise prey size "preference"**

  Compare the length distribution for each prey species that are deemed consumable (<40cm) for porpoises according to the NS-IBTS data against consumed size classes based on stomach content data. This will provide insight into porpoise prey size class "preference".

- **Energetic content of prey**

  To improve the seasonal energetic value of prey there are two projects that have recently commenced that will analyse different fish species for quality see section 5.1.5.

This study represents a multidisciplinary effort to inform spatial management via the integration of knowledge across taxa, principally the critical functional linkage between a marine mammal and some of their prey species. Future assessments will be improved by inclusion of more recent data available on stomach contents from stranded and bycaught porpoises from English/Scottish datasets (see section 5.1.2.2) and considerations of additional information on prey calorific content (see section 5.1.5). Therefore, to better understand this subject for harbour porpoises and other marine mammals, a multidisciplinary work of marine mammal scientists, environmental scientists and fish biologists would be extremely valuable to guide research to address fundamental questions in marine spatial planning, marine ecology and assessment of anthropogenic impacts.

Appendix 2.1

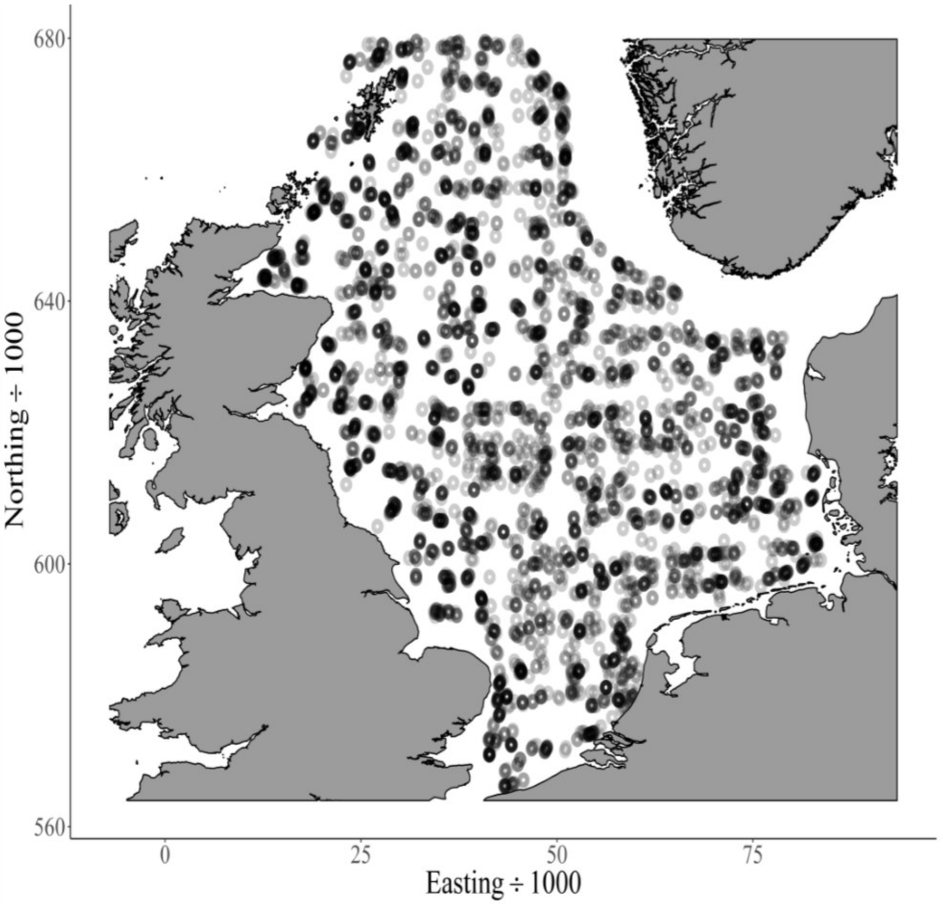

Figure A 2.1 Survey coverage of the NS-IBTS across the North Sea (2003-2017). Darker coloured circles represent locations that were more frequently sampled.

Appendix 2.2

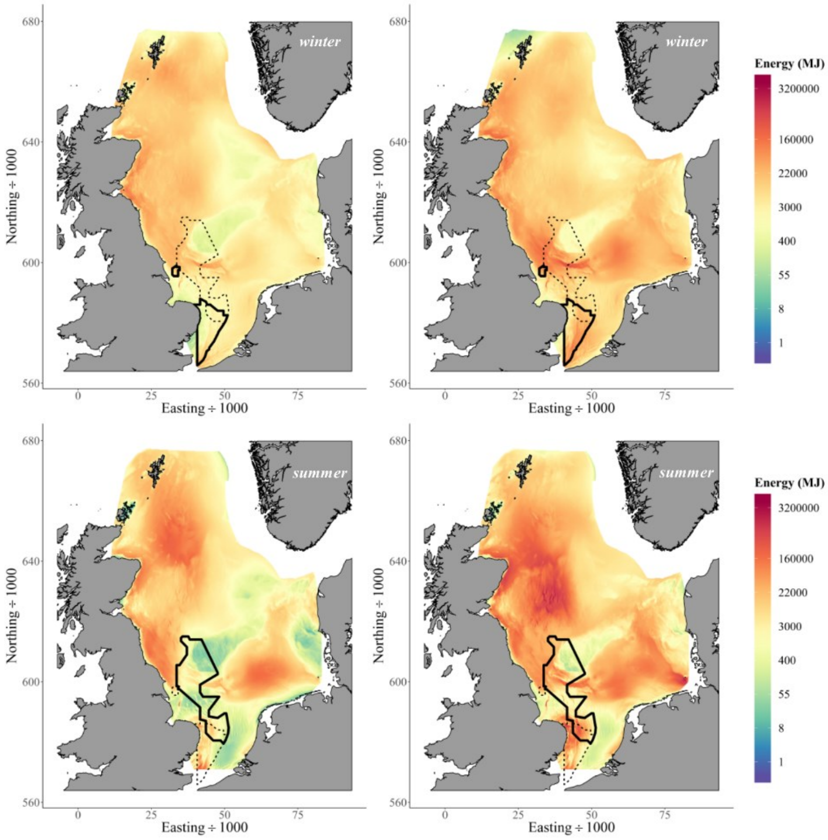

Figure A 2.2 Spatiotemporal winter (January-March) and summer (July-September) distribution of all porpoise prey species excluding sandeels energy per km2 for the North Sea, illustrated for 2005 on the left and 2016 on the right. Bold outlines represent the corresponding seasonal part of the SAC while the dotted lines represent the other part of the SAC.

Appendix 2.3

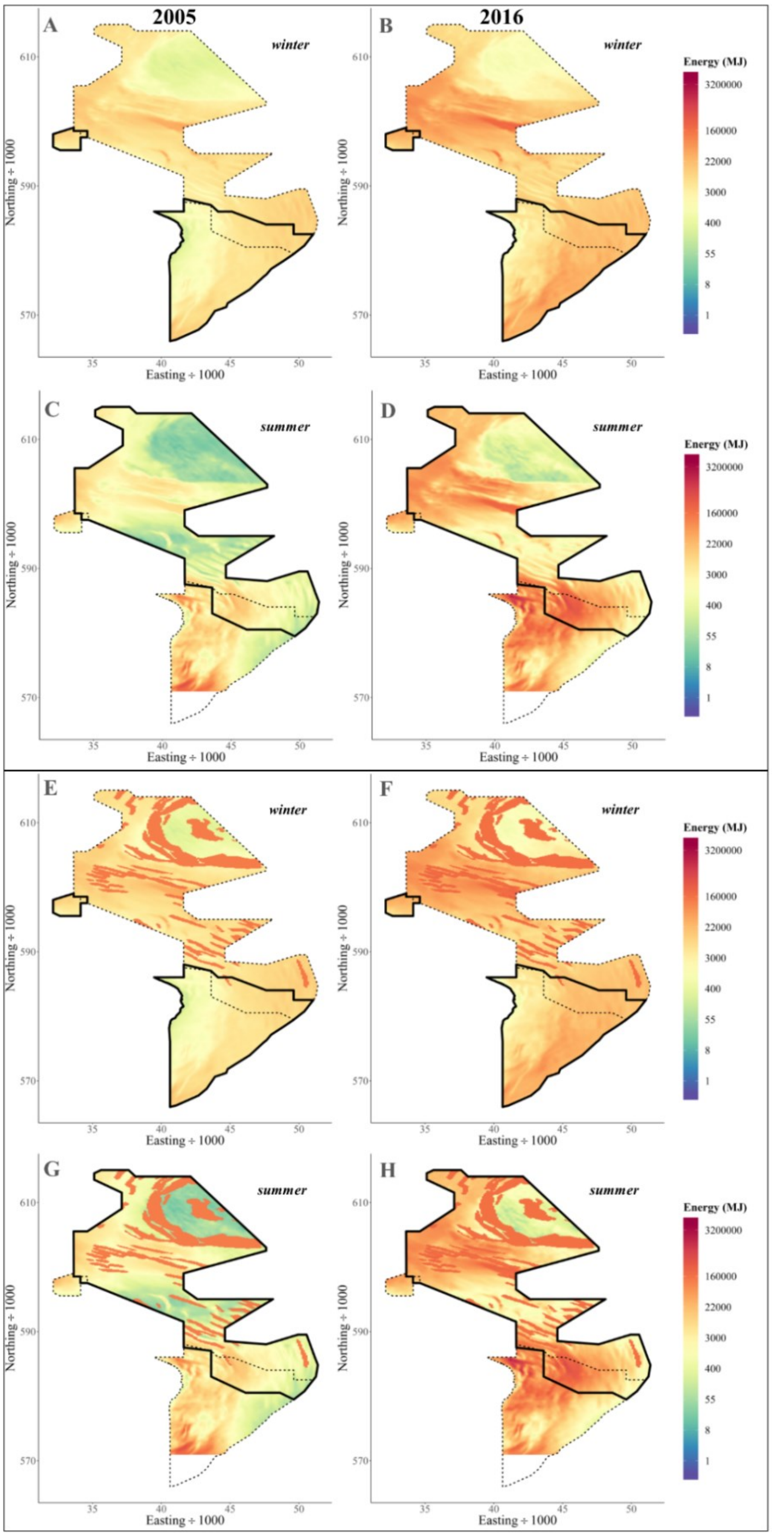

Figure A 2.3 Spatiotemporal winter (January-March) and summer (July-September) distribution of all porpoise prey species energy per km2 for the SAC, illustrated for 2005 on the left and 2016 on the right. A distinguish is made for total maps that included sandeels (bottom panels (E-H)) or not (top panels (A-D)). Bold outlines represent the corresponding seasonal part of the SAC while the dotted lines represent the other part of the SAC.

Appendix 2.4

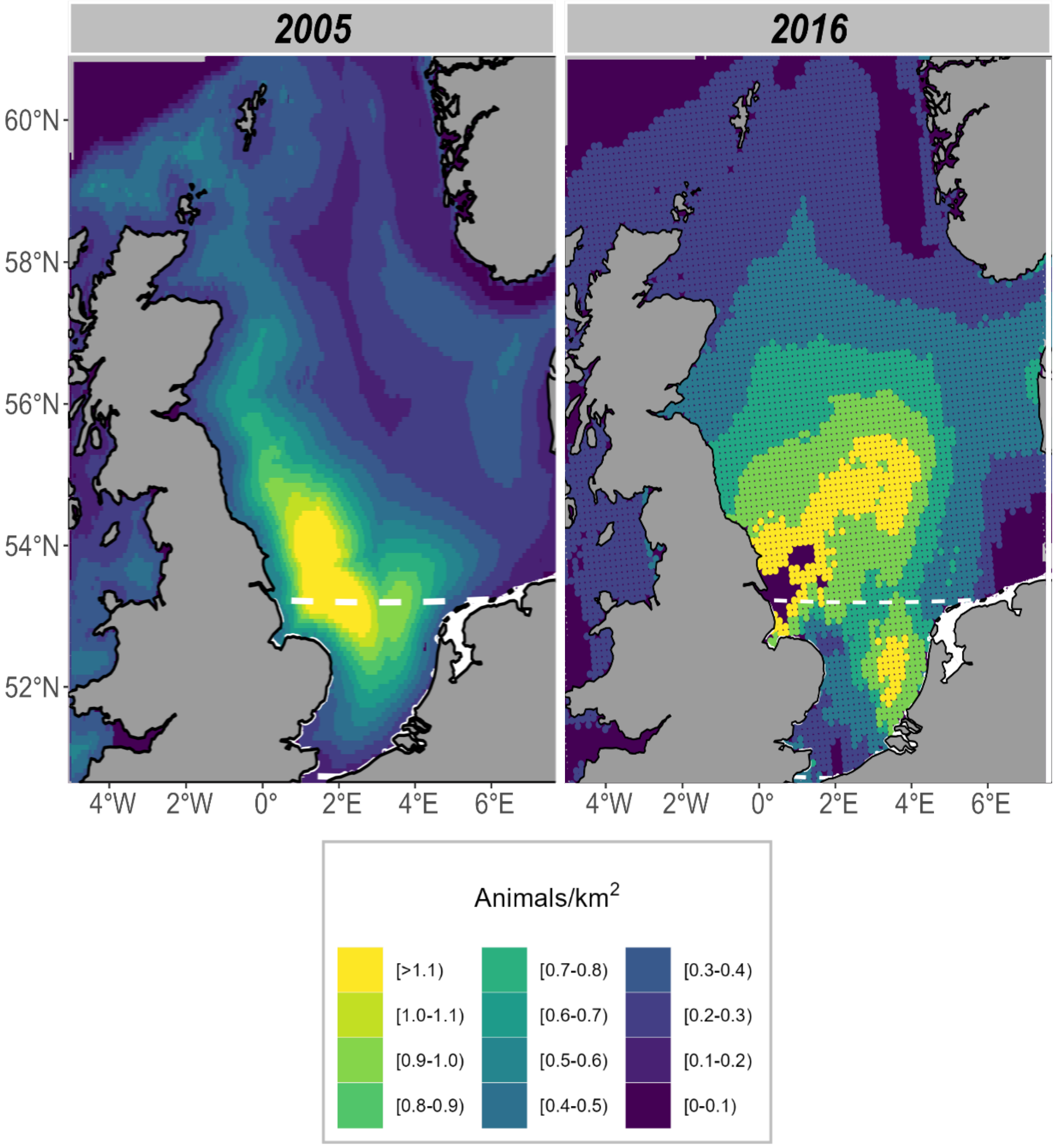

Figure A 2.4 Predicted harbour porpoise summer density in the North Sea from the SCANS II (2005) and SCANS III surveys.

CHAPTER 3

Integrating disparate datasets to model the functional response of a marine predator: a case study of harbour porpoises in the southern North Sea

This chapter has been published as:
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Authors' Contributions

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3.1 Abstract

1. Quantifying consumption and prey choice for marine predator species is key to understanding their interaction with prey species, fisheries, and the ecosystem as a whole. However, parameterising a functional response for large predators can be challenging because of the difficulty in obtaining the required data on predator diet and on the availability of multiple prey species.
2. This study modelled a multi-species functional response (MSFR) to describe the relationship between consumption by harbour porpoises (*Phocoena phocoena*) and the availability of multiple prey species in the southern North Sea. Bayesian methodology was employed to estimate MSFR parameters and to incorporate uncertainties in diet and prey availability estimates. Prey consumption was estimated from stomach contents data from stranded harbour porpoises. Prey availability to harbour porpoises was estimated based on the spatial overlap between prey distributions, estimated from fish survey data, and porpoise foraging range in the days prior to stranding predicted from telemetry data.
3. Results indicated a preference for sandeels in the study area. Prey switching behaviour (change in preference dependent on prey abundance) was confirmed by the favoured type III functional response model. Variation in the size of the foraging range (estimated area where harbour porpoises could have foraged prior to stranding) did not alter the overall pattern of the results or conclusions.
4. Integrating datasets on prey consumption from strandings, predator foraging distribution using telemetry and prey availability from fish surveys into the modelling approach provides a methodological framework that may be appropriate for fitting MSFRs for other predators.

3.2 Introduction

Prey populations are directly and indirectly affected by predation and their dynamics are influenced by long-term and short-term responses of predators (Holling, 1959; Murdoch & Oaten, 1975). The functional response helps to assess the potential impact that predators could have on their prey by describing the response of predator consumption rates to varying prey densities, providing insight into prey preference and general predator-prey interactions (Dale et al., 1994). High consumption rates indicate strong interactions between predators and prey, resulting from high encounter rates and/or active predator choice. Switching between prey species may occur if predator preference changes with prey density, for example when predators avoid scarce prey (Holling, 1959).

Although the functional response has been subject to extensive empirical research, most studies have been conducted within a laboratory setting or have described relationships among a small number of species (Morozov & Petrovskii, 2013). Modelling the multi-species functional responses (MSFR) for wild animals is challenging because observing both consumption and prey availability outside a controlled environment is difficult. Parametrising a MSFR requires substantial datasets on predator diet and distribution, and on the availability of multiple prey species covering a range of prey densities. It is not surprising, therefore, that the ecological role of most large predators has not been quantified and that we have an incomplete picture of their impacts in many ecosystems (Estes et al., 2011). However, the use of Bayesian methods can overcome the problem of data sparsity, allowing MSFR models to be fitted for top predators (Smout et al., 2014; Suryawanshi et al., 2017).

The aim of this study is twofold. Firstly, a framework to integrate long-term datasets on predator consumption is developed, predator distribution and prey abundance to model the

MSFR of a marine high trophic level predator. The framework consists of a number of methodological steps for modelling changes in diet in relation to prey abundance, which are appropriate for mobile marine predators for which diet is sampled at specific locations. The intention is that this methodological framework can serve as a model for other similar studies and thus help improve understanding of the ecological role of high trophic level marine predators. This framework was developed and applied using the harbour porpoise (*Phocoena phocoena*) in the southern North Sea as a case study to examine the methodology, model performance, model output and the sensitivity of the results to variation in assumptions. The harbour porpoise was chosen partly because there are data on prey consumption from the stomach contents of stranded porpoises in the Netherlands (Leopold, 2015), data on the distribution and movements of individual porpoises in the North Sea from satellite-linked telemetry (Sveegaard et al., 2011), and data on prey abundance from the ICES International Bottom Trawl Surveys (ICES, 2018).

Secondly, in choosing the harbour porpoise as a case study, the aim was to improve ecological understanding of an important marine predator in European Atlantic waters. The harbour porpoise is the most abundant large marine predator in the North Sea (Hammond et al., 2013) and its diet includes species that are also targeted by commercial fisheries (Santos & Pierce, 2003), such as whiting (*Merlangius merlangus*), Atlantic herring (*Clupea harengus*) and sandeels (Ammodytidae). Harbour porpoises have a high metabolic rate and only a limited energy storage capacity, which limits their ability to buffer against diminished food availability/quality and makes them more susceptible to starvation if they fail to meet their high metabolic demands (Rojano-Doñate et al., 2018; Spitz et al., 2012a). They have high ingestion rates and probably must consume prey on a daily basis (Kastelein et al., 2019; Wisniewska et al., 2016), unlike other cetaceans or pinnipeds that might move through certain areas while not foraging, and thus are particularly appropriate for this study. North Sea wide surveys showed a major north to south shift in the summer distribution of harbour porpoise from 1994 to 2005, maintained through 2016, which was likely linked to changes in prey distribution (Hammond et al., 2002, 2013, 2021). Information on the dynamic relationship between harbour porpoises and their prey is largely lacking but improving understanding of harbour porpoise predator-prey relationships may help to explain the observed shift in distribution.

3.3 Material and methods

As a framework for analysis, the following sequence of steps (described in detail below and illustrated in Figure 3.1) was followed to parameterize the functional response: 1. Estimation of diet composition; 2. Estimation of foraging range; 3. Estimation of prey availability; and 4. Fitting the multi-species functional response. All data processing and modelling was performed in software R (R Development Core Team, 2018) and MSFR fitting was carried out in WinBUGS (Lunn et al., 2000).

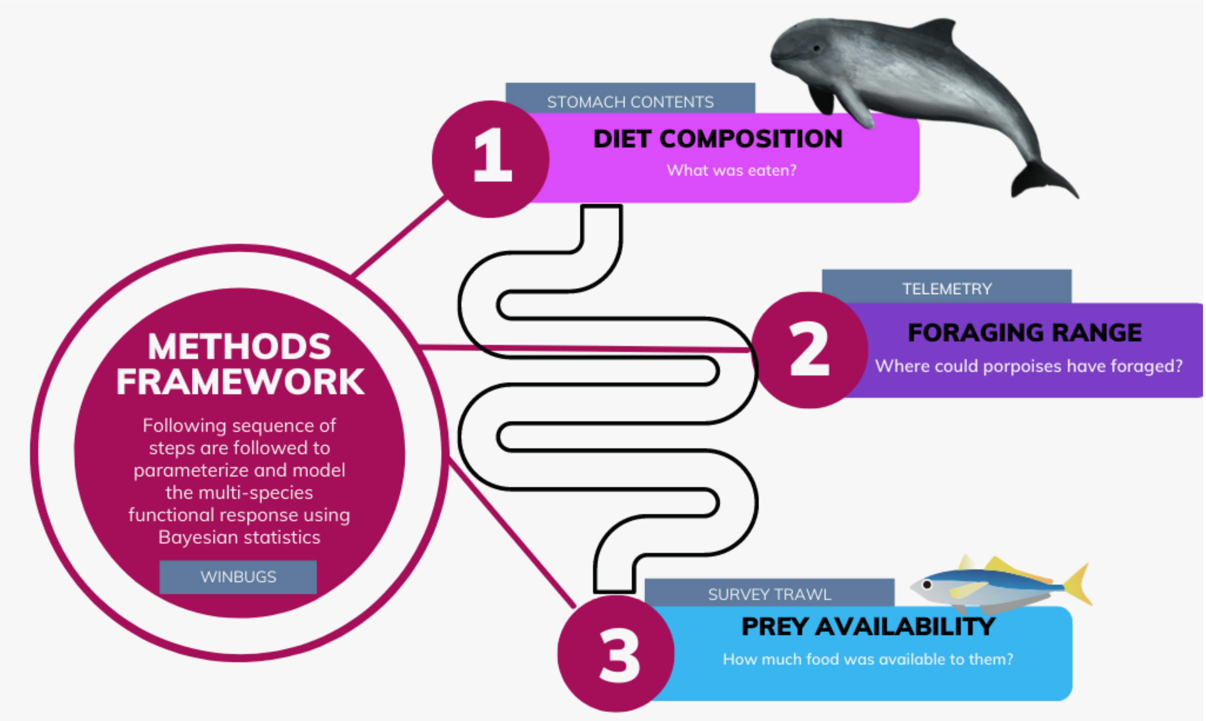

Figure 3.1 Flowchart depicting the methodological steps carried out in this chapter to fit the multi-species functional response of harbour porpoise. Firstly, stomach content data from stranded porpoises along the Dutch coastline were used to reconstruct diet composition. Secondly, the area where porpoises could have obtained their last meal were estimated from telemetry data. Thirdly, prey availability was predicted using scientific trawl data. Lastly, the MSFR was fitted using Bayesian statistics and the models were coded in WinBugs.

3.3.1 Data preparation

3.3.1.1 Diet composition

To obtain information on harbour porpoise prey consumption, diet composition was estimated from the hard remains of prey (fish otoliths) recovered from the stomachs of individual animals stranded along the Dutch coastline between 2006 and 2015. To match diet composition to availability of prey data strandings that occurred in November-April were assigned to quarter 1 and those in May-October to quarter 3 (see 3.3.1.3). Sample collection and analysis are described in Leopold (2015). Post-mortem examinations were carried out on stranded animals documenting standard measurements (*e.g.* body length). Prey species were identified to the lowest possible taxon. Otoliths were measured, paired when possible and graded for wear. Grade-specific correction factors were used to estimate undigested otolith size and prey weight was estimated by applying otolith size-fish mass relationships. Prey species that contributed ≥ 5 % of the total estimated prey weight were selected as main prey species.

Uncertainty in diet composition arises from measurement (estimation of prey weight) and sampling error (Hammond & Rothery, 1996). Sampling error was estimated by non-parametric bootstrapping using individual stranded porpoises as the sampling unit, stratified by season. To balance carcass freshness and retain an adequate sample size, only individuals with decomposition codes less than 4 were included in analysis (see Leopold, 2015). Measurement error was not estimated.

3.3.1.2 Foraging range

Foraging range was defined as the geographical range in which a stranded porpoise could have foraged. Note that this is different from the realised foraging area, which includes a component of predator "choice" regarding prey availability, which we want to avoid.

Estimating the foraging range of porpoises prior to stranding is difficult due to the unknown location of death. It is possible that a stranded porpoise was alive and swimming until just before it stranded, or carcasses could have drifted at sea for a considerable period of time (Peltier et al., 2013). This introduces uncertainty in defining the area where porpoises likely foraged. Information on the rate at which porpoises could have moved prior to stranding was used to obtain informed estimates of their potential foraging range.

The foraging range was estimated using telemetry data from satellite-linked tags deployed on harbour porpoises in the Kattegat, Belt Seas and Western Baltic between 1997 and 2015 (see

Teilmann et al. (2007) and Sveegaard et al. (2011) for tagging procedures, tag settings, and data filtering). The movements of harbour porpoises in the Kattegat and Belt Seas differ from those further north in the Skagerrak and in the North Sea (Sveegaard et al., 2011). To ensure the data were as representative as possible for porpoises that stranded in the southern North Sea, data from the southern Kattegat and further south (south of latitude 57.30°N and east of longitude 9.37°E) were excluded.

The use of stomach content data to estimate prey consumption depends on knowledge of the temporal window within which porpoises could have obtained their last meal, which is dependent on how long prey remains stay in the stomach. In the absence of information on passage rates of hard prey remains for harbour porpoises, information for similar sized grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina*, which consume similar prey species, was used. Two days after consumption > 50% of all otoliths were recovered in grey seal (Grellier & Hammond, 2006) and > 85% in harbour seals scats (Wilson et al., 2017). To estimate harbour porpoise foraging range, a minimum timeframe of 2 days was chosen. Additionally, timeframes of 4, 6, and 8 days were applied to explore how resilient the results were to variation in the likely foraging area, including to accommodate any drifting of carcasses post-mortem.

Prior to modelling the telemetry data, the track line of each tagged porpoise was processed to create positions at regular intervals. These positions were used to generate minimal enclosing circles (MECs) from sets of consecutive points for timeframes of 2, 4, 6, or 8 days (Figure 3.2). Using a generalized linear model (GLM) the MEC diameter (response variable assumed to follow a gamma distribution with log link) was modelled as a function of timeframe and age, sex, season (quarter of the year), and all two-way interactions. Model selection was based on AIC scores. The variance inflation factor (VIF) was used to detect multicollinearity using a threshold of 4 (Hair et al., 2010).

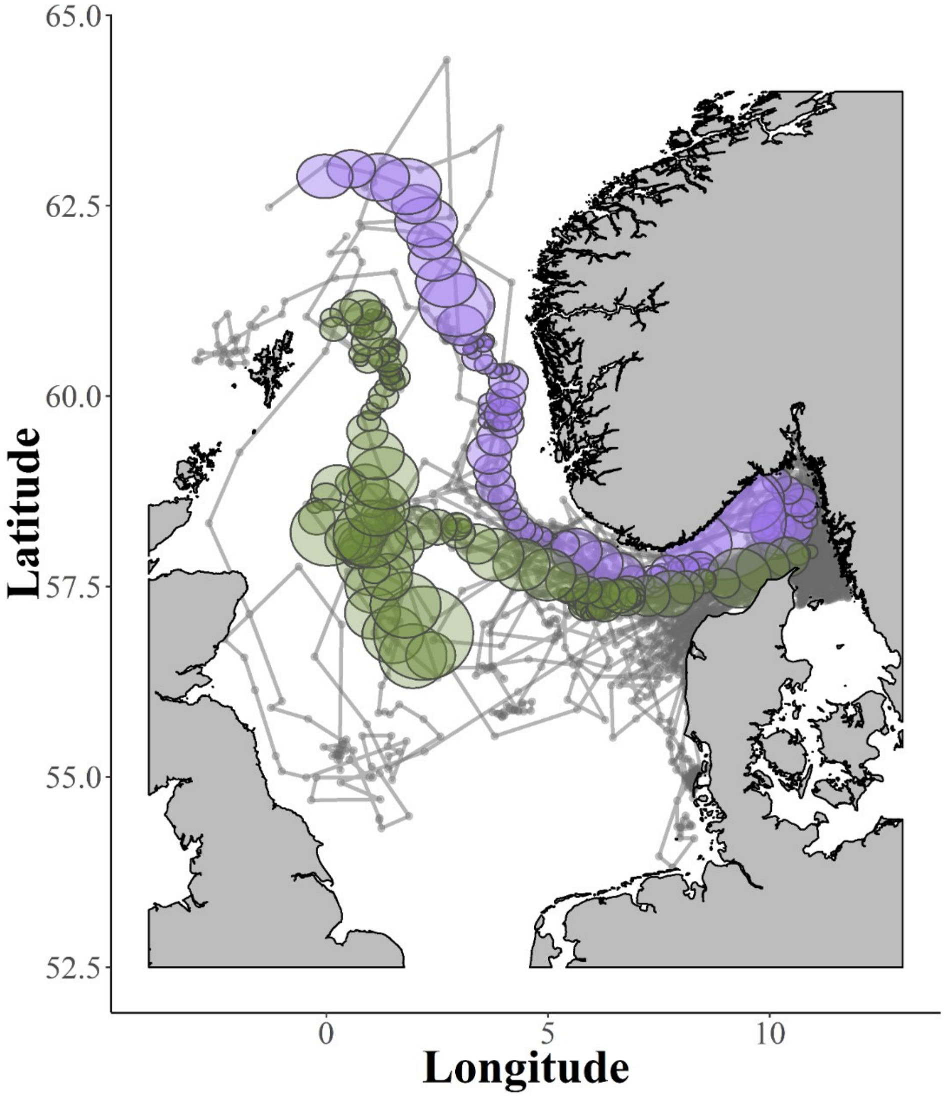

Figure 3.2 Track lines excluding Inner Danish Waters (south of latitude 57.30 and east of 9.37) of tagged harbour porpoises 1997-2015. For illustrative purposes, minimum enclosing circles (MECs) for two of the tagged harbour porpoises with a two-day time frame are shown. The green circles are the MECs for a juvenile male during the winter of 2003 and the purple circles are for a juvenile male during the summer of 2001. Grey dots represent the ARGOS positions of all porpoises.

Tagged individuals are measured repeatedly, so a generalized linear mixed model (GLMM) including a random effect for individual was also investigated. However, the GLM was better supported than the GLMM according to AIC scores and log-likelihoods.

Stranded porpoises are located on the coast, so the diameter of the MEC estimated from the GLM was used to predict the radius of a circular buffer, centred on stranding location, to approximate the foraging range (at sea) prior to stranding for each stranded individual (Figure 3.3). Uncertainty about foraging range was explored by fitting separate MSFR models (see 3.3.2) for each timeframe (2, 4, 6, 8 days).

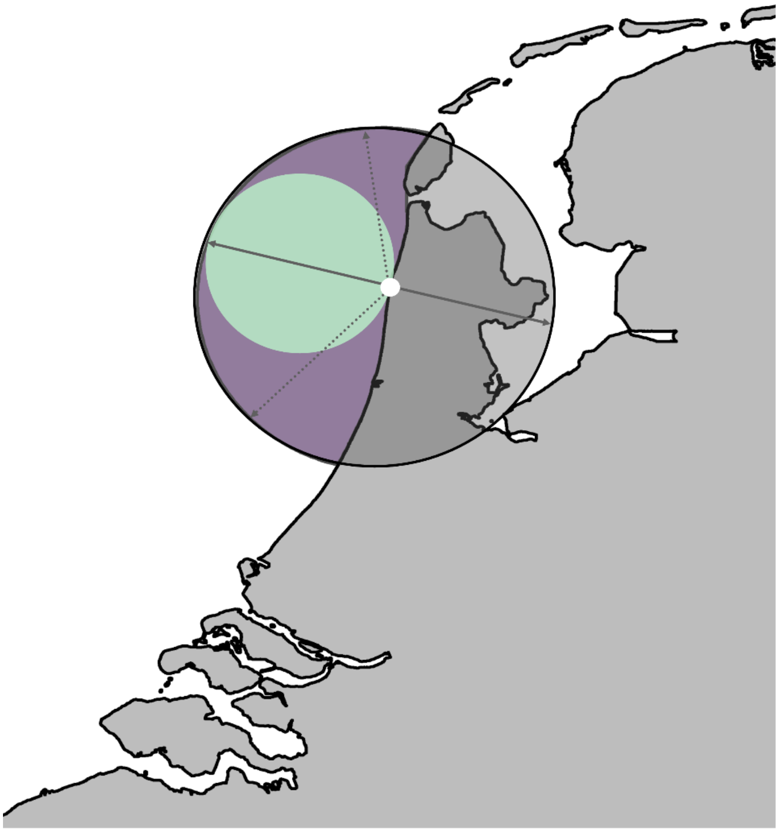

Figure 3.3 Predicted foraging range prior to stranding assuming 2 days foraging using telemetry data. Green buffer denotes the estimated minimum enclosing circle (MEC) from Danish telemetry data. White circle is the stranding location of one porpoise. Purple buffer represents the predicted foraging range prior to stranding. The diameter of the green buffer was used as the radius of the purple buffer.

3.3.1.3 Prey availability

Relative fish abundances were estimated using data from the North Sea International Bottom Trawl Survey (NS-IBTS), available from the International Council for the Exploration of the Sea (ICES) (datras.ices.dk). NS-IBTS data were available for quarter 1 (January-March) and quarter 3 (July-September).

Only size classes determined to be consumable by harbour porpoises (< 40 cm - Aarefjord et al., 1995) were selected. Catch per unit effort was transformed into biomass per unit effort (BPUE in g) by applying the length-weight relationship:

$$\mathrm{BPUE} = \sum\nolimits_{\mathrm{all}\ L<400\mathrm{mm}} a\left(\left(\frac{L}{10}\right)+(0.5e)\right)^{b} \times CPUE_L \qquad \text{(eqn 3.1)}$$

where L is length class (in mm), indicated by the lower limit of that class, e is the resolution of the length, either 5 or 10mm (depending on species), $CPUE_L$ is the catch per unit effort for length class L, and a and b are length-weight conversion parameters, the values of which were derived from (Wilhelms, 2013).

Generalised additive models (GAMs) were used to predict distribution for each prey species over the entire southern North Sea (south of 56°N latitude (Figure 3.4)). The response variable BPUE, log-transformed to reduce the effects of relatively high/low catches, was assumed to have a Gaussian error distribution. Covariates considered were longitude, latitude, depth, and year. Smoothing parameter selection was performed by restricted maximum likelihood (REML) (Wood, 2011). The model allowed the spatial pattern to change with time, by including a three-dimensional tensor product smooth for geographical space and year:

$$\mathrm{Log}(\mathrm{BPUE}_{it}) = \mathrm{s}\left(\mathrm{depth}_{it}\right) + \mathrm{te}\left(\mathrm{longitude}_{i}, \mathrm{latitude}_{i}, \mathrm{year}_{t}\right) \qquad \text{(eqn 3.2)}$$

For a given haul the biomass per unit effort is represented by $\mathrm{BPUE}_{i,t}$ having space coordinates i and a date/time t.

To avoid smoothing being adversely impacted by land boundaries a soap film smoother was applied (Wood et al., 2008). In generating the soap film, knots were placed over the data and land was set to zero which ensured smoothing towards data points and avoided predicting over the boundary.

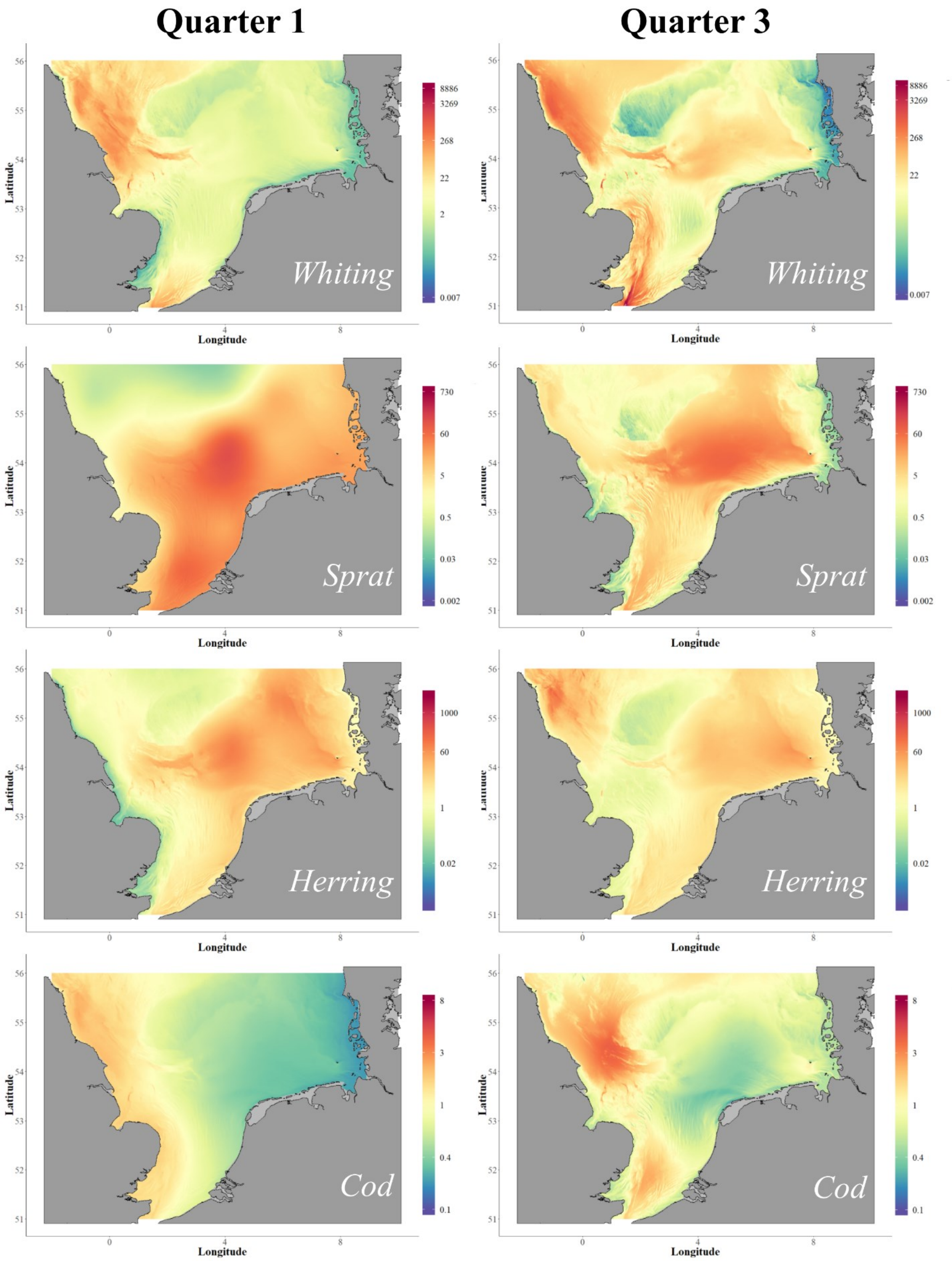

Figure 3.4 The spatial distribution of porpoise prey species for the southern North Sea illustrated for the year 2007, for quarter one (January-March) and quarter three (July-September). Density surfaces were produced from generalised additive models that were fitted to biomass per unit effort data (kg per half hour trawl, based on NS-IBTS catches). Note different scaling along Y-axes.

Comparing the soap film smoother with a conventional thin plate regression spline smoother, showed that the soap film improved the prediction of fish densities in areas with closely adjacent land boundaries (*e.g.* the Strait of Dover).

The predictions of the fitted model represent expected BPUE values. To estimate the true underlying fish biomass, predictions would need to be scaled using gear efficiency and catchability estimates. However, absolute estimates of fish biomass are not required to fit a MSFR (see 3.3.2).

Sandeels are not well represented in the NS-IBTS due to catchability issues. Therefore, for this species ICES estimates of sandeel spawning-stock biomass from other data sources were used, including commercial catches and dredge surveys (ICES, 2016). Gobies (Gobiidae) had to be excluded because they are almost absent in the NS-IBTS data due to their small sizes (Knijn et al., 1993) and there is no other source of data.

The relative availability, and associated uncertainty, of each main prey species to each porpoise prior to stranding was estimated as the relative amount of prey present within the area of sea within the estimated circular buffer (see 3.3.1.2). For each buffer the SD of the availability of each prey species was obtained by parametric re-sampling the estimated coefficients from the fitted GAMs.

3.3.2 Multi-species functional response

3.3.2.1 Model development

A general equation allowing a single species functional response to take the form of a type I, II or III is (Holling, 1959):

$$c = \frac{\alpha N^m}{1 + \alpha t N^m} \qquad \text{(eqn 3.3)}$$

where c is the predator consumption rate, α is the attack rate, N is prey availability, t is the consumption/handling time, and m is a shape parameter.

The equation can be re-written to include multiple prey species:

$$c_i = \frac{\alpha_i {N_i}^m}{1 + \sum_{j=1}^{Z} \alpha_j t_j {N_j}^m} \qquad \text{(eqn 3.4)}$$

where c_i is the consumption of focal prey species i; α_i and t_i are the attack rate and handling time of the focal prey species i and the denominator includes all prey species from 1 to the number of prey species included. There is a total of Z prey species in the system. I do not have information on harbour porpoise consumption rates, but the equation can be revised in terms of diet composition:

$$\frac{c_i}{\sum_j c_j} = \frac{\alpha_i N_i^m}{\sum_j \alpha_j N_j^m} \qquad \text{(eqn 3.5)}$$

where $\sum_j c_j$ is the sum of the consumptions of all prey species by the predator other than the focal prey species i. Not all species in the diet need to be included for this relationship to hold. Note that the denominator is identical for all prey types. Then for any subset of prey $\{1,2 \ldots p\}$ such that $p < Z$

$$\frac{c_i}{\sum_{k=1}^{p} c_k} = \frac{\frac{\alpha_i {N_i}^m}{1 + \sum_{j=1}^{Z} \alpha_j {N_j}^m}}{\sum_{k=1}^{p} \left(\frac{\alpha_k {N_k}^m}{1 + \sum_{j=1}^{Z} \alpha_j {N_j}^m} \right)} = \frac{\alpha_i {N_i}^m}{\sum_{k=1}^{p} \alpha_k {N_k}^m} \qquad \text{(eqn 3.6)}$$

It is therefore possible to model proportions of the diet of some prey relative to one another, leaving out some species. This is important because gobies had to be excluded even though they are important constituents of the diet (see 2.1.3, 3.1).

Catchability q_i relates the survey catch of each prey species B_i to the true abundance or biomass in the sea, N_i:

$$N_i = q_i \times B_i \qquad \text{(eqn 3.7)}$$

so equation 3.5 can be rewritten as:

$$\frac{c_i}{\sum_j c_j} = \frac{\alpha_i\,(q_i B_i)^m}{\sum_j \alpha_j (q_j B_j)^m} = \frac{(\alpha_i q_i^{m_i}) B_i^{m}}{\sum_j (\alpha_j q_j^{m_j}) B_j^{m}} \qquad \text{(eqn 3.8)}$$

Then defining constant $a_i = \alpha_i q_i^{m_i}$ we can write:

$$\frac{c_i}{\sum_j c_j} = \frac{a_i B_i^{m}}{\sum_j a_j B_j^{m}} \qquad \text{(eqn 3.9)}$$

Therefore, from diet composition and BPUE data we can estimate the value of the a_i parameters without needing to correct for catchability.

3.3.2.2 Model fitting

For model fitting, relative prey abundance was re-scaled so that the maximum observed value was 100 to assist numerical performance and convergence. The estimated values of a_i are thus a measure of prey 'preference' or attack rate in relation to an index of abundance and not to absolute estimates of biomass.

The shape parameter *m* determines how sigmoidal the response is and thus influences the form of the functional response. For a hyperbolic type II functional response, the shape parameter $m = 1$. If $m > 1$ the functional response defines a sigmoidal type III functional response (Real, 1977). Two model types were compared: a hyperbolic type II functional response with shape parameter $m=1$ (model 1) and a sigmoidal type III functional response with $m = 1.5$ (model 2).

The relationship between relative prey availability and consumption was estimated for each main prey species in turn by setting the availability of all other prey to one of three specific constant levels (minimum, mean, and maximum).

Markov chain Monte Carlo (MCMC) methods used for model fitting enabled uncertainty in diet composition and prey availability estimates to be incorporated. At each step in the Markov chain, for each prey species, random values of relative prey availability were drawn from a zero-truncated Normal distribution. For each model, the MCMC was run for 10,000 iterations after a burn-in of 1,000 samples with two parallel Markov chains.

Prey species that contributed < 5 % to the diet of harbour porpoises were grouped into a single category 'other prey'. All goby species were added to this category because no prey availability estimates for these species could be calculated (see 3.3.1.3).

It is difficult to create informative priors for a_i because diet composition data allow relative but not absolute values of attack rate a_i to be estimated (equation 3.9 holds if all the a_i are multiplied by any arbitrary constant). Consequently, to estimate relative values for a, a wide uniform prior U(0,10) was used for all prey species except sandeels, for which attack rate was fixed at a value of 1. This allowed for the relative values of attack rate a of other prey species to be larger or smaller than for sandeels. The marginal posterior distributions of a were checked after model fitting, to confirm that they had very low weights towards the prior's upper limit of 10, to ensure that the uniform priors were not over-constraining the exploration of parameter space. After fitting, models were compared using DIC scores (Spiegelhalter et al., 2002).

3.3.2.3 Model prediction

To illustrate the model's ability to predict consumption under different regimes of prey availability, the estimated parameters of the best fitting model were used to predict diet composition in 2011 (a year of high sandeel spawning stock biomass, SSB, in the southern

North Sea) and 2020 (a year of low sandeel SSB, and the most current advice from ICES for all prey species considered), assuming similar prey distribution and porpoise stranding locations. Prey availability of 2011 was rescaled using estimates of SSB from the ICES Stock Assessment Database for 2020, following Smout et al. (2014). Changes in diet composition were estimated relative to the daily biomass or energy consumption of an average adult male porpoise (i.e., 1.7 kg or 6.7 MJ per day (Gallagher et al., 2018)). Estimates from the literature were used to convert biomass to energetic content (Table 3.5). Energy values for gobies were used for the "other" prey category because they were the most prevalent species in that group.

3.4 Results

3.4.1 Diet composition

Stomach content data were available from 455 harbour porpoises. Juveniles of both sexes (n = 344 (74.8 %)) dominated the sample. The 'main' prey species included six different types of fish: whiting (27.1 % by biomass), gobies (20.8 %) and sandeels (18.5 %) were the most dominant species. Lesser contributions were made by herring (8.5 %), sprat (*Sprattus sprattus*) (6.9 %) and cod (*Gadus morhua*) (6.0 %). Other species comprised 12.2 % of the diet.

3.4.2 Foraging range

In total, 2448 locations of 54 harbour porpoises were included in the telemetry analysis (females: 15 juveniles, 3 adults; males: 24 juveniles, 12 adults). The number of tracking days per individual ranged from 8 to 350 days (mean = 93.9; SD = 87.3).

In models to estimate the diameter of minimum enclosing circles (MECs), all covariates had a VIF score lower than 1.4, therefore multicollinearity could be disregarded. Model results are summarised in Table 3.1. Age, quarter, sex, and timeframe were all found to be significant predictors ($p < 0.01$) for the foraging range (MEC diameter) and explained 24.5% of the variation. Predicted foraging range was smaller for males than for females, and for juveniles in comparison to adults. Foraging range was significantly smaller in spring in comparison to the other seasons.

Table 3.1 Summary of the generalized linear modelling to predict the foraging range of tagged harbour porpoises. Predicted mean diameter and SD (in parentheses) of minimum enclosing circle (MEC) in (km) for harbour porpoises according to time frame, quarter, age, and sex.

Time Frame	**Months**	**Adult**		**Juvenile**	
		Female	**Male**	**Female**	**Male**
2 days	January-March	34.9 (1.3)	32.6 (1.2)	30.5 (1.3)	28.2 (1.1)
2 days	April-June	42.3 (1.8)	39.9 (1.7)	37.9 (1.6)	35.5 (1.4)
2 days	July-September	33.2 (1.3)	30.8 (1.1)	28.8 (1.0)	26.4 (0.4)
2 days	October-December	33.5 (1.3)	31.1 (1.1)	29.1 (1.1)	26.7 (0.9)
4 days	January-March	58.4 (1.2)	56.0 (1.2)	54.0 (1.2)	51.6 (1.1)
4 days	April-June	65.8 (1.7)	63.4 (1.6)	61.4 (1.6)	59.0 (1.4)
4 days	July-September	56.6 (1.3)	54.2 (1.1)	52.2 (1.0)	49.9 (0.6)
4 days	October-December	57.0 (1.2)	54.6 (1.1)	52.6 (1.1)	50.2 (0.9)
6 days	January-March	81.9 (1.4)	79.5 (1.3)	77.5 (1.4)	75.1 (1.3)
6 days	April-June	89.2 (1.8)	86.9 (1.7)	84.8 (1.7)	82.5 (1.6)
6 days	July-September	80.1 (1.5)	77.7 (1.3)	75.7 (1.3)	73.3 (1.0)
6 days	October-December	80.4 (1.3)	78.1 (1.3)	76.0 (1.3)	73.7 (1.1)
8 days	January-March	105.3 (1.6)	102.9 (1.6)	100.9 (1.7)	98.6 (1.6)
8 days	April-June	112.7 (2.0)	110.3 (2.0)	108.3 (1.9)	105.9 (1.8)
8 days	July-September	103.5 (1.8)	101.2 (1.7)	99.1 (1.6)	96.8 (1.4)
8 days	October-December	103.9 (1.6)	101.5 (1.6)	99.5 (1.6)	97.1 (1.5)

3.4.3 Prey availability

Correlograms of the final models of relative prey abundance indicated very weak autocorrelation and deviance residuals were evenly spread. BPUE predictions in all grid cells, including unsurveyed cells, are shown in Figure 3.4. The final models explained between approximately one third to two thirds of the total observed variation in the BPUE values (Table 3.2).

As described above, the availability of each prey species was predicted for each individual porpoise, within the circular buffer that represented the foraging range for each timeframe (see 3.3.1.2). For illustration, Figure 3.5 displays the prediction of whiting availability for one porpoise for different timeframes.

Table 3.2 Percentage deviance explained values for the selected generalised additive models (GAMs) of relative prey availability (BPUE) per prey species and quarter.

Species	**Quarter 1** (January-March) % deviance explained	**Quarter 3** (July-September) % deviance explained
Cod	28.3	25.3
Herring	43.1	30.3
Sprat	32.9	32.8
Whiting	60.7	54.0

3.4.4 Multi-species functional response

The best MSFR model in terms of timeframe according to DIC scores (Table 3.3) was the 4 days model. Model 2 (DIC = 97202) with a type III functional response was selected over model 1 (DIC = 117216) with a type II functional response. Consequently, predictions are only presented for the 4 days type III functional response model.

Table 3.3 Deviance Information Criterion (DIC) (lower DIC scores indicate better models) scores of multi-species functional response (MSFR) models according to different foraging range as determined by buffer sizes estimated for different time periods.

Time period	2 days	4 days	6 days	8 days
DIC score type III	113090	97202	133846	107295
DIC score type II	125161	117216	147177	138544

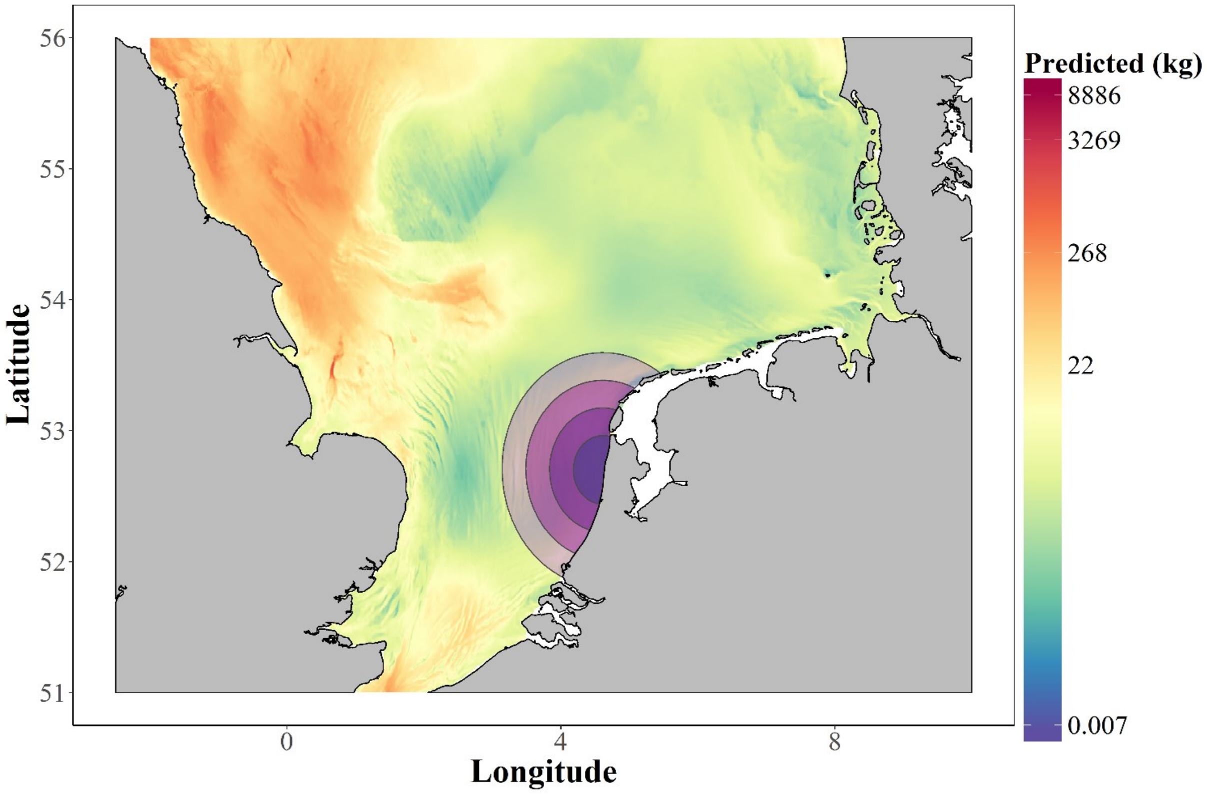

Figure 3.5 Predicted availability of whiting for a stranded harbour porpoise along the Dutch coastline in quarter one (January-March), 2014. Purple buffers represent different assumptions about the foraging range prior to stranding: the size of the buffers corresponds to 2, 4, 6, or 8 days spent foraging, based on the analysis of telemetry data. The coloured background denotes the predicted relative abundance of whiting in terms of biomass per unit effort values (kg per half hour trawl, based on NS-IBTS catches).

The posterior distributions for a were well defined given the wide uniform priors (Figure 3.5). The relative attack rate was considerably higher for sprat (mean = 0.238, 95% CI [0.226, 0.254]) in comparison to whiting (mean = 0.120, 95% CI [0.114, 0.129]), herring (mean = 0.101, 95% CI [0.095, 0.108]), 'other prey' (mean = 0.089, 95% CI [0.085, 0.095]), and cod (mean = 0.058, 95% CI [0.055, 0.063]). Recall that these estimates are in relation to a relative attack rate for sandeel fixed at a value of 1.

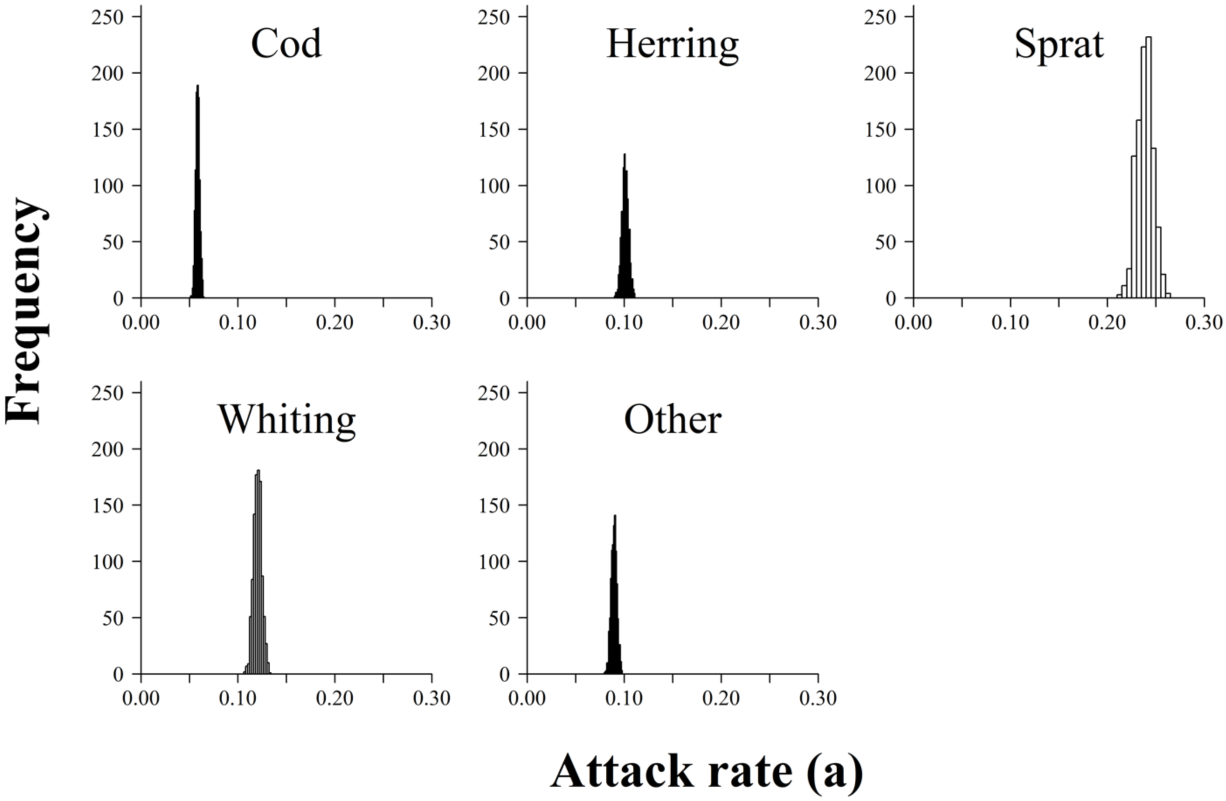

Figure 3.6 Posterior distribution for the attack rates for the porpoise prey species in model (*a*). Sandeels are not displayed as they were set at a fixed value of 1.

Model predictions of diet composition captured the overall pattern in the observed diet (Table 3.4). The model predicted higher proportions of sandeels and cod, and lower proportions of other species in comparison to the observed diet, but all predictions fell well within the range of uncertainty indicating that the model predictions were robust.

Table 3.4 Predicted diet (for the 4 days MSFR model) of harbour porpoises and observed diet derived from bootstrapping stomach content of stranded animals. Expressed as mean (SD) percentages of total prey mass.

Prey species	Predicted	observed
Cod	5.0 (0.5)	2.1 (10.0)
Herring	6.4 (4.0)	4.8 (10.0)
Sandeel	25.1 (8.2)	17.2 (14.2)
Sprat	7.0 (3.8)	7.7 (14.2)
Whiting	8.6 (1.8)	12.7 (15.8)
Others	47.6 (18.9)	55.0 (12.2)

The model predicted a strong relationship between relative prey availability and relative prey consumption by harbour porpoises (Figure 3.7). Overall, consumption of the selected prey species decreased as more alternative prey (all other species) was available. However, the relative consumption of sandeels remained relatively high over all three levels of alternative prey availability (Figure 3.7).

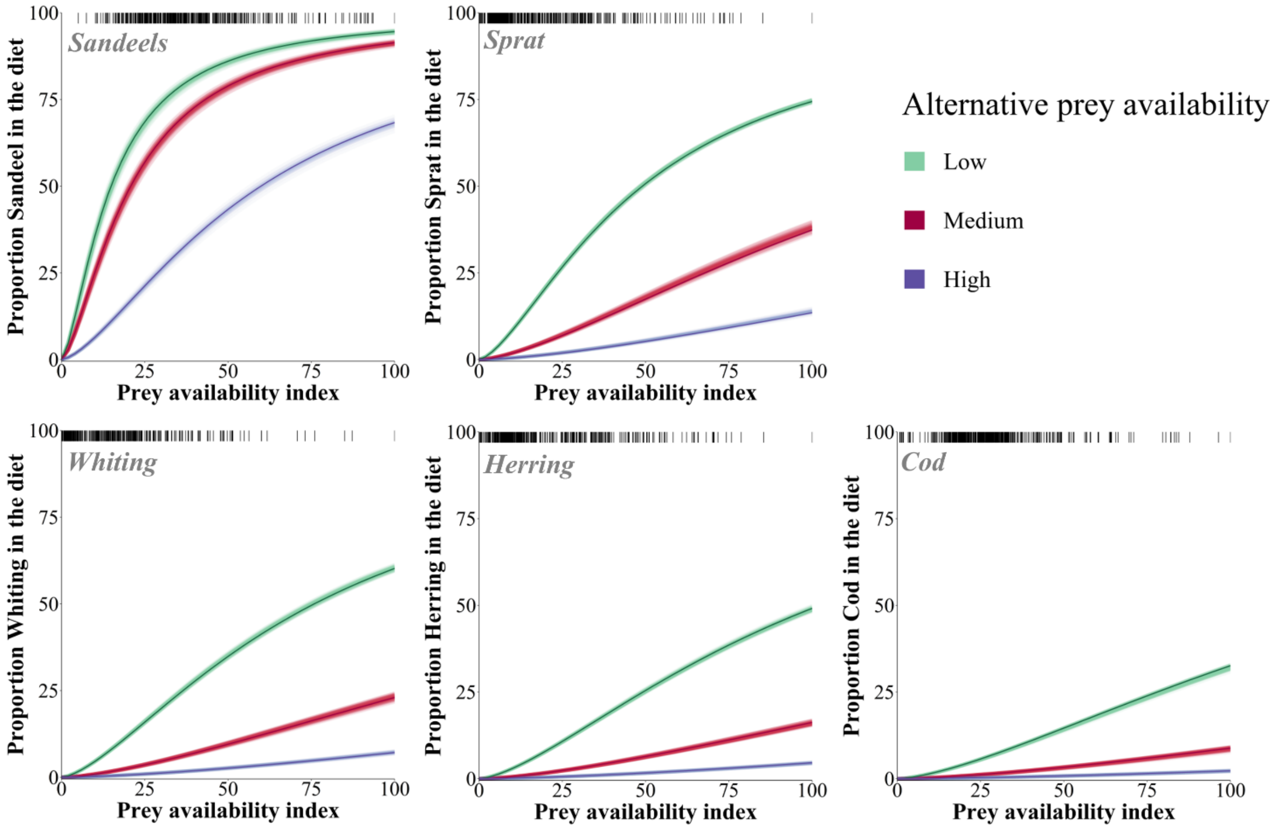

Figure 3.7 Relationship between prey availability and consumption by harbour porpoises for the 4 days MSFR model. Relationships are shown as a single-species plot at three different levels of alternative prey (all other prey) availability. The relationship between relative prey availability and consumption was estimated for each main prey species in turn by setting the availability of all other prey to one of three specific constant levels (minimum, mean, and maximum).

The relative change in predicted diet composition between 2011 and 2020 was most noticeable for sandeels (-63%), whiting (+61%), herring (-56%), and sprat (+50%). The change in prey availability resulted in a relatively small predicted change of ~2% in daily consumption (either an increase in kg consumed or a reduction in energy intake). If porpoises forage to meet energy requirements, intake of biomass would have needed to increase by ~27 g per day in 2020 compared to 2011. Conversely, if porpoises forage to consume constant biomass, this would have led to a reduction in energy intake of ~163 kJ per day in 2020 in comparison to 2011.This decrease in energy for a fixed intake of biomass was because of a reduced consumption of sandeels, substituted mainly by an increase in consumption of sprat and whiting, from 2011 to 2020.

Table 3.5 Predicted change in harbour porpoise diet composition in terms of percentages of total prey biomass (%M) and energy (%E) for 2011 and 2020, and prey energy density.

species	**%M 2011**	**%M 2020**	**%E 2011**	**%E 2020**	**Prey energy ($kJ.g^{-1}$)**
Cod	5.9	3.8	5.0	3.3	4.2[1]
Herring	4.1	1.8	5.1	2.3	6.2[2]
Sandeel	26.6	9.8	31.2	11.7	5.8[3]
Sprat	3.8	9.5	5.8	14.9	7.6[3]
Whiting	9.5	15.3	8.3	13.6	4.3[2]
Others	50.1	59.8	44.6	54.2	4.4[4]

[1](Lawson et al., 1997) [2] (Pedersen & Hislop, 2001) [3](Wanless et al., 2005) [4](Plimmer, 1921)

3.5 Discussion

Integrating disparate datasets to model the MSFR for harbour porpoises in the southern North Sea provides a methodological framework that may be appropriate for other predators. Results from the case study show that sandeels are an important and possibly a preferred prey for harbour porpoise, thus increasing knowledge of the foraging ecology of this important marine predator.

3.5.1 Method evaluation and sensitivity

Setting suitable spatial scales can be a major challenge in ecological studies and the accuracy of any modelled relationship between prey consumption and availability is strongly dependent on achieving realistic spatio-temporal overlap. In this study, the foraging distributions of porpoises prior to stranding (our source of diet information) are unknown, so it is crucial to explore whether assumptions made about the foraging range of these animals are reasonable. The novel approach was to find the most likely foraging area prior to stranding by predicting the range used as a function of time period based on telemetry data, and using the MSFR model fit to determine the appropriate time period of 4 days. There is little relative difference in modelled prey distribution for each prey species in the areas where porpoises could have been foraging in the vicinity of the Dutch coast (Figure 3.4, Figure 3.5) indicating that the overall pattern of results is unlikely to vary much over the range of time periods modelled (2 - 8 days). This is confirmed by lack of variation in the emerging patterns of estimated attack rates or the shape of the functional response (Table 3.6; Figure 3.8). In this case study the methodology thus appears rather robust to this aspect of uncertainty.

Table 3.6 Attack rate according to different foraging ranges. The posterior mean and 95% Bayesian credible intervals of attack rate a, for all "main" prey species and different foraging ranges (represented by different timeframes). Recall that the attack rate for sandeel was set at a fixed value of 1 in the model.

Prey species	**Foraging range (timeframe)**			
	2 days	4 days	6 days	8 days
Cod	0.046 [0.040, 0.053]	0.058 [0.055, 0.063]	0.055 [0.052, 0.058]	0.055 [0.053, 0.058]
Herring	0.101 [0.095, 0.107]	0.101 [0.095, 0.108]	0.104 [0.099, 0.110]	0.100 [0.093, 0.106]
Sprat	0.227 [0.214,0.241]	0.238 [0.226, 0.254]	0.207 [0.197, 0.220]	0.224 [0.219, 0.238]
Whiting	0.116 [0.109, 0.122]	0.120 [0.114, 0.129]	0.106 [0.101, 0.113]	0.115 [0.109, 0.121]
Others	0.082 [0.079, 0.087]	0.089 [0.085, 0.095]	0.095 [0.091, 0.103]	0.090 [0.085, 0.094]

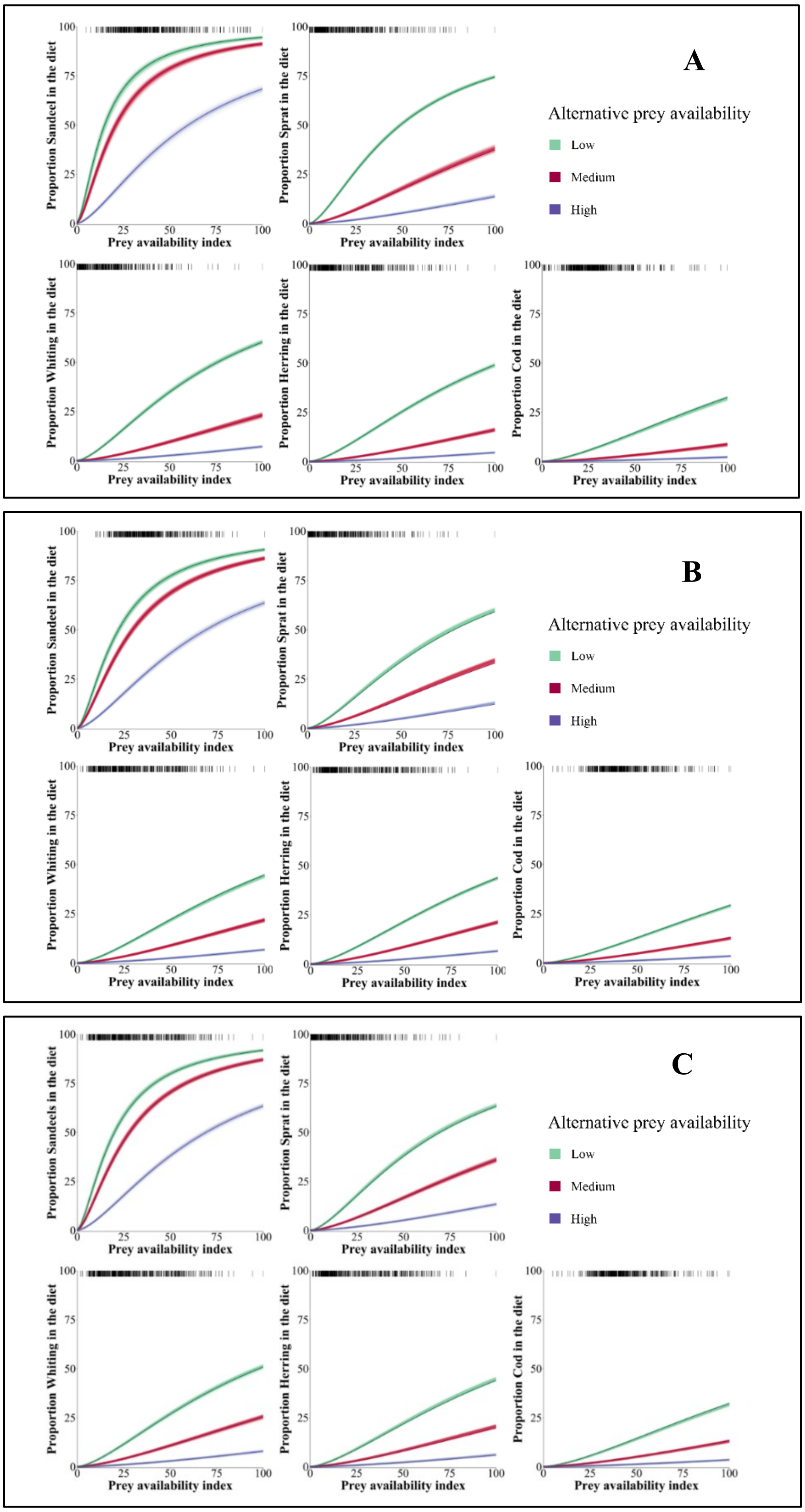

Figure 3.8 Functional response shapes to different foraging ranges. Relationship between prey availability and consumption by harbour porpoises to different foraging ranges. Relationships are shown as a single-species plot at three different levels of alternative prey (all other prey) availability. (A) assumed 2 days of foraging prior to stranding, (B) 6 days and (C) 8 days.

3.5.2 Data limitations

Foraging range was estimated from telemetry data collected in areas of the North Sea outside the study area. To minimise error in the estimated foraging range, only data from the area believed to be most similar to the study area was included. Estimates of foraging range using movement data are uncertain and conservative. Active swimming is faster than drifting, so true foraging range will be larger than that estimated from drifting alone. The fitted MSFRs gave similar results for different assumptions about the foraging area available to porpoises before stranding, so the lack of telemetry data from the study area should not affect the conclusions appreciably. ARGOS data from telemetry tags are subject to location error which was not quantified in this study but is believed to be negligible in this context.

The prey availability estimates assume that relative prey abundance is proportional to true abundance. Furthermore, the assumption was made that prey abundance reflects prey availability to predators; however, the relationship between prey abundance and prey availability is largely unknown, not least because differences in prey behaviour (*e.g.* diurnal and seasonal variation in schooling and burying behaviour) may affect this. The methodology is appropriate if spatio-temporal trends in relative abundance reflect those in absolute abundance of prey, which seems a reasonable assumption.

Most fisheries surveys, including the North Sea IBTS, sample at a coarse spatial and temporal resolution. Some species, especially sandeels and gobies in this study, are poorly sampled. Given the importance of sandeels for many marine predators (Engelhard et al., 2013; Gilles et al., 2016; Wanless et al., 2005; Wilson & Hammond, 2019) and the lack of knowledge regarding spatio-temporal variability in their distribution and abundance, improving effective sampling and modelling of sandeel distribution would improve the quality of the inferences made from future studies. The inability to model sandeel and goby distributions spatially could have led to error in availability estimates, especially because sandeel distribution is extremely patchy (Wright et al., 2000) and largely unknown for gobies. The importance of gobies could have been underestimated because they were excluded from the prey availability analysis. Although information on goby distribution and abundance is largely lacking, gobies are extremely abundant within Dutch coastal waters (Tulp et al., 2008). Therefore, it might be reasonable to assume that these species have a relatively consistent availability.

Care should be taken in making inferences from stranding data because they do not represent an unbiased sample of the population; there is likely an over-representation of individuals that are inexperienced, old, and/or in poor health (Pierce et al., 2004). Indeed, a large proportion of the stranded individuals in this study were juveniles so the results are biased towards this age class. Thus, it is uncertain to what extent the results reflect the functional response of a ‘typical’ porpoise. Most information on cetacean diet derives from stomach contents analysis. Using diet data from stomachs of animals that have been bycaught in fishing nets, or even killed by grey seals or bottlenose dolphins (Ross & Wilson, 1996; van Neer et al., 2020), would be an alternative way to look at harbour porpoise diet. However, the diet of bycaught porpoises diet could be biased towards target species of the fishery and “net selection” of inexperienced individuals (Santos & Pierce, 2003), and porpoises killed by seals or dolphins may be more vulnerable to predation and not representative of the population.

The predicted diet for 2011 and 2020 for an adult male porpoise assumed sampling the same porpoise stranding locations, fish distributions having the same pattern scaled by North Sea wide stock assessment estimates, and that the relationship between fish biomass and energy was constant for each species. However, these assumptions could be violated in several ways.

For example, the distribution of porpoises and/or fish could have changed, there are differences in porpoise prey consumption according to sex, age (Booth, 2020; Leopold, 2015), and prey energy densities vary by size class, season, etc. (Pedersen & Hislop, 2001). Therefore, a more elaborate analysis is required to explore the impact of changing these factors on the predictions.

3.5.3 Ecological inference

Different shapes of the predator functional response have different implications for prey populations, especially at low prey densities. In the best fitting model with a sigmoidal type III functional response, predation mortality decreases when a prey species becomes rare and is indicative of prey switching when prey is at low abundance (that is, there is a change in preference dependent on prey abundance). This may result in persistence and/or stabilizing effects on predator-prey dynamics (Murdoch & Oaten, 1975) because it may prevent one prey species from outcompeting others (Roughgarden & Feldman, 1975). A type III response may result from a number of ecological mechanisms, including prey refuge (McNair, 1986), and learning time (Tinbergen, 1960).

Classically, the attack rate parameter a in the functional response equation can be interpreted as a form of relative preference of the predator for a certain prey type. Here these values are interpreted cautiously because of the nature of the prey abundance estimates used. These were indices, scaled in proportion to maximum values, and they were not estimates of overall total biomass (which is difficult to calculate). Thus, for example the ‘maximum’ value of sandeel abundance was 100 and so was the maximum value for whiting.

In this study, porpoises consumed a disproportionately larger proportion of the most abundant prey. Sandeel consumption remained high even when other prey were abundant and was considerably higher than the consumption of other prey at equal availability index values. At prey abundances similar to those available to the study animals, harbour porpoise diets often have a high proportion of sandeels (Jansen, 2013; Santos et al., 2004), and it also implies that sandeel availability might have a particularly strong effect on the consumption by porpoises of other prey species in this area. Habitat models of harbour porpoise in the North Sea have found that harbour porpoise density increases with decreasing distance to sandeel grounds (Gilles et al., 2016), suggesting that porpoises could be attracted to those areas.

Harbour porpoises in better body condition have been found to be more likely to have higher amounts of fatty fish, such as sandeels, in their diet (Leopold, 2015). The results add to the body of evidence that sandeels are important to porpoises. Sandeels have high energy content and are abundant in the southern North Sea, forming an important forage fish resource that supplies a number of predator species including harbour porpoises, seabirds (Rindorf et al., 2000), and grey and harbour seals (Wilson & Hammond, 2019).

Despite considerable differences in predicted diet composition in 2011 and 2020 (Table 3.5), differences in predicted consumption were relatively small (~2 %), illustrating little variation in overall biomass or energy intake. However, if energy-rich prey species (i.e. clupeids and sandeels) were reduced to low levels, this could result in porpoises needing to increase biomass consumed to avoid failing to meet their energetic requirements.

Sandeel abundance in the northwestern North Sea has declined since 2000 (MacDonald et al., 2019). Poor seabird breeding success in the northwest North Sea has been linked to a reduction in the availability and quality of sandeels (Wanless et al., 2005, 2018). The results confirming the importance of sandeels to harbour porpoise and indicating their possible preference for this prey, are consistent with the reduction of sandeel biomass in the northern North Sea being a driver of the distributional shift of porpoises from the northern to the southern North Sea between 1994 and 2005 (Hammond et al., 2013). However, this needs further exploration of the impact of other potential drivers such as competition with other sandeel predators (*i.e.* sea birds, other marine mammals, foraging fish as well as fisheries).

3.5.4 Context and applications

Applying a Bayesian approach to model the MSFR appears to work well, allowing incorporation of uncertainty in prey availability and consumption estimates. These features, together with the resilience of the results, suggest that the modelled MSFR provides a strong methodological framework that can be applied (generalized) to a range of other species and might aid in quantifying the ecological role of other predators that consume a variety of prey. For example, similar data exist for seabirds (Wanless et al., 2005), grey seals and harbour seals in the North Sea (Carter et al., 2020; Wilson & Hammond, 2019) and applying this framework could provide valuable new insights into their population dynamics, especially in the context of possible competition for prey between these two seal species (Wilson & Hammond, 2019). To take this further, the MSFR could be integrated into ecosystem models to predict and test how prey and predator populations are expected to change under different fisheries management and climatic scenarios that impact prey availability. This could also shed light on the extent of direct and indirect competition between marine mammals, seabirds, and fisheries and possibly on the outcomes of fisheries management and stock recovery programmes.

3.6 Ethics statement

Porpoises were tagged by Aarhus University in collaboration with the DTU Aqua, National Institute of Aquatic Resources, the Fjord and Belt Centre, University of Southern Denmark and the Institute for Terrestrial and Aquatic Wildlife Research at University of Veterinary Medicine Hannover under permissions from Danish Forest and Nature Agency (SN 343/SN-0008) and the Animal Welfare Division (Ministry of Justice, 1995-101-62).

CHAPTER 4

Predator-prey interactions: modelling the multi-species functional response of grey and harbour seals in the North Sea

4.1 Abstract

Resource uptake is the fundamental process that links trophic levels through predator-prey interactions. The critical component that describes how consumption rate of a predator varies in relation to prey density is the functional response and is crucial to understand trophic interactions, predation pressure, prey preference and population dynamics.

This study modelled the multi-species functional response (MSFR) of grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in the North Sea to describe how consumption will vary dynamically depending on the availability of multiple prey species. Bayesian methodology was employed to estimate MSFR parameters and to incorporate uncertainties in diet and prey availability estimates. Diet composition was based on information from seal faecal samples. Prey availability estimation was based on combining prey distributions, estimated from fish survey data, with predictions of the geographical area that was accessible to the predator, given food passage time, from telemetry data.

Results indicated that both seal species have a type III functional response. Sandeels are important but more strongly preferred by grey seals. While harbour and grey seals are sympatric and consume similar prey species, results also suggested that they might be functionally distinct predators, with harbour seals having a more diverse diet and exhibiting a more sigmoidal response that may indicate a greater tendency to switch prey. Depending on what kind of other prey is available and their associated profitability (i.e. obtained energy divided by costs of acquiring that prey (search, capture, and handling time)) could lead to circumstances that are unfavourable for harbour seal populations.

4.2 Introduction

There is a push to progress towards adopting a broader ecosystem approach (Garcia & Cochrane, 2005; Greenstreet & Rogers, 2006) which is fundamental to our understanding of the regulation of biodiversity and for decision-making regarding conservation and management of natural resources. This is a significant step towards sustaining human livelihoods (Pikitch et al., 2004). However, ecosystems are complex dynamic systems which can be challenging to understand. Resource uptake is the fundamental process that links trophic levels through predator-prey interactions in food-web-based ecosystem models. The critical component that describes how consumption rate of a predator varies in relation to prey density is the functional response. For predators that consume multiple prey species, this relationship is more appropriately described by a multi-species functional response (MSFR), in which consumption will vary dynamically depending on the availability of several food sources. The functional response is important to understand trophic interactions and provides information on predation pressure, prey preference and population dynamics. However, there are only a few studies that inform parametrization of functional response in marine ecosystems (Smith & Smith, 2020; Smout et al., 2014; Smout & Lindstrøm, 2007).

High trophic-level predators such as grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) consume a variety of species (Wilson & Hammond, 2019). Seals are considered to be important predators of commercial fish species and identified to be sensitive to changes in forage fish availability (Aarts et al., 2019; Engelhard et al., 2014; Hammond & Wilson, 2016). There are concerns about how to balance possible conflicts between conservation and potential predation pressure of seals (i.e. especially grey seals) on commercially valuable fish stocks (Matthiopoulos et al., 2008). Despite this, there is no information for harbour seals and only one published study on grey seals (Smout et al., 2014) regarding their predation pattern in a multi species context.

Around Britain, harbour and grey seals have considerable overlap in the prey species consumed (Wilson & Hammond, 2019) and spatial distribution (Carter et al., 2020). Although their annual breeding and moulting cycles are asynchronous (SCOS, 2017), their foraging distribution overlaps. The two seal species have contrasting population trends. Generally, grey seals are increasing in the North Sea and stable around the Northern Isles and Western Isles (Morris et al., 2021; Russell et al., 2019; SCOS, 2022; Thomas et al., 2019). Harbour seals are declining along the north-east coast of Scotland, in the Northern Isles and recently in the southern North Sea but stable or increasing in the Western Isles (Morris et al., 2021; SCOS, 2022; Thompson et al., 2019). The causes of harbour seal declines in some areas are not yet understood, but several potential drivers have been considered including biotoxins (Jensen et al., 2015), nutritional stress (Arso Civil et al., 2019) and interactions with shipping (Brownlow et al., 2016). Drivers that involve seal predation and/or foraging success include reduced prey availability, competition and/or direct predation of grey seals (Arso Civil et al., 2019; Thompson et al., 2019; Wilson & Hammond, 2019). Around the Northern Isles where grey seals are reaching carrying capacity harbour seals are declining, which could be evidence of resource induced density-dependence and increased competition with harbour seals which may not be such strong competitors (Russell et al., 2019; Thomas et al., 2019; Thompson et al., 2019).

Improving understanding the predator-prey relationships of seals may aid in explaining regional differences in population trajectories and assist management decisions regarding seals and fish stocks. The aim of this study was to provide and compare information on the dynamic relationship between two seal species (i.e. grey and harbour) and their prey by estimating the parameters of their MSFR in the North Sea.

4.3 Material and methods

As a framework for analysis, the following sequence of steps (described in detail below and illustrated in Figure 4.1) was followed to parameterize the functional response: 1. Estimation of diet composition; 2. Estimation of surface accessible for seals to forage; 3. Estimation of prey availability; and 4. Fitting the multi-species functional response. All data processing and modelling was performed in software R (R Core Team 2020) and MSFR fitting was carried out in Stan (Stan Development Team 2021).

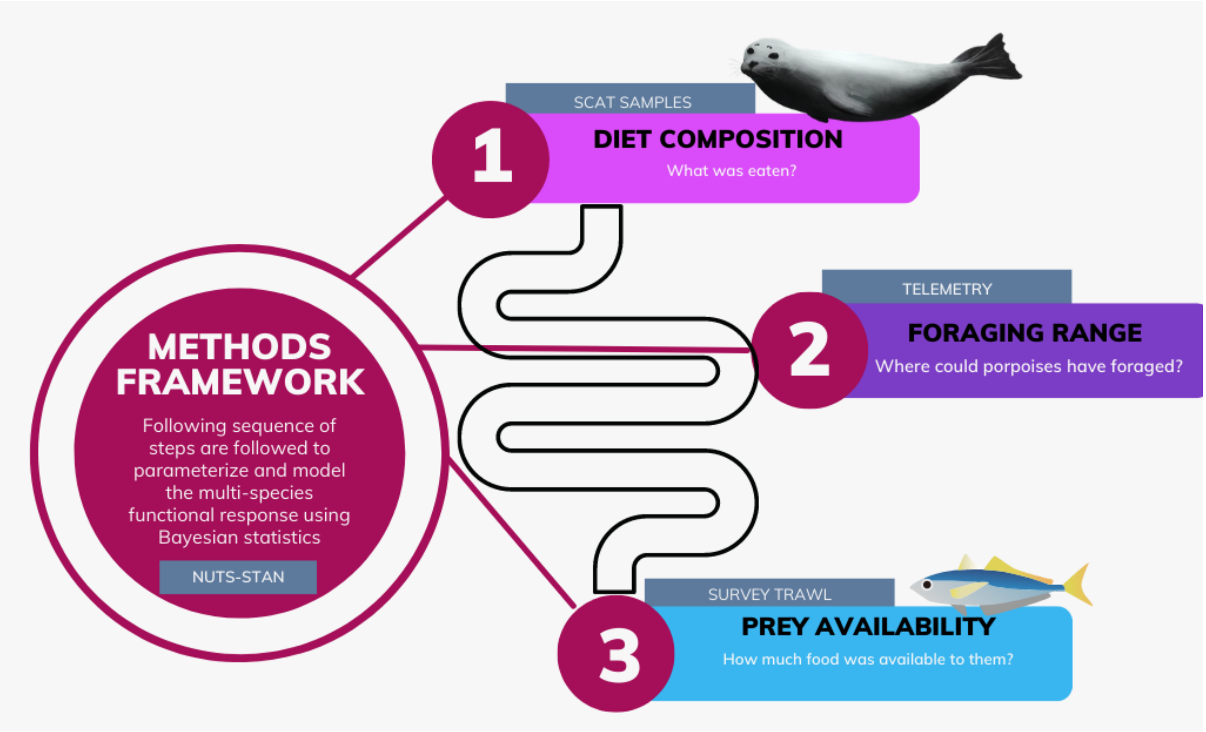

Figure 4.1 Flowchart depicting the methodological steps carried out in this chapter to fit the multi-species functional response of grey and harbour seals. Firstly, scat samples were used to reconstruct diet composition. Secondly, the area where seals could have obtained their last meal was estimated from telemetry data. Thirdly, prey availability was predicted using scientific trawl data. Lastly, the MSFR was fitted using Bayesian statistics and the models were coded in STAN.

4.3.1 Diet composition

Estimates of grey and harbour seal diet composition were available from previous studies (Hammond & Wilson, 2016; Wilson & Hammond, 2019), but it is important for this analysis that some details of the methods are set out clearly because they impact the treatment of the spatiotemporal datasets and the consideration of observation errors. Diet estimates were based on diet information from fish otoliths and cephalopod beaks in seal faecal samples (i.e. scats). Collection, processing, and analysis of scat samples are described in detail in Grellier & Hammond (2006), Hammond & Grellier (2006), Hammond & Wilson (2016), Harris (2007), Wilson & Hammond (2016), Wilson et al. (2017). In these studies, fish otoliths and cephalopod beaks were identified, and measured, corrected for partial digestion using experimentally derived species- and grade-specific correction factors. Prey weight was estimated by applying otolith size – fish mass, or beak size -cephalopod mass, relationships. Prey weights were adjusted using experimentally derived species-specific rates of complete digestion (recovery rates).

Scats were previously collected around Scotland and the east coast of England. Grey seal samples were collected in three periods: the mid-1980s, 2002, and 2010-2011. The majority of the 1980s data were collected in 1985 but there were also some data for eastern England from 1983-1988. Harbour seal scats were collected mainly from April 2010 until March 2011 but also in the Wash (southern England) through 2012.

Diet composition was estimated for quarter 1 (January-March) and quarter 3 (July-September) using existing methods but stratified differently compared to previous work (Wilson & Hammond, 2019) to match to availability of prey data (see section 4.3.3) and estimated for several regions along the British North Sea coast based on seal management units (SMUs) (ICES, 2013; Thompson et al., 2019) for which scat and tracking data were available (Figure 4.2, Figure 4.3). The regions were: Shetland, Orkney and northern North Sea, Moray Firth, central North Sea, and southern North Sea. Scat collections (i.e. defined by year, quarter, region) were included in the analysis if they contained ≥ 25 scats (Appendix 4.1). These scat collection groupings are hereafter referred to as scat sampling units.

Prey species that contributed ≥ 5 % of the estimated prey weight and occurred in $\frac{1}{6}$ or more of the scat sampling units were selected as main prey species. Prey species that contributed < 5 % to the diet were grouped into a single category 'other prey'.

Uncertainties in diet composition arise from measurement (estimation of prey weight) and sampling error and were estimated using the method described by Hammond & Rothery (1996) using a combination of parametric and non-parametric random sampling. Measurement error was estimated by parametric resampling the coefficients that describe the relationship between otolith/beak measurements and diet composition. Sampling error was incorporated using non-parametric bootstrap resampling by resampling a scat sampling unit 1,000 times with the individual scat as the sampling unit. These two sources of variance were combined to estimate diet composition uncertainty.

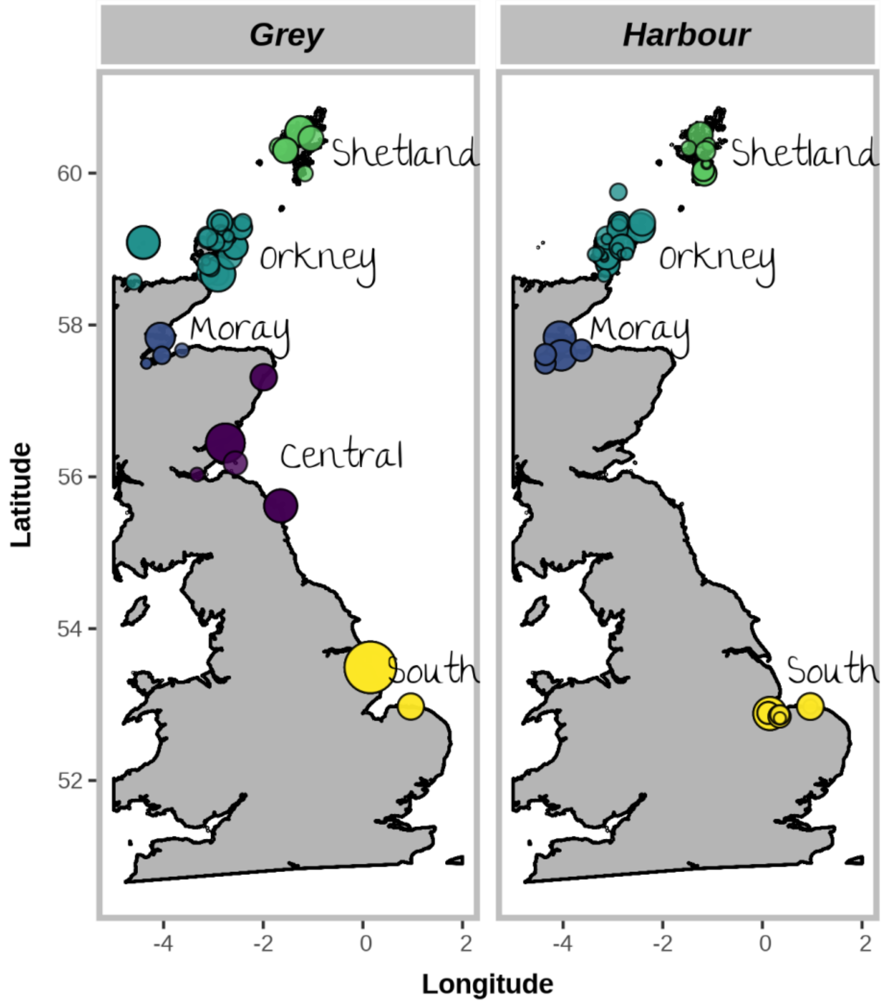

Figure 4.2 Grey and harbour seal diet collection sites by region along the British North Sea coast**.**

4.3.2 Accessibility surface

To link prey consumption to prey availability there is a need to define the geographical area in space that is accessible to the predator. Data processing and analysis largely followed Carter et al. (2020).

Accessibility is most easily thought of as the total area that could be occupied by a predator that may depend on different inter-specific and environmental factors (Aarts et al., 2016; Matthiopoulos, 2003). Assuming that different points in space are equally accessible might hold depending on the species biology (Beyer et al., 2010). However, for central place foragers such as seals, accessibility is greatest close to the central place, and decays with distance from the central place (Matthiopoulos et al., 2004). Previous studies on grey and harbour seals around Britain showed that their habitat preference is mainly driven by distance from the haul-out site (Aarts et al., 2008; Grecian et al., 2018; Matthiopoulos et al., 2004).

To identify areas of likely seal-prey encounters this should be considered. The goal here is to create a weighted accessibility surface for each scat sampling unit location. Furthermore, because the accessibility of space is used to estimate prey availability, the temporal window within which predators could have obtained their last meal is linked to the passage rate of hard prey remains.

Food passage times have been reported for both grey and harbour seals (Hammond & Grellier, 2006; Wilson et al., 2017). The reported cumulative daily passage rates show an asymptotic relationship that eventually levels of at ~100 % of recovered hard prey remains. However, most of the hard parts of prey consumed are passed within a few days. Therefore, seal scats likely represent the final few days of a foraging trip. Different time frames for harbour and grey seals were chosen depending on the day after which the increase of recovered remains was minimal. For harbour seals > 98 % of all fish otoliths were recovered within three days after consumption (Wilson et al., 2017) and for grey seals > 99 % were recovered after four days (Grellier & Hammond, 2006). These timeframes were used to restrict the trip duration if a trip exceeded this time threshold (i.e. 18% of trips for grey and 11% for harbour seals).

4.3.2.1 Data

Grey and harbour seal telemetry data from GPS tags (i.e. GPS-GSM and GPS-GSM/SRDL) throughout 2008-2018 were used to estimate a weighted accessibility surface. GPS-GSM tags transmit data via the Global System for Mobile Communications (GSM) phone network (McConnell et al., 2004) while GPS-GSM/SRDL can relay data either through GSM or the Advanced Research and Global Observation Satellite (ARGOS) system.

These tags have relatively little position error < 50 m, however some erroneous locations were still observed. Russell et al. (2015) was followed to remove inaccurate location fixes and determine accurate haul-out positions. Inaccurate location fixes were removed using residual error thresholds and number of satellites. Additional to positional data the tags also record haul-out events determined by conductivity (i.e. wet/dry) and pressure sensors.

A haul-out was recorded when the tag had been continuously dry for 10 minutes and was classified to end when it had been wet for 40 s. The position of a haul-out event was approximated by taking the mean of all recorded locations during the haul-out time interval. When no location fixes were transmitted within the haul-out time interval the haul-out position was estimated as the midpoint of a linear interpolation between location fixes before and after the haul-out event. Haul-out locations were classified as unreliable if no adjacent location was recorded within 6 hr before and/or after the haul out event. Additionally, each interpolated haul-out event was visually examined and removed if it occurred at sea. The location data were interpolated to a two-hour resolution to create regularly sampled trips between haul-out events. Trips were only included in the analysis if the haul-out event was deemed reliable at the start and end.

For this analysis we are interested in foraging trips and want to exclude the behaviour when seals wait for tidal sites to become available (Thompson, 1989). Therefore, trips that were shorter than 8 hr and occurred completely within 500 m from land were excluded (Carter et al., 2020; Russell et al., 2015). Additionally, data from the first week after tag deployment were removed to reduce incorporating potential post-capture effects on behaviour.

4.3.2.2 Data analysis

Accessibility was modelled assuming a case-control/use-availability design (Aarts et al., 2008). To account for possible regional differences in accessibility (due to differences in the environment e.g. currents; Chevaillier et al., 2014; Hastie et al., 2016) each region was modelled separately Figure 4.3).

There are no tracking data for seals in Shetland, so data from the area believed to be most similar to Shetland (i.e. Orkney and northern North Sea region) were used to predict accessibility for seals in Shetland.

The geographical space that is accessible to an individual was defined by using the maximum geodesic distance (i.e. smallest distance at sea) (Carter et al., 2020; Grecian et al., 2018) using the R package ‘gdistance’, given the likely foraging timeframe (i.e. 3 days harbour seals, 4 days grey seals).

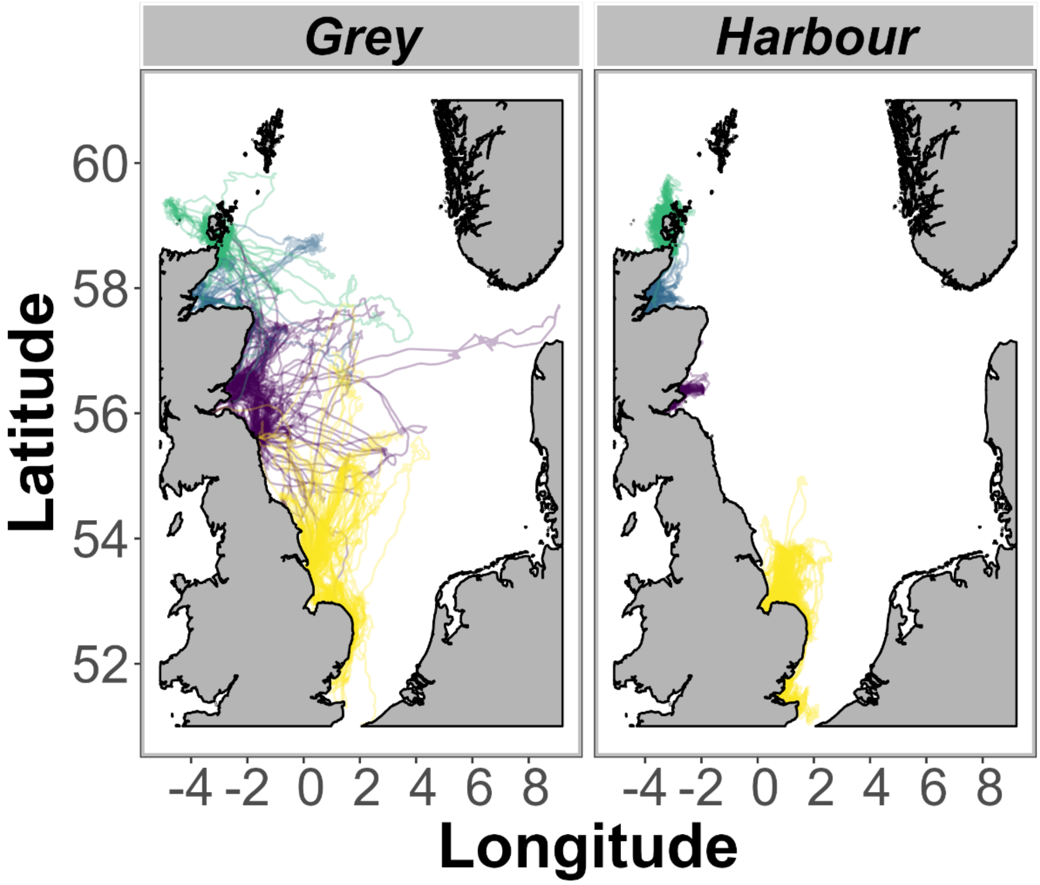

Figure 4.3 Grey and harbour seal trips from GPS tracking data by region along the British North Sea coast**.**

4.3.2.3 Pseudo absence

Telemetry data only represent presence. To provide contrast to model a weighted accessibility map based on distance from the haul out site absences are also needed. Therefore, artificial absences known as pseudo-absences were randomly generated within the geographical space that was assumed accessible based on the maximum distance travelled from each haul out site within a region.

These pseudo-absences thus provide a contrast between locations that are used versus those that are deemed available (Beyer et al., 2010). The ratio of presence versus pseudo-absence data influences model accuracy (Barbet-Massin et al., 2012; Beyer et al., 2010). The number of pseudo-absences needed to approximate a good modelled response while minimizing computational cost was explored by using a ratio between (1:1 to 1:30). For each ratio a binomial generalised linear mixed model (GLMM) was fitted using the R package 'lme4'. The GLMM included distance to the haul out site as a fixed effect and individual was included as a random effect. The coefficient value of distance to haul out was plotted against the ratio of pseudo-absences to visually identify the ratio of pseudo-absences needed for a stabilised model coefficient (see Figure 1c from Beyer et al., 2010).

4.3.2.4 Thinning

Serial autocorrelation in presence data violates the assumption of independence and if not corrected for could overestimate the strength of effects and underestimate uncertainty. Data were thinned using a time-to-dependence approach to account for this. This consisted of subsampling the data to every n^{th} observation. The accessibility model (i.e. one for each region) was fitted with the subsampled dataset and autocorrelation in model residuals of each individual seal was explored by correlograms. The amount of thinning required was based on the value of n for which all individuals returned values that fell within ~95% confidence interval for independent time series of the autocovariance function (i.e. within the blue lines of the correlogram, Figure 4.4).

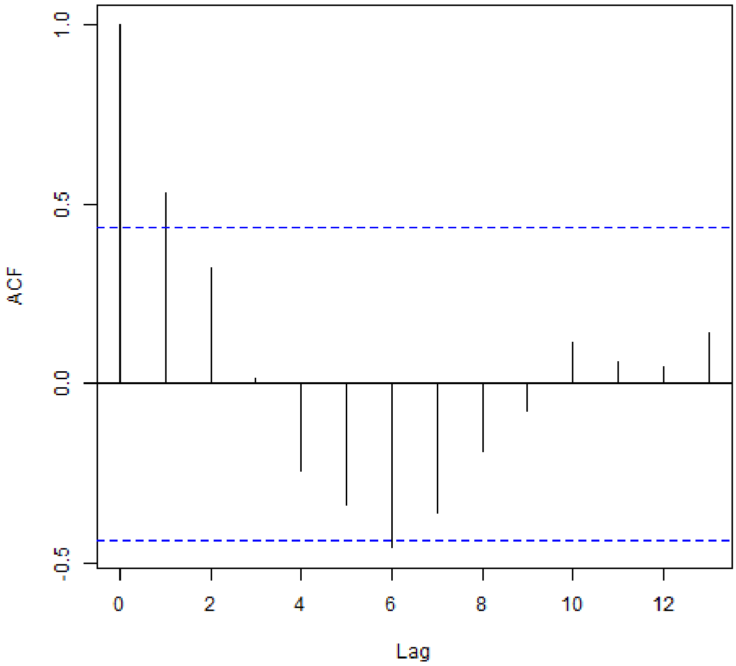

Figure 4.4. Correlogram of one individual seal, autocovariance function (ACF) by lag and 95% confidence intervals represented by dashed blue lines.

4.3.2.5 Model

The probability of observing a presence in the use-availability modelling design is expected to be a non-linear function of distance to haul out site. To capture this, hierarchal generalized additive models (HGAMs) were fitted using the R package "mgcv". Within the HGAM the response variable presence/pseudo-absence is binary and modelled with a binomial error structure and logit link function. Only distance to the haul out site was included as a fixed effect and modelled as a cubic shrinkage spline. Shrinkage smoothers use an additional penalty that helps to avoid overfitting by allowing the smooth function to shrink beyond a linear function towards zero. Individual was included as a random effect to account for variability in individual responses over which we want to generalize. Different types of random effects that share a global trend (i.e. a single common smoother (model G), a global smoother plus group-level smoothers that have the same wiggliness (model GS), or a global smoother plus group-level smoothers with differing wiggliness (model GI)) can be specified within the HGAM framework (Pedersen et al., 2019). These different options were tested, compared using AIC and fitted relationships visually examined, to see which assumption was best supported by the data.

For final model fitting the pseudo-absences were weighted so that they contributed the same weight as all presence data. The number of knots were set so that model predictions returned biologically understandable relationships to distance to haul out site (i.e. decreasing function of presence with distance). Smoothing parameter selection was performed by restricted maximum likelihood (REML) (Wood, 2011).

4.3.3 Prey availability

Fish abundance was estimated for different main prey species (identified in 4.3.1) for harbour and grey seals in the North Sea (see Table 4.1). Longspined sea-scorpion (*Taurulus bubalis*) and bull-rout (*Myoxocephalus Scorpius*) were grouped into scorpion fish and sandeel was grouped on the family level (Ammodytidae) due to difficulties in species identification (Daan, 2001). Furthermore, sandeels are not well represented in the NS-IBTS due to catchability issues (Daan, 2001; Jensen et al., 2011) and therefore a different approach was applied (see section 4.3.3.6).

Table 4.1 All prey species included in analysis, including common and scientific name, most appropriate survey type and percentage of zeros (i.e. % of hauls were the species was absent).

Common name	Scientific name	survey	% zero
Scorpion fish	*Myoxocephalus scorpius*	both	87.9
	Taurulus bubalis		98.7
Cod	*Gadus morhua*	IBTS	30.2
Dover sole	*Solea solea*	BTS	85.7
Dragonet	*Callionnymus lyra*	both	59.5
Haddock	*Melanogrammus aeglefinus*	IBTS	39.5
Herring	*Clupea harengus*	IBTS	24.7
Ling	*Molva molva*	IBTS	90.6
Mackerel	*Scomber scombrus*	IBTS	71.1
Plaice	*Pleuronectes platessa*	BTS	25.2
Saithe	*Pollachius virens*	IBTS	81.7
Sandeel	*Ammodytidae*	section 4.3.3.6	
Whiting	*Merlangius merlangus*	IBTS	5.3

Distribution modelling has seen rapid development over the last decades, motivated by the need to understand changes in time and space to assist conservation and resource management (Araújo et al., 2019; Zurell et al., 2020). However, the analysis of fish catch data remains far from straightforward because there is substantial variation in catchability and abundance among species. Furthermore, their occurrence in space can be patchy and many species aggregate in schools. This means that fish abundance data may have an unusual statistical distribution that needs to take account of zero-catches, and occasionally extraordinarily high values. There are several different statistical approaches that can be applied to resolve some of these challenges. However, the "best" approach is dependent on the species and the severity of these processes. Here the following approaches were compared:

1) Ad-hoc model.

   Historically this is the most used approach in fisheries science. It adds a small constant to the response which is then log transformed. The constant is uniformly added to the catch data and allows for zero catches to be incorporated. It is uncertain what kind of value this constant should take. Although the literature mentions a recommendation of 10% the reason for this is not evident (Campbell, 2004). Here the error distribution was assumed to be Gaussian.

2) Hurdle models.

   This approach which is also commonly applied in fisheries (Maunder & Punt, 2004) uses a combination of two models, one to model the process of presence-absences and the other for non-zero values. A binomial model is fitted to all the data to estimate the probability of occurrence while the second model predicts fish density given that the catch is non-zero. Different error distributions can be applied to the second model. Here, the most commonly used ones were considered (i.e. Gamma distribution or log-transformed response with Gaussian error distribution).

3) Tweedie model.

   More recently, several studies have applied the Tweedie distribution to the zero-catch problem of fish data (Augustin et al., 2013; Shono, 2008). When the power-parameter (p) is >1 and < 2 the Tweedie distribution is known as "compound Poisson-gamma" with point mass at zero and support on positive reals characterised by Poisson mixtures of gamma distributions. This type of the Tweedie distribution thus seems as an elegant approach as it uniformly deals with zero-catch data.

4.3.3.1 Dataset

Prey availability to seal predators in the North Sea was based on estimating fish biomass from survey data coordinated by the International Council for the Exploration of the Sea (ICES). Data were mainly from two surveys using different gear types: the North Sea International Bottom Trawl Survey (NS-IBTS) and the Netherlands Beam Trawl Survey

(BTS). Otter trawls that are carried out within the North Sea mostly use the Grande Ouverture Vertical (GOV) as gear type. The BTS carried out by the Netherlands has a beam width of 8m. Both surveys aim to monitor the relative abundances of commercial and non-commercial fish species. However, due to different gears used they are more efficient in catching certain species. The BTS is designed for flatfish species while the IBTS is more aimed at mid-water fish species.

The Netherlands BTS survey started in 1985 but from 1996 its coverage was expanded from Dutch coastal waters to locations in the Central North Sea and from 1998 most of the North Sea that can be reasonably sampled by the beam trawl was covered. The BTS is caried out in quarter 3 (August-September).

A detailed description of the NS-IBTS data is described in section 2.3.1.1. However, some raw IBTS data that were removed due to low sampling in the Marine Scotland Science dataset were considered beneficial to estimate prey availability West of Orkney and Shetland. Furthermore, as grey seal diet data were collected in winter on Sule Skerry, a remote skerry off the north coast of Scotland, some data from the Scottish West Coast IBTS that started in 1985 and takes place in quarter 1 were included in the analysis (Figure 4.5). However, some critical information to estimate the area of seabed swept (i.e. wingspread (width of the net in m) or towed distance) was missing for 23% of the hauls. Missing wingspread was estimated using GAMMs per quarter including depth as a smoothing spline and a random intercept of vessel explaining 81.6% in quarter 1 and 82.6% in quarter 3 of the observed variation in wingspread. The inclusion of vessel as a random effect was done to account for wingspread from the same vessel may be more similar then that of other vessels (Moriarty et al., 2017).

When towed distance was missing, a linear model with haul duration was used and explained approximately 82% of the data for both quarters.

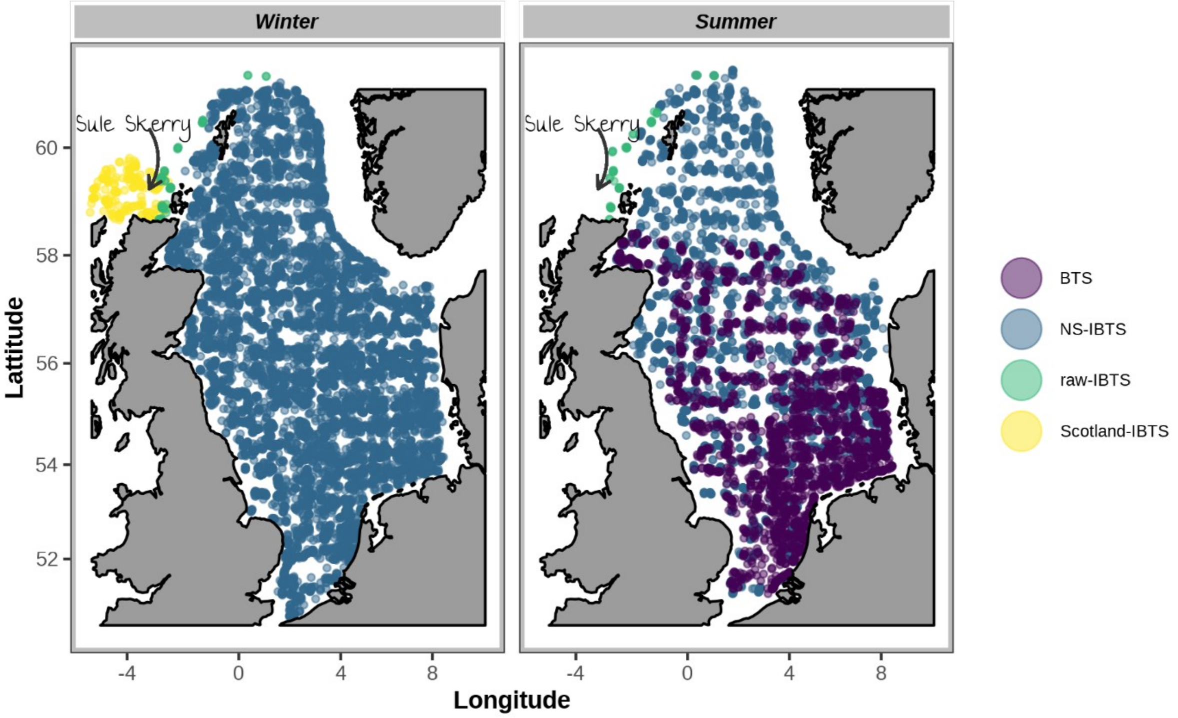

Figure 4.5 Coverage of selected ICES survey data for winter (January-March) and summer (July-September) in the North Sea. Netherlands Beam Trawl Survey (BTS) in purple, cleaned North Sea International Bottom Trawl Survey (NS-IBTS) data from Marine Scotland Science in blue, additional raw NS-IBTS data in green, and the Scottish-IBTS in yellow. Additional northernly distributed data was needed to predict fish distribution to seal diet sampling located West of Orkney, Shetland and Sule Skerry.

4.3.3.2 Data selection

Data from 1983-2017 were used to predict for the years for which estimates of grey and harbour seal diet data were available (Appendix 4.1). Only quarter 1 and quarter 3 were surveyed consistently within the time period. To reduce the overrepresentation of extraordinary catch events biomass values were winsorized (e.g. values that fell beyond the mass 95 % off the range were assigned the value at 95 %).

4.3.3.3 Gear efficiency

Survey catches do not represent true amounts of fish in the area surveyed as fishing gear does not catch all fish in the path of the net. To account for this relative gear efficiency factors per species, gear type and size class from Walker et al. (2017) were used.

4.3.3.4 Distribution modelling

Prey density within the North Sea was estimated by generating a spatio-temporal distribution model of each species using generalised additive models (GAMs). Two different approaches were taken according to which survey was most applicable per species (i.e. IBTS, BTS, or both, see Table 4.1). For both survey type models the response variable was biomass per unit area (BPUA, kg/km^2) and covariates considered included depth, year, season, latitude, and longitude.

For species that are best sampled with the IBTS only, data from that survey were used and modelling was split by season. Otherwise, data from both the IBTS and BTS were used, and quarter and gear type were included within the model. This allowed predicting fish density for both quarters and years of seal diet data that are better sampled by the BTS which is only carried out in summer with good coverage from the mid-90s.

Prediction surfaces were generated over a bathymetry grid publicly available from the European Marine Observation Data Network (EMODnet) Seabed Habitats project[5]. This raster, with a resolution of 115 m^2, was re-gridded to a resolution of 10 km^2 and restricted to the area that was covered by the data per quarter.

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[5] emodnet-seabedhabitats.eu

4.3.3.5 *Model selection*

The model selection procedure was a two-step process.

Step 1 model structure selection

First, for each modelling type (i.e. ad-hoc, hurdle-gamma, hurdle-lognormal, and Tweedie), the level of complexity for the space-time interaction was determined (see Table 4.2). Each different space-time effect was fitted for each different modelling type depending on the most applicable survey type. For BTS species, the complexity level of a four-dimensional space-time effect model (4D) was compared to a double three-dimensional model (3DD), and a single three-dimensional space-time effect model (3D). For IBTS species, models were fitted separately by quarter and therefore only a single three-dimensional space-time effect was fitted.

Table 4.2 GAM model definitions for the space-time effect by survey type.

Dataset	**Space-time effect**	**Model terms**
BTS	4D	$f1(depth_i) + f2(north_i, east_i, year_i, quarter) + survey$
	3DD	$f1(depth_i) + f2(north_i, east_i, year_i) + f3(north_i, east_i, quarter) + survey$
	3D	$f1(depth_i) + f2(north_i, east_i, year_i) + survey + quarter$
IBTS	3D	$f1(depth_i) + f2(north_i, east_i, year_i)$

Within the 4D model the spatial pattern could change by year and quarter simultaneously. For the 3DD model the spatial model could change with time separately by year and quarter. Within the 3D model the spatial pattern could change by year and the intensity could change with quarter for non IBTS species.

Models were fitted using a penalized thin-plate regression spline basis. Space-time interactions were modelled as tensor products with an isotropic smoother for space. Year was included as a penalized cubic regression spline and depth was modelled as a smoothing spline. For the BTS species both quarter and survey type were included as a factor. The Tweedie power parameter (p) was estimated ($1 < p < 2$) during model fitting. Smoothing parameter selection was performed by restricted maximum likelihood (REML) (Wood 2011). Model selection for each modelling type was based on Akaike's Information Criterion (AIC).

Step 2 model type selection

Secondly the best modelling types/error distribution per species were selected based on comparing their predictive power using k-fold cross-validation. 5-fold cross-validation was used, while balancing the ratio between survey type for BTS species, and both the Root Mean Squared Error (RMSE) and Pearson's correlation coefficient were used to evaluate the models' predictive accuracy. Additionally, model performance was checked by manually comparing spatial predictions against observations.

4.3.3.6 Sandeels

Due to catchability issues and the vertical distribution pattern of sandeels neither the IBTS nor BTS are representative for this species. Therefore, a distribution model, described in detail in Langton et al. (2021), of the occurrence of this species in the North Sea in combination with annual sandeel spawning-stock biomass (SSB) estimates for different assessment areas from ICES Stock Assessment Database were used.

The distribution model from Langton et al. (2021) was developed with data on sandeel occurrence from grab sampling and environmental covariates. Here only the binomial component of the hurdle model was used and scaled by annual estimates to reflect spatio-temporal variation in sandeel biomass. The extent of the distribution map is however smaller for one of the sandeel assessment areas for which ICES estimates SSB (Figure 4.6). Therefore, SSB was rescaled for ICES sandeel area 1r (i.e. southern North Sea). This was done by calculating the proportion of sandeel fishing grounds (Jensen et al., 2011) that fell within the range of the distribution model outputs and used as a multiplier for the SSB values. Note that ICES does not provide stock assessment advice for Shetland and Orkney and sandeel availability for these regions was estimated by the MSFR model (see section 4.3.4).

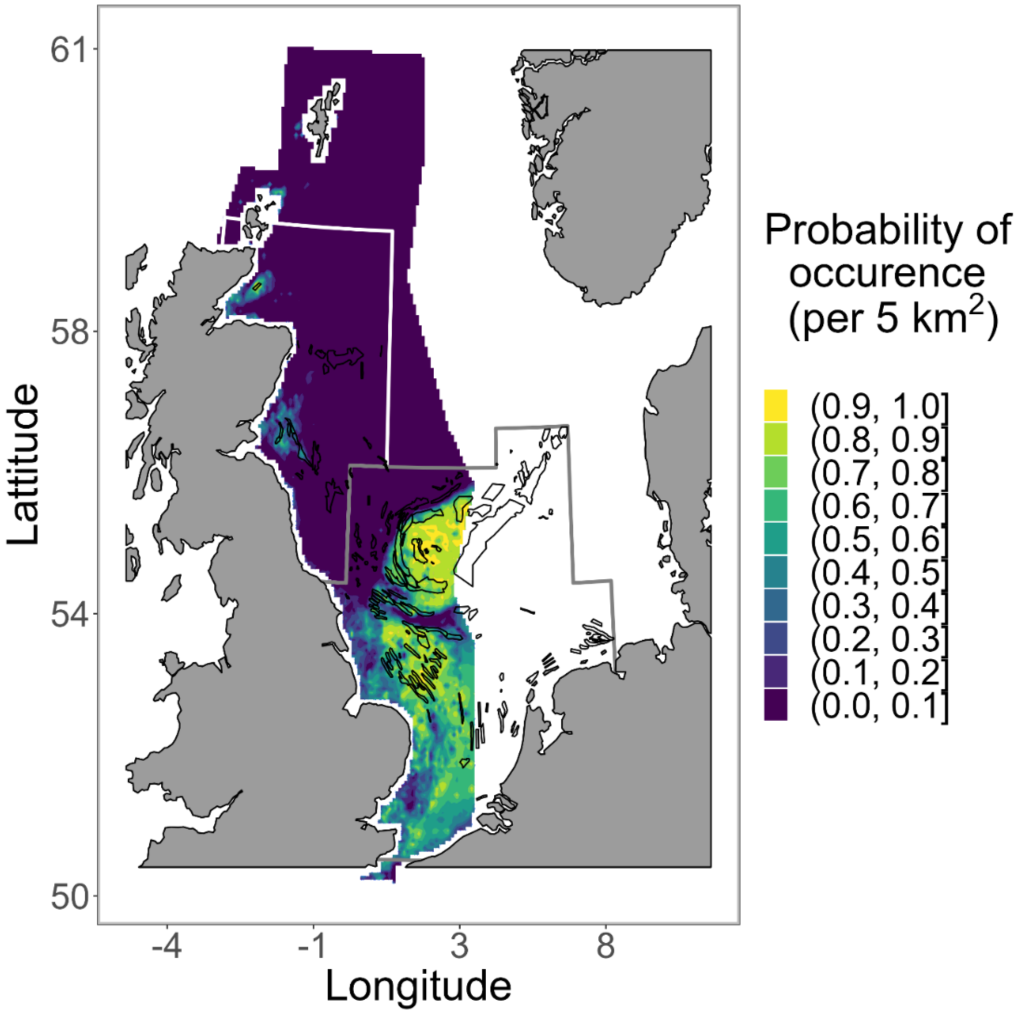


Figure 4.6 Probability of sandeels occurrence per 5 km2 for the North Sea (Langton et al., 2021), sandeel fishing grounds in black polygon outlines (Jensen et al., 2011), and extent of ICES sandeel assessment areas 1r in grey and 4r in white borders.

4.3.3.7 *Propagating uncertainty*

Uncertainty in prey availability to predators was estimated by re-sampling values of gear efficiency correction factors and re-sampling the parameters of the fitted prey distribution and seal accessibility models.

For each prey species (except sandeels) and gear type, uncertainty in gear efficiency correction factors was represented by their CVs and assumed constant across length classes. To create an appropriate distribution of uncertainty for the gear efficiency correction factors the uncertainty estimates reported by Walker et al. (2017), the upper and lower 95% confidence limits, were used to estimate a species-specific CV by gear type, which were resampled using a non-parametric bootstrap. For each prey species, (1000) independent random samples were drawn with replacement using this CV across all length classes. A normal distribution with a mean of 1 and a SD of the CV was assumed. This allowed for this density function to be used as a multiplier for the entire prey surface.

Simulations from the posterior distribution of parameters (Wood, 2007) were used to obtain uncertainty estimates in the predictions of both seal accessibility and fish distribution models. For sandeels, uncertainty was based on re-sampling the occurrence model predictions from Langton et al. (2021), and associated uncertainty in interpolated sediment layers.
Overall diet was estimated for each scat sampling unit (i.e. year, quarter, region). To account for difference in scat numbers the accessibility surface was weighted by the sample size at each location (Figure 4.7a).

For each prey species and scat sampling unit, a bootstrapping procedure of 1,000 iterations was applied to combine the sources of uncertainty. In every iteration, one sample of the gear efficiency correction factors was taken and multiplied by one new prediction of the re-sampled parameters of the prey distribution model. The map of prey biomass generated was then multiplied by a prediction of the re-sampled accessibility model (Figure 4.7b) to obtain a surface of weighted prey availability. Given co-ordinates (*x,y*) and time (*t*) total prey availability (*Pa*) of fish species *s* is given by the product of resampled gear efficiency (*G*), resampled accessibility of seals (*S'*) and resampled fish distribution model (*F'*).

$$Pa_s(x,y,t) = G_s * F'_s(x,y,t) * S'_s(x,y) \qquad \text{(eqn 4.1)}$$

Each surface was summed to obtain a total prey availability estimate and after all iterations were completed the mean and standard deviation of total prey availability per species were calculated.

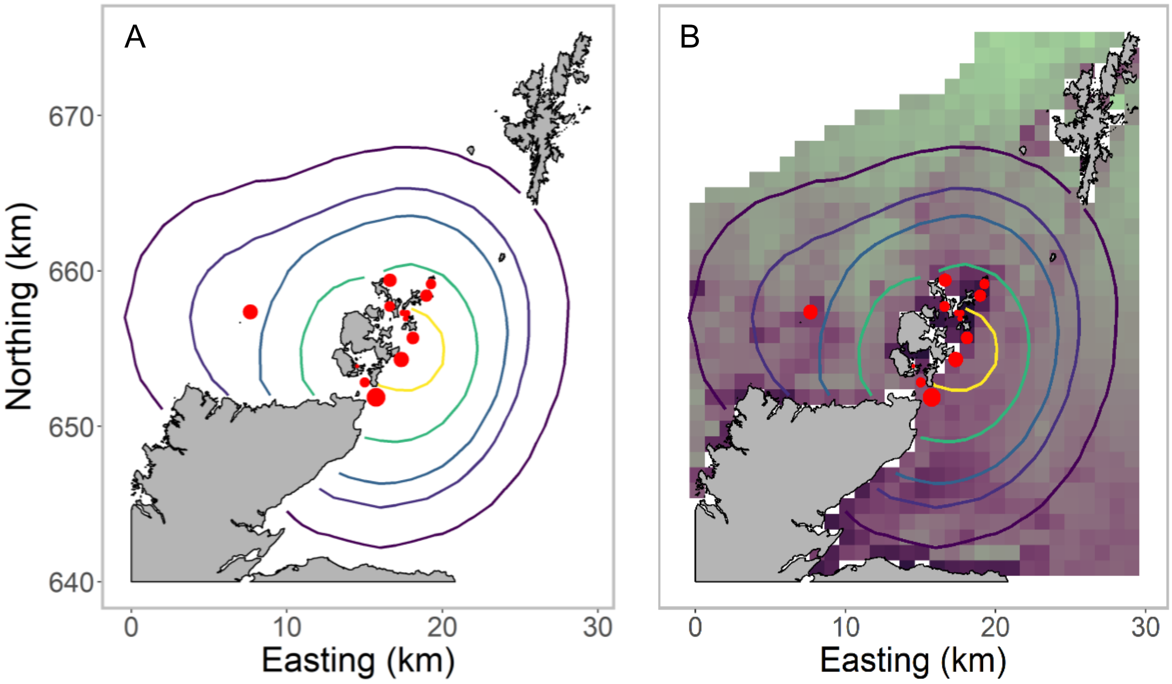


Figure 4.7 Predicted availability of cod to grey seals around Orkney during the winter of 2002. Seal scat sampling locations are represented by red dots, seal accessibility is illustrated by coloured contours (i.e. with higher probability of accessibility closer to shore) and the background in panel B represents the relative biomass of cod per km2.

4.3.4 MSFR

4.3.4.1 Model development

A single species functional response is often described by the generalized Holling formula (Holling, 1959):

$$c = \frac{\alpha N^m}{1+\alpha t N^m} \qquad \text{(eqn 4.2)}$$

where c is the predator consumption rate, α is the attack rate, N is prey availability, t is the consumption/handling time. The shape parameter m determines the shape of the functional response: $m = 1$ yields a hyperbolic saturating functional response (type II), and $m > 1$ produces a sigmoidal response (type III) (Real, 1977).

The equation can be revised to include multiple prey species and in terms of diet composition (see Chapter 3):

$$\frac{c_i}{\sum_j c_j} = \frac{\alpha_i N_i^m}{\sum_j \alpha_j N_j^m} \qquad \text{(eqn 4.3)}$$

where c_i is the consumption of focal prey species i and α_i is the attack rate of focal prey species i and the denominator includes all prey species from 1 to the number of prey species.

For a type III response, with a fixed attack rate, the value m will determine the sigmoidal shape at the start of the curve which becomes particularly important when looking at the prey mortality risk (Figure 4.8).

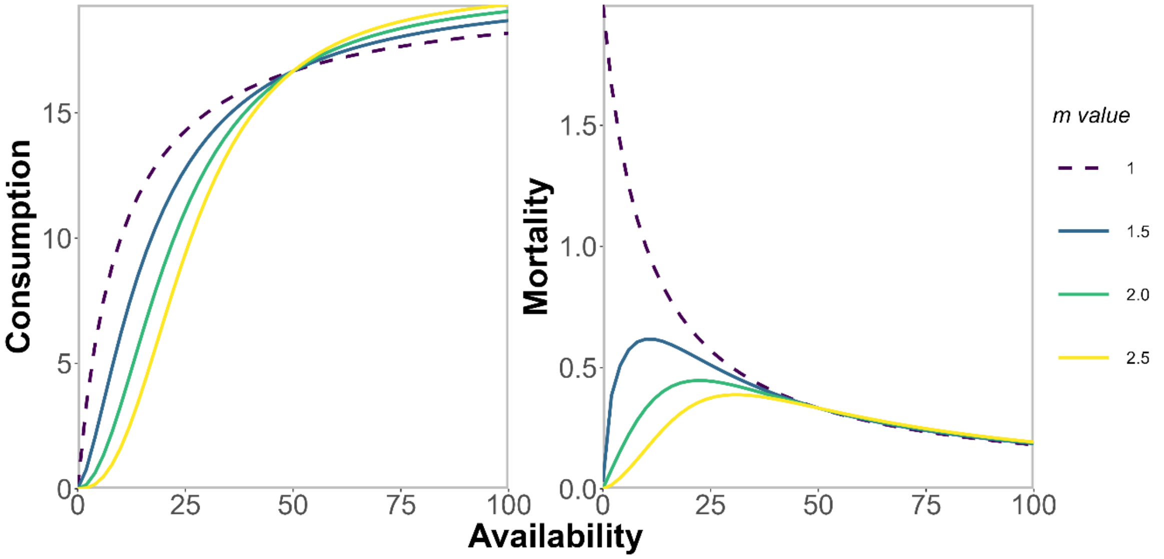


Figure 4.8 Single species functional response curves showing prey consumption and prey mortality risk against prey availability for different shape parameter m values.

When considering multiple prey species, the shape of the response might be prey specific. Therefore, four candidate model types were compared differentiated by shape parameter values to determine the functional response: a hyperbolic type II functional response with shape parameter $m = 1$ for all prey species (model 1), a sigmoidal type III functional response with $m = 1.5$ for all prey species (model 2), an single overall value of m estimated for all prey species (model 3) and a model that estimated species-specific shape parameter values (model 4). However, as the two different parameters that we would like to estimate here (i.e. α and m) jointly determine the shape of the relationship there is a potential problem of unidentifiable parameters. To mitigate this, the MSFR was fitted using Markov chain Monte Carlo (MCMC) methods, a Bayesian approach which allows prior information to be included and is useful for ecological models with poorly identifiable parameters (Reichert & Omlin, 1997). Furthermore, Stan's no-U-turn-sampler, which is more efficient at sampling the posterior and less sensitive to correlated parameters than Gibbs sampling, was used as the MCMC algorithm sampling method (Hoffman & Gelman, 2014). The Bayesian framework offered the additional strength of allowing for uncertainty in both response (diet composition) and independent variables (prey availability) to be included in the analysis, and for the imputation of missing covariate values (in this case, missing values of sandeel abundance around Shetland and Orkney).

4.3.4.2 Model fitting

For each model, two parallel Markov chains were generated, and each chain was run for 40,000 iterations with a burn-in period of 20,000 samples. Convergence was assessed using the Gelman–Rubin diagnostic $\hat{R}$ (Gelman & Rubin, 1992) and visual inspection of trace plots.

To expedite model fitting, all prey availability estimates were re-scaled so that the maximum observed biomass was 100 for each prey species, and zero-truncated Normal distributions were fitted to bootstrap samples of prey availability for each sampling unit. Sandeel availability could not be estimated for all scat sampling units (section 4.3.3.6). For those sampling events a prior N(50,20) was used to estimate sandeel availability. The availability of ‘other prey’ was assumed constant in space and time and was set at a value of 100. Priors for α and m were set i) to rule out unrealistic parameter estimates based on ecological theory ii) previous work from Smout et al. (2014) and iii) checked for independence. Attack rate α, was fixed at 1 for sandeels. For other prey species, a Gamma(1,1) prior was used. This allowed for the relative values of a of each prey species to be considerably larger or smaller than for sandeels. For models 3 and 4 the functional response could take on either a type II or type III functional response and the shape parameter m was given a Gamma(2,1) prior and restricted to values ≥ 1. The marginal posterior distributions of α and m (model 3 and 4) were checked using prior posterior overlap (PPO) plots after model fitting to assess identifiability of these parameters. When the degree of overlap is substantial, the prior is dictating and the data have little effect on the posterior distribution. A rough guideline for weak parameter identifiability is 35% (Gimenez et al., 2009).

Fitted models were assessed by visual posterior predictive checks and compared by the predictive performance of the model indicated by the difference in the expected log pointwise predictive density (ELPD) and its standard error obtained from Pareto-smoothed importance sampling (PSIS) leave-one-out cross-validation (LOO-CV) (Vehtari et al., 2017). Moment matching (Paananen et al., 2021) was used as some Pareto $\hat{k}$ values were large ($\hat{k}$ >0.7) indicating unreliable estimates. An ELPD difference (ELPD diff) > 4 might be relevant for predictive performance and should be compared with respect to their SE (Sivula et al., 2020; Vehtari, 2020). However, there is no strict threshold rule on what ELPD diff in conjunction with SE would result in appropriate model selection. Therefore, the general rule of at least a difference > 2 SE was applied here. When models were similar in their predictive performance the simpler model was favoured.

Marginal relationships between availability and consumption were estimated for each prey species by setting the availability of all other species to one of three specific observed constant levels (minimum, mean, maximum).

4.4 Results

4.4.1 Diet composition

Seal diet was based on 2,367 scats samples for grey and 1,316 for harbour seals. Diet composition of the main prey species by region and sampling time is shown in Figure 4.9 for grey seals and Figure 4.10 for harbour seals.

The main prey species of grey seals included seven different fish species/groups (cod, dragonet, haddock, saithe, sandeels (i.e. again grouped at the Family level, see Table 4.1), scorpion fish (i.e. grouped Longspined sea-scorpion and bull-rout, see Table 4.1) and harbour seal diet included eleven main species (cod, dragonet, herring, ling, mackerel, plaice, saithe, sandeels, scorpion fish, Dover sole, and whiting). For both seal species there was considerable spatio-temporal variation in diet composition but sandeel dominated the diet in most instances. However, the contribution of sandeels to the diet was considerably higher for grey seals.

Of the gadid species cod was important in all regions for grey seals but only in Orkney for harbour seals. Other gadids (i.e. haddock and saithe for grey seals and saithe and ling for harbour seals) were mainly consumed in the central and northern areas of the North Sea. Whiting only made substantial contribution to harbour seal diets in the southern North Sea. Pelagic species (i.e. mackerel, herring) were also important contributors for harbour seals around the Northern Isles. Diets were more diverse in the southern North Sea and other species (i.e. dragonet, scorpion fish, and sole) made substantial contributions in that region.

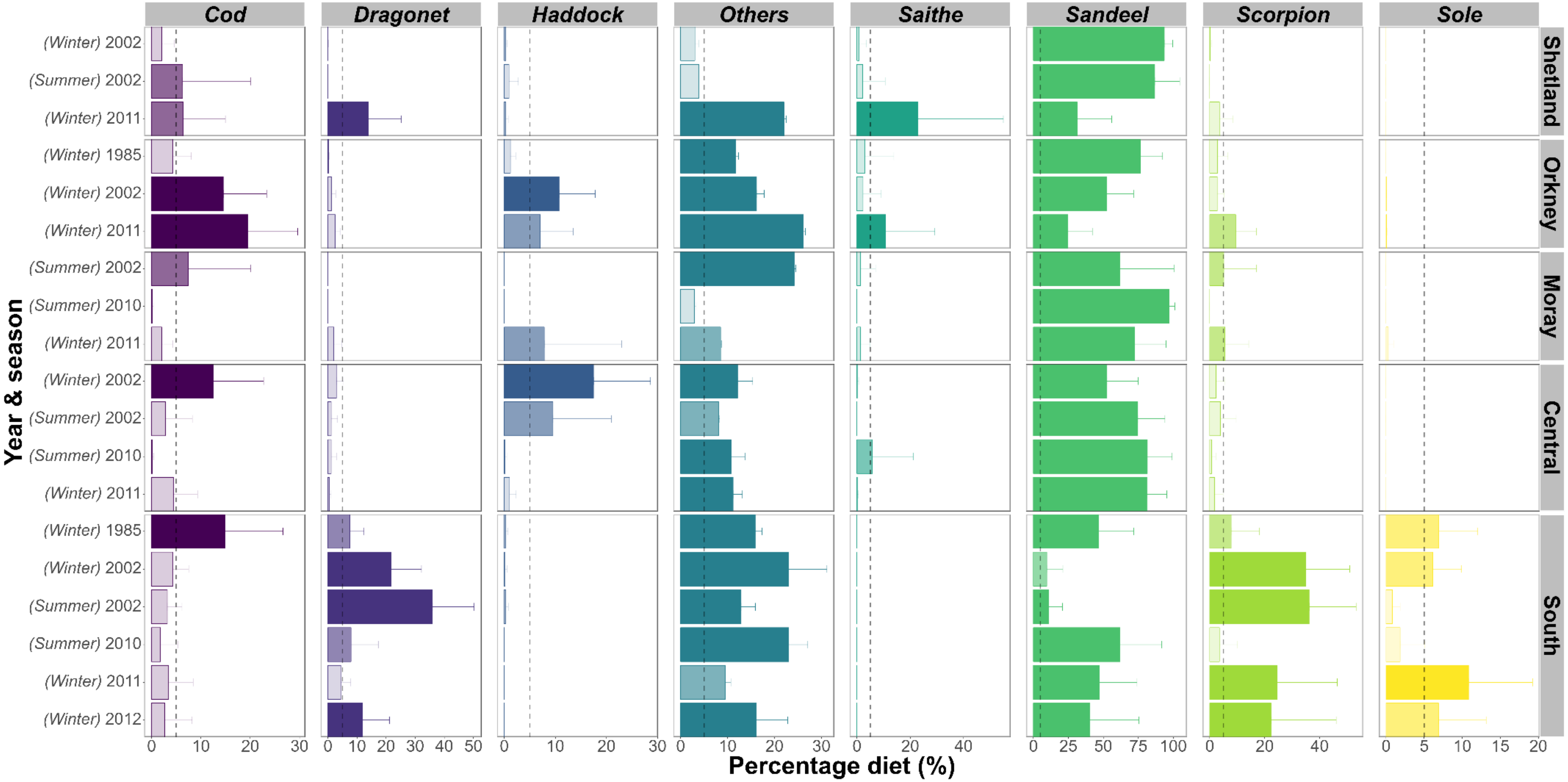


Figure 4.9 Grey seal diet composition by species, region, year and season in terms of percentage by biomass. Bars represent mean value and error bars upper 95 confidence limits. Transparency of bars (i.e. three levels < 5%, <10%, ≥ 10% of mean percentage biomass) and dotted vertical line shows importance threshold of ≥ 5%.

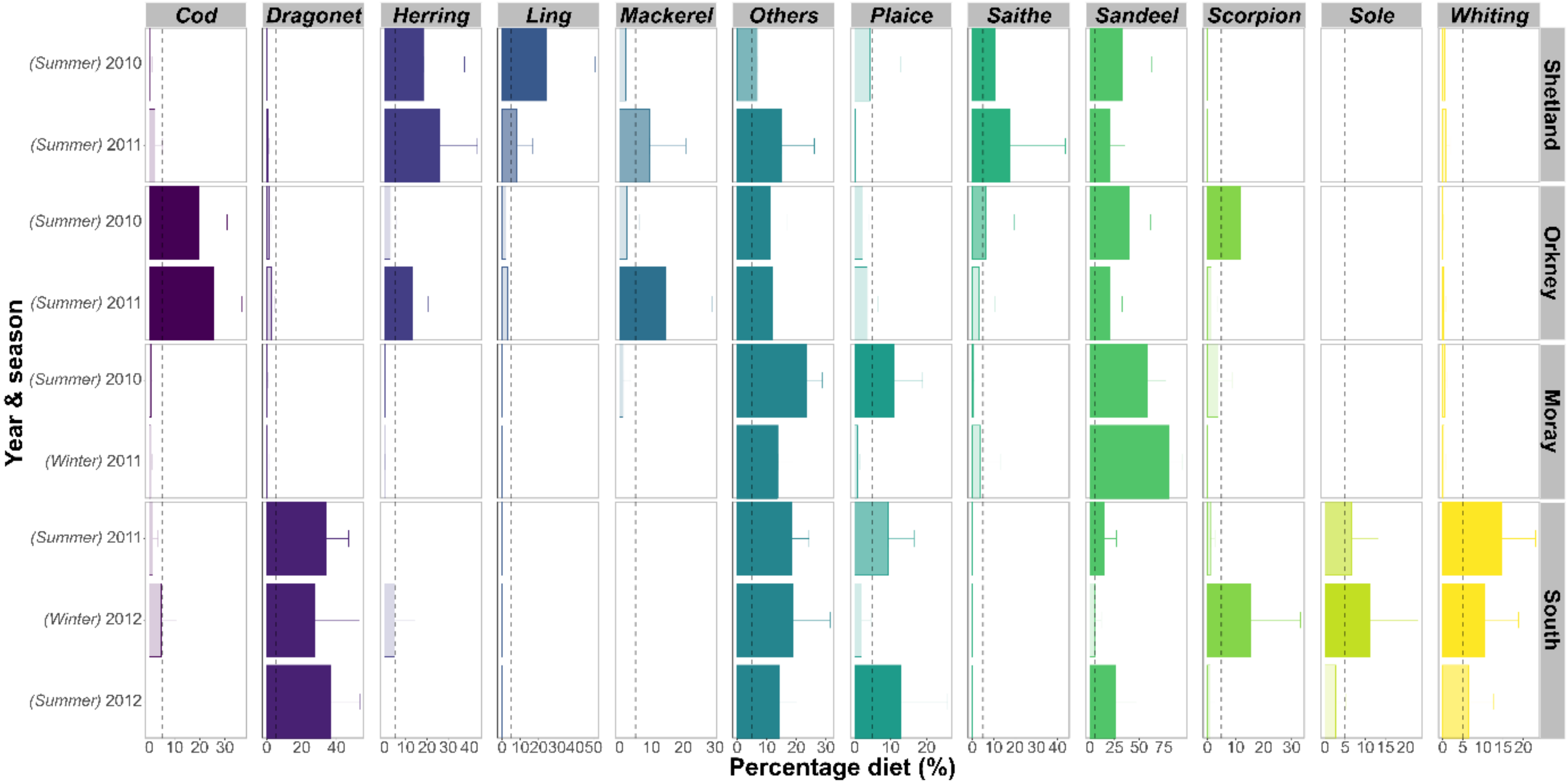


Figure 4.10 Harbour seal diet composition by species, region, year and season in terms of percentage by biomass. Bars represent mean value and error bars upper 95 confidence limits. Transparency of bars (i.e. three levels < 5%, <10%, ≥ 10% of mean percentage biomass) and dotted vertical line shows importance threshold of ≥ 5%.

4.4.2 Accessibility surface

In total data from 55 grey and 166 harbour seals were included into the analysis. The number of trips for individual harbour seals ranged from 4 to 107 (mean = 32.6; SD = 19.1) and 2 to 113 (mean = 28.9; SD = 21.7) for grey seals. For all regions and both seal species the GS model (i.e. a close analogue to a GLMM with varying slopes (Pedersen et al., 2019)) was the best modelling type (Table 4.3).

Final models explained between 52.5 % to 86.1% of the total observed variation. Predicted accessibility according to distance to haul out was greater for grey seals than harbour seals (Figure 4.11). Distances covered were smaller in Orkney for both seal species and harbour seals tended to go further from the haul out site in the southern North Sea.

Table 4.3 AIC scores and % deviance explained (DEV) for grey and harbour seal accessibility models according to random effect type by region.

Random effect type	**Region**								**Species**
	Orkney		Moray		Central North Sea		Southern North Sea		
	AIC	DEV	AIC	DEV	AIC	DEV	AIC	DEV	
intercept	223	79.1	224	72.1	233	69.7	440	54.5	Grey seals
slope	**220**	**83.0**	**202**	**74.6**	**214**	**71.8**	**415**	**57.1**	
Intercept & slope	226	83.9	228	74.8	242	71.9	440	57.5	
intercept	660	81.3	552	85.2	741	48.9	974	73.1	Harbour seals
slope	**608**	**82.6**	**500**	**86.1**	**648**	**52.5**	**902**	**75.1**	
Intercept & slope	623	82.7	510	86.1	673	55.2	918	75.4	

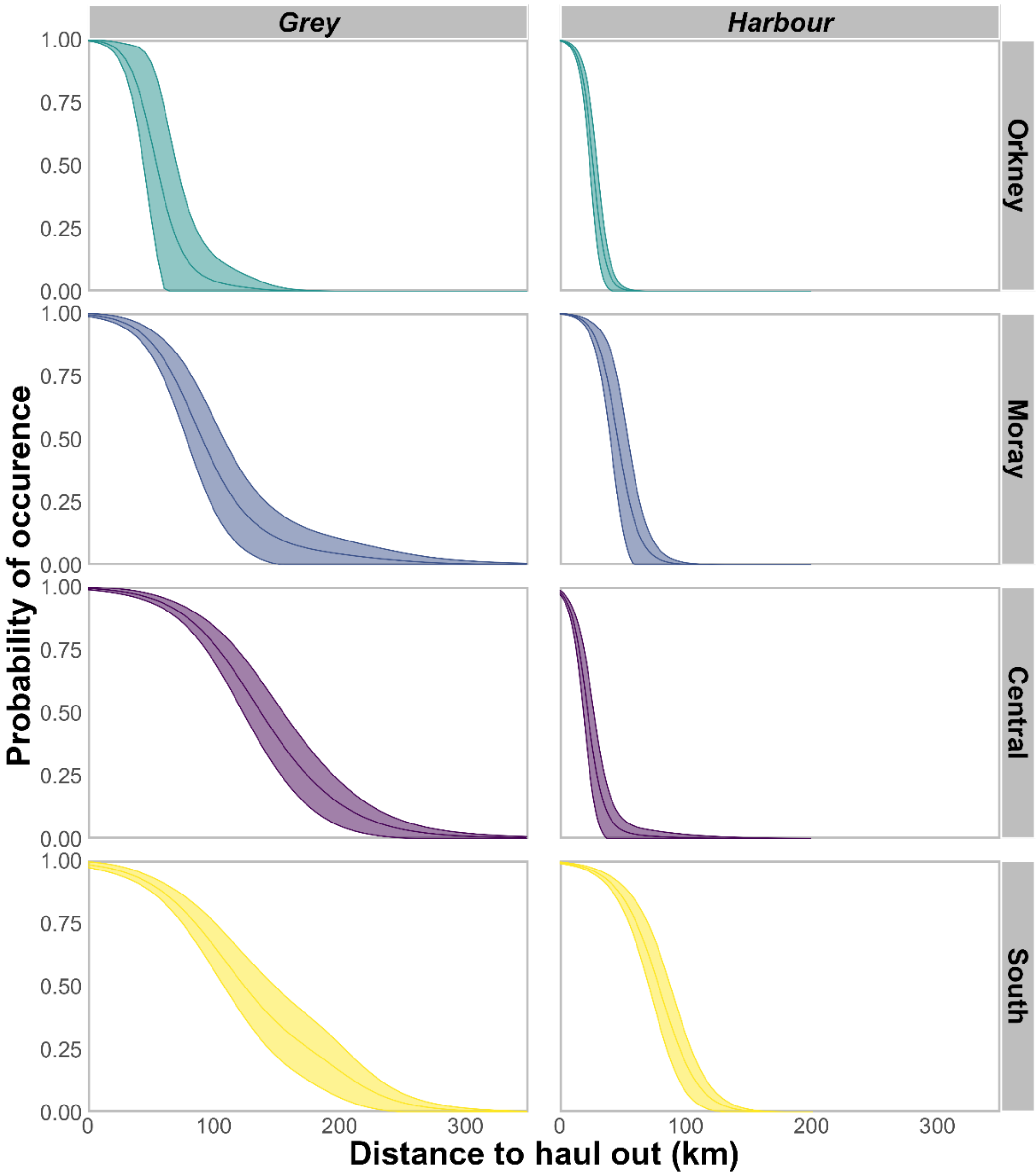


Figure 4.11 Probability of seal accessibility from HGAM by seal species and region depending on distance from the haul out in km. Band represent 95% confidence intervals.

4.4.3 Prey availability

The selected model structure for BTS species was different according to model type and species (Appendix 4.2). However, the inclusion of quarter in the space-time effect, either in the 3DD or 4D, always had a better fit compared to the 3D model, illustrating that distributional did not solely change in terms of intensity by season but that the patterns changed.

Hurdle gamma and Tweedie models were selected as best models and were similar in both RMSE and Pearson's correlation estimates from 5-fold cross-validation, while the log traditional was the worst model followed by hurdle log in all cases (Table 4.4).

Table 4.4 Model comparison based on Pearson's correlation (p) and root mean squared error (RMSE) for each prey species and quarter (depending on survey type) from 5-fold cross-validation. The suitability of the different models according to RMSE and p values are colour coded. Yellow and bold represents the best model, light green second, teal third, and blue least suitable model.

species	**survey**	**quarter**	**Model**							
			Tweedie		Hurdle gamma		Hurdle log		Log trad	
			RMSE	p	RMSE	p	RMSE	p	RMSE	p
Cod	IBTS	1	**477**	**0.5**	478	0.5	518	0.5	561	0.4
		3	373	0.7	**371**	**0.7**	391	0.6	424	0.6
Haddock	IBTS	1	9767	0.5	**9758**	**0.5**	10144	0.5	10172	0.5
		3	16642	0.5	**16593**	**0.5**	17066	0.4	17081	0.4
Herring	IBTS	1	3953	0.3	**3940**	**0.3**	4337	0.3	4387	0.2
		3	**7964**	**0.5**	7988	0.5	9054	0.5	9222	0.4
Ling	IBTS	1	**974**	**0.3**	975	0.3	976	0.3	978	0.2
		3	**1056**	**0.4**	**1056**	**0.4**	1057	0.4	1062	0.3
Mackerel	IBTS	1	**193**	**0.5**	194	0.4	203	0.4	216	0.4
		3	1957	0.3	**1955**	**0.3**	2119	0.3	2230	0.3
Saithe	IBTS	1	1283	0.7	**1260**	**0.7**	1405	0.6	1585	0.5
		3	1978	0.7	**1874**	**0.7**	2034	0.7	2271	0.6
Whiting	IBTS	1	**3843**	**0.6**	3858	0.6	4219	0.5	4281	0.5
		3	**11137**	**0.5**	11291	0.4	12090	0.4	12225	0.4
Scorpion	both	both	**11**	**0.6**	**11**	**0.6**	**11**	**0.6**	12	0.5
Sole	BTS	both	245	0.5	**239**	**0.6**	249	0.6	284	0.3
Dragonet	both	both	**76**	**0.5**	**76**	**0.5**	78	0.5	86	0.5
Plaice	BTS	both	1325	0.7	**1320**	**0.7**	1432	0.7	1562	0.6

As the Tweedie models allow one-stage modelling of zero-inflated data thereby simplifying the modelling procedure this model type was chosen to predict prey availability for all species. Final models explained between ~32% and ~65 % for BTS species and 16% and 78% for IBTS species of the total observed variation in the biomass values (Appendix 4.2). All Tweedie power-parameter estimates were between 1.3 and 1.8 indicating a good fit of the compound Poisson-gamma distribution (Appendix 4.2). These models enabled predicting biomass per km^2 in unsurveyed grid cells resulting in distribution maps illustrated in Figure 4.12for summer in 2012 for each main prey species (except sandeels).

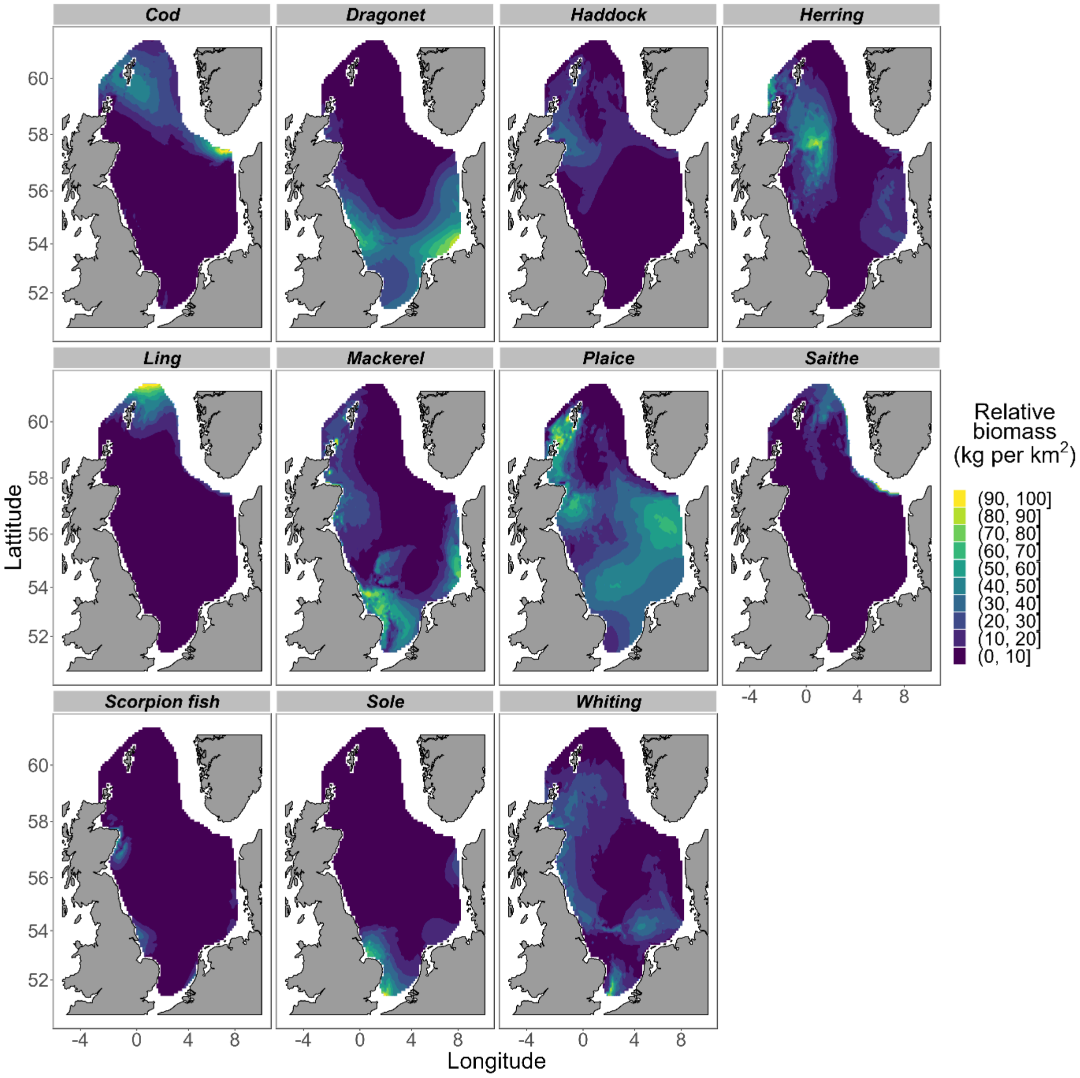


Figure 4.12 Spatiotemporal winter (January-March) distribution of seals (i.e. grey and harbour seal) main prey species excluding sandeels for the North Sea in 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value per species.

Overall patterns in spatio-temporal variation in abundance and distribution of prey species are described and displayed in more detail in Appendix 4.3 .

4.4.3.1 *Sandeels*

The proportion of sandeel fishing grounds covered by Langton's distribution map was ~54% and used as a scaler for area 1r (i.e. southern North Sea) SSB estimates. The SSB values and associated uncertainty used to scale the sandeel distribution map are shown inFigure 4.13.

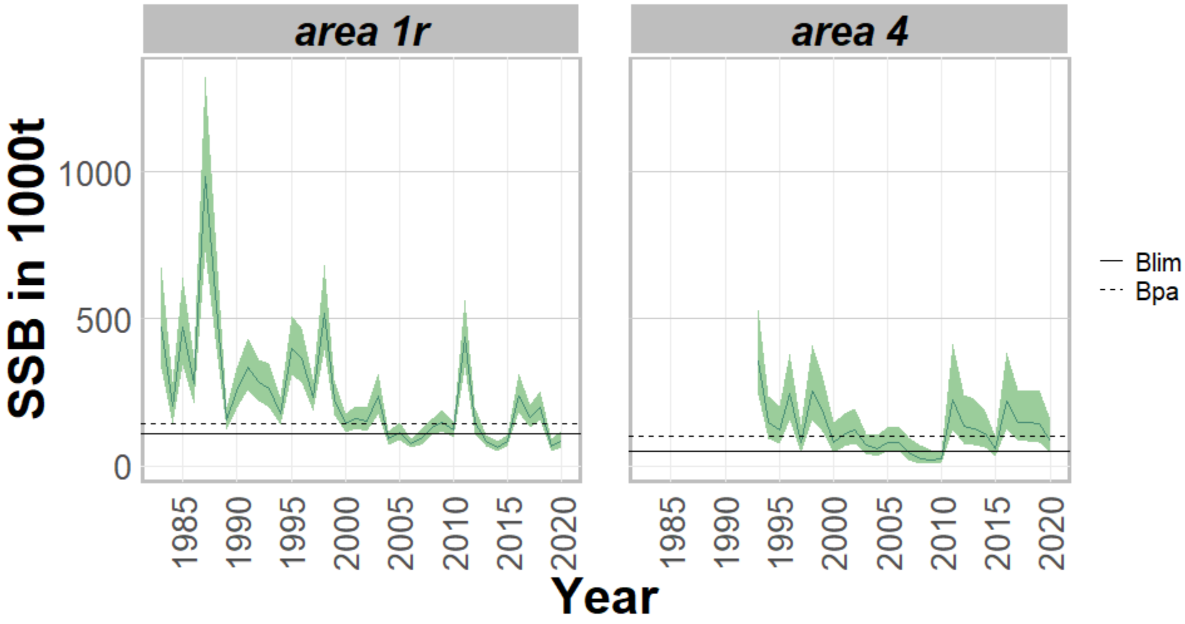


Figure 4.13 Sandeel spawning stock biomass (SSB) from ICES stock assessments for area 1r and (southern North Sea) area 4 (central North Sea).

4.4.4 MSFR

4.4.4.1 *Model selection*

MCMC trace plots showed good mixing of chains, and Gelman-Rubin statistics of $\hat{R}$ <1.1 confirmed convergence for all models considered. For both grey and harbour seals model 1, with a type II functional response, was the least suitable model (Table 4.5). For grey seals the best model was model 3 (*m* overall); it had more predictive power then models 1 and 2 while similar in predictive power but simpler than model 4. Furthermore, PPO of attack and shape parameter(s) diagnosed weak identifiability of parameters for model 4 (Appendix 4.5).

For harbour seals, model 3 was clearly a better fit to the data than models 1 and 4, and the small difference given uncertainty between model 2 and 3 precluded evidence to distinguish between their predictive performance (Table 4.5). Model 3 with an overall *m* parameter was chosen as the best model so attack rates between the two seal species were more comparable. Only predictions from model 3 are presented. The posterior distributions for both a and *m* were well defined given the weakly informative priors (Appendix 4.5).

Table 4.5 Expected log predictive density (ELPD) differences of multi-species functional response models for grey and harbour seals, along with their standard error (SE). Selected models are highlighted in grey and best models are bold.

Grey seals			**Harbour seals**		
Model	**ΔELPD**	**ΔSE**	**Model**	**ΔELPD**	**ΔSE**
Model 4	**0.0**	**0.0**	**Model 3**	**0.0**	**0.0**
Model 3	**-2.8**	**3.0**	**Model 2**	**-7.9**	**5.5**
Model 2	-23.7	8.0	Model 4	-13.6	5.3
Model 1	-58.2	14.3	Model 1	-31.3	8.1

4.4.4.2 Model predictions

Model predictions of diet composition captured the overall pattern in the observed diets of both seal species well (Appendix 4.5). However, the proportion of whiting in harbour seal diets in the southern North Sea (i.e. the only region where whiting contributes considerably to the diet) was not captured by the model as it was considerably underestimated.

Parameter estimates of attack rates and shape parameter are displayed in Figure 4.14 and Table 4.6. Attack rate was highest for sandeel, fixed value of 1, for both seal species. Relative to sandeels harbour seals had higher attack rates for other species compared to grey seals. Attack rates were highest for ling (mean = 0.70, 95% CI [0.44, 1.05]), herring (mean = 0.68, 95% CI [0.22, 1.02]), saithe (mean = 0.59, 95% CI [0.29, 0.95]) and cod (mean = 0.47, 95% CI [0.33, 0.65]) for harbour seals. Scorpion fish (mean = 0.37, 95% CI [0.25, 0.52]) and saithe (mean = 0.29, 95% CI [0.15, 0.49]) were relatively preferred by grey seals. Shape parameter *m* estimates were higher for harbour (mean = 2.78, 95% CI [2.31, 3.37]) than grey (mean = 2.15, 95% CI [1.84, 2.52]) seals, with values indicating a sigmoidal type III functional response.

Strong relationships between prey availability and consumption by seals were predicted by the final models and are illustrated in Figure 4.15 for grey and Figure 4.16 for harbour seals. Prey consumption of a particular prey was reduced when more ‘alternative’ prey (i.e. other prey species in the system) were available (illustrated by the different colours in Figure 4.15, Figure 4.16). For grey seals, the availability of sandeel had the strongest effect on consumption of other prey types and sandeel consumption remained high over all levels of “alternative” prey availability. Although the functional response for harbour seals was also mostly impacted by sandeel availability, strong effects of other species (i.e. ling, herring and saithe) were also observed.

Table 4.6 Posterior mean and standard deviation (SD) of attack rate by prey species and overall shape parameter for grey and harbour seals.

		Grey seal		**Harbour Seal**	
		mean	**SD**	**mean**	**SD**
Attack rate	Cod	0.18	0.03	0.47	0.08
	Dragonet	0.14	0.02	0.16	0.03
	Haddock	0.09	0.02		
	Herring			0.68	0.17
	Ling			0.70	0.15
	Mackerel			0.05	0.04
	Others	0.13	0.02	0.11	0.02
	Plaice			0.18	0.05
	Saithe	0.29	0.09	0.59	0.16
	Sandeel	Fixed at 1			
	Scorpion	0.37	0.07	0.15	0.05
	Sole	0.07	0.02	0.08	0.02
	Whiting			0.03	0.01
Shape parameter		2.15	0.17	2.78	0.27

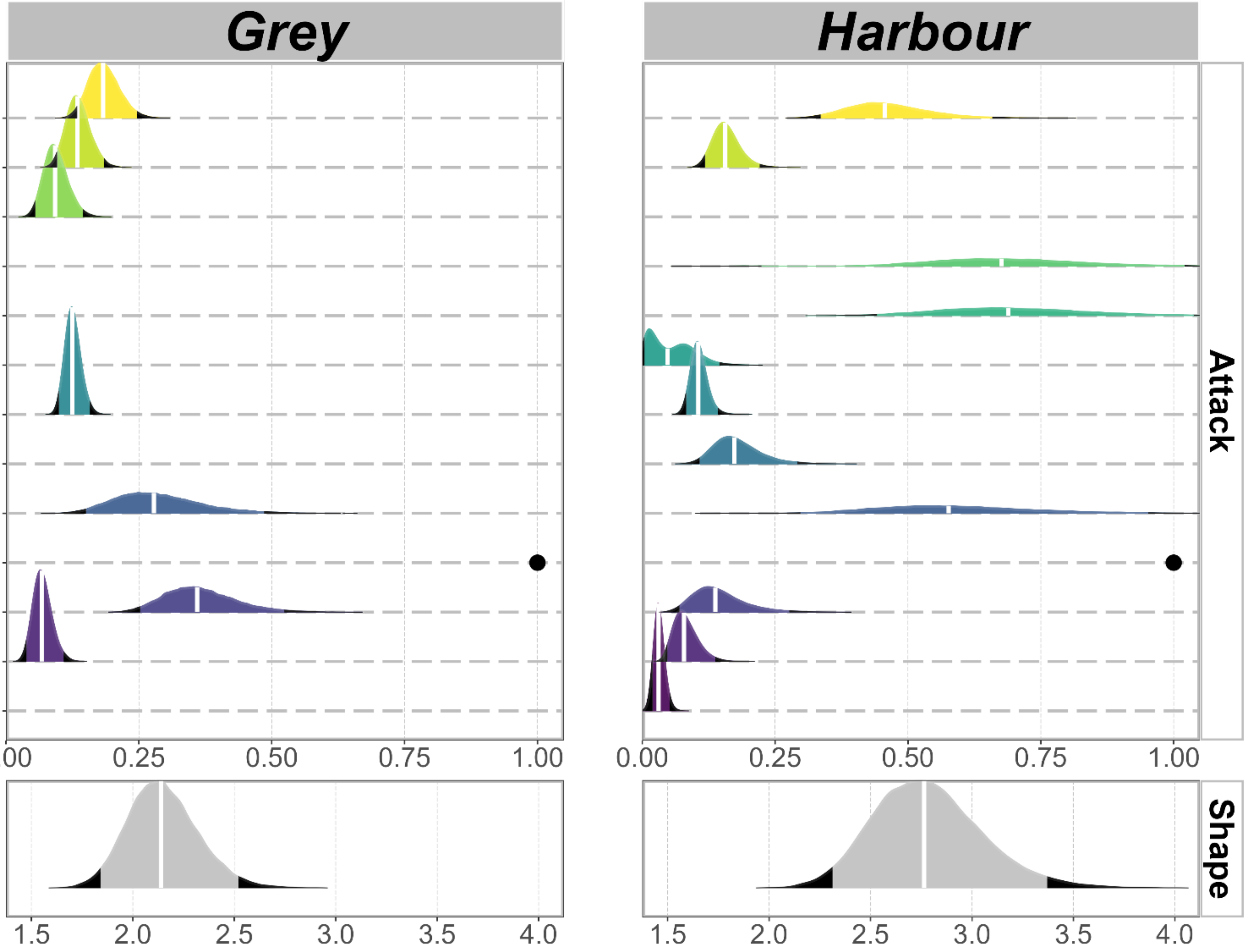


Figure 4.14 Posterior distribution of attack rate ($\boldsymbol{\alpha}$) by prey species and overall shape parameter (m) for grey and harbour seals. 90% confidence intervals are coloured and outer 10% are in black, note the attack rate of sandeels had a fixed value of 1.

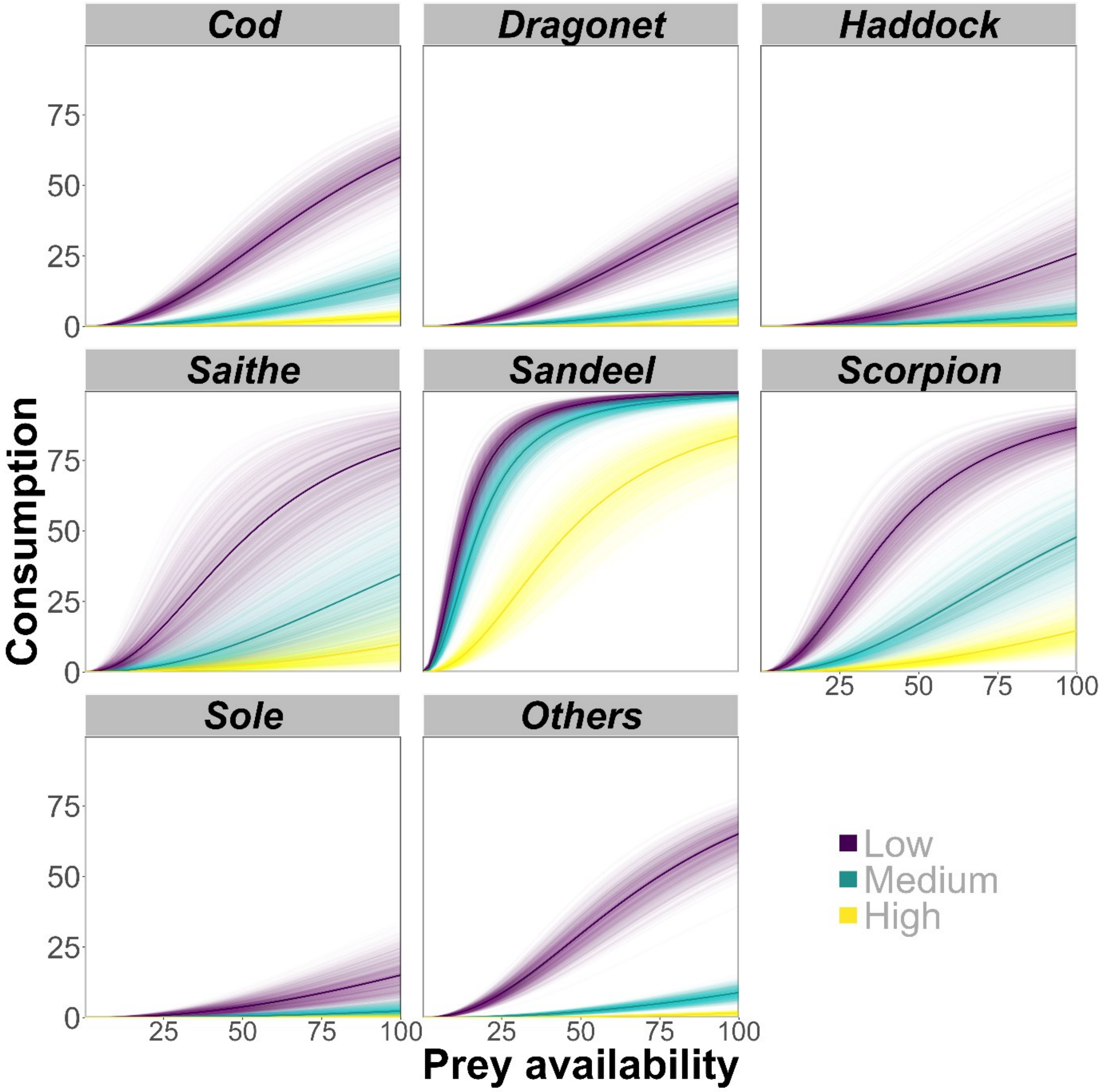


Figure 4.15 Functional response of grey seals for each prey species. Relationships between consumption and availability are shown as a single-species plot at three different levels of alternative prey (all other prey) availability. Each line represents a simulation (N=1000), and the solid line represents the model median. The relationship between relative prey availability and consumption was estimated for each main prey species in turn by setting the availability of all other prey to one of three specific constant levels (minimum, mean, and maximum).

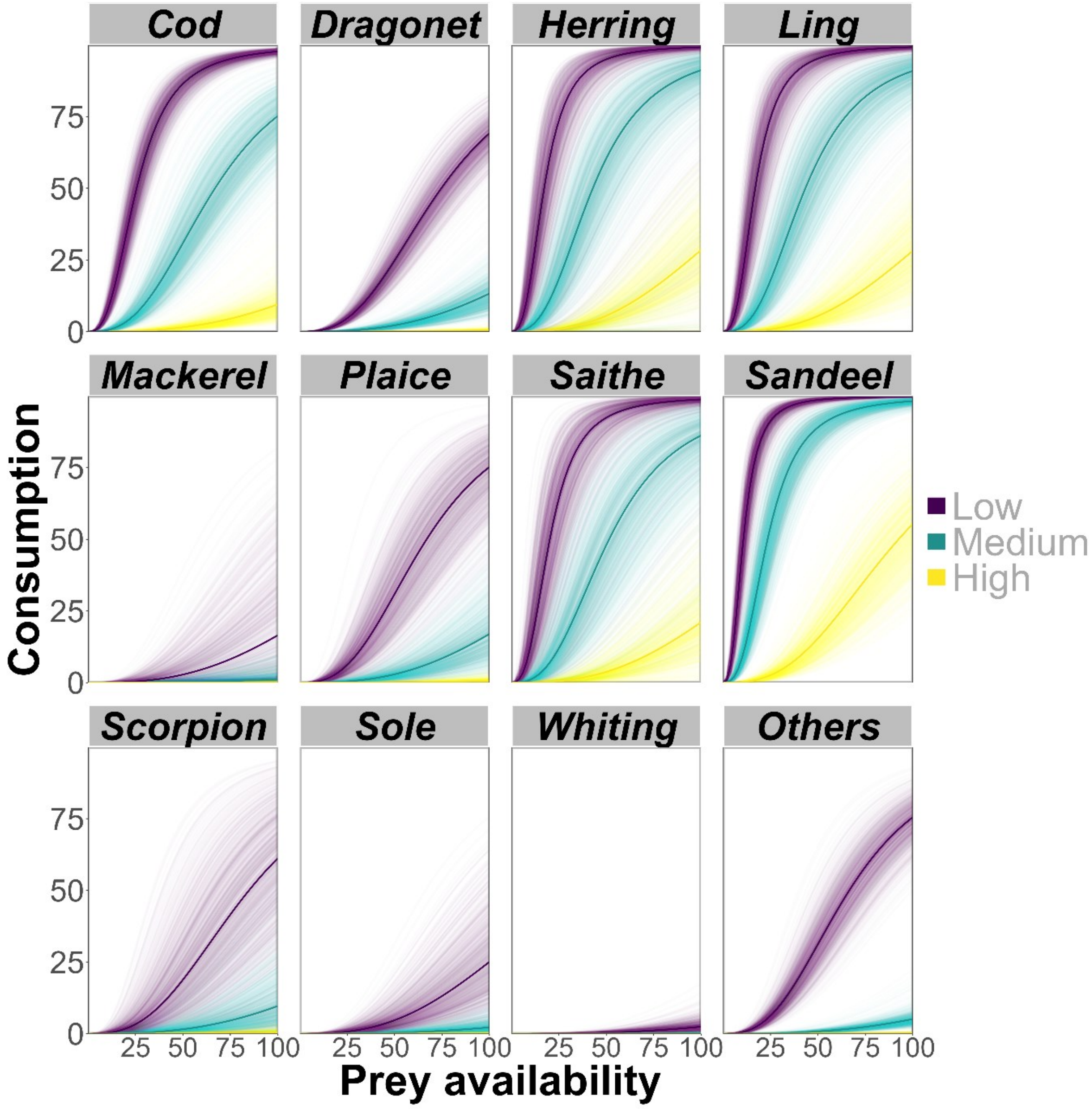


Figure 4.16 Functional response of harbour seals for each prey species. Relationships between consumption and availability are shown as a single-species plot at three different levels of alternative prey (all other prey) availability. Each line represents a simulation (N=1000), and the solid line represents the model median. The relationship between relative prey availability and consumption was estimated for each main prey species in turn by setting the availability of all other prey to one of three specific constant levels (minimum, mean, and maximum).

4.5 Discussion

This chapter revealed the shape of the multi-species functional responses of grey and harbour seals which are important high trophic level predators within the North Sea ecosystem. The MSFR modelling approach in Chapter 3 was further developed by increasing the reliability in prey availability estimates by incorporating gear efficiency estimates, a more elaborate approach to estimate sandeel availability, transitioned to Stan's no-U-turn-sampler, and explored different models to estimate the shape parameter(s) m. The most important finding is that a type III functional response is clearly preferred over a type II functional response for both grey and harbour seals. Furthermore, sandeels are important for both seal species but are more strongly preferred by grey seals (evidenced by a relatively higher ranked attack rate).

While harbour and grey seals are sympatric and consume similar prey species, results also suggested that they might be functionally distinct predators (i.e. predators that have different functional roles in the ecosystem), with harbour seals having a more diverse diet and exhibiting a stronger sigmoidal response that may indicate a greater tendency to switch prey.

4.5.1 Data and Methods

Incorporating suitable spatial scales is one of the major challenges in ecological studies (McCann et al., 2005) and the accuracy of the modelled relationship between prey availability and consumption relies critically on achieving exact spatial and temporal overlap. Foraging tactics of predators could be different in space and time and therefore functional responses would ideally be fitted separately among regions in the North Sea. However, due to the limited amount of seal diet data the functional response was modelled on a population level assuming that broad scale variation in prey availability is linked to changes in diet composition (which might encompass differences in foraging strategies or preference) and that these two types of data match temporally (i.e. fish survey data match with diet estimates). The accuracy of the results is large depended on how accurate the predator accessibility surface corresponds with the area wherein seals could have foraged prior to defecating on land and how well the prey availability estimates represent the true food availability to seals. These and other caveats of the data and methods are described in more detail below.

4.5.1.1 Method evaluation

MSFR model 3, that estimated an overall *m* parameter, was the favoured model for both seal species, with estimated values of *m* representing strong sigmoidal type III functional responses, while the fixed type II functional response model which had the least amount of support was clearly rejected. These results emphasize the complex foraging behaviour of these two predator species that have a tendency to switch prey depending on the availability of different species. Although the species-specific shape parameter model was also a good fit for the grey seal data (model 4, Table 4.5) the prior posterior overlap (PPO) indicated weakly identifiable parameters given the data and priors (Appendix 4.1). Importantly, the attack rate and shape parameter jointly determine the shape of the functional response and an increase in *a* has a similar effect on the shape as a decrease in *m*. The lack of informative priors and the limited amount of data with associated uncertainty illustrates the difficulty and potential redundancy of fitting all these parameters. However, additional data might help address the challenges of parameter identifiability and/or new information from tags that synchronously sample predator movement, prey fields, and capture attempts (Goulet et al., 2019; Vance et al., 2021; Wisniewska et al., 2016) could support constructing more informative priors for species-specific attack rates which would theoretically allow a better fit of this type of model.

Uncertainty in attack rates is greater for higher attack rates (Figure 4.14) in terms of absolute uncertainty, but relative uncertainties are similar (e.g. coefficient of variation). With a lower sample size (i.e. fewer scat sampling units) for harbour seals and more included prey species, parameter uncertainty is expected to be greater. For saithe the relatively high uncertainty in the diet estimates might also be a source of uncertainty in these estimates.

One of the biggest potential caveats is that sandeel availability for the Northern Isles had to be estimated within the modelling framework. A prior of N(50,20) was used and should theoretically allow for a broad range of values to be estimated. The number of scat sampling units for which sandeel availability had to be estimated was considerably higher for harbour seals compared to grey seals. Figure 4.14 shows that high attack rates apart from sandeel were identified for species (i.e. ling, saithe, herring, and cod) that only substantially contributed to harbour seal diet around the Northern Isles (i.e. were sandeel availability had to be estimated) where they also only occur in high numbers. This could be indicative of an overestimation of sandeel availability in those places and thus an overestimation of the attack rates of ling, saithe, herring, and cod and these results should therefore be interpreted cautiously. Apart from probably being able to use more diet data information in the future (Russell et al., 2021), and the need for more reliable sandeel data, the use of a more informed prior (e.g. using seabirds breeding success, which is sensitive to sandeel abundance, as a proxy for sandeel availability) might be another solution to improve the reliability of the results.

The MSFR captured variation in diet well except for underestimating whiting in harbour seal diets. This could be for various reasons but most likely is due to opportunistic feeding on this prey species. Diet composition estimates were incorporated assuming a Normal distribution.

However, a Dirichlet distribution which is a multivariate generalization of beta distributions might be a better representation of the data because the proportions of different species are dependent on each other (Ainsworth et al., 2010). However, parametrising the Dirichlet distribution within this framework would make the functional response model and fitting more difficult (e.g. amongst other things the need to incorporate species- and grade-specific correction factors). Therefore, the method applied here to fit a simple MSFR model that is analytically tractable and estimate diet composition beforehand through a bootstrapping routine (described in section 4.3.3.7) seems acceptable.

The MSFR model used here is simple and does not include inter or intra specific competition. Future studies could build upon this work by including predator (e.g. grey seal, harbour seal, harbour porpoise) abundance within the MSFR to asses potential competition within or among different predator species which might be highly relevant to address the possibility of competition between the two seal species and harbour porpoises. Furthermore, size-based preference could be explored by grouping prey in multiple size classes (as further discussed in the general discussion, Chapter 5). The impact of predation on prey populations is a combination of the predator's functional, aggregative, numerical response and the nature of density dependence in the prey's per capita reproductive rate (Matthiopoulos et al., 2008). Within a multi-species ecosystem with complex trophic interactions, some of which may interact trophically or competitively, predation impact will also depend on other sources of prey mortality (e.g. fishing, predation by other predators). Therefore, to fully explore the consequences of predation by seals on prey species, the MSFRs modelled here should be incorporated within an ecosystem model to predict and access how prey populations are expected to change under different scenarios of predator populations, fisheries management regimes and climatic scenarios.

4.5.1.2 Data limitations

Although diet composition and movement are known to be affected by demographic factors (e.g. sex and age (Beck et al., 2007; Carter et al., 2017; Lundström et al., 2010; Wilson & Hammond, 2016)) and individual seals could display different preferences (Gallon et al., 2017) which could affect the functional response, these processes could not be incorporated into the analyses both due to the limited sample size of telemetry data and the nature of the diet data which is not associated with individual identity, age or sex.

Diet composition

Prey consumption was based on seal scat samples and assumed to describe the average diet for scat sampling units (i.e. defined by year, quarter, region). Sample size was considerably larger for grey seals compared to harbour seals and consisted of a larger temporal range in terms of years. Furthermore, samples between the two species differed considerably by season with harbour seals being mainly sampled in summer and grey seals in winter (Appendix 4.1) but relate to similar ecological processes (i.e. just after the breeding season which occurs June-July for harbour seals and August-December for grey seals (SCOS, 2017)).

The minimum number of samples needed to reduce sampling error and identify moderate changes was previously identified to be ~ 100, and ~60 to identify main prey species which also depended on the number of prey species consumed (Hammond & Rothery, 1996; Trites & Joy, 2005). Here a minimum sample size of ≥ 25 scats per sampling unit was chosen to balance diet accuracy and precision with maintaining enough scat sampling units to provide a range in prey availability indices to fit the MSFR models. Here this focus is on overall diets and the decision on minimum sample size should still provide a reliable representation of the main (most consumed) prey species but might underestimate the contribution of rarer species.

Species- and grade-specific factors were applied to correct for differences in partial and complete digestion but other sources of potential bias from using scat samples include: higher representation of prey consumed close to haul out sites (partially accounted for here by restricting accessibility areas by food passage time); underrepresentation of large prey by failure to consume the heads; and secondary prey ingestion (Hammond & Grellier, 2006; Tollit et al., 1997). These sources have been considered to result in minimal bias in estimates of grey and harbour seal diet around Britain (Hammond & Grellier, 2006; Hammond & Wilson, 2016; Wilson & Hammond, 2016b). Although species- and grade-specific correction factors were applied to correct for differences in partial and complete digestion, the contribution of smaller prey might still be underestimated because smaller otoliths have lower recovery rates and correcting for complete digestion is complicated (Wilson et al., 2017). However, for similar amounts of individual fish, small fish make a small contribution to the diet in terms of biomass compared to bigger fish; only when seals would feed extensively on small size classes their contribution to the diet would become important and thus it seems reasonable to assume that their influence is probably minor.

Prey availability

The methodology used here is appropriate if spatio-temporal trends in relative prey abundance reflect those in absolute abundance of prey, which seems a reasonable assumption provided that all the data are subject to the same bias. Here, size-specific net efficiency by gear type and species was accounted for. However, catch efficiency can also vary with fish abundance (Cadrin et al., 2016) and herding effects might be progressively greater with increasing depth (Dean et al., 2021) which might be especially important if species exhibit abundance changes in specific areas (e.g. cod (Hedger et al., 2004)). These limitations are expected to induce moderate to minor bias in the spatio-temporal estimates of relative prey availability.

Cross validation revealed that hurdle gamma and Tweedie models of spatiotemporal variation in the distribution of prey were similar in predictive power and performed better than the other statistical models considered. This is consistent with previous studies comparing different model types, which identified the usefulness of the Tweedie distribution for dealing with zero-inflated catch data (Lecomte et al., 2013; Shono, 2008; Thorson et al., 2021).

The fisheries surveys (i.e. IBTS and BTS) used here sample at a coarse spatio-temporal resolution, allowing the prediction of large-scale variation in prey availability over the entire North Sea. However, local variations, especially close to the coast or in inaccessible trawling areas, which might be important for predators, might have gone undetected. The suitability of these surveys for species that occur in coastal or rocky habitats might thus be less, which might be problematic. The low number of scorpion fish in survey catches and large number of hauls without any catches of this species (Table 4.1) might result in underestimated relative abundance of this species. This would affect the results of the MSFR model if the underestimation was not constant over time and/or space but this seems unlikely. For pelagic shoaling fish species (e.g. herring, sprat, mackerel) acoustic survey (AS) data have been generally thought to be better suited to estimating their abundance, and could be incorporated to make more robust predictions. However, the availability of AS data is limited in space and time and a recent study combining data from disparate fish surveys showed that the IBTS provides the most precise estimates even for pelagic species (Nnanatu et al., 2020).

One of the challenges in this study was to assess the availability of sandeels, which was estimated by combining a distribution model on sandeel occurrence (Langton et al., 2021) with annual SSB estimates from ICES. For Orkney and Shetland, information is inadequate for ICES to evaluate the stock and sandeel availability in those regions was estimated within the MSFR model-fitting process. Although the assumption of this approach that the large-scale stock assessment estimates relate to what is available to predators seems reasonable, the inability to include intra-annual (e.g. seasonal burying behaviour, growth, and spawning) and small-scale variability might have led to a misrepresentation of sandeel availability estimates. There is an indication that the availability of sandeels has been overestimated for harbour seals (see section 4.5.1.1). Additional data for sandeel stock assessment would therefore be very informative for this MSFR modelling exercise and, given the importance of sandeels in the North Sea ecosystem and the lack of knowledge regarding local spatio-temporal variability in their abundance, which can vary considerably even on small spatial scales (Wright et al., 2000), increasing the coverage of effective sampling would in general strongly enhance our understanding of their role within the food web.

Accessibility

Accessibility (decaying function of distance from the haul-out) was modelled using hierarchal generalized additive models (HGAM). However, different methods, such as a GLMM or the framework proposed by Matthiopoulos, 2003 could also have been deployed. Especially, the framework from Matthiopoulos, 2003 who constructed an accessibility surface by the simple relationship:

$$\alpha = \left(\frac{d}{5}\right)^{-1.98} \quad \text{(eqn 4.4)}$$

where α is accessibility and *d* represents the distance from the haul out in km, would have led to different parameter estimates with the relationship form of a decreasing power function. The greatest consequence of such an approach would be that prey availability close to the haul out would be disproportionally weighted (higher contribution) compared to the approach applied here (Figure 4.177). In the context of this work where estimates of where seals could have foraged are required (e.g. a use-availability design was applied with only distance to haul out as explanatory variable), solely using the accessibility model from Matthiopoulos, 2003 would have led to un underestimation of space use further from the haul out. Furthermore, this might also have translated in usage which is evident from comparing the maps from Matthiopoulos, 2003 and Carter et al. (2020) .

Seal telemetry data from 2008-2018 were used to link prey availability to prey consumption by creating an accessibility surface from land (weighted by scat sampling unit sample size). Predictions relied on the assumption that accessibility did not change throughout the time-period considered which seems sensible even though foraging behaviour might have altered. However, seasonal differences in accessibility as a result of life history processes (e.g. breeding and moulting) might be considerable and should be given priority when additional future telemetry data would result in a sample size that allows the exploration of such variation.

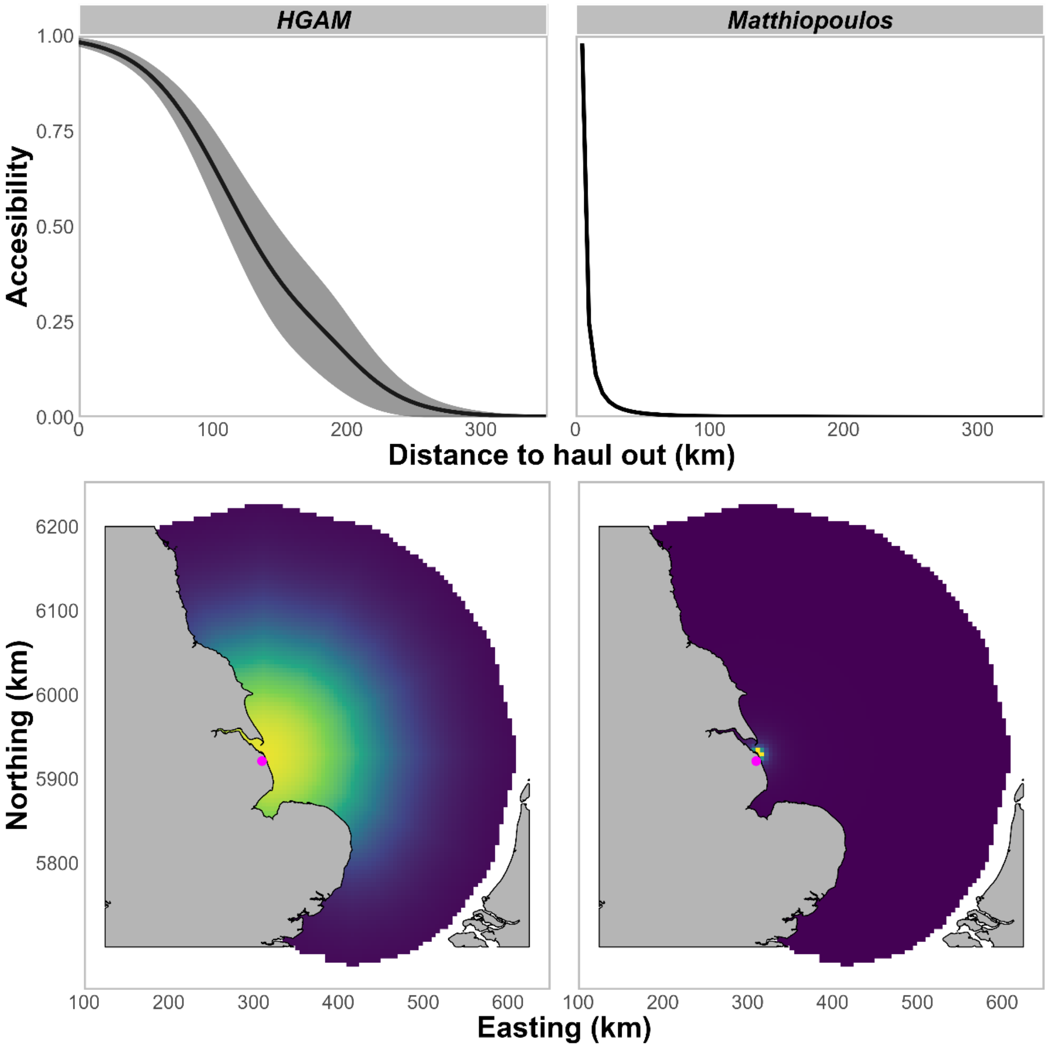


Figure 4.17 Comparison prediction accessibility from HGAM and framework of Matthiopoulos (2003) for grey seals in the southern North Sea. Top row indicates probability of seal accessibility and bottom row predicted accessibility for one scat sampling location Donna Nook.

4.5.2 Ecological inference

Functional response type has considerable implications for the stability of food-chain dynamics due to the difference in induced predation mortality (Figure 4.8**8**). Sigmoidal type III functional responses can result in persistence in predator-prey dynamics because switching to alternative prey relieves predation pressure at low prey density (Van Baalen et al., 2001; Yodzis & Innes, 1992). For the favoured models with a sigmoidal type III functional response the predation mortality for a given prey species thus decreases when that species becomes less available. The shape parameter *m* was larger for harbour seals indicating a more sigmoidal relationship and a greater tendency to switch prey compared to grey seals. Several ecological mechanisms might give rise to a type III such as prey refuge (McNair, 1986), learning time (Tinbergen, 1960), varying foraging effort with prey density (i.e. due to the higher foraging cost at low prey density) (Abrams, 1982), and switching (Van Baalen et al., 2001). Switching between prey species might be a way for predators to optimally satisfy their energetic requirements and such predators might have preferred primary food sources which are supplemented by other prey only when those alternative prey are very abundant.

Seal consumption of any given species decreased with higher availability of other prey in the system (Figure 4.15, Figure 4.16). For both grey and harbour seals, sandeel consumption remained high even when other prey was abundant. For harbour seal, consumption of ling, saithe, herring, and to a lesser extent cod were also relatively high (Figure 4.16). Sandeel consumption was considerably higher than that of other prey at equal availability index values, particularly for grey seals. This implies that the availability of sandeels has a particularly strong effect on the consumption of other prey species and indicates that seals “prefer” sandeels which is more amplified for grey seals.

4.5.2.1 Sandeels

Previous studies have demonstrated the importance of sandeels to seals diet (Hammond & Wilson, 2016; Wilson & Hammond, 2016, 2019) and habitat preference (Aarts et al., 2008; Jones et al., 2017; McConnell et al., 199a9). Although, the functional response does not specifically indicate the cost of attacking certain prey, sandeels might be preferred because they are a relatively easy and predictable food source to utilise due to their immobility, and aggregated and restricted distribution (Wright et al., 2000).

The highly energy-rich sandeels are major food web energy conveyers (Christensen et al., 2013) forming an important link between zooplankton and marine predators in addition to seals, such as fish (Daan et al., 1990; Engelhard et al., 2013; Temming et al., 2004), seabirds (Rindorf et al., 2000; Wanless et al., 2005), and harbour porpoise (Gilles et al., 2016; Leopold, 2015; Ransijn et al., 2021), within the North Sea food web. A lack of sandeels seem to have played a role in the breeding failure of various North Sea seabird populations (Macdonald et al., 2015) and their importance is likely larger further north where there is less alternative prey available (Furness & Tasker, 2000; Wanless et al., 2018). Seabird sensitivity to reduced sandeel abundance has been linked to bird size, foraging range, and ability to switch diet (Furness & Tasker, 2000). Furthermore, sandeels have become smaller and lower in energy content particularly in the north-western North Sea (Frederiksen et al., 2011; Rindorf et al., 2016) suggesting that their predators would have to increase their foraging effort to meet their energetic requirements.

4.5.2.2 Foraging restrictions and the harbour seal decline

Central-place foragers such as seals and breeding seabirds are restricted in their spatial usage because they must return to land to moult and provision their offspring. According to optimal foraging theory, central-place foragers are expected to disproportionally utilize resources closer to the coast while further patches are only used when they are more beneficial (e.g. more prey, easy to catch prey, energy rich prey). However, prey patches closer to shore will be reduced more rapidly (Ashmole, 1963) due to increased inter and intra specific competition. As colonies grow, so will the prey-depletion zone (i.e. Ashmole's halo) which can be compensated by increased traveling or foraging time (Ashmole, 1963; Kuhn et al., 2014; Wakefield et al., 2011). However, cognitive processes and movement modes depending on landscape characteristics (e.g. spatial distribution, size, and replenishment/predictability of food patches) are also important drivers of where and how predators should forage to optimize their energy intake (Chudzinska et al., 2021; Nabe-Nielsen et al., 2013).

The smaller harbour seal, which is less wide ranging than the grey seal (Aarts et al., 2019; Jones et al., 2015; Sharples et al., 2012; Thompson et al., 1996) and may not be as able to exploit offshore prey due to transportation costs, might be particularly sensitive when prey abundance close to the colony is low. Food shortages due to interspecific competition with grey seals has been attributed as a potential cause of a decline in harbour seals in Canada (Bowen et al., 2003) while intraspecific competition for prey was assumed to have led to reduced body growth in Danish and Swedish harbour seals (Harding et al., 2018). The harbour seal decline in eastern Scotland and the Northern Isles might be linked to reduced sandeel availability and/or increased competition with grey seals (Wilson & Hammond, 2019). Regional harbour seal population trajectories (Thompson et al., 2019) seem to coincide with seabird breeding success patterns (i.e. declining from north-western to south-western North Sea (Olin et al., 2020)) attributed to distinct sandeel spatial dynamics.

Previous studies indicated that harbour seals in regions around Britain in which they are declining did not seem to compensate for reduced food availability by increasing foraging effort (e.g. trip duration or distance) or resting; however, comparing foraging effort as a measure of prey availability among regions might be unreliable as local habitat conditions (e.g. physical environment, distance to profitable feeding grounds) impose different constrains on foraging movement (Russell et al., 2015; Sharples et al., 2012). Increasing search effort (i.e. time spent foraging) or becoming more versatile through diversifying diet are other mechanisms that counteract reduced food availability due to preferential selection of high-quality prey items near the colony. The results seem to suggest that harbour seals have a greater tendency to switch prey (confirmed by the larger estimated value of the shape parameter m) and potential foraging plasticity around the Northern Isles where very different prey species (i.e. ling, saithe, herring, and cod) were consumed and had high attack rates compared to grey seals. Additionally, Damseaux et al. (2021) found a larger diet bivariate standard ellipse area for harbour seals around Orkney compared to grey seals which could be related to foraging plasticity due to increased competition or decreased prey quality.

Trophic niches for harbour and grey seals in the North Sea seem to be segregated by more diverse diets (e.g. measured by prey evenness in Wilson & Hammond (2019)) for harbour seals obtained from inshore waters while grey seals had greater amounts of sandeels in the diet that seem to be taken from offshore waters (Damseaux et al., 2021; Wilson & Hammond, 2019). Damseaux et al. (2021) found a geographical foraging distinction along the Scottish and German coasts where isotopic composition was pelagic for grey seals and more benthic for harbour seals. However, at the southern limit of harbour and grey seals European range (Eastern English Channel) harbour seals isotopic niche was nested within that of grey seals which could be because of the difference of the population stage (i.e. recent arrival of seals at their range limit hence less measurable competition at present) (Planque et al., 2021) .

In conclusion, the final MSFR models effectively predicted the overall diet composition and associated variation for both grey and harbour seals. Results from the MSFR modelling confirm a higher tendency for harbour seals to switch prey and the importance of sandeels for both seal species, though they are more strongly preferred by grey seals. Prey species that also had high attack rates by harbour seals (i.e. ling, saithe, herring, and cod) only substantially contributed to the diet around the Northern Isles (i.e. where sandeel availability had to be estimated), which could imply that these species are compensating reduced sandeel availability in those areas. The high attack rate for sandeels could imply that reduced sandeel availability in inshore waters forces harbour seals to consume other species and thus they have a higher foraging plasticity. Depending on what other prey are available and their associated profitability (i.e. obtained energy divided by costs of acquiring that prey (search, capture, and handling time)) this could lead to circumstances that are unfavourable for harbour seal populations.

4.6 Ethics statement

All UK capture, handling and other licenced procedures were carried out under UK Home Office project licence PF84B63DE (and previous iterations: 60/3303, 60/4009 and 70/7806) under the Animals (Scientific Procedures) Act 1986. The capture of seals was conducted under licence from Marine Scotland (Scotland) and the Marine Management Organisation (England). Telemetry data collection was approved by the University of St Andrews Animal Welfare and Ethics Committee. Appropriate site-specific approvals were obtained, with any associated mitigation measures observed for designated sites. For detailed information on capture and handling see (Sharples et al., 2012).

Appendix 4.1

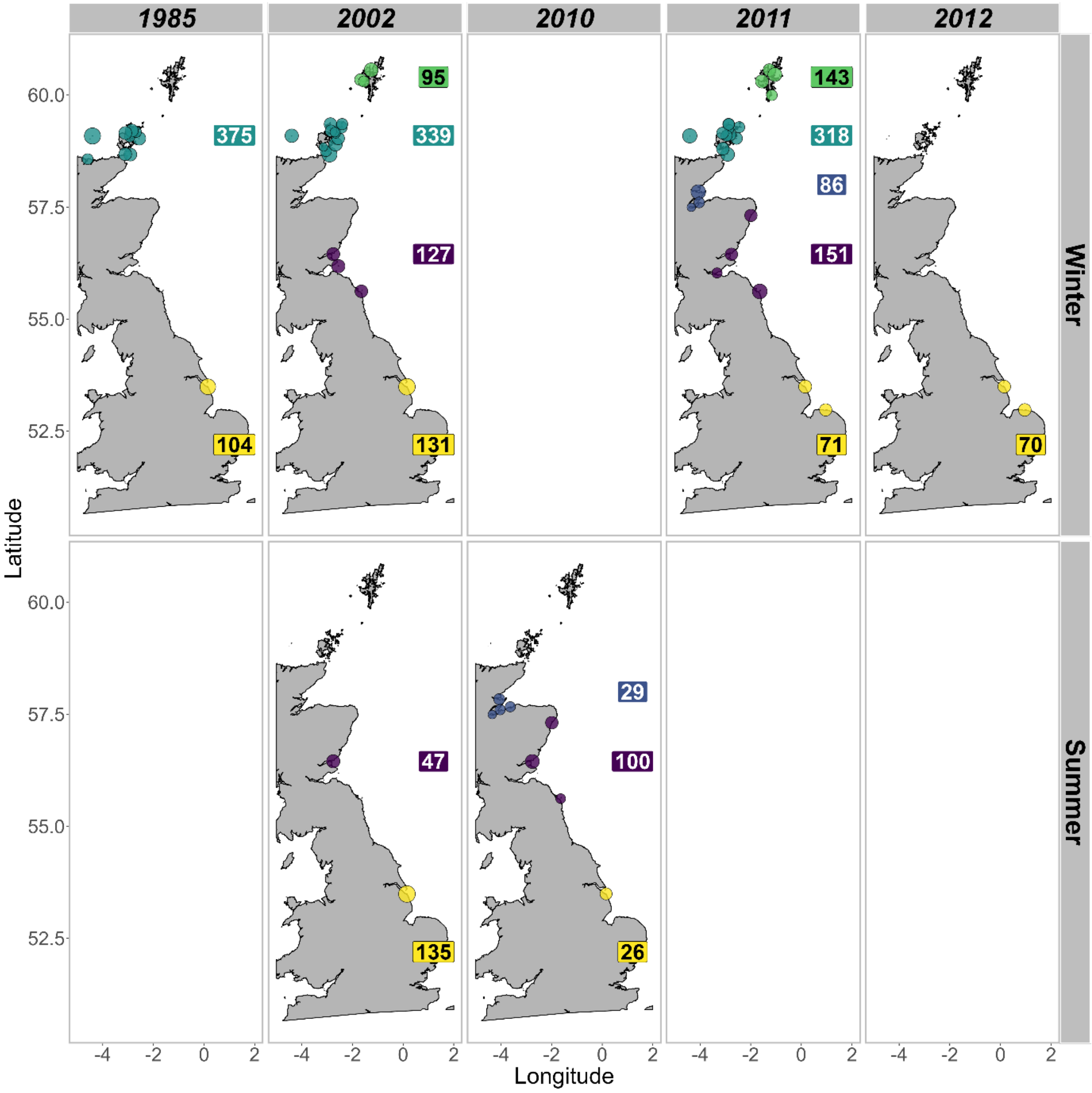


Figure A 4.1 Locations and sample size of grey seal scat collection units by region and year.

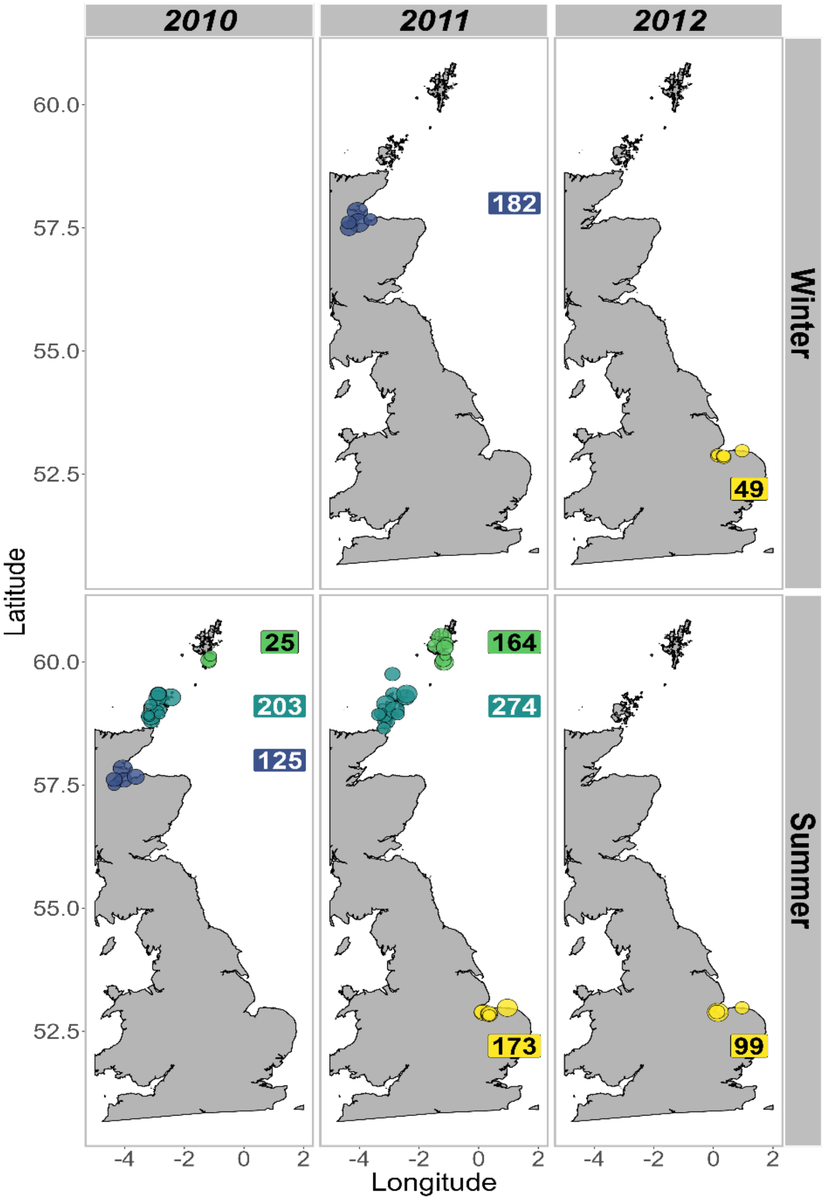


Figure A 4.2 Locations and sample size of harbour seal scat collection units by region and year.

Appendix 4.2

Table A 4.1 AIC score (A) for model structure selection, percentage deviance explained values (D), and Tweedie power-parameter (p) for the selected generalised additive models (GAMs) for BTS species per model type and prey species. Final Tweedie models highlighted in grey best model structure per model type in bold. Space time structure is described in section 2.3.5.

Species	**Model type**	**Space time structure**						**p**
		3D		3DD		4D		
		A	D	A	D	A	D	
Scorpion	Hurdle Binomial	8384.1	43.6	**8117.0**	**45.3**	8357.8	44.3	
Sole	Hurdle Binomial	7468.2	54.8	**7231.6**	**56.4**	7233.7	56.7	
Dragonet	Hurdle Binomial	19013.8	28.4	18866.3	29.0	**18691.2**	**29.9**	
Plaice	Hurdle Binomial	10961.3	51.1	10856.0	51.7	**10812.8**	**52.1**	
Scorpion	Hurdle Gamma	19648.0	28.0	19636.9	28.7	**19569.1**	**32.1**	
Sole	Hurdle Gamma	38740.7	43.9	38657.7	45.5	**38584.6**	**47.5**	
Dragonet	Hurdle Gamma	86820.3	22.6	86737.8	23.6	**86526.2**	**26.0**	
Plaice	Hurdle Gamma	239013.9	32.9	238397.7	35.6	**238105.1**	**37.0**	
Scorpion	Hurdle Log	6578.3	23.5	6540.2	25.2	**6521.2**	**27.5**	
Sole	Hurdle Log	8439.9	40.6	8370.7	42.3	**8302.6**	**44.5**	
Dragonet	Hurdle Log	22730.5	24.6	22586.3	26.3	**22476.1**	**28.0**	
Plaice	Hurdle Log	43979.4	37.2	43570.5	39.2	**43169.4**	**41.2**	
Scorpion	Tweedie	36599.5	62.4	**36433.4**	**64.6**	36544.6	64.2	1.35
Sole	Tweedie	57407.7	56.2	**57084.6**	**59.6**	57134.7	59.7	1.46
Dragonet	Tweedie	109526.5	30.5	109208.3	32.2	**109017.1**	**33.3**	1.42
Plaice	Tweedie	252100.6	51.1	**250693.8**	**54.4**	250748.1	54.5	1.47
Scorpion	Traditional	46264.7	34.4	**44743.5**	**39.6**	45793.9	36.4	
Sole	Traditional	71225.1	42.2	**69851.8**	**46.3**	70325.8	45.0	
Dragonet	Traditional	77054.9	33.5	76580.3	35.3	**76229.1**	**36.7**	
Plaice	Traditional	82081.6	60.6	81232.5	62.4	**81157.9**	**62.7**	

Table A 4.2 Percentage deviance explained values (D) and Tweedie power-parameter (p) for the final generalised additive models (GAMs) per prey species and quarter.

Species	Quarter	D	p
Cod	1	24.3	1.56
	3	45.6	1.50
Haddock	1	74.9	1.56
	3	76.9	1.55
Herring	1	25.9	1.81
	3	32.3	1.79
Ling	1	54.8	1.47
	3	62.8	1.45
Mackerel	1	57.1	1.59
	3	18.0	1.68
Saithe	1	75.1	1.59
	3	77.8	1.59
Whiting	1	46.5	1.78
	3	43.5	1.83

Appendix 4.3

Overall patterns in distribution and abundance

Cod distribution changed markedly from 1985 to more recent years, it once was widely distributed but now abundance is highest in northern deeper waters. Whiting is widely distributed throughout the North Sea except for the Dogger Bank. In the southern North Sea, dragonet, sea scorpion and sole are prevalent species while ling and saithe occur mainly around the northern isles. Plaice is distributed both around Orkney and the south-eastern part of the North Sea. High abundances of haddock are concentrated in the central and northern areas. A clear distributional change of high abundance between the seasons was found for herring with higher biomass in the summer in central-northern areas compared to lower biomass more widely spread in winter. Mackerel also had a clear distributional change by season, mainly occurring in low numbers around the edge of the continental shelf in winter while during summer their density increases and are distributed in the southern North Sea and northern North Sea around Scotland and the northern isles.

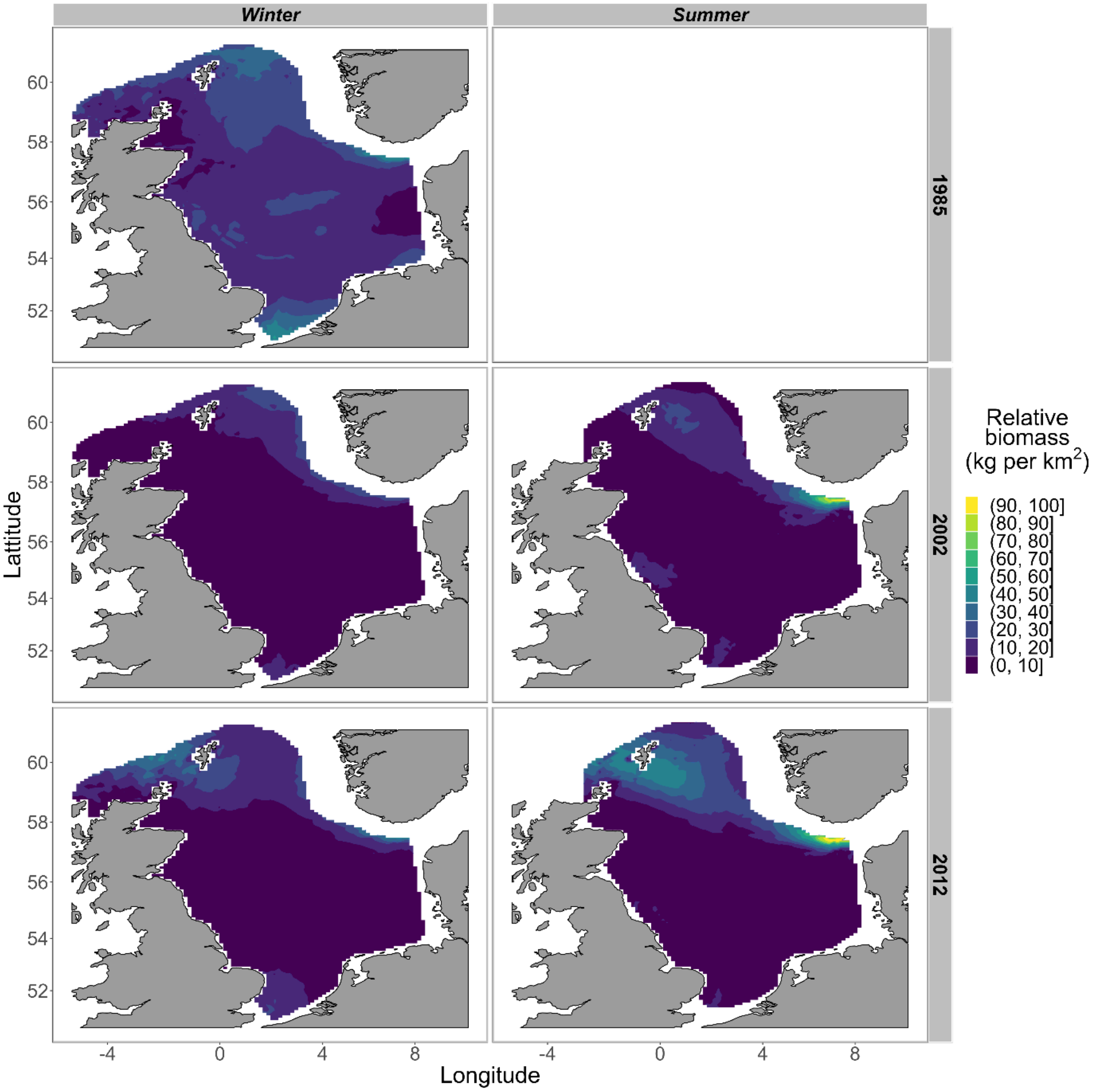


Figure A 4.3 Spatiotemporal winter (January-March) and summer (July-September) distribution of cod for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

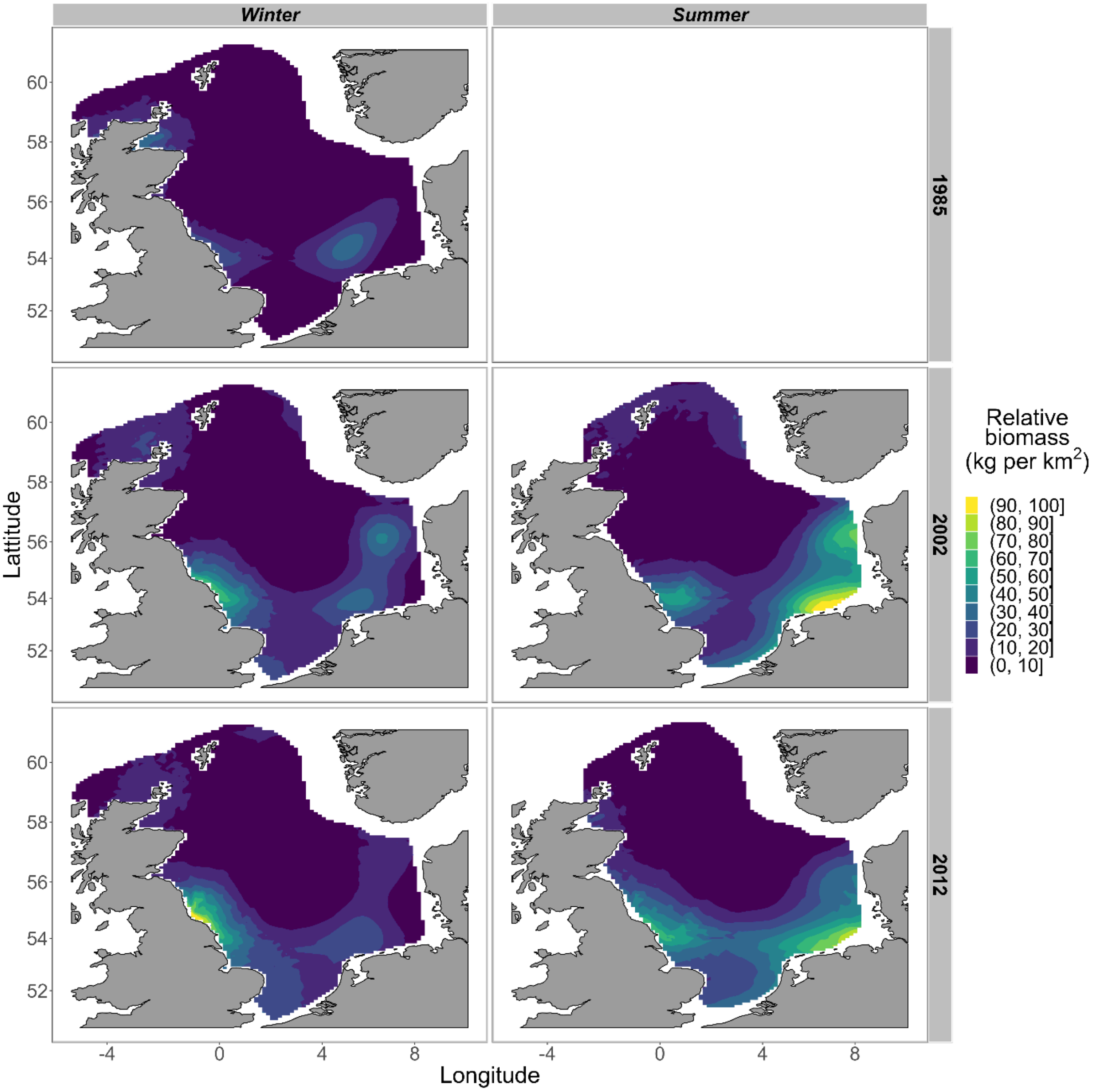


Figure A 4.4 Spatiotemporal winter (January-March) and summer (July-September) distribution of dragonet for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

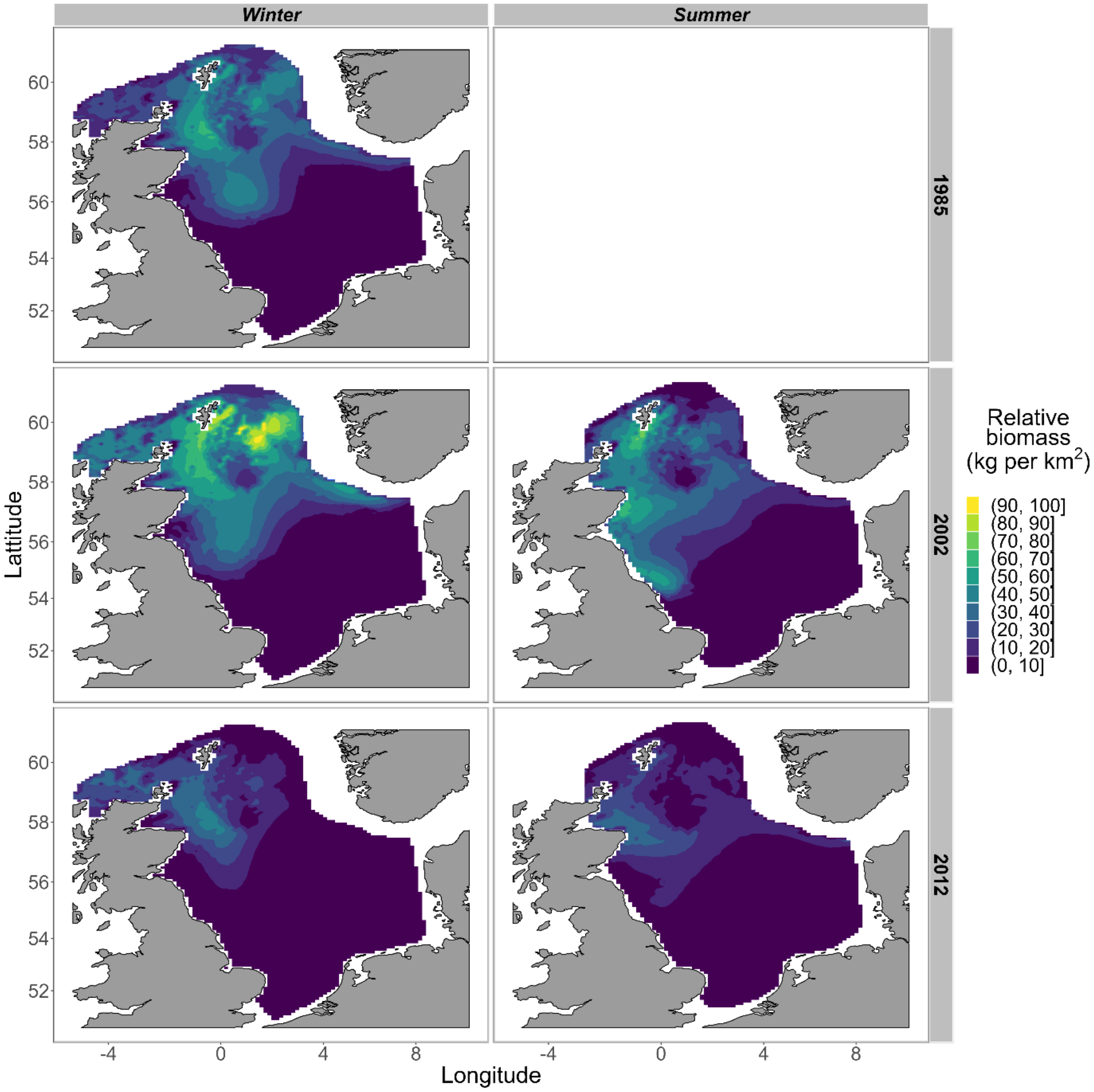


Figure A 4.5 Spatiotemporal winter (January-March) and summer (July-September) distribution of haddock for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

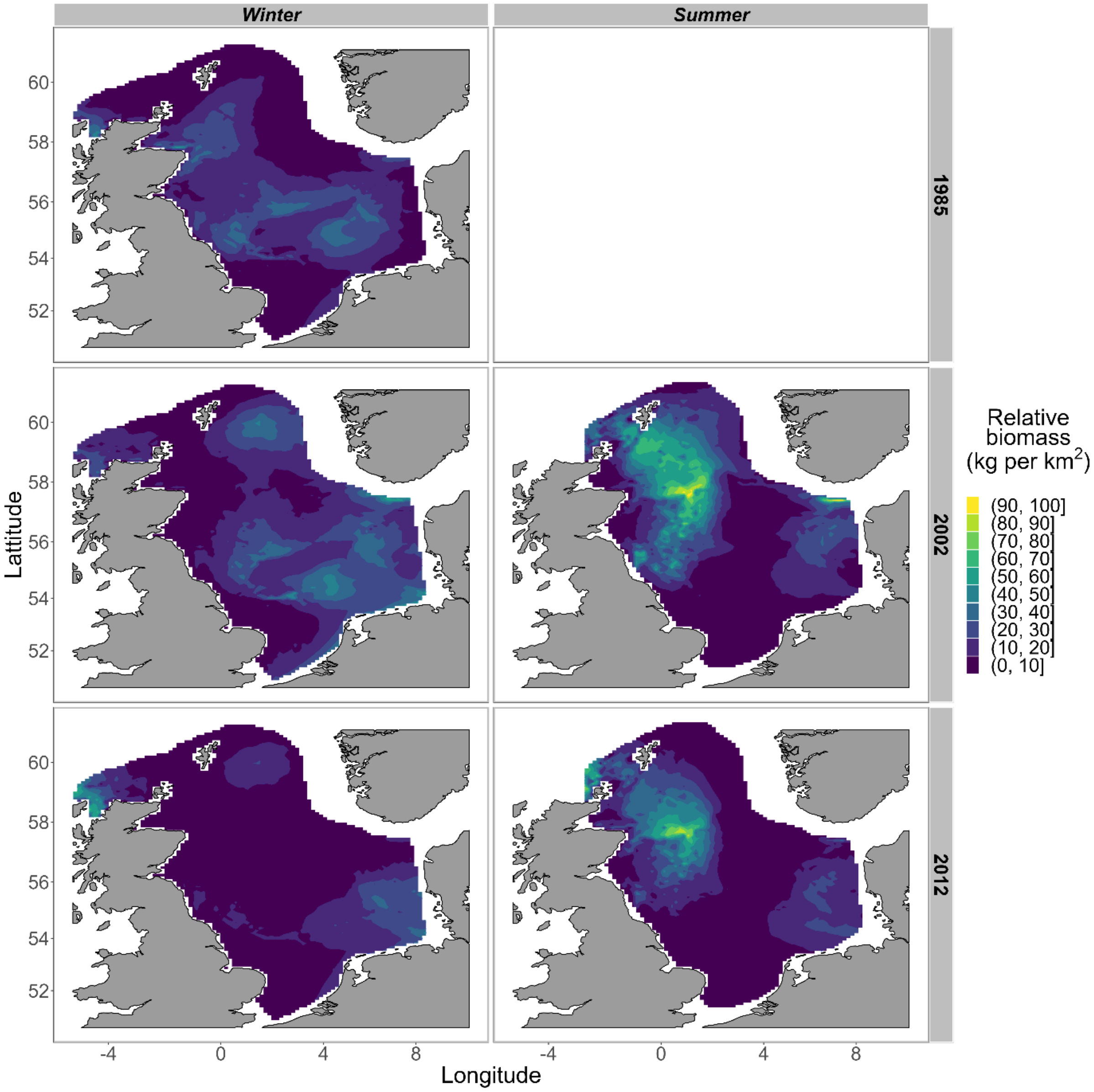


Figure A 4.6 Spatiotemporal winter (January-March) and summer (July-September) distribution of herring for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

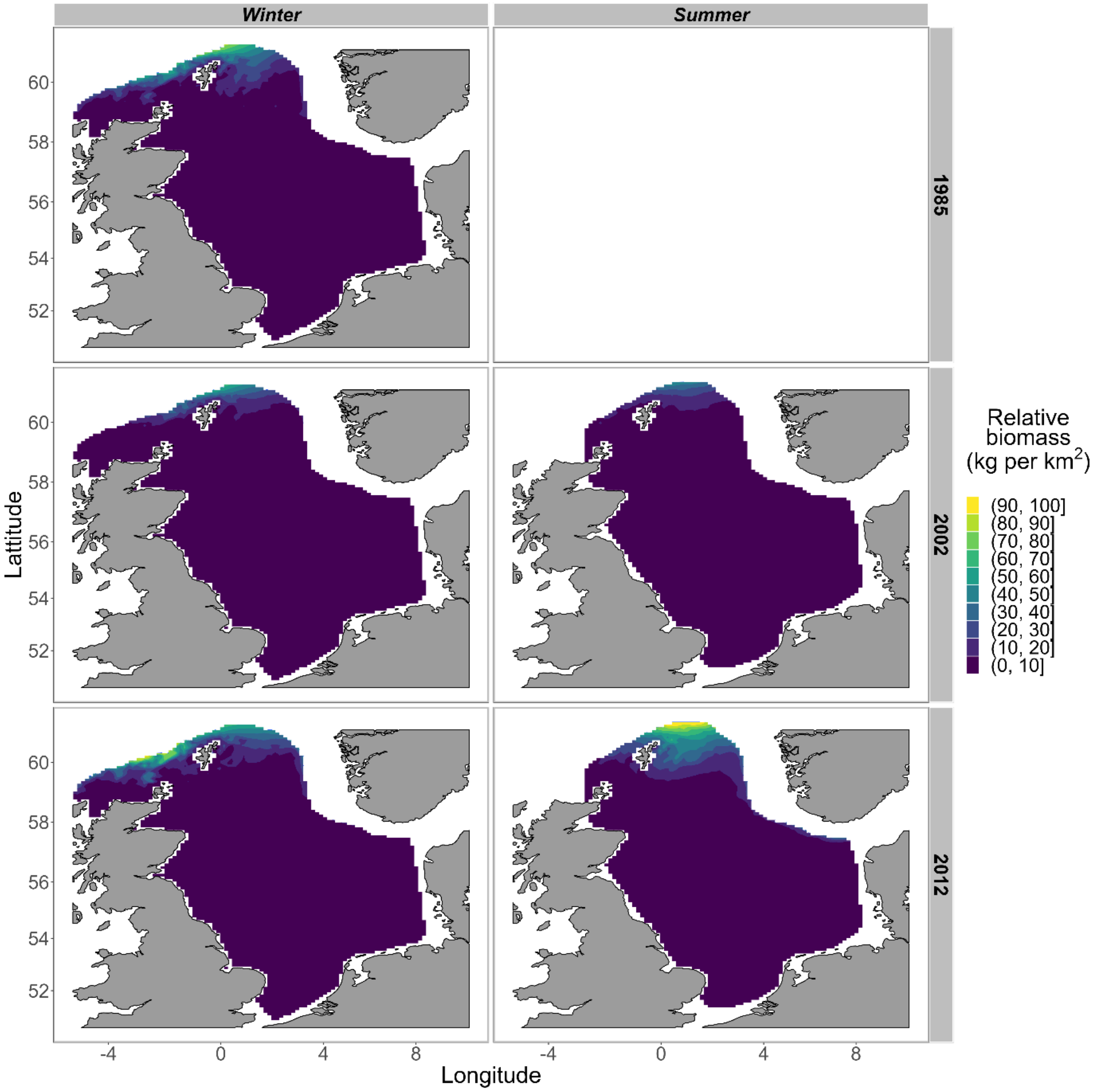


Figure A 4.7 Spatiotemporal winter (January-March) and summer (July-September) distribution of ling for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

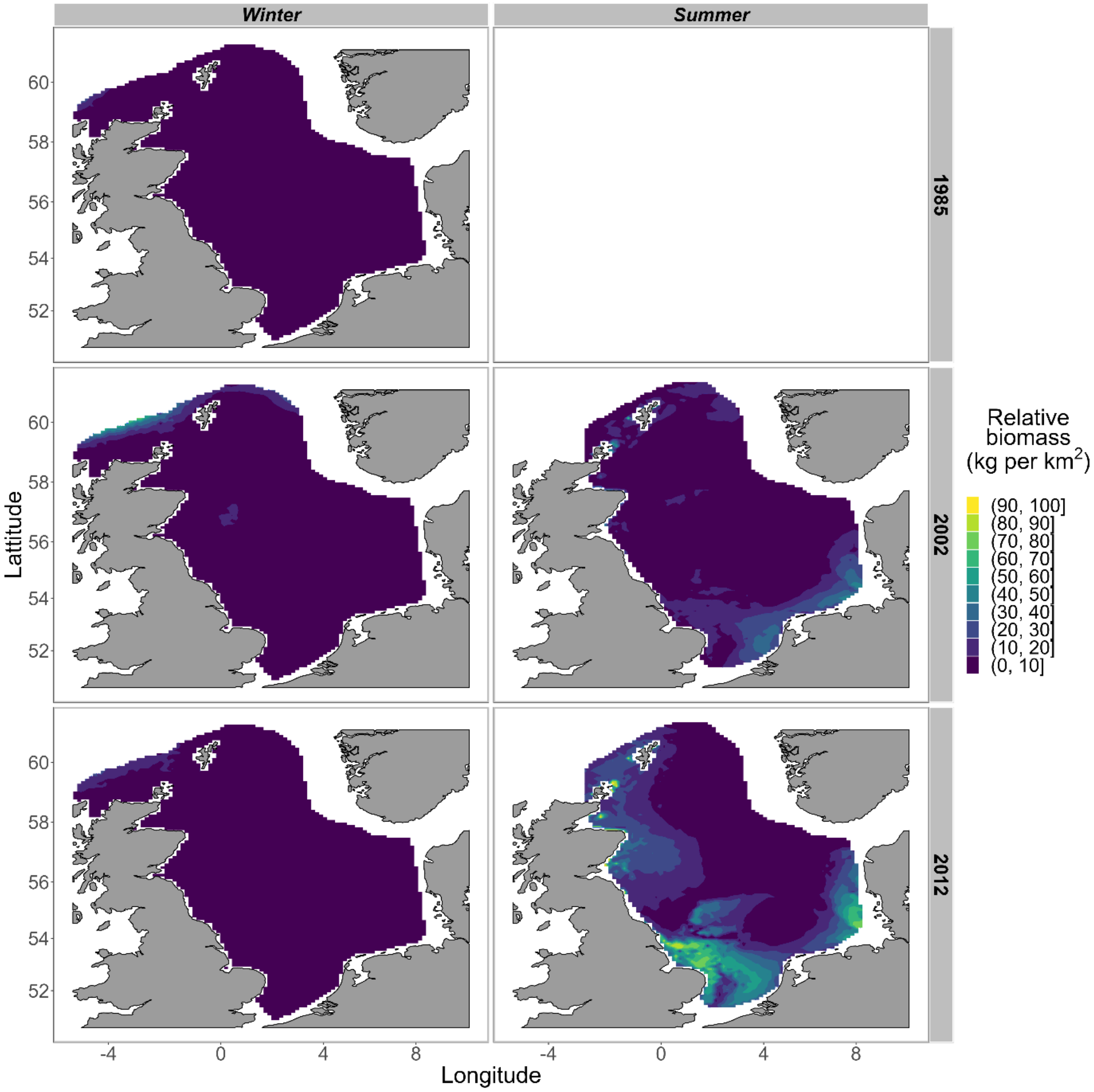


Figure A 4.8 Spatiotemporal winter (January-March) and summer (July-September) distribution of mackerel for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

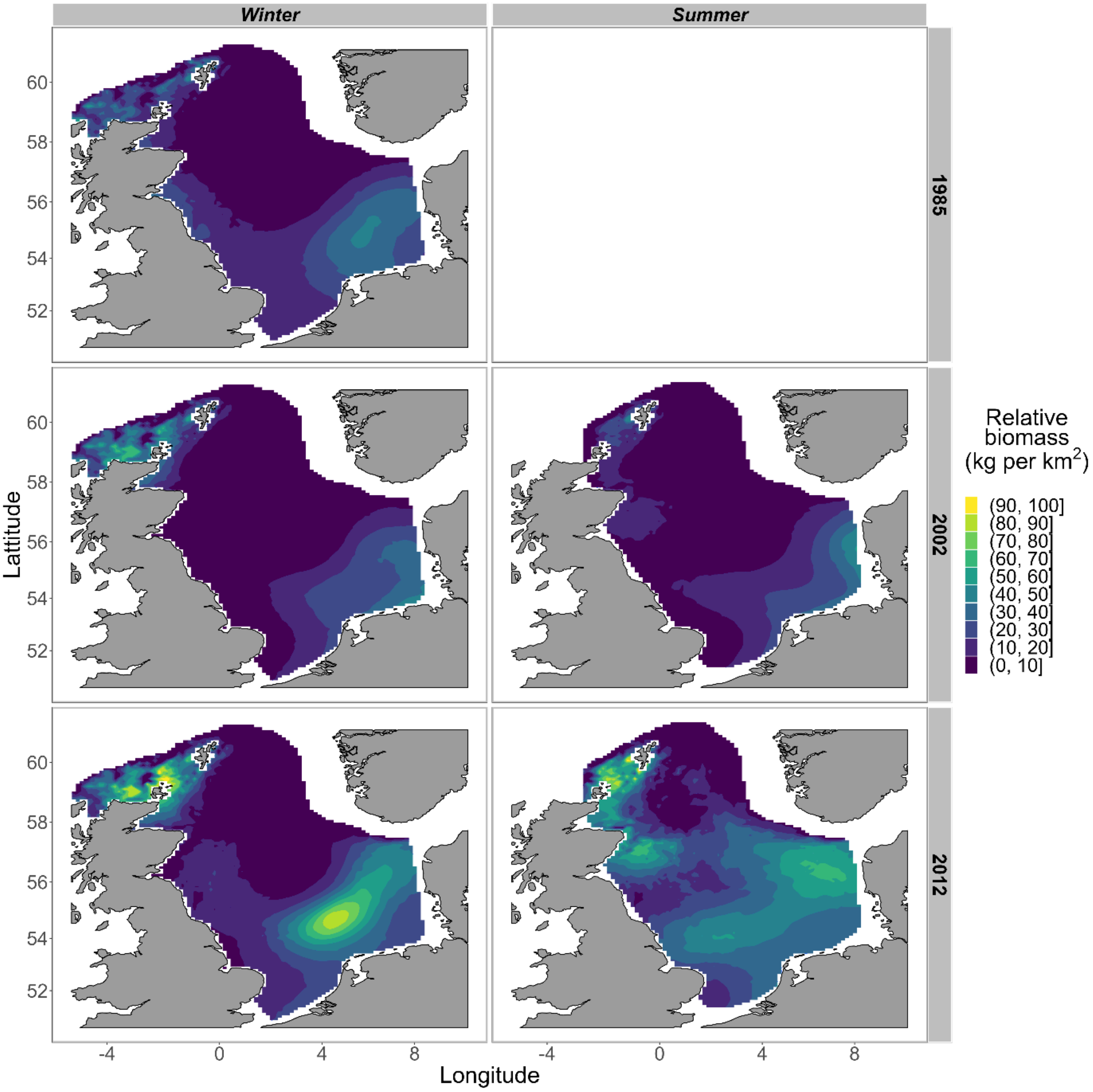


Figure A 4.9 Spatiotemporal winter (January-March) and summer (July-September) distribution of plaice for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

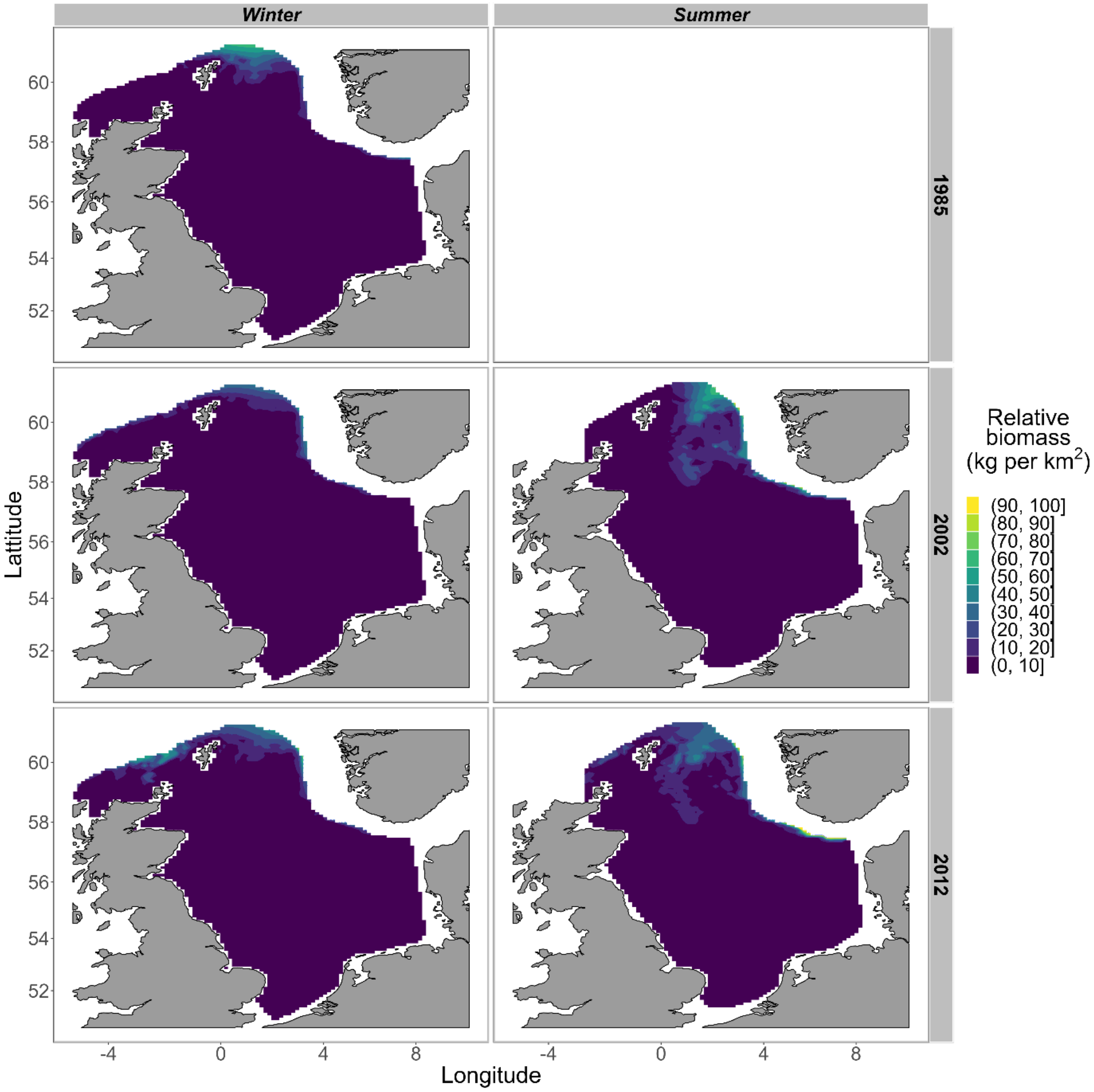


Figure A 4.10 Spatiotemporal winter (January-March) and summer (July-September) distribution of saithe for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

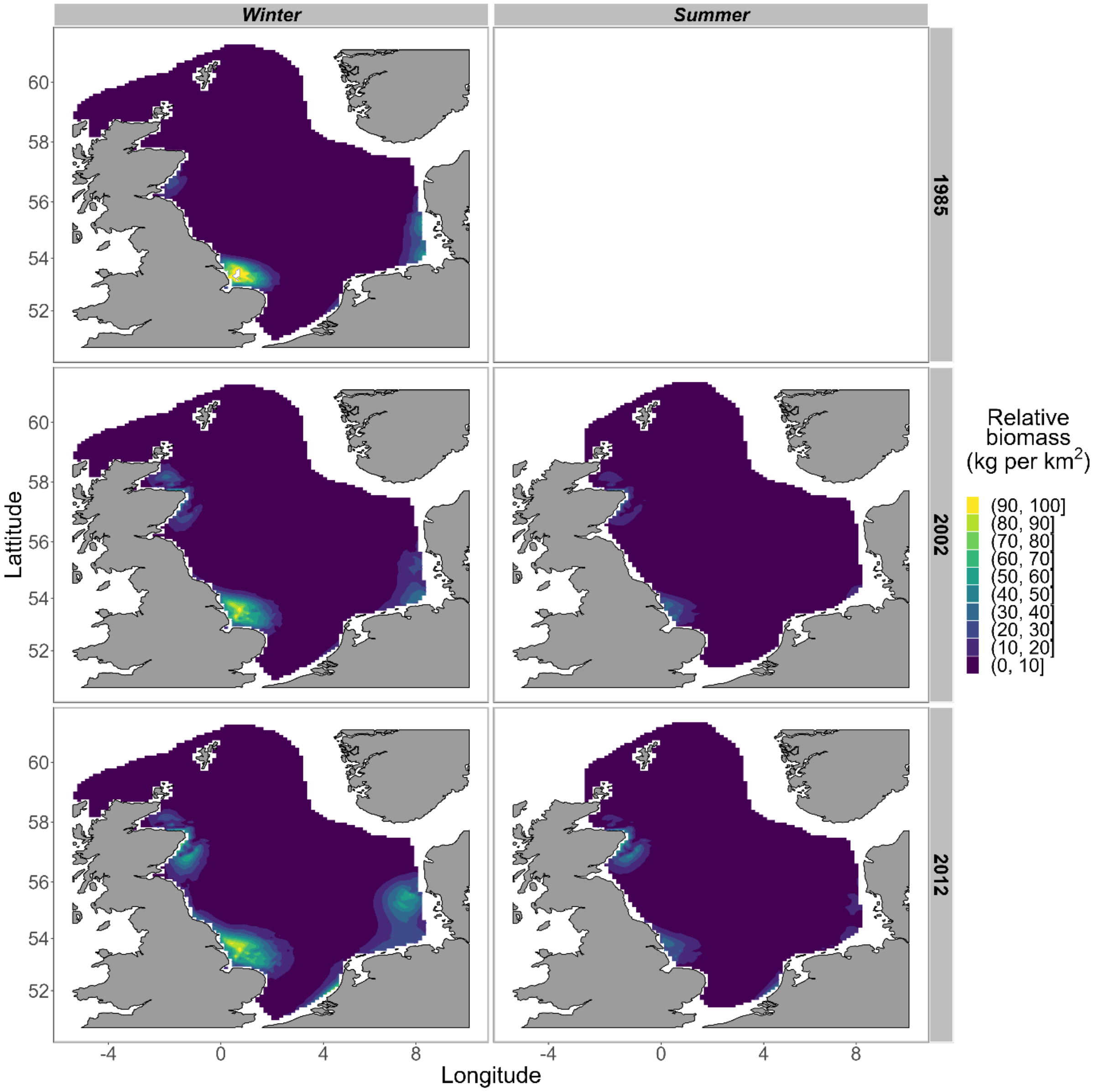


Figure A 4.11 Spatiotemporal winter (January-March) and summer (July-September) distribution of scorpion fish for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

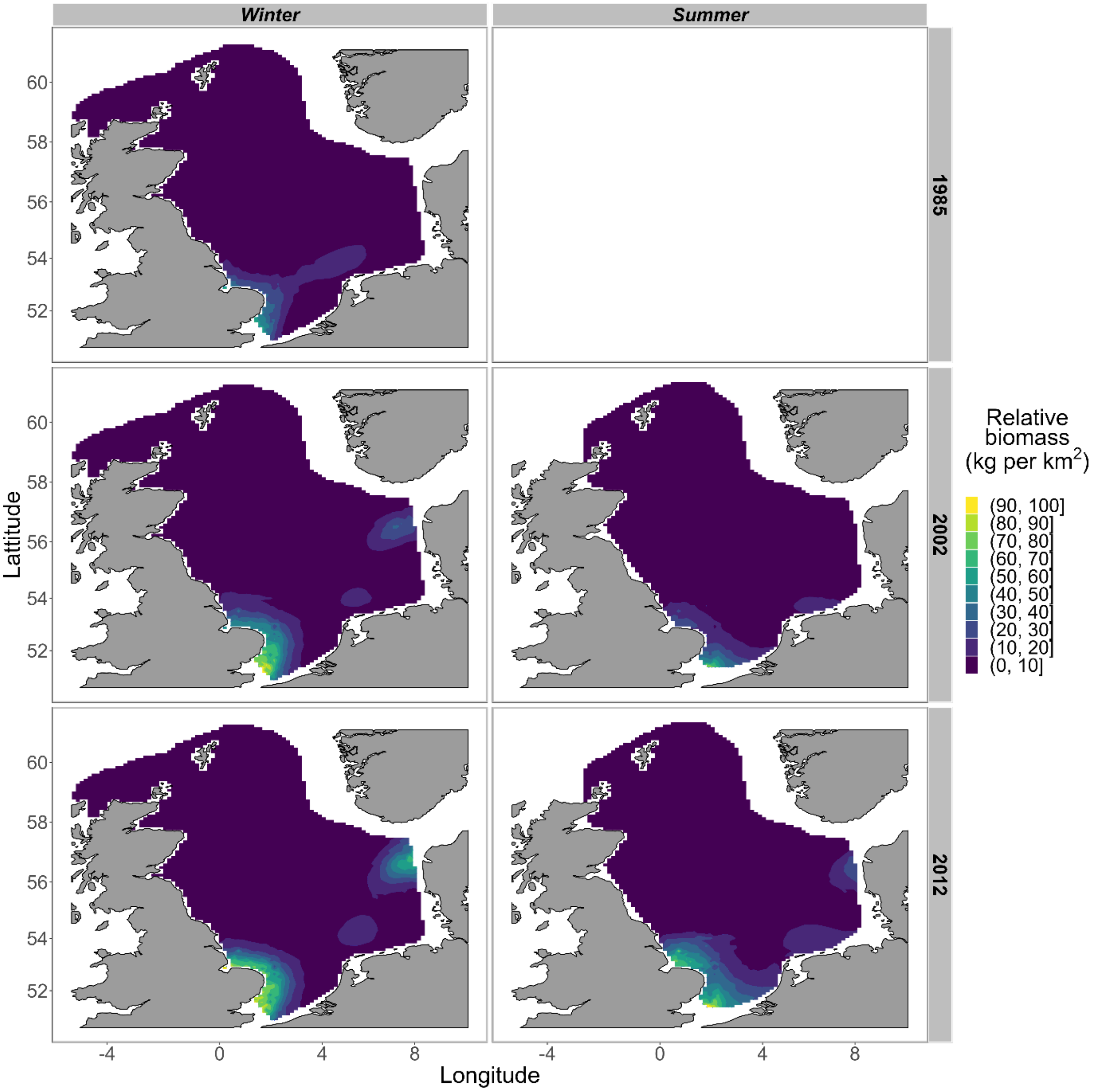


Figure A 4.12 Spatiotemporal winter (January-March) and summer (July-September) distribution of Dover sole for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

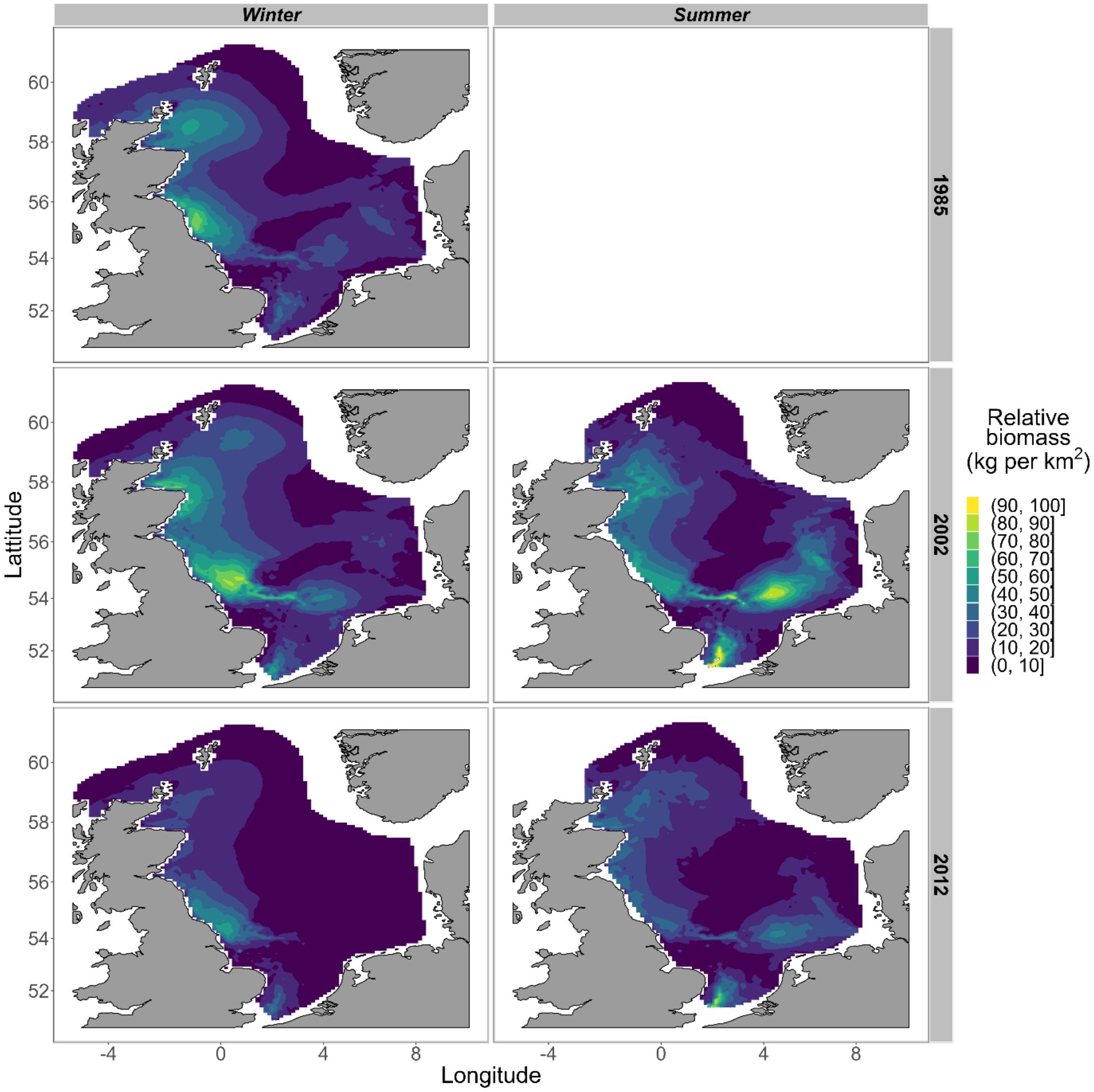


Figure A 4.13 Spatiotemporal winter (January-March) and summer (July-September) distribution of whiting for the North Sea in 1985, 2002, and 2012. Plots indicate relative biomass (kg per km2) scaled by the maximum observed value.

Appendix 4.4

Table A 4.3 Prior posterior overlap (PPO) for attack and shape parameter(s) of multi-species functional response model 3 and 4 for grey and harbour seals. Weak parameter identifiability represented in bold.

Grey seals					**Harbour seals**				
Model	**attack**	**PPO**	**shape**	**PPO**	**Model**	**attack**	**PPO**	**shape**	**PPO**
Model 3	a[1]	11.9	m[0]	22.5	**Model 3**	a[1]	19.3	m[0]	20.0
	a[2]	8.7				a[2]	8.4		
	a[3]	23.2				a[3]	24.3		
	a[4]	6.8				a[4]	24.9		
	a[5]	9.6				a[5]	10.7		
	a[6]	19.5				a[6]	15.7		
	a[7]	6.6				a[7]	26.2		
						a[8]	15.8		
						a[9]	3.2		
						a[10]	23.2		
						a[11]	6.5		
Model 4	a[1]	**58.1**	m[1]	21.8	**Model 4**	a[1]	**44.2**	m[1]	28.8
	a[2]	18.3	m[2]	**78.3**		a[2]	**57.3**	m[2]	**62.3**
	a[3]	**76.6**	m[3]	**44.6**		a[3]	25.7	m[3]	26.4
	a[4]	8.6	m[4]	**48.0**		a[4]	13.3	m[4]	10.9
	a[5]	8.6	m[5]	26.5		a[5]	**42.0**	m[5]	26.4
	a[6]	**64.0**	m[6]	**40.3**		a[6]	13.1	m[6]	**76.0**
	a[7]	33.7	m[7]	**35.9**		a[7]	**60.5**	m[7]	**43.2**
						a[8]	**58.8**	m[8]	28.6
						a[9]	**68.9**	m[9]	**41.8**
						a[10]	27.2	m[10]	**44.0**
						a[11]	**42.9**	m[11]	34.3

Appendix 4.5

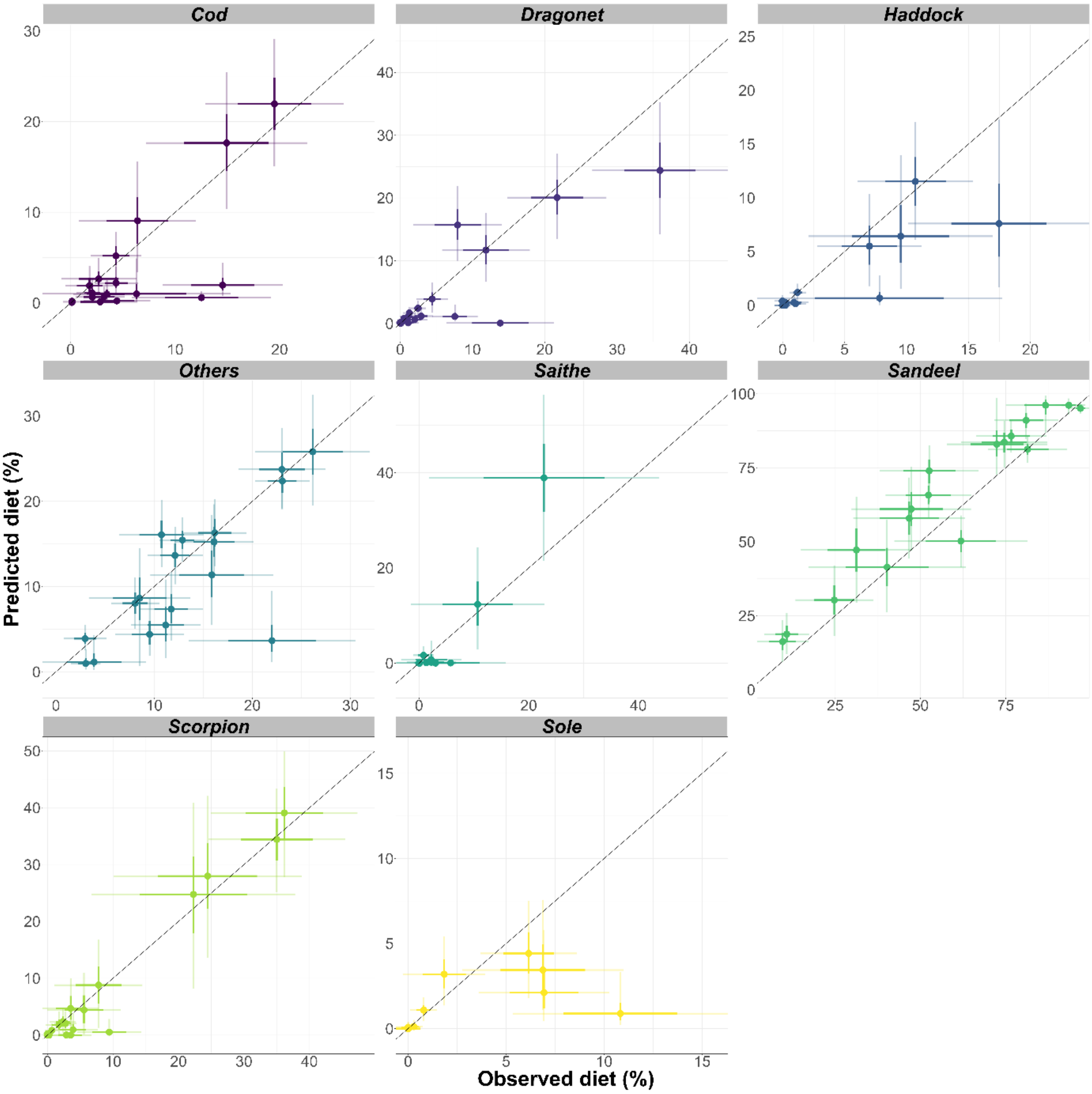


Figure A 4.14 Observed vs predicted diet grey seal. Note lesser fit for sole.

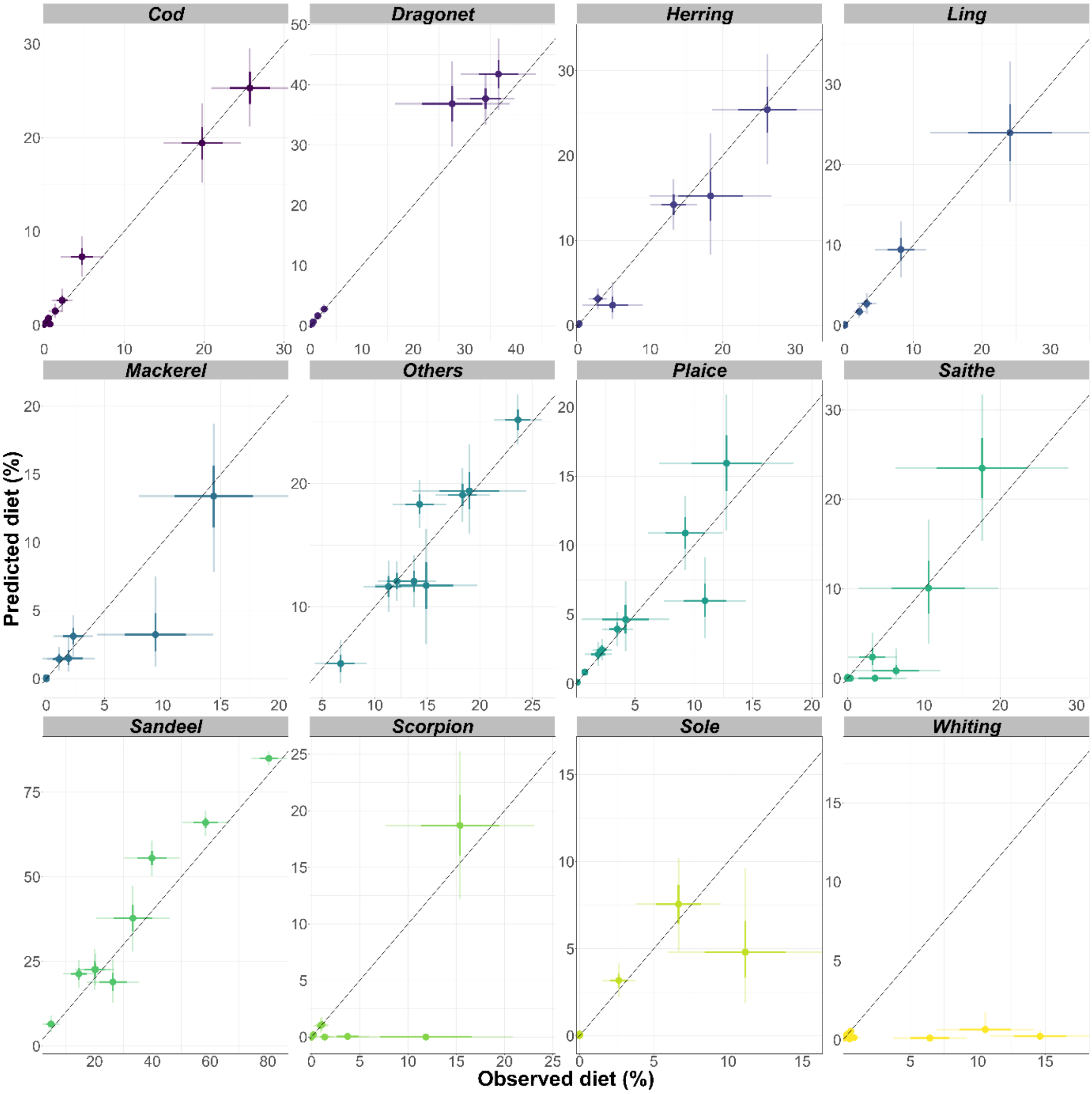
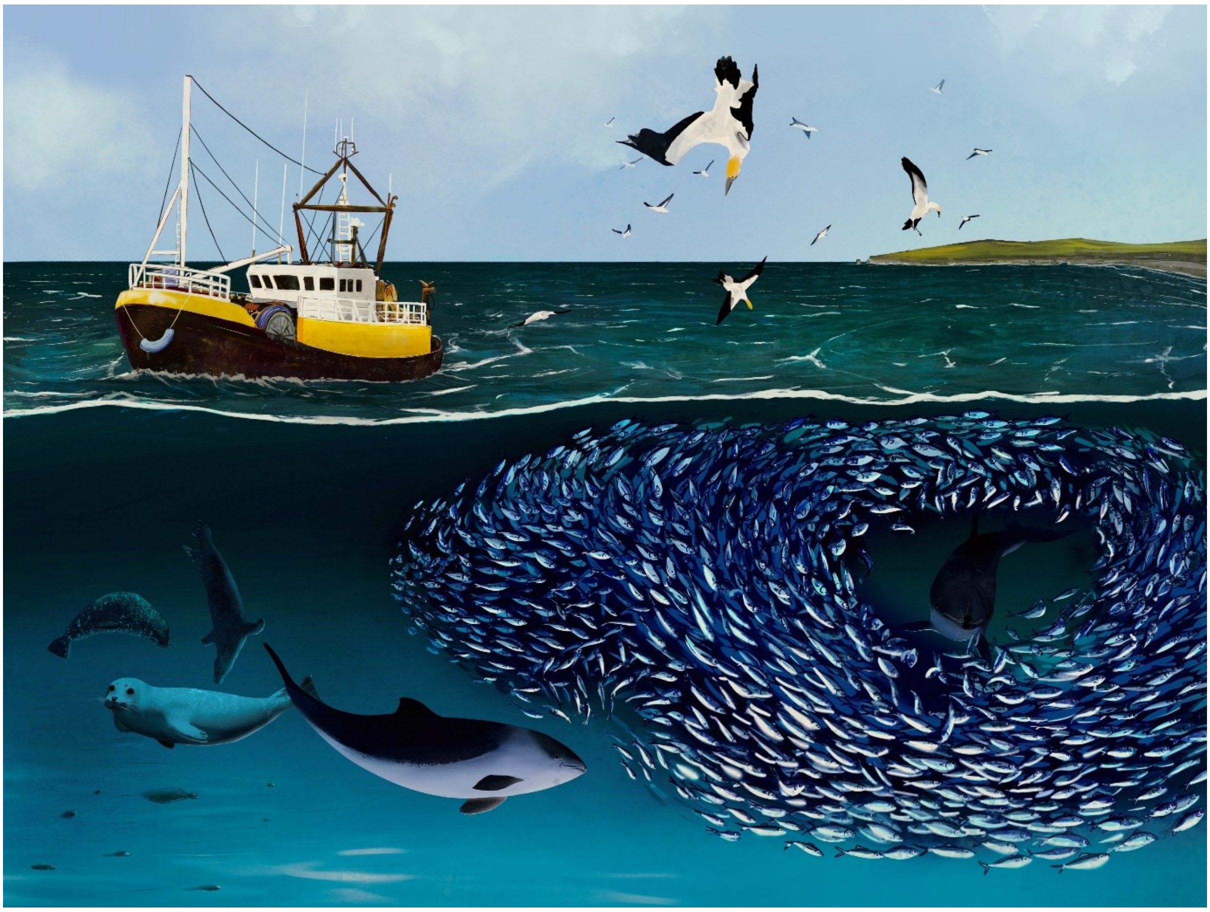


Figure A 4.15 Observed vs predicted diet harbour seal. Note the poor fit for whiting.

CHAPTER 5

General discussion



A major focus of contemporary ecology is understanding ecosystem interactions which is also fundamental for decision-making regarding conservation and management of natural resources. Food web complexity and stability depend on the various population dynamics within and among species. A crucial component in food web models, that links the various functional groups, is the functional response and their description has provided crucial insights into the dynamics of communities (Gentleman & Neuheimer, 2008; Lindstrøm et al., 2009; Murdoch & Oaten, 1975). Predator diet composition varies depending on the context (e.g. prey community and availability) and for predators that consume multiple prey types a multi-species functional response (MSFR) can be modelled to describe how the consumption of particular prey varies according to overall prey availability.

In depth modelling of foraging ecology of three marine mammal predator species was explored by revealing the form of the MSFR. The MSFR for harbour porpoise was parameterised in the southern North Sea (Chapter 3). This modelling framework was further developed and applied to both grey and harbour seals along the British part of the North Sea (Chapter 4). Parameter estimates indicate that all three marine mammal predator species exhibit a type III functional response and that sandeels are important but more strongly preferred by grey seals and harbour porpoise compared to harbour seals. Harbour seals have more diverse diets and exhibiting a more sigmoidal response that may indicate a greater tendency to switch prey.

The exploitation of natural resources generally goes hand in hand with a perceived conflict between humans and wildlife. Marine mammals are “charismatic” species valued and legally protected by society, they are relatively large requiring substantial amounts of food and are visible in contrast to other marine predators such as piscivorous fish, while some of their prey is commercially valuable and sustains livelihoods and food provisioning. The degree of competition with fisheries depends on predator prey preference and fisheries target species and how this varies with changes in that prey’s availability and other components of the system. Therefore, modelling the functional response is crucial.

Assessments of competition have mainly focused on amounts of prey taken by predators and fisheries (e.g. Hammond & Wilson, 2016; Trites et al., 1997). Although such assessments provide a rough indication of the level of competition, they can be misleading as they only provide a static snap shot of the system while a more structural, dynamic and spatio-temporal understanding is required (Matthiopoulos et al., 2008). Ecosystem models that incorporate the trophic interactions of various species over time and space might be better suited (Pauly et al., 2000). However, these complex models are typically impeded by a lack of necessary data/information. In this final chapter, I suggest a different approach in which I outline a proposed methodological framework to quantify and compare the amount of fish taken by predators and the fishing industry in the North Sea. Firstly, the information required to support each component of this framework is briefly described and the state of knowledge and available data are reviewed. Thereafter, a case study is applied for illustrative purposes using the currently best available information and the MSFR models and results are discussed in a wider context. Lastly, recommendations are made regarding opportunities to improve outstanding limitations and knowledge gaps and future research directions regarding the MSFR highlighted.

5.1 Estimating marine mammal consumption in the North Sea: background

The following information (reviewed in detail below) is needed to fit MSFRs for marine mammals in the North Sea and to then estimate consumption rates over the Southern North Sea area for the case study in section 5.2: 1. Marine mammal distribution and abundance; 2. Predator diet; 3. Predator consumption rate; 4. Predator energetic requirements; 5. Prey calorific content; 6. Prey availability; 7. Fisheries catch and stock assessment.

5.1.1 Marine mammal distribution and abundance

To obtain consumption estimates of marine mammal species, estimates of their distribution (as this is indicative of where the forage) and abundance are required. For harbour porpoises and other cetacean species, the most encompassing time series that covers the North Sea are the summer SCANS surveys (i.e. 1994, 2005, 2016 (Hammond et al., 2002, 2013, 2021)) that provide robust abundance and distribution estimates. However, they have only taken place once a decade and in summer and are thus unable to infer short-term, seasonal, and/or more spatially detailed changes. The Netherlands and Germany have dedicated smaller scale aerial survey programmes that cover their national waters (Gilles et al., 2009; Scheidat et al., 2012). Collating these and other data, seasonal scale distribution maps have been produced by Paxton et al. (2016) and Waggitt et al. (2020). However, this is not straightforward due to different data collection standards, leading to the creation of the Joint Cetacean Data Programme (JCDP)[6] which aims to provide a platform for collation, standardisation, and access of cetacean survey data. Alternatively, solely systematic surveys could be used as per Gilles et al. (2016) to minimize dissimilarities in data sources.

Estimates of at-sea distribution of seals in the North Sea have most recently been generated by Carter et al. (2020) based on large scale telemetry deployments around the UK. This work could be expanded by integrating telemetry data collected in European countries (e.g. France and the Netherlands (Brasseur, 2017)) to increase the spatial extent.

5.1.2 Predator diet

The multi-species functional response models in this thesis have been fitted using the most extensive datasets for the predator species involved. However, the spatial extent has been a limiting factor; grey and harbour seal MSFR models were fitted to scat data collected in the British part of the North Sea while harbour porpoise models were restricted to the vicinity to

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[6] https://jncc.gov.uk/our-work/joint-cetacean-data-programme

the Dutch coast. To gain insight into predator-prey interactions on a wide scale, data from other regions would be needed. This would allow updating the current models to a North Sea wide scale and/or fitting the MSFR models separately among regions. This will suggest whether there are considerably different foraging tactics and/or preferences of predators in space and time, or if an overall functional response is appropriate. Additionally, it would be possible to validate the predictive power of the current models by using the new data as a test dataset (e.g. similar to cross-validation). Sources of published and unpublished marine mammal diet information in the North Sea and adjacent waters were recently summarised (ICES, 2021c).

5.1.2.1 Seals

Diet data for both seal species are available in the UK but, although some historic data is published from European countries (e.g. Netherlands, Belgium, Germany, and France), most biological samples still need to be analysed. Seal diet data are available for locations on the west coast of Scotland (Hammond & Wilson, 2016; Wilson & Hammond, 2019) and new seal diet samples have been collected in the Wash (i.e. Southeast England) but still need to be processed (Russell et al., 2021).

5.1.2.2 Harbour porpoise

Harbour porpoise diet data are regularly updated in the Netherlands, currently two datasets are being finalised in the UK, while several European countries hold historical data but need to process more recent data.

One of the work packages from the EcoSTAR (Ecosystem level importance of STructures as Artificial Reefs; 2020- 2023)[7] project that is currently underway will extend the multi-species functional response work for harbour porpoise from Chapter 3. Diet data for porpoises will be derived from an analysis of a comprehensive long-term University of St Andrews dataset of stomach contents from stranded and bycaught animals collected around the UK. This will allow fitting the functional response to a wider area in the North Sea.

5.1.2.3 Other diet information

It may also be possible to use other sources of diet information in fitting multi-species functional responses. For instance, information from stable isotope ratios (Damseaux et al., 2021; De La Vega et al., 2016; Jansen et al., 2012; Planque et al., 2021) or quantitative fatty acid analysis (QFASA: Gilles, 2008; Jansen, 2013; Kavanagh et al., 2010) could be considered. These data may provide a broader view of the importance of prey species over time as they represent diet over a longer time scale then scat or stomach content analysis. But the lack of specificity in stable isotope ratio results and issues regarding interpretability in QFASA results mean that use of such data in MSFR modelling will be challenging.

5.1.3 Predator consumption rate

For a type II or III functional response, individual consumption rate is limited by a saturation level, which depends on digestive constraints and handling time (Real, 1977; Rosen & Trites, 2004; Williams et al., 2001). Harbour porpoises need relatively large amounts of food given their body mass as a result of their high metabolic rate and limited energy storage capacity (Bjørge, 2003; Kastelein et al., 1997) and thus need to feed at high rates (Wisniewska et al.,

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[7] http://www.smru.st-andrews.ac.uk/ecostar/

2016, 2018). Consequently, there is concern porpoises are particularly vulnerable to starvation. However, porpoises with extensible forestomaches have been observed to be capable of ingesting up to 98% of their daily food mass requirements in a single feeding bout illustrating they might be capable to compensate for short fasting periods (Kastelein et al., 2019).

Seals also need considerable amounts of energy, and their energetic requirements vary throughout the year. They need to build up their energy reserves before they fast during the moult and during the breeding season, especially female grey seals, which do not feed during lactation, while harbour seals still forage during the nursing period.

Due to the diet information available, the MSFR models presented in Chapter 3 and Chapter 4 were fitted to diet composition rather than foraging rates. Estimates of food intake are limited for marine mammals and either based on observations of captive animals (Kastelein et al., 2019) or from bioenergetic models (Gallagher et al., 2021; Sparling, 2003a). Without additional information the assumption was made that marine mammals on average meet their estimated energy requirements which is in line with previous prey consumption estimates for seals (Hammond & Wilson, 2016).

However, the question of whether animals can obtain enough energy is also dependent on the availability of high-quality prey. If energy-rich prey is replaced by lean prey an animal would need to consume considerably more to compensate for the difference in energy density and digestion costs (Rosen & Trites, 2000). However, the ability of marine mammals to compensate might be limited for instance if they are restricted to a certain amount of mass they physically can consume. The junk-food hypothesis, that states that animals face reduced fitness if this occurs, was supported for Steller sea lions (*Eumetopias jubatus*) that were fed *ad libitum* (Rosen & Trites, 2000) and the body condition of porpoises was found to be dependent on the amount of fatty fish in the diet (Leopold, 2015).

5.1.4 Predator energetic requirements

Obtaining energy is crucial for animal existence and it is balanced between intake and expenditure. A detailed consideration of the components and processes that affect energy intake is currently under review (Booth et al., in review). Reported energy intake rates cover a broad range of values for all predator species considered: energetic requirements are dependent on life history processes (*e.g.* individual mass, reproductive status) and environmental factors (*e.g.* season, water temperature) (Santos et al., 2014; Gallagher et al., 2021; Lockyer, 2003; Rosen & Renouf, 1998; Silva et al., 2020; Sparling, 2003). For instance, harbour porpoise ingest less energy in spring and summer and more in fall and winter (Gallagher et al., 2021), while published estimates of grey seal daily energy expenditure increased throughout the first year for pups and differed by season for adults with males having higher expenditure then females (Sparling, 2003a). However, this variation was not considered in the following case study in section 5.2 due to the lack of sufficient information on temporal variation and population demography (e.g. age structure and sex ratios). Additionally, as the functional responses that were fitted in this thesis represented "average" individuals it seems appropriate to scale these with "average" energy intake values.

For the case study in section 5.2 the availability of published energy intake estimates per predator species are summarised below.

5.1.4.1 Harbour porpoise

As described in Chapter 2, published estimates for harbour porpoise energy intake of tagged porpoises varied between 0.57 - 0.99 MJ per hour for juveniles, 0.92 - 2.45 MJ per hour for adults (Booth, 2020) or 0.39 - 1.29 MJ per hour (Rojano-Doñate et al., 2018), 8 - 35.5 MJ per day for captive porpoises (Kastelein et al., 1997; Lockyer, 2003; Rojano-Donãte et al., 2018). Estimates from an energetic model of wild adult harbour porpoises ranged from 6.7 (± 2.1) MJ per day for males and 16 (± 5.3) MJ per day for pregnant and lactating females (Gallagher et al., 2018), while the predicted overall intake rates from an agent-based model was **19.2** (±8.8) MJ per day (Gallagher et al., 2021).

5.1.4.2 Grey seal

Average daily energy expenditure has been estimated at 11.23 (± 1.7) MJ per day for wild juvenile grey seals, 20.10 (± 4.2) MJ per day for adults (Sparling et al., 2008) while the estimate of daily energy consumption for an 'average' grey seal was 25.3 (22.8-27.8) MJ or **5497** (4964-6042) Kcals per day (Sparling, 2003a).

5.1.4.3 Harbour seal

Harbour seal average daily energy requirement has been estimated to be **4,680** Kcals (Härkönen & Heide-Jørgensen, 1991) and average gross energy intake of captive individuals has been estimated at ~ 25.4 (± 4.1) MJ per day (Kastelein et al., 2005; Rosen & Renouf, 1998).

Bold values in section 5.1.4.1, 5.1.4.2, and 5.1.4.3 are selected values an chosen for consistency with previous studies on seal diet composition (Hammond & Wilson, 2016; Wilson & Hammond, 2016) and to represent an average estimate.

5.1.5 Prey calorific content

An organism's fitness and distribution is determined through the relationship it has with its environment (i.e. resources, risks, and conditions) (Matthiopoulos et al., 2020). Consequently, the population size and individual fitness of a predator is linked to prey availability (Øigård et al., 2013; Trites & Donnelly, 2003) and quality (Österblom et al., 2008). The extent to which animals can compensate for reduced food availability depends on the ability to buffer or counteract it (e.g. use of energy reserves stored in blubber, altering their diet, foraging area, metabolic costs) and further depends on prey calorific content.

As discussed in detail in Chapter 2 and Chapter 3 harbour porpoises might be particularly sensitive to diminished food availability. The observed distribution shift of porpoises from the north to the south of the North Sea in summer between 1994 and 2005 is likely linked to changes in prey distribution (Hammond et al., 2002, 2013, 2021). Results from Chapter 3 confirmed the importance of sandeels in the diet that are energy-rich prey and their biomass reduction in the northern North Sea (MacDonald et al., 2019) may have being a driver of this shift. Furthermore, the work carried out in Chapter 2 which estimated and compared the spatiotemporal variation in energetic availability of harbour porpoise main prey species between the Southern North Sea SAC and in the wider North Sea indicated that overall, large amounts of prey energy were available to harbour porpoises and highlighted the importance of sandeels. They are a key driver for the energy distribution in both the SAC region and other areas of the North Sea which was clearly illustrated in the overall map of energy content highlighting the sandeel banks.

Energy intake estimates are based on bioenergetics studies that combine foraging effort or estimated from diet composition and information on food availability and quality (Chudzinska et al., 2021; Rosen & Trites, 2005; Trites et al., 1997). However, as prey energy content varies substantially by species, size, and spatio-temporally, a more nuanced exploration of these factors is required.

Diet composition varies greatly per marine mammal species. Broadly, baleen whales mainly consume *Euphausiids*, while toothed whales mostly consume fish but deep diving cetaceans such as sperm whales (*Physeter macrocephalus*) also eat large amounts of squid, other species such as walrus (*Odobenus rosmarus*) and sea otters (*Enhydra lutris*) forage on benthic invertebrates and clams while the marine mammal predators considered in this thesis (i.e. harbour porpoise, grey and harbour seal) eat fish almost exclusively. According to Booth et al. (in review) of all marine mammal prey species the energy content of fish is most variable compared to other taxa. Thus, for predators that consume mainly fish, prey energy density and predator energetic requirements might fluctuate more compared to predators that feed on species that have more consistent energy densities. However, as described in Chapter 2, currently there are only limited published fish energy density data records and new data are required to improve the understanding of energetic availability to predators. The recently commenced PrePARED[8] (Predators and Prey Around Renewable Energy Developments) project will carry out fish surveys in the Moray Firth and Firth of Forth and samples will be subsequently analysed for quality (e.g. species, size, and energy content through bomb calorimetry). Similarly, the seals & sandeels (NIOZ-NWO) research project will carry out bomb calorimetry of caught sandeels and other fish species in the Dutch exclusive economic

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[8] https://www.thecrownestate.co.uk/en-gb/media-and-insights/news/the-crown-estate-invests-over-12million-in-new-research-to-help-protect-the-uk-marine-environment/

zone (EEZ). This will provide insight into how prey energy changes through time and space and could also be integrated into other modelling (e.g. impact assessment tools, bioenergetic models, MSFR models).

5.1.6 Prey availability

To fit the MSFR information on prey availability is needed for the time and places that diet information is available, additionally this information is needed to predict consumption for other times or places.

Estimating prey availability to predators is difficult as it requires estimation of the spatio-temporal overlap between predator and prey species and its accuracy relies profoundly on how exact this overlap is in time and space. Depending on the research question, large-scale stock trends may or may not be representative of food availability to a predator but could help understanding broader spatial patterns, especially if prey distribution is persistent. However, the productivity of many fish species has undergone changes due to climate variability, commercial harvest, habitat degradation and/or alterations in competition (Baudron et al., 2020; Brander, 2007). Therefore, prey density estimates on a smaller spatio-temporal scale are required to increase understanding of foraging ecology. These could come from species distribution models (as was done throughout this PhD), real-time monitoring (Friedlaender et al., 2006) or inter-prey spacing (i.e. prey density within a patch) (Southall et al., 2019).

The work presented in this thesis (Chapter 2, Chapter 3, and Chapter 4) estimated prey density using scientific trawl surveys (i.e. IBTS and BTS) coordinated by ICES and improved previous work by incorporating catchability factors of different gears used. To estimate prey availability information on predator movement was included and uncertainty was incorporated by using a combined bootstrapping routine (e.g. for seals this consistent of resampling the spatio-temporal prey species distribution model, catchability correction factors, and space availability to predator model). However, small-scale variability, especially in areas that are inaccessible to fishing gear (e.g. rocky substrate) and/or close to the coast might have gone undetected. As discussed in detail in section 4.5.1.2 the fisheries surveys used throughout this thesis are long-term and large-scale datasets allowing predictions of fish over the entire North Sea. However, the survey sampling coverage in space and time is limited and small-scale variability, that might be important for foraging predators, may go undetected. A similar approach as for the marine mammal distribution modelling covered in section 5.1.1 could be taken to improve the current predictions. Existing datasets and/or new sampling data could be used to complement the current surveys carried out by ICES. However, combing different survey data may not be straightforward especially as catchability differs considerably by gear type. A project currently in the planning stage will combine the IBTS survey with an additional trawl dataset around the coastal waters of Shetland (Fraser et al., 2020) using a similar approach as described in Paradinas et al. (in prep.). To understand and predict species distribution Paradinas et al. (in prep.) used integrated species distribution models, that use flexible joint modelling that can accommodate combining multiple data sources and scale different gear efficiencies, to combine fishery independent trawl survey and a fishery dependent trammel net survey on Dover sole (*Solea solea*). This would allow improving (i.e. especially close to the coast) and comparing with the current predictions. Additional to the MSFR work, these kind of predictions, for example whether seals target specific areas of prey, might be useful to explore by linking telemetry and fish distribution data. When other data for different regions become available this approach could be spatially extended.

Regarding prey availability, one of the biggest challenges was to estimate the availability of sandeels. Throughout this thesis, various approaches were taken but sandeel availability could not be estimated for Orkney and Shetland as ICES does not evaluate the stock in those regions. The seals & sandeels project that is currently taking place in the Dutch exclusive economic zone (EEZ) will employ specific sandeel surveys, estimate fine-scale spatio-temporal distribution of sandeels, and measure predation pressure by fish, seabirds, harbour porpoise and grey and harbour seals. This could potentially be used to update and extend the sandeel distribution model by Langton et al. (2021). Additionally, when diet data of seals or more up to date porpoise diet data becomes available, new sandeel information could be integrated in MSFR models for the Dutch part of the North Sea (Chapter 3) and/or incorporated within the current framework.

As previously mentioned in section 4.5.1.1 another possibility to consider is to use seabird breeding success as a proxy for sandeel availability. This might improve the reliability of the results but could also shed light on the extend to which sandeel availability to birds is similar/dissimilar to that experienced by marine mammals.

5.1.7 Fisheries catch and stock assessment

To compare removals by predators with fisheries and provide context to those estimates, information on the total stock size is required. In the North Sea this is provided in stock assessments from ICES.

Underreported catch is a fairly common practice in fisheries and a global problem (Pauly & Zeller, 2016) that could affect stock abundance estimation and potentially the effectiveness of their management. However, underreporting can be taken into account in assessment methods and abundance trends might still be correct even though absolute numbers might not be (Van Beveren et al., 2017). The extent of underreporting in the North Sea, was a significant problem in the past but due to increased reporting in recent years, is no longer considered a major issue (ICES, 2011). Although ICES incorporates underreporting into its assessments, raw recorded landings might still be considerably affected. For instance, the landings reported between 2005-2008 only accounted for 30-55% of total removals (ICES, 2009).

The spatial extent of stock assessments differs considerably by species. For example, the assessment area for mackerel is the Northeast Atlantic and adjacent waters (ICES, 2021d) while cod is assessed in different parts of the North Sea, Skagerrak, and English Channel (ICES, 2021a). This complicates direct comparison between predator consumption estimates, fisheries landings, and stock assessment estimates.

Although ICES produces stock assessments at the population/stock level it would be beneficial if they could produce regional specific stock trends as they used to in the past. In the absence of this information, a solution applied here was to estimate the proportion of the stock in the region where consumption is estimated to make the predictions more comparable (note that the fish distribution maps from Chapter 3 and Chapter 4 were restricted to the North Sea only and therefore stocks that are assessed over a wider range might be difficult to attribute to specific areas).

5.2 Case study

The consumption by three marine mammal species (i.e. grey seals, harbour seals, and harbour porpoises) was estimated for the summer of 2005 using the multi-species functional response models and fish distribution predictions from Chapter 3 and Chapter 4 and combining predator density (Figure 5.1) with abundance estimations.

Prey availability to predators was calculated by summing the product of the fish density with predator density in each grid cell:

$$\sum_i \sum_j Prey\ availability = \sum(Npredator_{ij} * Nprey_{ij}) \qquad \text{(eqn 5.1)}$$

where ij is the spatial position on the grid, i (row) is the x coordinate while j (column) y coordinates.

Thereafter, these estimates were rescaled to the maximum fish availability from either Chapter 3 and Chapter 4 which was fed into the predator species specific MSFR model to predict consumption.

Currently, information on harbour porpoise distribution at a North Sea wide scale is only available from the SCANS surveys undertaken in summer. To allow comparison between the different predator species, consumption estimation was restricted to summer in the southern North Sea (Figure 5.1, ICES division IVc) for one of the three (2005) harbour porpoise abundance estimates from the SCANS surveys.

Seal density estimates were derived from usage maps (Carter et al., 2020) fitted to seal tagging data from the British part of the North Sea. Abundance estimations were obtained from (SCOS, 2006) for seals and Hammond et al. (2013) for harbour porpoises.

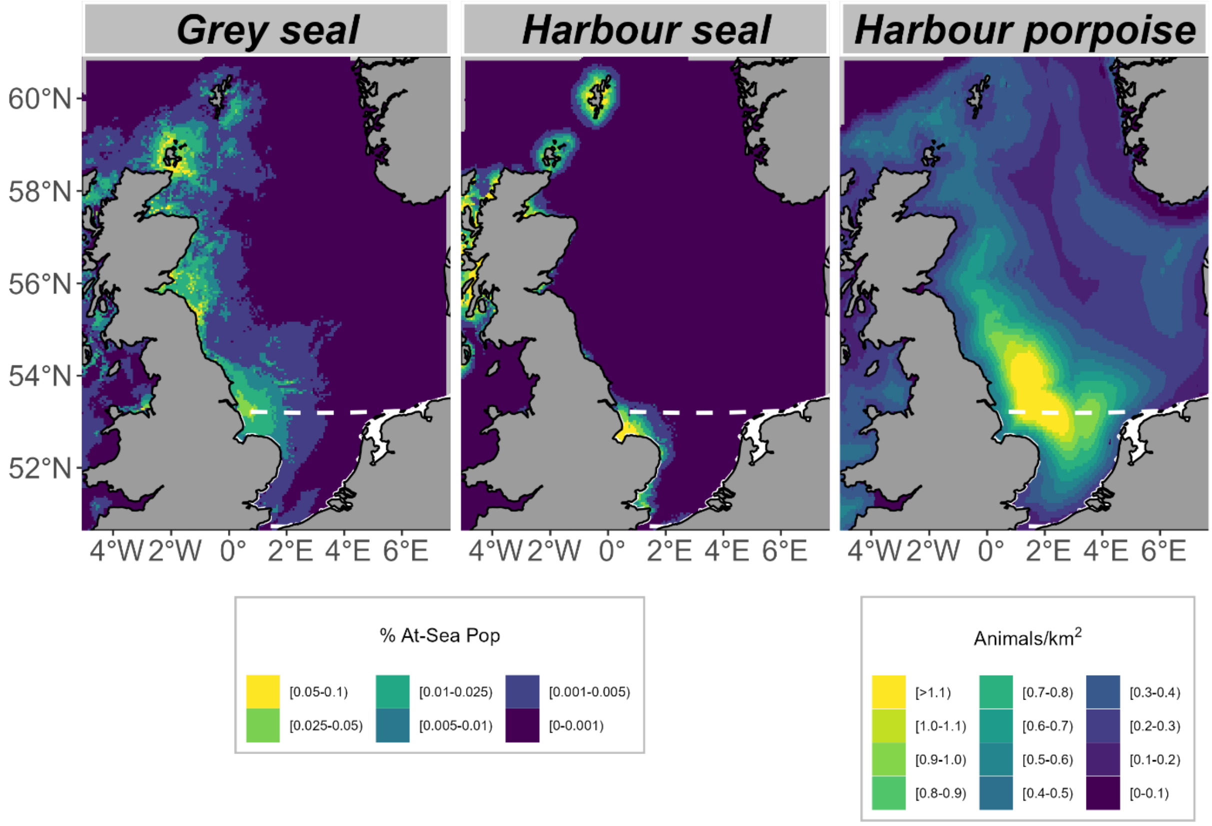

Figure 5.1 Relative density at-sea for grey and harbour seals from haulouts in the British Isles (Carter et al., 2020) and summer density of harbour porpoises in 2005 (Hammond et al., 2013). Upper border of southern North Sea according to ICES division IVc in white dashed line.

As the multi-species function response models were fitted to diet composition data there was a need to use published energetic requirements to estimate the consumption rates of the three marine mammal predator species assuming that on average these predators meet their energy requirements.

Daily per capita consumption was based on published daily energetic requirements estimates as described in section 5.1.4.

To compare the removals of fish by predators and fisheries the Percentage Predator Fisheries (PPF) was calculated as:

$$PPF_i = \left(\frac{Predator\ consumption_i}{Fisheries\ landings_i}\right) * 100 \qquad \text{(eqn 5.2)}$$

where i is the prey species. The commercial importance of species in marine mammal diet was estimated by constructing the Percentage Predator Consumption Price (PPCP) that each species contributed to the total commercial value using UK landing price (Dixon et al., 2017):

$$PPCP_i = \left(\frac{Predator\ consumption_i * Fish\ price_i}{\sum Predator\ consumption_i * Fish\ price_i}\right) * 100 \qquad \text{(eqn 5.3)}$$

where i is the prey species.

5.2.1 Results and implications

Consumption by marine mammals and fisheries landings are summarized in Table 5.1. Of the marine mammal species, harbour porpoise had the highest consumptions estimates, mainly due to the larger number of animals in the area (i.e. > 4 times for harbour seals and > 6 times for grey seals). Porpoise consumption was highest for sandeels and whiting. Seals mainly consumed dragonet and dover sole, while scorpion fish were also highly consumed by grey seals. Of these species only sole is of commercial interest. Generally, marine mammal consumption was relatively low compared to fisheries landings (on average around or below 20%) except for whiting consumption by porpoises (171%). The biggest consequences for fishing revenues due to predator consumption was on dover sole and sandeel which are also caught in relatively high numbers by fisheries. From the UK landing price data, it seems that 2005 was an exceptionally high price year for sandeels also compared to a previous study on seal consumption and fish prices by Harwood & Croxall (1988).

Consumption estimates for marine mammals were generated based on combining various datasets and model outputs and could serve as minimum estimates of natural mortality in stock assessment models. Knowledge gaps that need to be filled to better understand and improve the reliability of the estimations of direct competition for resources between marine mammals and fisheries are highlighted below.

- **Geographical area and spatio-temporal detail**

  Ideally, consumption would be estimated for the entire North Sea. However, the porpoise MSFR model was parametrised using data from within the vicinity of the Dutch coast and to avoid over-extrapolating the area for estimation was restricted to ICES division IVc (Figure 5.1). However, one could extend this area with the assumption that the functional response would hold in other areas of the North Sea, which might be justifiable given the studies considered in Chapter 2 (Table 2.1) that reflected only small differences in diet, or when new data become available the MSFR model could be refitted to a wider area.

  As mentioned in section 5.1.1 currently there is a lack of more detailed information on marine mammal distribution change over time on a North Sea wide scale, but various recommendations are mentioned to improve this. Similarly, the prey availability modelling is currently limited to large-scale predictions. Ideally, both predictions would be enhanced to predict natural mortality on fish stocks by these predators incorporating distributional changes on a more spatio-temporally detailed scale.

- **Energy values of prey and predator requirements**

  Although there are numerous studies on marine mammal bioenergetics and foraging behaviour is relatively well studied, knowledge gaps remain in other components and processes that affect estimation of biologically useful net energy intake from ingested gross energy (Booth et al., under review). For instance, information on true successful prey capture rates and calorific content of prey species is limited. As these parameters affect the estimated energetic requirements, an accurate prediction of these components is required. As mentioned in section 5.1.4 projects are currently underway to shed further light on prey calorific content changes among species and in time and space.

- **Assimilation efficiency**

  Assimilation efficiency was not included in the analysis because there is currently not enough information for all predator and prey species combinations (Booth et al., under review). This would have led to an underestimate of the estimated amount of prey consumed (Table 5.1). However, as assimilation efficiencies of fish and the marine mammal predator species is considered to be high (e.g. ~ 90%) this is believed to be a relatively small short coming given the other sources that have not been considered (e.g. population age structure, seasonal energetic requirement change).

- **Implementation of the MSFR into ecosystem/economic models**

  The case study estimation of predator consumption in terms of biomass and price is restricted to a single point in time. To better understand the predation pressure of these predators more detailed information is needed particular regarding size classes of prey consumption and how predation changes. Additionally, information on other predator-prey interactions and the effect of climate change are required to better predict how fish stocks and consumption is expected to change in future scenarios. A good next step would be to integrate the functional response in whole ecosystem or bioeconomic models. A more detailed description on this is provided in section 5.4.

Table 5.1 Estimated consumption of main prey species by marine mammal predators (i.e. grey seals, harbour seals, and harbour porpoise) and fisheries landings in the southern North Sea (i.e. ICES division IVc) during the summer of 2005 in tonnes (t). Estimates of predator population size and individual daily energy requirement (MJ per day) are also reported. Energy density values of prey species are represented by a single value from the literature. Fisheries annual landings were derived from ICES for division IVc and spawning stock biomass (SSB) and total landings are for the entire North Sea[10] in tonnes. The percentage of the fish species that are in division IVc compared to the entire North Sea were estimated from distribution maps from Chapter 3 and Chapter 4. Fish UK landing price in £ per tonne from Dixon et al. (2017). Furthermore, to compare the amount of fish taken by predators versus fisheries PPF (which sums to 100%) and PPCP (which is relative predator consumption to fisheries landings) were calculated. The other prey category included several species, but main contributions were made by dab, unidentified flatfish, flounder, and Norway pout for harbour seals, dab, unidentified flatfish, lemon sole, and poor cod for grey seals and smelt, Atlantic mackerel, and Dragonet for harbour porpoise.

	Predator consumption (t)			**Energy density** (KJ per gram)	**Fisheries landings IVc** (t)	**North Sea wide**		**Fish in IVc vs North Sea** (%)	**Price** (£ per t)	**PPF** (%)	**PPCP** (%)
	Grey seal	**Harbour seal**	**Harbour porpoise**			**Stock assessment** (SSB t)	**Landings NS** (t)				
Population size	8008	5167	33272								
Daily energy	22.9	19.6	19.2								
Cod	1.4	0.2	211.3	4.2[a]	1794.0	45758	29727	2.5	1,585	11.9	1.2
Sole	1106.9	535.0		5.0[e]	11186.0	32541	16355	72.5	6,940	14.7	41.5
Sandeel	277.3	86.2	4808.7	5.8[c]	22985.0			45.0	2,646	22.5	49.8
Other	720.6	528.4	4037.5	4.4[d]	-						
Scorpion fish	1070.8	18.3		4.1[f]	-			25.8			
Whiting		1.5	3145.2	4.3[b]	1836.0	145341	15471	12.2	635	171.4	7.3
Dragonet	429.5	704.2		5.2[e]	-			26.5			
Plaice		8.5		5.8[e]	13519.0	12492	3485	14.3	1,292	0.1	0.0
Herring		0.2	48.2	6.2[b]	6935.0	2522543	663813	2.0	209	0.7	0.0
Sprat			108.8	7.6[c]	4426.0			10.8	268[9]	2.5	0.1
Mackerel		1.7		7.9[e]	854.0	238917	51528	16.5	648	0.2	0.0
Haddock	0.0			3.3[d]	6.0			0.0	813		
Saithe	0.0	0.0		4.2[e]	1.0	255341	118625	0.0	473		
Ling		0.0		3.7[f]	1.0			0.1	1,081		
Total	3606.5	1884.2	12359.7		63543	3252933	899004				

[a](Lawson et al., 1997) [b](Pedersen & Hislop, 2001) [c](Wanless et al., 2005) [d](Plimmer, 1921) [e](Spitz et al., 2010) [f](Murray & Burt, 1977)

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[9] Note no price of sprat so price of other pelagic category assigned.

[10] Note that for certain species the North Sea area differs (e.g. mackerel stock is assessed in the Northeast Atlantic and adjacent waters (ICES, 2021d)).

5.3 Future directions

5.3.1 Technological advances

Technological advances can provide opportunities to gain more insight into the foraging behaviour of predator and prey species. As identified in Chapter 3 and Chapter 4, additional information derived from tags that synchronously sample predator movement, prey fields, and capture attempts (Goulet et al., 2019; Vance et al., 2021; Wisniewska et al., 2016) could support constructing more informative priors for species-specific attack rates which would theoretically allow a better fit of the MSFR models. For instance, tags that measure location and active-acoustic (Wisniewska et al., 2016), or that capture orientation and accelaration (Vance et al., 2021), or measure stomach temperature (Kuhn & Costa, 2006) or pH (Papastamatiou & Lowe, 2004) could be used to estimate prey capture attempts. Capture attempt and success is dependent on prey density, predictability, and behaviour (e.g., diurnal or nocturnal, shoaling or burring, escape strategies) which will vary by species and spatiotemporally. Therefore, to estimate variation in capture attempts under different prey regimes, local prey abundance and aggregations must be quantified. Those type of studies could also provide more insight into ecological complex predator-prey interactions and predator preference by improving predictions on the use of space by predators and their prey over time.

5.3.2 Size-selective predation

Fish body size composition plays a fundamental role in ecological processes with implications for population dynamics, predator-prey interactions, and fisheries management (Emmerson & Raffaelli, 2004; Winemiller, 2005; Zhou et al., 2010). Size-based indicators have therefore been used as indicators of ecosystem health and resilience of stocks (Shin et al., 2005).

Simply because predators and fisheries target the same species does not necessarily imply that they are competing for the same portion of the resources. Fisheries are primarily size selective because, larger fish are disproportionally economically valuable (Heino & Dieckmann, 2008), and they thus alter size structure and fish assemblage functioning (Pauly et al., 1998). Fishing-induced mortality can be severe and exceed natural mortality. It typically increases with fish size, while mortality from natural predators mostly declines with fish size (Sogard, 1997). Natural predators also target specific size classes of prey. Size-selective predation arises from certain fish sizes being actively preferred or easier to capture/handle and influenced by mechanistic processes arising from ontogenetic and allometric changes (e.g. mouth gape, learning, digestive capacity, diving capability, and swimming speed). As predators age, their ability to consume a broader range of prey types thus generally increases. However, marine mammals generally target fish < 30 cm which for some prey is at the smaller end of their size spectrum (Etnier & Fowler, 2010).

Estimating the broader impact of fishery removals and/or predation pressure by natural predators on fish stocks requires quantifying the magnitude both in terms of amount and size targeted. Additionally, insight is required into size-selectivity by comparison between landings/consumption and availability. The functional response models described in Chapter 3 and Chapter 4 could be applied for this purpose. For instance, to gain insight into size-preference, prey species could be grouped into different age classes for both diet and prey availability estimates. As the number of parameters to be estimated within the MSFR models is already high, adding in extra groupings into the diet data would require either additional diet data to become available or a more restricted range of prey species to be considered.

5.3.3 Multiple predator functional response

Predator-prey interactions are always simplified in a functional response model (Asseburg, 2006). In this thesis the functional responses are prey-dependent assuming that predator consumption is solely based on prey availability. It surpassed single or few prey type models by including multiple prey species which is a useful conceptual starting point as the North Sea is a complex ecosystem with a wide range of interacting species.

The generalized Holling functional response model (estimating the shape parameter *m*) used in Chapter 4 can theoretically be altered to include other drivers of consumption (e.g. temperature (Englund et al., 2011), hunger level (Li et al., 2018), predator-density (Kratina et al., 2009) or body size (Aljetlawi et al., 2004)). For instance, interference (e.g. either from inter or intra specific competition) can be integrated in predator-dependent functional responses, either as a component of the functional response itself by adding in the predators density (Arditi & Akçakaya, 1990; Beddington, 1975; DeAnglis et al., 1975) or prey to predator ratios can be used in ratio-dependent models (Ardit & Ginzburg, 1989). Which functional response model may be most appropriate depends on the system and relative predator abundance. For example, if predator abundance is low the functional response can be considered prey-dependent, while a predator-dependent response might be more appropriate at high predator abundance (Arditi & Ginzburg, 2012). Therefore, the functional response modelled could be viewed as falling somewhere on a gradient of potential responses depending on where on this continuum the predator population falls. Comparing between different functional response types (e.g. prey or predator dependent) could aid in assessing the extent of potential competition among predators. However, due to logistical, data, and statistical limitations predator-dependent models have been used infrequently and only for specialist predators consuming few prey species in experimental set ups (Novak et al., 2017).

Thus, the importance of predator-dependence for most non-specialist predators within a multi-prey context has not been quantified. Additionally, predator-prey relationships are affected by prey species that interact with each other in complicated ways (e.g. intraguild predation, cannibalism) and the spatio-temporal heterogeneity of environmental features (e.g. temperature, seafloor characteristics such as structures that act as prey refuge, and oceanographic features such as fronts). Functional responses can be integrated into ecosystem models that can accommodate multiple trophic interactions within an ecological system and allow prediction of consumption by predators, depending on various factors/drivers/variables (e.g. prey size, fisheries management, climate change).

5.3.4 Other predators

The functional response models could be applied to other species such as seabirds but also terrestrial predators. Currently, a PhD student at the University of Sheffield is planning to fit functional response models for several seabirds in the North Sea. Seabird species that heavily rely on sandeels might be of specific interest and their diets and/or breeding success could potentially serve as a proxy for sandeel availability. Another interesting application might be to fit a functional response to fishing fleets (Murray et al., 2011) to identify factors affecting the intensity of fishing.

5.4 Ecosystem modelling

Ecosystem modelling is a valuable tool for disentangling the confounding factors that influence ecosystem dynamics because large-scale ecosystem experiments are seldom feasible (Mackinson et al., 2009). These models can assess the cumulative effect of antropogenic pressures suchs as removals by fisheries and future climate change on different species. Additionally, species' thermal ranges can be integrated (Serpetti et al., 2017). Bioeconomic models have been used to quantify the impact of seal predation on fisheries revenue on the west coast of Scotland (Trijoulet et al., 2018). Ecopath with Ecosim (EwE) models are biomass-dynamic simulations that use the principle of conservation of energy. Ecopath models describe mass balance (Christensen & Pauly, 1992; Polovina, 1984) where biomass flows between different functional groups within the ecosystem. Other parts of the modelling package allow for examining dynamic alteration using Ecosim (Walters et al., 1997) and Ecospace (Walters et al., 1999) allows for exploring spatial changes. These tools have been used to explore the impacts of anthropogenic and environmental change (Lassalle et al., 2012; Österblom et al., 2007) and bottom-up and top-down control (Skaret & Pitcher, 2016). For example, ecosystem models including the Steller sea lion populations in the western Gulf of Alaska indicated that fishing, ocean productivity, predation, and competition all contributed to seal lion decline (Guénette et al., 2006).

The application of these models is limited by conceptual shortcomings and data limitations. Long-term data sets on a large number of trophic links are required and have to be linked both spatially and temporally which increases the amount of uncertainty in the model's predictions. However, with current statistical advances some elements of uncertainty can be quantified. EwE models have the ability to aid our understanding in topics (*e.g.* predation and climatic change) that single-species models cannot address (Hollowed et al., 2000). However, the ecological validity of these ecosystem models further depends on the underlying theory and the associated assumptions (ICES, 2015). One of the problems of particular importance arises from the assumptions made about predator functional responses (Mackinson et al., 2003). A predator's functional response describes how consumption of prey alters at varying prey densities and provides insight into predator-prey interactions. Hence, they provide fundamental information on trophic interactions and incorporating them correctly into an ecosystem model might be essential (Yodzis, 2000).

The ability to incorporate marine mammals within ecosystem models at an appropriate level of ecological detail remains limited. Regarding diet, as the North Sea Ecopath model (Mackinson & Daskalov, 2007) has 1991 as baseline year, ideally predator diet of that year would be used to initialize the model. However, due to data sparsity diet data from other periods would be required. The need to estimate an average diet through averaging samples from multiple locations and during various periods is challenging. However, in the ICES WGMME (Working Group on Marine Mammal Ecology) report of 2021 an outline of a proposed methodology for combining and analysing diet data needed for the Ecopath model is described.

The MSFR models from this thesis will be incorporated within an ecosystem model under one of the work packages from EcoSTAR. They will provide estimates of marine mammal prey preference and this integration will offer insight into total removals by marine mammal predators and the impacts of this on interacting fish stocks and enable the exploration of the consequences of fishing, environmental and climate change, predation, competition and the role of trophic interactions for the wider marine community. Additionally, it will allow predicting and testing how prey and predator populations are expected to change under plausible future scenarios.

The MSFR models of this thesis will also be integrated in various food selection models focusing on the role of size and predator-prey overlap under the SEAwise[xi] project, that recently commenced, to further understand the impact of predation on fishing revenues. A suite of biological, economic and social indicators and bio-economic models (e.g. BEMTOOL, FLBEIA, DISPLACE, EwE with Ecospace) will be employed in a multispecies and multi-fleet mixed fisheries context to provide advice for policy making.

[xi] https://cordis.europa.eu/project/id/101000318

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