Moving Targets: Safeguarding Migratory Pelagic Species in a Changing Ocean

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Abstract

Migratory and other highly mobile species, which rely on multiple, often spatially discrete and heterogeneous environments throughout their life cycles, play critical roles in the functioning and dynamics of communities and ecosystems. However, migratory species face multiple anthropogenically driven threats to their survival as they move between and use different areas. Understanding migratory species distributions and drivers of those distributions is essential to develop effective strategies that reduce or remove anthropogenic threats to their wellbeing and persistence. Yet, the spatial-temporal dynamism of migratory species movements and distributions, particularly under changing conditions, presents additional challenges for researchers and managers. Here, I use distribution modelling and quantitative analysis tools to examine the changing distributions of suitable habitat for marine pelagic species over horizontal (longitude and latitude) and vertical (depth) space, time and between ocean climates, and deconstruct how modelled distributions of prey can inform the design and management of area-based management tools for migratory seabird predators. First, I applied a species distribution model (Maxent) to explore the average monthly spatial-temporal dynamics of suitable habitat of the migratory pelagic forage fish capelin (*Mallotus villosus*) in Atlantic Canadian waters. I found that the distribution of habitat suitability varied across horizontal and vertical axes and among monthly models. Furthermore, I found that the importance of modelled covariates such as temperature varied between models. Next, I used a series of spatial and temporal analyses to examine how shifts in the North Atlantic Oscillation influenced the availability of suitable habitat over horizontal and vertical axes between 1998 and 2014. I found substantial stability in the location of predicted suitable capelin habitat between positive and negative phases. However, in six of the ten months modelled, predicted habitat suitability scores showed a declining trend over time. Finally, I present a framework for explicitly integrating changing prey availability into adaptive area-based management for seabirds throughout their migratory cycle. This framework focuses on using existing modelling, forecasting, and analysis tools to identify potential seabird foraging spaces, and allows for the input of new knowledge and data to provide managers with the best available information for iterative and adaptive decision-making.

General Summary

Migratory species, such as whales and seabirds, move to different locations throughout their lives. These locations may be quite different from one another. As migratory animals move, they influence the other species they interact with. However, it is hard to know where they are. Here, I use tools that take information about the environment, such as how warm it is, to model (predict) where an individual of a migratory species is most likely to be and where it might move. I start by modelling where capelin, an important prey fish for many animals such as cod, whales, and seabirds, is most likely to occur in the sea around Atlantic Canada. I also evaluate how different environment features such as temperature might be very important aspects of their habitat in one month but unimportant in another. Next, I consider whether their suitable habitat in one month always occurs in the same location or whether it moves, for example, because of warmer water in one year and colder water in another. Capelin and other fish are food for other migratory animals, such as seabirds that fly long distances to find and consume them. I created a guide for using models of fish such as capelin to help identify the places the seabirds are most likely to go to feed, even if the fish do not always go to the same place at the same time. The information available on a given species increases all the time, so I ensured that this guide includes a way for researchers to add new information about the seabirds and the fish they consume. Additional information should improve predictions on where seabirds will go to feed. Although no tool can clarify with absolute certainty where an animal will be, using the best available information will help to sustain wildlife.

Acknowledgements

"*Start where you are. Use what you have. Do what you can*" ~ Arthyr Ahse

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In science, we often talk about progress by standing on the shoulders of giants, but some of the most important giants are not scientists at all. I am incredibly grateful to my friends and family who have supported me throughout this journey. In particular, I would like to thank Ashley Jehan for always reminding me to "cry in the dojo, laugh on the battlefield"; Kerrie Le Meur, whose wisdom helped me get across the finish line; Matteo Rizzuto for repeatedly listening to me despair over that programming language/software which shall not be named; Isabel Cameron for tea on the banks at Glasney Parc and keeping me grounded over the years; Denise Byrne whose infectious optimism and drive in the face of the greatest of adversity has been an inspiration beyond all measure; Simon Beaton for reminding me of the importance of one step at a time; Rachel de Caen for being a friend to my friends and family to my family when I could not be there; my mum, dad, and sister for their unwavering support from the moment I decided to go back to school at the age of 28; my husband who learned the importance of swiftly bringing tea and cake when a crisis begins. I love you all and could not have finished this without you.

Finally, to the ocean, whom we have loved and mistreated for too long. This thesis started with you. It is just one chapter in a story to help repair some of the damage we have done to you. The story does not end here. The future has yet to be written.

"Take what you have learned, take your skills, knowledge, critical thinking, and use them. Spread your knowledge to those around you, shed light on misunderstanding, use your skills, help others write their stories, show kindness, and never put your pen down." ~ Elizabeth Andrews (sister).

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Chapter 1: Introduction and overview

There is little argument that the ocean is increasingly degraded by habitat loss and deterioration, climate change, invasive species, and pollution (Sala & Knowlton 2006, Halpern et al. 2015). The overexploitation of marine populations, however, is widely regarded as one of the most pervasive threats to marine biodiversity (Pauly & Palomares 2005b, McCauley et al. 2012), with effects rippling throughout all marine ecosystems (coastal, mangrove, benthic, pelagic, coral reefs, kelp forest, among others; Coleman & Williams 2002, zu Ermgassen et al. 2013). To protect and ensure sustainable use of marine ecosystems, managers are shifting their focus from single-species management towards community and ecosystem-based approaches. These approaches integrate multiple biotic and abiotic interactions and consider the cumulative impacts of human activities (Levin et al. 2013, Long et al. 2015). In particular, area-based management tools (ABMTs) are increasingly being used to manage human activities (e.g. fisheries area closures, Wright et al. 2019) and to meet biodiversity conservation objectives (e.g. marine protected areas and networks, Day et al. 2019).

A growing body of literature suggests that populations of marine species with largely sedentary or sessile adult life stages, such as scallops, or with limited home ranges, such as coral reef herbivorous fish, do not exist in discrete, isolated populations (Chapman & Kramer 2000, Twist et al. 2016). Rather, populations operate as a part of a larger metapopulation, in which the movement of larvae links otherwise spatially discrete subpopulations (Kritzer & Sale 2004). In turn, these populations are nested within a broader set of metacommunities, with each sub-community linked by the movement of multiple species that interact directly and indirectly (Leibold & Chase 2018). Although the importance of maintaining population connectivity for sessile or range-limited species in conservation planning is increasingly recognised (Carr et al. 2017), the spatial protection of highly mobile species such as migratory species remains a considerable challenge (Martin et al. 2007, Runge et al. 2014). Migratory species, which may also operate in a metapopulation structure (Esler 2000, Gerlotto et al. 2012), occupy a range of spatially discrete habitats that may shift in time and space depending on oceanographic conditions (Refsnider & Janzen 2010, Davoren & Halden 2014) and/or with the spatial-temporal dynamics of interacting heterospecifics such as prey (Furey et al. 2018). Furthermore, the current and projected novel climates (Veloz et al. 2012a) and communities (Williams & Jackson 2007b) present additional complications predicting species distributions and designing marine protected areas (hereafter MPA) networks that are future-proofed to potential changes in space use.

Although we lack the knowledge needed to know precisely how species will respond to changing ocean conditions, with the continued degradation and increasing zonation of the ocean for one human activity or another, it has never been more important to identify and protect the spaces that could be important for population persistence and ecosystem resilience (Jones et al. 2016, Schmitz et al. 2015, Queirós et al. 2016).

1.1: Marine species in a changing ocean

The ocean is a highly dynamic environment, with conditions fluctuating on spatial scales from a few meters to several thousands of kilometres, and temporally on daily, weekly, monthly, seasonal, annual, decadal, and longer scales (Ottersen & Stenseth 2001, Durazo & Baumgartner 2002, Risebrobakken et al. 2010, Muller-Karger et al. 2015). By moving among spatially homogeneous or heterogeneous environments throughout their life cycle, migratory species can avoid suboptimal conditions and exploit areas where conditions are better for survival (Sims et al. 2004, McCauley et al. 2012, Cherry et al. 2013, Kimirei et al. 2013, Ebel et al. 2016).

Marine migratory species are taxonomically diverse, representing mammals such as humpback whales (*Megaptera novaeangliae*), sea turtles such as green sea turtles (*Chelonia mydas*), bony fish such as Pacific herring (*Clupea pallasii*), cartilaginous fish such as blue sharks (*Prionace glauca*), and birds such as Arctic terns (*Sterna paradisaea*) (Shaffer et al. 2006, Veríssimo et al. 2017, Bishop & Eiler 2018, Andrews-Goff et al. 2018, Dalleau et al. 2019). Migratory species vary in distances they travel and the number of areas they use. Many traverse coastal and open-ocean waters, including those of multiple jurisdictions and Areas Beyond National Jurisdiction (ABNJs). For example, Arctic tern (*Sterna paradisaea*) tracking studies have revealed annual migration distances of 81,600 km between Arctic and Antarctic waters, with routes encapsulating the coastal waters of multiple South African or South American countries, as well as Canadian, Icelandic, and Danish (Greenland) waters and ABNJ in the north and south Atlantic (Egevang et al. 2010).

Spaces used (e.g. location and habitat type) by migratory species may surround fixed features such as seamounts, dynamic features such as oceanographic fronts, and where oceanographic conditions, such as temperature, mixed layer depth, or prey availability are suitable for survival (Rose 2005, Morato et al. 2010, Williams et al. 2015, Waggitt et al. 2018, Lewallen et al. 2018, Lerma et al. 2020). Migratory species may consistently visit the same location during a particular migration stage (e.g. always overwinter in the same area) or periodically (e.g. if conditions in that area are more variable from one year to the next) (Davoren & Halden 2014, Runge et al. 2014). As migratory species move between different locations/areas, they often influence otherwise spatially separated communities and contribute to ecosystem productivity, resiliency, and ecosystem connectivity (Kremen et al. 2007, Massol et al. 2011, McCauley et al. 2012, Erisman et al. 2017).

Humans pose myriad threats to marine biodiversity both within nations' exclusive economic zones (EEZ) and ABNJs. Threats include direct and indirect exploitation, pollution, development, and climate change-induced alterations to biotic and abiotic factors (Halpern et al. 2015, UN 2021). As a result of their dependence on multiple spatially discrete areas and potentially wide-ranging movements, migratory species may be exposed to different combinations of threats at different migration stages (Lascelles et al. 2014). Land-based threats add additional concern for migratory species who also rely on terrestrial habitats, such as seals and seabirds. Responses to changing biotic and abiotic conditions resulting from threats depend on individual species' sensitivity and adaptability to change and the nature, magnitude, frequency, and severity of change they experience (MacLean & Beissinger 2017). Today, fishing and hunting, and to a lesser albeit growing extent, climate change is directly and indirectly (e.g. through trophic cascades), comprise the greatest anthropogenic threats to marine species persistence (Payne et al. 2016). Where adaptation is possible (i.e. where species mortality/extinction is avoided), marine species responses to changing conditions include spatial and/or temporal shifts in spawning (Davoren 2013, Murphy et al. 2018), switching to lower quality prey in the absence of preferred prey (Grémillet et al. 2008, Divoky et al. 2015, Reynolds et al. 2019), and range shifts across longitude, latitude, and depth (Poloczanska et al. 2013, Cheung et al. 2014, Robinson et al. 2015, Pecl et al. 2017). Indeed, multiple marine taxa are redistributing at faster rates than their terrestrial counterparts, and species with highly mobile adults are redistributing faster than species whose ability to move large distances is restricted to their larval stages (Pinsky et al. 2020, Lenoir et al. 2020). However, limitations in suitable habitat could prevent redistribution, even where relocation might be physically possible. For example, polar species typically have narrower tolerance ranges than their mid-latitude counterparts and thus may be unable to find suitable cold waters in the future, putting them at greater risk of extinction (Morley et al. 2019). Alongside range-shifters potentially altering the ecosystems and food-webs across their new and old ranges (Pinsky et al. 2020), the redistribution of one species can cause knock-on effects in co-dependents. For example, changing conditions that alter the movement and distributions of prey could cause predators to alter their spatial-temporal patterns (Grémillet & Boulinier 2009, Loredo et al. 2019).

1.2: Predator-prey spatial dynamics

Marine migratory species are typically carnivorous, though some species, such as olive ridley sea turtles (*Lepidochelys olivacea*), are omnivorous (Peavey et al. 2017). Migratory species feed on multiple trophic levels, including zooplankton (e.g. capelin *Mallotus villosus*, Rose 2005), pelagic bony fishes (e.g. common murres *Uria aalge*, (Maxwell & Morgan 2013), and cartilaginous fishes (e.g. northern elephant seals *Mirounga angustirostris*, (Condit & Le Boeuf 1984). In particular, forage fish species – small, schooling, planktivorous species – form a key prey base for many marine migratory species. Forage species include capelin (*Mallotus villosus*), Japanese anchovy (*Engraulis japonicus*), Gulf menhaden (*Brevoortia patronus*), European sardine (*Sardina pilchardus*), and common jack mackerel (*Trachurus declivis*), and can be migratory themselves.

The dynamic heterogeneity of marine environmental conditions, combined with physiological requirements and interactions with conspecifics and heterospecifics, results in patchy distributions of prey species such as forage fishes globally. Prey patches can exist in a hierarchical spatial structure, with patches of high prey density nestled within larger patches of lower density (Kotliar & Wiens 1990), and can fluctuate in time and space in line with the ocean and biotic covariates that govern the characteristics of the patch (Charnov 1976, McClatchie et al. 2017).

Optimal foraging theories suggest predators make foraging decisions based on their ability to maximise energy intake and fitness (MacArthur & Pianka 1966), with migratory species optimising their foraging by exploiting disparate and temporally-variable prey patches. In particular, resource tracking theory suggests that predator migration routes, timing, and foraging spaces are partly determined by the abundance, timing, ephemerality and predictability of prey patches, as well as the spatial configuration and variance of those patches in the wider seascape (Abrahms et al. 2021). For example, seabird colonies along the Norwegian coastline occur in locations with stable abundances of suitable prey for parent and chick survival, even if higher prey abundance – albeit more variable – occur elsewhere (Sandvik et al. 2016). Furthermore, prey exploited during the breeding season may also be migratory or only reach sufficient abundance levels to support parents and chicks during certain times of the year. In such situations, migratory seabirds time their migrations to breeding colonies to match prey availability and appear to have high breeding site fidelity (Regular et al. 2014, Arneill et al. 2019).

Although co-occurrence does not guarantee interaction between predator and prey (Blanchet et al. 2020), it is the first prerequisite for identifying predator-prey interactions. A key challenge facing migratory species is to be in the right place at the right time to exploit available prey. However, human activities, including climate change, may change the spatial-temporal availability of resident or migratory prey at future foraging spaces (Bertrand et al. 2012). For example, over the past 50 years, the emigration of Atlantic salmon (*Salmo salar*) into the North Atlantic Ocean has occurred increasingly earlier, potentially resulting from warming sea, river, and air temperatures (Otero et al. 2014). In Japan, non-migratory black rock fish (*Sebastes cheni*) have adjusted the timing and location of their spawning grounds (Shoji et al. 2011). It is worth noting that patterns of climatological and oceanographic changes are not synchronous across the globe (Pecl et al. 2014), nor are the cues that trigger a migration linked to climatological changes at the destination (e.g. changes in day-length). Nevertheless, with prey distributions playing a significant role in the spatial-temporal dynamics of their predators (Wisz et al. 2013, Furey et al. 2018, Ratcliffe et al. 2021), it is perhaps unsurprising that some migratory species are adapting their spatial-temporal patterns to match changing availability of their prey as well as to other conditions that influence their spatial-temporal dynamics. For example, Atlantic bluefin tuna (*Thunnus thynnus*) appears to be re-establishing historic migration and distribution patterns, likely due to a combination of reduced fishing pressure, changes in oceanographic conditions, and redistribution of their prey (Horton et al. 2021), whereas common guillemots (*Uria aalge*) have delayed breeding in response to climate-driven changes to the spawning migrations of their prey (Regular et al. 2009).

1.3: Predicting distributions

Among the management options employed to reduce human pressure on marine species are area-based management tools (ABMTs), such as marine protected areas and fishery closures (Day et al. 2019). When designed and managed well, ABMTs can be particularly effective in protecting against point-based threats, such as fishing, although they cannot protect against diffuse threats such as ocean acidification (Agardy et al. 2011, Slooten 2013, Edgar et al. 2014, De Santo 2018). Since ABMTs are, by their very nature, spatial, knowing the distribution of species targeted for protection is essential for placing ABMTs where they will be most effective and ecologically relevant (Moilanen et al. 2009). However, the lack of knowledge about the spatial-temporal dynamics of migratory species distributions significantly impedes the implementation of ABMTs that can offer meaningful protection (Martin et al. 2007, Runge et al. 2014).

Species distribution models (SDMs), also known as habitat suitability models among other names, are a family of quantitative tools that combine abiotic and, to a lesser extent, biotic covariates with species observations to predict the distribution/habitat suitability of a focal species (Guisan et al. 2017) or community (Norberg et al. 2019). A wide range of models can fit with diverse species data types, including presence-absence data (e.g. generalised linear models (Barbosa et al. 2009)), presence-background data (e.g. Maxent (Phillips et al. 2006)) and presence-only data (e.g. BIOCLIM (Booth et al. 2014)). Where abundance or density data are available, some SDMs, such as random forest, can also predict the abundance/density distributions of the targeted species (Luan et al. 2020). Although SDMs for marine species lag their terrestrial counterparts (Robinson et al. 2017), they are increasingly used to resolve marine species distributions, including for migratory and other highly mobile species (Maxwell et al. 2015, Hays et al. 2019).

SDMs for migratory and other highly mobile marine species face several challenges. First, SDMs are usually applied to flat, two-dimensional surfaces, whereas marine species may move through three-dimensional space (i.e. throughout the water column). With the ocean exhibiting a dynamic vertical structure, accounting for changing conditions across depth is particularly valuable to matching proximal covariates with species occurrence samples and predicting distributions over depth (Duffy & Chown 2017). Second, oceanographic conditions vary greatly over time. Using oceanographic data averaged over long temporal windows (e.g. decadal, annual) may provide sufficient information to model the distributions of relatively sedentary species, but for migratory and other highly mobile species, more contemporaneous resolutions (e.g. monthly or daily) may reveal important information about their spatial responses to changing conditions (Mannocci et al. 2017). Third, SDMs only predict a species' modelled realised niche rather than its fundamental niche, which can be much broader (Hutchinson 1957). As a result, SDMs assume that a species is in equilibrium with conditions throughout its range and over time. In reality, variations can arise due to spatial-temporal dynamics inherent in conditions and resources, including prey (Trainor & Schmitz 2014). For example, relationships between covariates can vary over space and time (Kavanaugh et al. 2016), and relationships between marine species and modelled covariates can vary over seasons, during heatwaves, and between cycles of the North Atlantic Oscillation (an oscillation in atmospheric surface pressure between the Icelandic Low, a semi-permanent low-pressure system between Iceland and southern Greenland in the North Atlantic/sub-Arctic, and the Azores High, a semi-permanent high-pressure system in the sub-tropical Atlantic) (Roberts et al. 2019, Muhling et al. 2020, Lloret-Lloret et al. 2021).

The use of SDMs for migratory predators, including community-based SDMs, joint SDMs that seek to predict multiple species distributions within a single model, and stacked SDMs, which ‘stack’ SDMs fit for individual species to determine multi-species distributions (Norberg et al. 2019), is challenged by the need to include spatial-temporal variations in the prey as well as the predator for several reasons. First, predators do not necessarily use the same prey species throughout their migration cycle. Second, predator and prey may respond to changing conditions differently due to differences in physiology and external factors such as interactions with other species. Third, predators do not necessarily experience the same conditions as their prey. The latter point is perhaps best exemplified by seabirds, which breed on land, migrate through the air, and catch prey in the ocean. Although water temperature may be an important determinate for a prey fish species (Lenoir et al. 2020), it is the availability of that prey (e.g. are the prey located in an area the predator can reach) rather than the temperature *per se* that is the key determinate of the seabird (Waggitt et al. 2018). Indeed, several studies argue that oceanographic covariates are not necessarily good predictors of seabird distributions (Grémillet et al. 2008, Kane et al. 2020, Afán et al. 2021) and that predator-prey interactions and environmental relationships can drive predator distributions to varying degrees over geographic space and time (Grémillet et al. 2008, Aragón et al. 2018).

1.4: Thesis overview

My thesis combines empirical modelling research with a conceptual framework to quantify changes in the habitat suitability of migratory pelagic species over space and time and explore how area-based management tools such as marine protected area networks can capture and manage the shifting distributions of marine species. Overall, my thesis is one of the few examples of efforts to predict habitat suitability at short timescales (monthly) and across depth and explicitly integrate predator-prey dynamics into management processes.

In Chapter Two, I conduct an empirical study to quantify the monthly drivers of the distributions of suitable habitat for a highly migratory keystone forage fish species, capelin (*Mallotus villosus*), in Atlantic Canada and explore how predicted habitat suitability scores change over longitude, latitude, and depth axes (see Appendix A for a primer on capelin). I highlight the importance of (1) capturing potential variation in habitat suitability over multiple depths and (2) assessing potential variation in the relative importance of modelled covariates over time for migratory and other highly mobile species.

In Chapter Three, I build on the work of Chapter Two by exploring the stability of modelled habitat distributions between different ocean ‘climates’ (here, phases of the North Atlantic Oscillation). I use the same species and environmental datasets as in Chapter Two and modify the modelling technique and output to allow area-based comparisons. I use an emerging hotspot analysis and landscape metric tools to quantify the degree of stability of suitable habitat between ocean ‘climates’. Alongside highlighting the importance of spatial stability of suitable habitat for area-based management, I also identify several areas for model development that can assist in providing more robust measurements of pelagic species habitat suitability changes over space and time.

In Chapter Four, I propose a novel conceptual framework to incorporate the changing spatial-temporal distributions of prey into the design and implementation of area-based management tools such as marine protected area networks for seabirds. I review and synthesise key literature on seabird movements, and the impact of changing prey availability on their spatial ecology and population persistence. I also present a workflow to model and forecast prey availability and analyse spatial-temporal trends using commonly available tools such as those presented in Chapters Two and Three. I discuss the application for predicted seabird foraging spaces in adaptive management processes.

1.5: Co-authorship Statement

This thesis is the result of my independent research. The breakdown of contributions by each author is as follows:

Chapter 2: Modelling the spatial-temporal distributions and associated determining factors of a keystone pelagic fish.

I developed the research, processed and analysed the data, and wrote the manuscript. S. Leroux and M-J. Fortin contributed to question development, data analysis, and writing.

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Chapter 3: Influence of the North Atlantic Oscillation on the distribution of a keystone pelagic fish.

I developed the research, processed and analysed the data, and wrote the manuscript. S. Leroux and M-J. Fortin contributed to question development, data analysis, and writing.

A version of this Chapter has been submitted to the journal *Marine Ecology Progress Series (MEPS)* and is currently under review.

Chapter 4: Incorporating the spatial-temporal distributions of prey availability into area-based management tools for marine ecosystems

I developed the research, processed and analysed the literature, and wrote the manuscript. S. Leroux and M-J. Fortin contributed to research development and writing.

Additional:

In addition to the chapters presented in this thesis, I collaborated with Tianna Peller, a PhD student who is also working in the Second Canadian Healthy Oceans Network (CHONe2):

From Marine Metacommunities to Meta-ecosystems: Examining the Nature, Scale and Significance of Resource Flows in Benthic Marine Environments.

T. Peller and I developed the research, processed and analysed the literature/data. T. Peller wrote the manuscript and I contributed to the writing. S. Leroux and F. Guichard contributed to research development, analysis, and writing.

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Chapter 2: Modelling the spatial-temporal distributions and associated determining factors of a keystone pelagic fish

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Abstract

Mobile pelagic species habitat is structured around dynamic oceanographic and ecological processes that operate and interact horizontally and vertically throughout the water column and change over time. Due to their extensive movements, pelagic species distributions are often poorly understood. I use the Maxent species distribution model to assess how changes in the relative importance of modelled oceanographic (e.g. temperature) and climatic variables (e.g. the North Atlantic Oscillation) over 17 years affect the monthly average horizontal and vertical distribution of suitable habitat for a keystone pelagic forage species, Atlantic Canadian capelin (*Mallotus villosus*). I show that the range and distribution of relative habitat suitability scores vary across horizontal and vertical axes over time, with binary suitable/not suitable habitat predictions indicating suitable habitat occupies between 0.72% (April) and 3.45% (November) of the total modelled space. Furthermore, the analysis reveals that the importance of modelled oceanographic variables, such as temperature, varies between months (44% permutation importance in August to 2% in May). By capturing the spatial dynamics of capelin habitat over horizontal, vertical, and temporal axes, the analysis builds on work that improves our understanding and predictive modelling ability of pelagic species distributions under current and future conditions for proactive ecosystem-based management.

2.1: Introduction

Mobile pelagic species have critical functions in marine systems, occupying multiple trophic levels (Sarà & Sarà 2007, van der Lingen et al. 2010), acting as agents for resource flows (Gounand et al. 2018), and as ecosystem engineers (Breitburg et al. 2010). However, their extensive movements mean that they are typically poorly surveyed. Consequently, the abundance, distribution, and population structures of mobile pelagic species are not well understood.

Species distribution models (SDMs), which combine abiotic and biotic variables with species location data, are commonly used to predict habitat suitability (Guisan et al. 2017). SDMs have been applied to a wide range of marine species, including invertebrates (Eger et al. 2017), reef fish (Young & Carr 2015), and sponges (Knudby et al. 2013). Modelling pelagic species habitat suitability remains challenging, however, because pelagic habitat is structured around dynamic oceanographic and ecological processes, operating and interacting horizontally and vertically throughout the water column, and changing over time (Angel 1993). Oceanographic conditions that influence pelagic species habitat include temperature and salinity (Rose 2005), dissolved oxygen content (Bertrand et al. 2011), sea surface height (Zainuddin et al. 2017), and mixed layer depth (Williams et al. 2015). Prey abundance and distribution also plays a pivotal role in pelagic predator habitat distributions, with chlorophyll concentration often acting as a proxy for zooplanktivorous prey (Zainuddin et al. 2017). Furthermore, large-scale climate oscillations such as the North Atlantic Oscillation and Atlantic Multidecadal Oscillation influence regional oceanographic conditions and have been implicated in changing distributions of marine species (Roberts et al. 2019).

While distribution models are typically applied to two-dimensional environments that lack temporal variability, resolving the dynamic vertical structure of the ocean to account for changing conditions across depth is particularly valuable for mobile pelagic species which can be distributed throughout the water column. Whereas oceanographic data averaged over long temporal windows (e.g. decadal, annual) may provide sufficient information to model the distributions of relatively sedentary species, using such data can lead to loss of information about how pelagic species are responding spatially to variations in conditions than more contemporaneous resolutions (e.g. monthly or daily) (Mannocci et al. 2017). Furthermore, as species-environment relationships can vary over time (Marques et al. 2011), temporally-constraining models may be beneficial for predicting habitat suitability (Gschweng et al. 2012, McClellan et al. 2014).

Dynamic SDMs for marine species that consider change through time are increasing in number (e.g. Brodie et al. 2018). The availability of ocean models that provide data at multiple depths is increasing (Becker et al. 2016; Kavanaugh et al. 2016), however SDMs that incorporate conditions at depth are rare (Duffy & Chown 2017). Although ocean models are not truly three-dimensional, instead offering snapshots at specific depths creating a "2.5-dimensional" environment (Duffy & Chown 2017), they have advantages over in-situ measurements in that they offer continuous spatial coverage over time at each modelled depth (Becker et al. 2016). Incorporating both depth and time in SDMs may improve our ability to predict current and future pelagic species habitat suitability and explore biological responses to global change.

Capelin (*Mallotus villosus*) is a migratory zooplanktivorous pelagic fish species with four genetically distinct populations– two in the Pacific, one around West Greenland, and one in the Northeast Atlantic around Atlantic Canada containing several sub-populations (Præbel et al. 2008, Kenchington et al. 2015). Within Atlantic Canadian waters, capelin is regarded as a keystone species (Rose 2005, Davoren et al. 2006). This temperate to sub-Arctic region is dominated by the cold, fresh Labrador Current, with the warm, more saline Gulf Stream increasing temperatures in the southern portions. During the 1990s, Atlantic Canada experienced a substantial change in ocean climate, notably marked by a freshening of shelf waters and lower temperatures (Greene et al. 2008), generating a regime shift impacting multiple fish species in the region (Pedersen et al. 2020). Alongside numerous groundfish species, capelin abundance declined, shifted distributions, began maturing at younger ages and smaller sizes, and spawned later in the year (Carscadden & Nakashima 1997). Capelin have not recovered to their former state, and these changes have been implicated in the lack of recovery of Canada's Atlantic cod (*Gadus morhua*) (Mullowney & Rose 2014). Despite the ecological and cultural importance of capelin in Atlantic Canada, their year-round distributions and spatial responses to changing conditions throughout the region are not fully understood.

In this study, I address the following research objectives: (1) quantify variation in the average monthly distribution of suitable capelin habitat across longitude, latitude, and depth to capture their horizontal and vertical movements, and (2) assess changes in capelin's species-environment relationships via the relative importance of modelled oceanographic and climatic variables to estimated capelin distributional changes. I construct monthly "2.5-dimensional" distribution models with Maxent (Phillips et al. 2006), predict average monthly relative habitat suitability scores across the 2.5-dimensional geographic space, and derive the relative importance of modelled variables using Maxent's permutation importance metrics. The analysis broadly contributes to the application of distribution models for mobile pelagic species.

2.2: Methods

2.2.1: Study region

The study region includes the ocean lying within and adjacent to the Canadian territorial sea (0 – 12 nautical miles from the low-water line along the coast) and Exclusive Economic Zone (EEZ) (12 – 24 nautical miles from the low-water line along the coast), broadly extending from 40^{o} latitude to 70^{o} latitude. To avoid imposing unnatural breaks in capelin distributions, I include France's EEZ surrounding Saint Pierre and Miquelon, disputed territories with the USA, and areas adjacent to Canada's EEZ, such as the Flemish Cap and Georges Basin, as part of the study region (Figure 2.1).

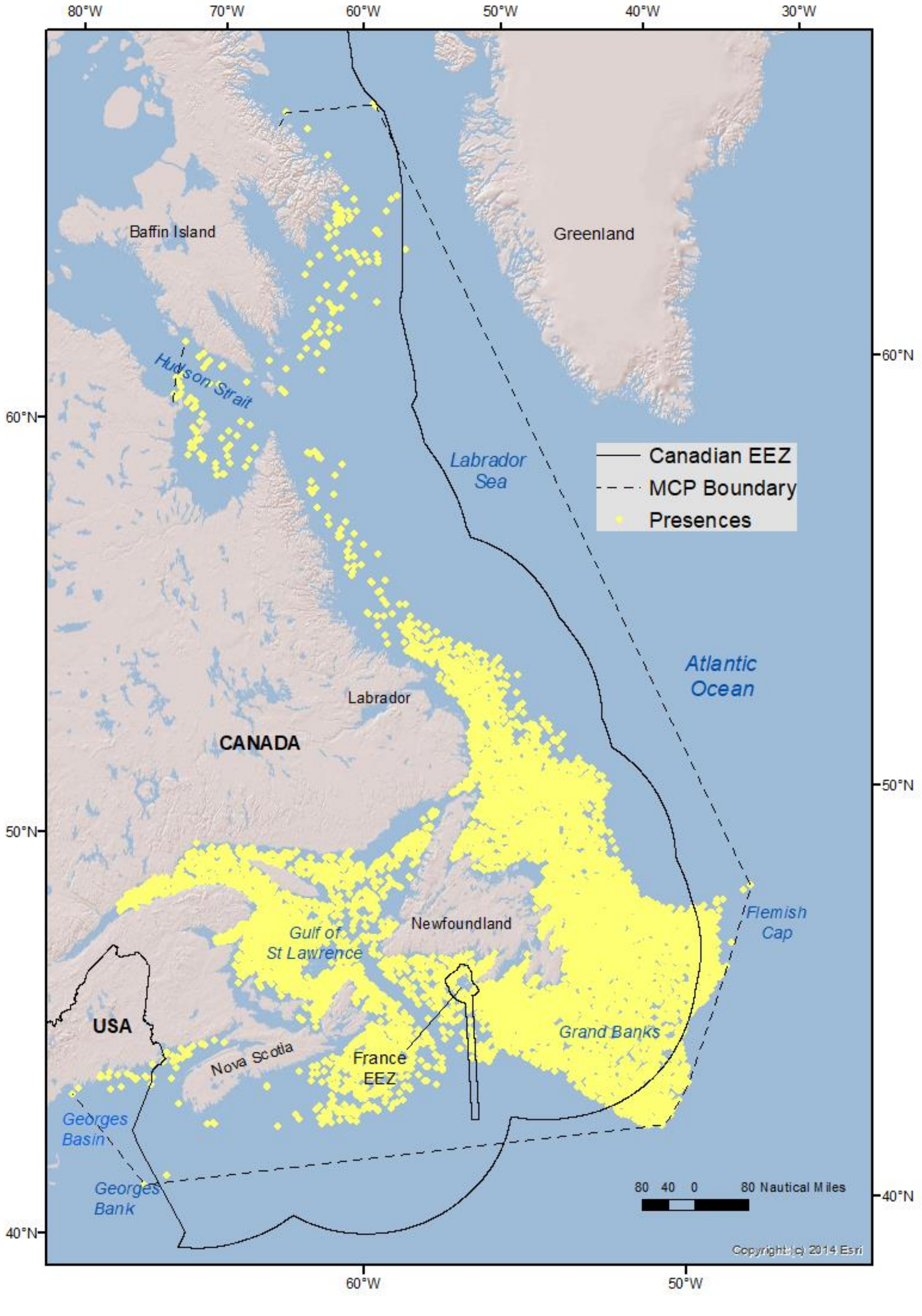

Figure 2.1: *The study region includes waters inside the Canadian EEZ, the French EEZ contained within the Canadian EEZ, and adjacent areas of the Flemish Cap, Grand Banks, Georges Bank, and Georges Basin. Analyses were restricted to the Minimum Convex Polygon (MCP) boundaries, which was derived from capelin presence data.*

2.2.2: Data – Environmental variables

I obtained oceanographic data (chlorophyll α concentration, density mixed layer depth, dissolved oxygen, salinity, sea surface height, and temperature), as well as bottom depth, from the numerical modelling products GLORYS V4.1 (CMEMS 2018a) and BIOMER V3.2 (CMEMS 2018b). Both products offer global gridded monthly average measurements at a horizontal resolution of 0.25˚ across 75 depth levels (0.5 meters to 5,902 meters at varying intervals) for the years 1998 to 2015 inclusive (Appendix B.1).

I also obtained monthly mean index values for two climate oscillations; the Atlantic Multidecadal Oscillation (AMO) index (ESRL, 2019) calculated from detrended spatially averaged sea surface temperature anomalies between 87.5°S – 87.5°N, 2.5°E – 357.5°E, and the North Atlantic Oscillation (NAO) index (NCAR, 2019) calculated from the leading empirical orthogonal function sea level pressure anomalies between 20° – 80°N, 90°W – 40°E. Broadly, fresher, cooler waters characterise positive NAO phases than negative phases. AMO trends operate on longer timescales than the NAO, and a positive AMO value trend dominates the study period, though the strength (values) varies. Water temperatures are generally warmer during positive AMO phases than during negative phases.

2.2.3: Spatial-temporal grid

I created a series of grids representing each depth delineated in the oceanographic models. Because the distribution model (Maxent, see below) assumes an equal-area surface, I projected all layers into an Albers Equal Area (25 km^2) grid for modelling. The grid was duplicated to create one grid per month-year period, thus giving each grid cell a unique *x*, *y*, *z*, and *t* location. Throughout the remainder of this text, I refer to grids that include only a spatial element as the ‘spatial grid’ and grids that include the month-year period as the ‘spatial-temporal grid’.

2.2.4: Data – Capelin presences

I obtained georeferenced capelin presence data from the Ocean Biogeographic Information System (OBIS, now known as the Ocean Biodiversity Information System) database (OBIS, 2018, Appendix B.2). I subset the dataset to the years 1998 to 2014 to match the oceanographic data availability (excluding 2015 because there were only ten presences recorded in the dataset for the entire year). I removed duplicate entries or those lacking sampling month information. I removed entries that could not be appended to environmental data (see below for details on environmental data extraction). To reduce over-representation of conditions that may arise from over-sampling of cells, I then reduced the number of presences to one per spatial-temporal grid cell (Elith et al. 2006; Bentlage et al.*;* 2013).

For individual species and size classes, sampling gears differ in their ability to capture individuals, influencing detectability of presences and potentially biasing SDMs (Knudby et al. 2013). I gleaned sampling gear information from the metadata submitted to OBIS by data contributors, from which I identified nine broad gear type categories (Appendix B.3).

2.2.5: Modelling Process

I used Maxent (Phillips et al. 2006, Appendix B.4) to model the average spatial distribution of suitable habitat scores on a month-by-month basis (e.g. one model for March including March data from all years between 1998 and 2014 for which there is observation data). I chose Maxent because of the presence-only nature of the species data and its performance, which arguably performs on par with more robust presence-absence models (Elith et al. 2006). By building a model for each month, I could better match environmental dynamics (e.g. temperature changes over time and space) and potential variations in the species-environment relationship to the distribution of capelin. I carried out all analyses in R version 3.5.3 (R Core Team 2019), with the *Raster* (Hijmans 2019), *Dismo* (Hijmans et al. 2017), *EcoSpat* (Broennimann et al. 2018), and *enmSdm* (Smith 2019) packages.

2.2.6: Background Point Generation

Maxent uses background points to characterise the study area. I derived the capelin's horizontal geographic range using a 100% minimum convex polygon (MCP) (Syfert et al. 2014) (Figure 2.1). To include depth with the MCP, I also excluded depth layers falling below the maximum depth of capelin presence. I generated 10,000 background points for each monthly model (Appendix B.5). To prevent over-representation of oceanographic conditions, I permitted only one background point per spatial-temporal grid cell (Elith et al. 2006).

To account for between-month-year variability (e.g. March 1999 vs March 2000) in oceanographic conditions, I weighted the number of background points to the number of presences recorded in each month-year period. For example, if 22% of the unique observations by cell occurred in 2003, 49% in 2004, 29% in 2005, 22% of the background points for that model came from 2003, 49% from 2004, 29% from 2005. To ensure I sufficiently captured conditions across the capelin's range, I also weighted points by the number of spatial grid cells represented in each Northwest Atlantic Fisheries Organization (NAFO) division and the area of the Hudson Strait represented in the MCP (NAFO 2019). For example, I subdivided the 22% of the background points from 2003 so that 8.8% of the cells came from NAFO division 3K, 7.4 from 3L, 4% from 3Ps, etc. (Appendix B.6). This double-weighting of background points reduces the influence of sampling bias, which may impact model performance (Elith et al. 2006).

2.2.7: Data extraction for presence and background points

I extracted ten oceanographic, six climatic, and one static (bathymetry) environmental predictor variables (Table 2.1) for the presence and background points. I included both surface values and values at the depth-layer closest to capelin presence/background points as predictors (Appendix B.1) except for sea surface height, density mixed layer depth, seafloor depth, the AMO, and the NAO because these are single layer values only. To account for the potential lagged influence of AMO and NAO on distributions, I included three metrics for the AMO and NAO predictors: the value of the oscillations during the sampling month, the value during the previous sampling month, and the mean value from the previous winter (December to February). The winter NAO, in particular, exerts an influence over oceanographic conditions in spring, summer and autumn months following, and is associated with shifts in species distributions in the North Atlantic (Fisher et al. 2008, Petrie 2007).

2.2.8: Variable selection

To minimise the impact of collinearity, I selected variables for each monthly model a-priori using Spearman correlation coefficient and variance inflation factor (VIF) (Dormann et al. 2013) (Appendix B.7). I removed variables with correlation coefficients above 0.7 and VIF values above 5.0. I gave variable retention preference to oceanographic variables closest to sampling depth because, given their proximity, they likely have a more direct impact on species occurrence than more distal values. Although Maxent performs well even with small sample sizes (Pearson et al. 2007), I employed a minimum events per variable (EPV) rule which states that a minimum of five samples per predictor variable is required to run a distribution model (Yalcin & Leroux 2018). As such, I only modelled those months with a minimum of 45 samples (five x eight predictor variables) to avoid erroneous estimation of predictor variance.

2.2.9: Maxent modelling

I executed monthly models using Maxent version 3.4.1. To allow entropy to be reached, I set the maximum number of iterations to 5000 for each model. I also set regularisation (β) multiplier values for each model to reduce overfitting and complexity. To determine regularisation values, I constructed a series of test models for each month with regularisation values ranging from 0.25 to 4 at 0.25 step intervals. Optimal regularisation values were determined using Akaike's Information Criterion adjusted for small sample size (AICc) (Warren & Seifert 2011). Final models used the regularisation value that resulted in the lowest AICc.

I used temporally-split cross-validation to train and test each model, using one year for the training data to test against all other years, repeating until all years were used for training. This approach ensured training and testing data independence and minimised the risk of performance overestimation arising from environmentally correlated folds (Radosavljevic & Anderson 2014). I assessed models performance using testing and training area under the curve (AUC) scores (Phillips et al. 2006), true skill statistic (TSS) (Allouche et al. 2006), and the continuous Boyce index (CBI) (Boyce et al. 2002) (Appendix B.8). I calculated each metric separately for each temporal fold, which I then averaged to produce mean performances for each model. Finally, I created permutation plots for each model to measure the mean variable importance of each of the environmental variables used.

2.2.10: Spatial predictions

I created average monthly maps based on Maxent's complementary log-log (cloglog) transformation, which provides an estimated probability of presence (habitat suitability) (Phillips et al. 2017). In order to predict habitat suitability across the 2.5D space as a whole (i.e. across all depth layers), for each oceanographic variable, I concatenated individual depth layers to create a continuous grid, which retains each depth layer and its associated variable values (Bentlage et al. 2013, Appendix B.9). I produced habitat suitability score maps for each temporal fold, which I then averaged to create the average monthly maps.

To explore general patterns in the habitat suitability scores, I also converted the maps into binary suitable/not suitable habitat maps using a Maximum Kappa derived threshold. This threshold is used in a wide range of distribution modelling studies (e.g. Davidson et al. 2017, Scherrer et al. 2018), demonstrates resiliency to prevalence which cannot be accurately determined with presence-only data, and shows good agreement with the AUC (Nenzén & Araújo 2011).

2.3: Results

I obtained a total of 11,516 presence points that matched the required spatial and temporal extent from OBIS. After cleaning the data (see Methods), a total of 6,350 presence points remained. Presence point data availability for modelling varied by month, with June having the highest number of presences (*n* = 1,263) and February the lowest (*n* = 10) throughout the study period (1998-2014) (Appendix B.2).

Of the eighteen variables selected a-priori, multicollinearity analysis indicated only six, five, and nine variables could be included in the final models for January, February, and March to December, respectively. However, following the EVP rule, I did not run a February model because there were insufficient presence points. I also chose not to run a January model due to the smaller number of sampling years compared to the others (four years vs eleven+ years for March to December). Selected variables for the March to December models are presented in Table 2.1.

Table 2.1*: Variables used before and after a-priori variable selection based on Spearman Correlation and VIF for the March – December models.*

Data	**Variables**
All Variables prior to selection	Chl (surface); Chl (depth); Depth; MLP; O2 (surface); O2 (depth); Salinity (surface); Salinity (depth); SSH; Temperature (surface); Temperature (depth); NAO (prev); NAO (sample); NAO (winter); AMO (prev); AMO (sample); AMO (winter); Gear
Variables selected for the March – December models	Chl (surface); O2 (depth); Salinity (depth); Temperature (depth); NAO (prev); NAO (sample); NAO (winter); AMO (sample); AMO (winter)

Variable abbreviations: depth – value of the variable at presence depth; surface – value of the variable at the sea surface; Chl – Chlorophyll concentration (mmol.m $^{-}$3); Depth – Seafloor depth; MLP – Mixed layer thickness (meters); O2 – Dissolved Oxygen (mmol.m $^{-}$3); Salinity – Salinity (PSU); SSH- Sea Surface Height (meters) Temperature – Temperature (kelvin); NAO – North Atlantic Oscillation; AMO – Atlantic Multidecadal Oscillation; sample – value during the sampling month; prev – value from the previous month; winter – value during the previous winter; Gear – Gear Type (Table B.3 in Appendix B.3).

2.3.1: Maxent model results

On average, the monthly models performed very well (metrics Train AUC, Test AUC, TSS, and CBI; Appendix B.8). Overall, mean performance of the models was highest in December (mean Train AUC 0.95, mean test AUC 0.97, mean TSS 0.89, mean CBI 1) and lowest in October (mean Train AUC 0.92, mean test AUC 0.89, mean TSS 0.72, mean CBI 0.99).

The average permutation importance of the variables for each model also varied (Figure 2.2). Temperature contributed the most to predicting capelin distribution in the June (41%), July (27%), August (44%), September (41%), October (46%), and November (31%) models, and the least to the March (11%), April (3%), and May (2%) models. Salinity had the strongest influence in the March model (38%) and was never ranked the least important variable in other months. Chlorophyll α had the strongest influence on predicted distribution in the December model (41%) and was least important in the May (5%), June (9%), August (1%), and September (3%) models. Dissolved oxygen was the most important predictor of capelin distribution in the May model (51%) and the least in the July (10%), October (8%), and December (12%) models. In all monthly models, the climate oscillations were the least important of all the variables (range <1% for NAO value from the previous month in June, to 16% for the NAO value from the previous winter in April).

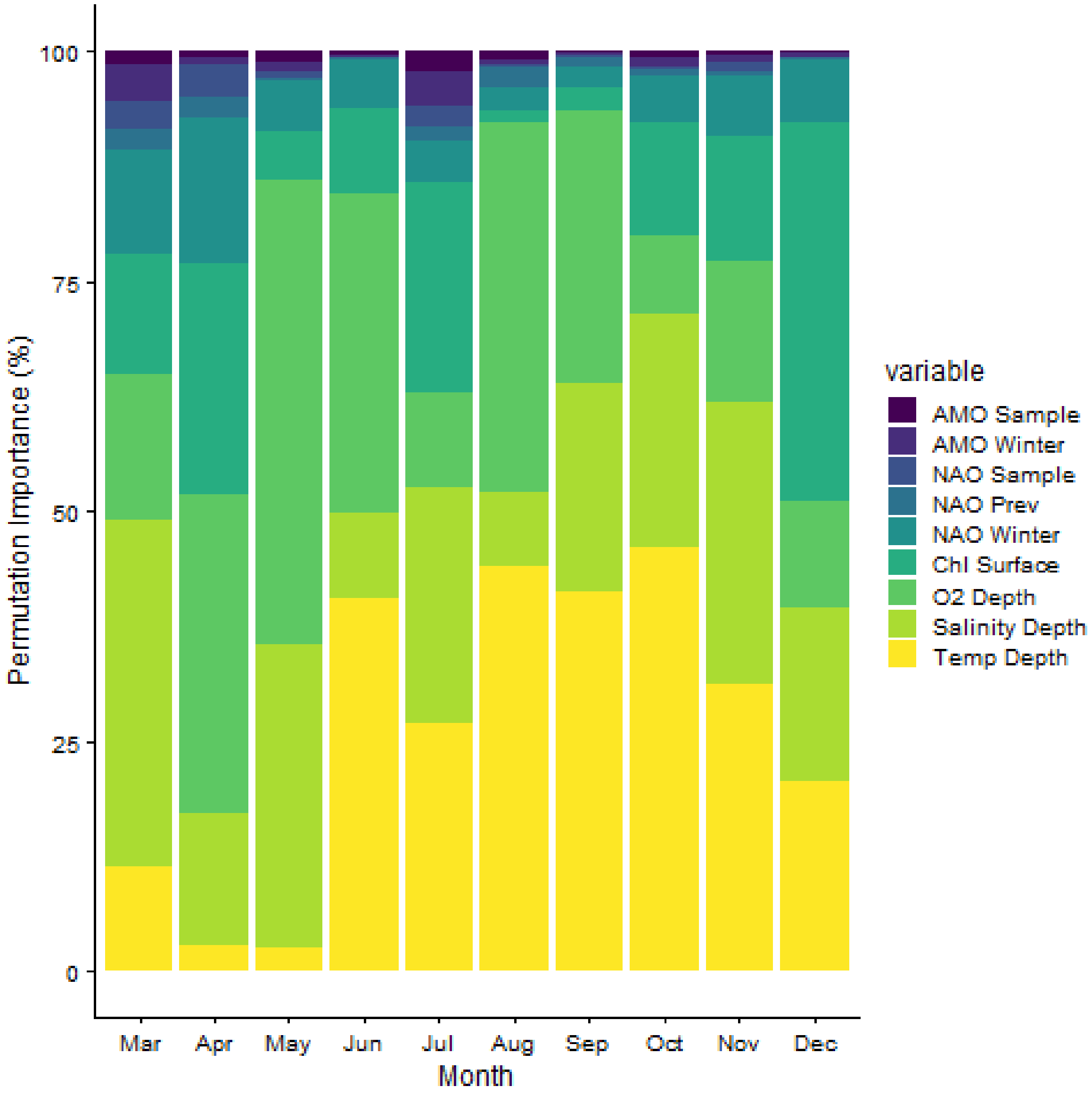

Figure 2.2: *Average permutation importance of environmental variables used in the models. Values represent averages (across temporal folds) for each month. See Table 2.1 for a definition of the variables.*

2.3.2: Monthly habitat suitability maps

I produced average habitat suitability maps based on Maxent's cloglog transformation, depicting habitat suitability scores from ~0.5 meters depth to ~1,045 meters depth between March and December inclusive. The habitat suitability maps reveal variability in the spatial extent and location of areas with high suitability scores (Figures 2.3 and 2.4), including over depth (Figure 2.5). Across all depth layers, October had the largest areas of high suitability than all other months, and September the smallest. On average, the highest suitability scores corresponded to depths of ~244 meters and shallower, except for October, November, and December, where higher suitability scores corresponded to greater depths.

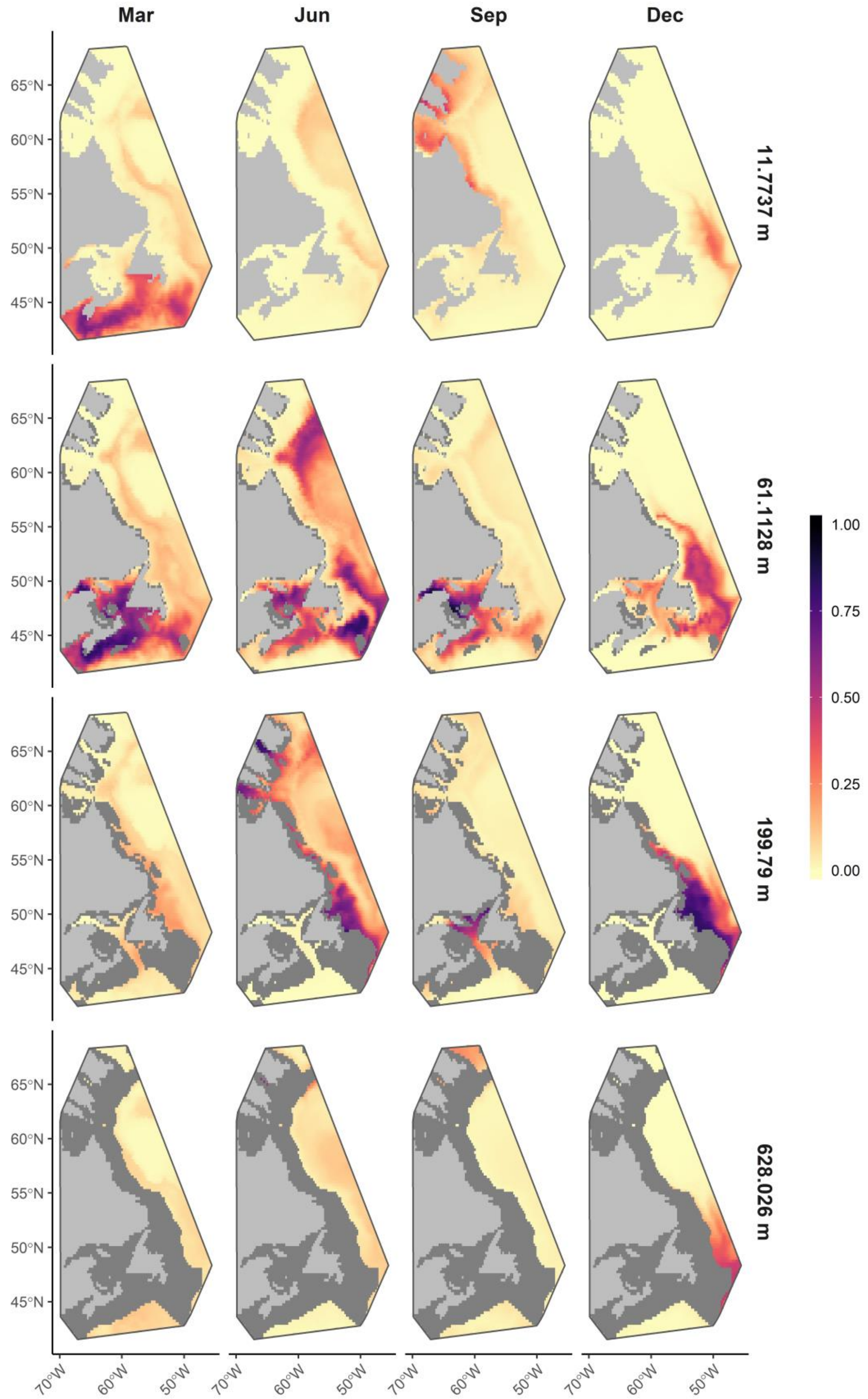

Figure 2.3*: Sample of predicted habitat suitability maps for March, June, September, and December over four different depth layers. Dark grey indicates the seafloor and light grey landmass. Lighter colours indicate lower suitability and darker colours higher. Months and depths have been selected arbitrarily for illustrative purposes only.*

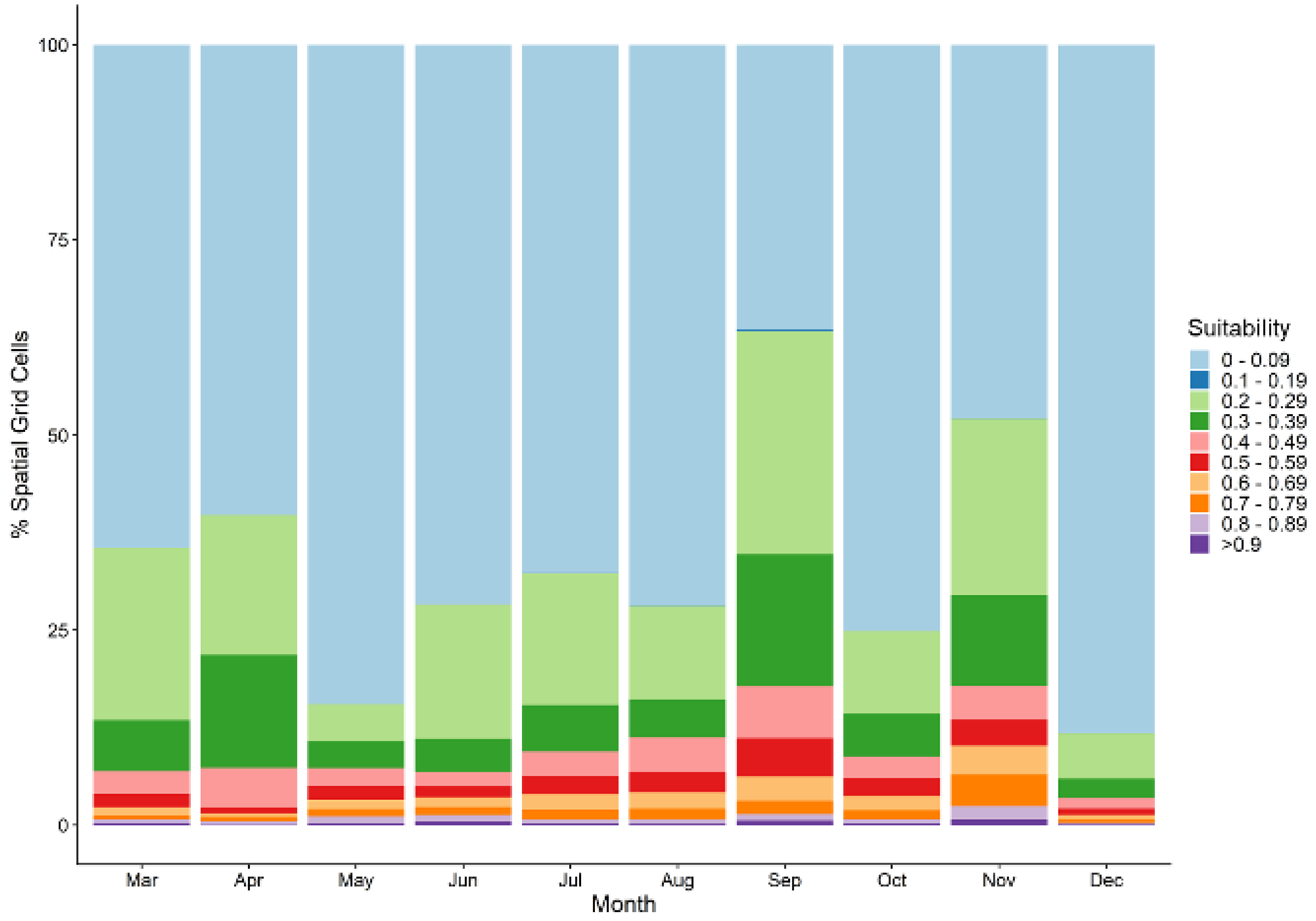

Figure 2.4*: Percentage of spatial grid cells falling into suitable habitat for each of the modelled months.*

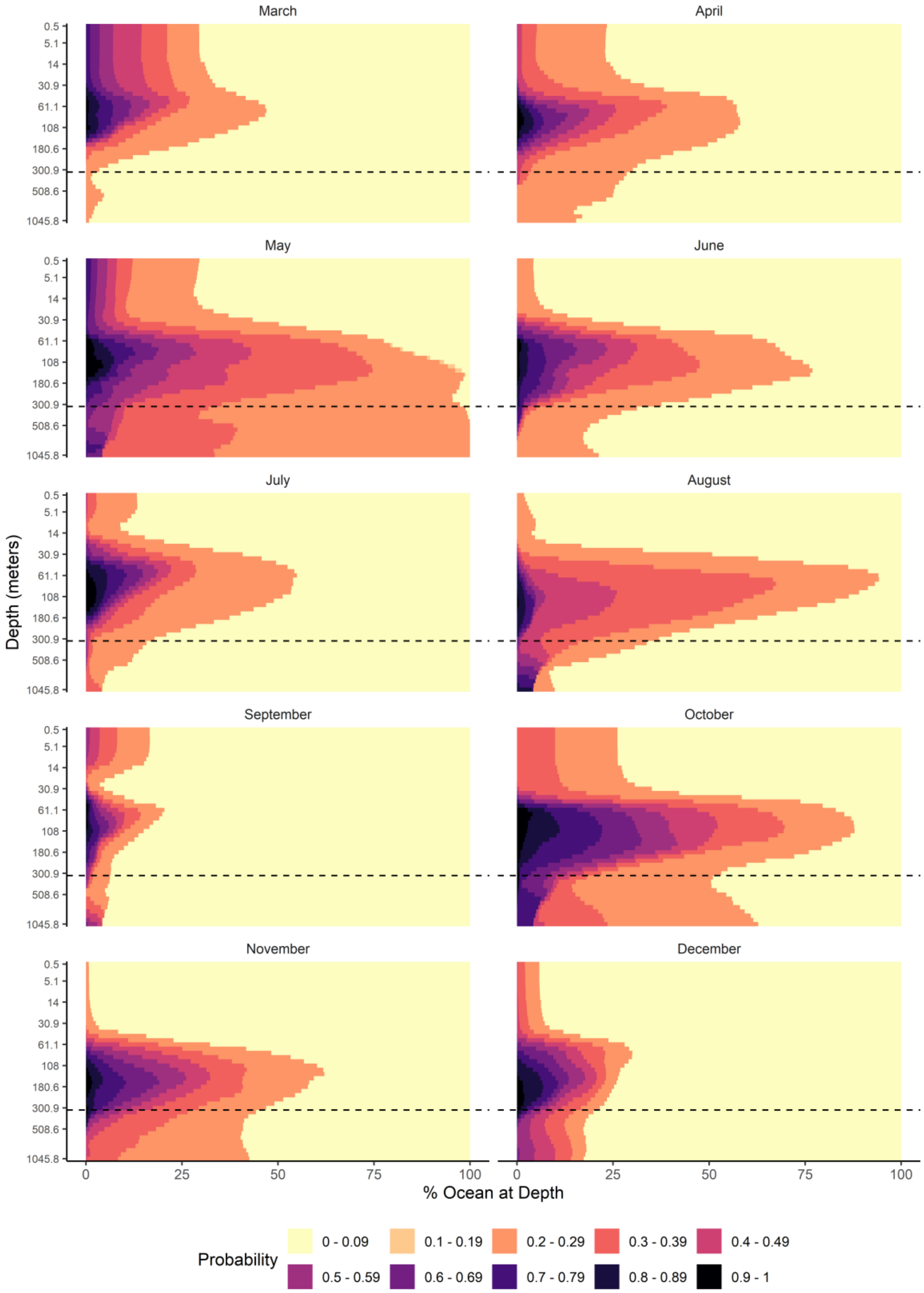

Figure 2.5*: Vertical distribution of predicted habitat suitability from March to December relative to the ocean available at each depth. Note the greater area of ocean at higher depths than lower depths due to increasing intrusion of the seafloor and that depth layers are not evenly spaced (see Appendix B.1). Lighter colours indicate lower suitability and darker colours higher. The dashed line represents the median seafloor depth for the study area (~313 meters).*

By converting the habitat suitability maps into binary predicted suitable/not suitable habitat, I highlighted differences in the horizontal and vertical distribution of suitable habitat across the study area (Figures 2.6 and 2.7). From March to June, predicted suitable habitat shifted eastwards, extending from the Gulf of St Lawrence and around Nova Scotia to encompass eastern Newfoundland and the Grand Banks (western trailing cell centroid in March 67.75°W to 64.5°W in June, eastern leading cell centroid in March 55.25°W to 46.25°W in June), with some cells classified as suitable habitat appearing further north. The vertical distribution of suitable habitat also expanded, with cells occupying depth layers from ~0.5 meters to ~147 meters in March to ~42 meters to ~656 meters in June. From July to September, suitable habitat cells largely shrunk back to the Gulf of St Lawrence (western trailing cell centroid in July 69.25°W to 69°W in September, eastern leading cell centroid in July 52.5°W to 57.5°W in September), before expanding in October to encompass the eastern side of Nova Scotia and Newfoundland. During August, suitable habitat cells occupied the greatest number of depth layers (~27 meters to ~1,046 meters). In November, cells shift eastwards (western trailing cell centroid in October 62.0°W to 59.5°W in November, eastern leading cell centroid in October 48.0°W to 46.75°W in November) and northwards along Labrador (southern trailing cell centroid in October 43°N to 44.75°N in November, northern leading cell centroid in October 51.0°N to 54.75°N in November) before contracting to eastern Newfoundland in December. The number of depth layers with suitable habitat also reduced (~69 meters to ~509 meters in November, and ~69 meters to ~458 meters in December). Following these distribution patterns, the percentage of spatial grid cells predicted to be suitable habitat in all months remains relatively small – from 0.72% of the total spatial grid in April to a maximum of 3.45% in November (Figure 2.6).

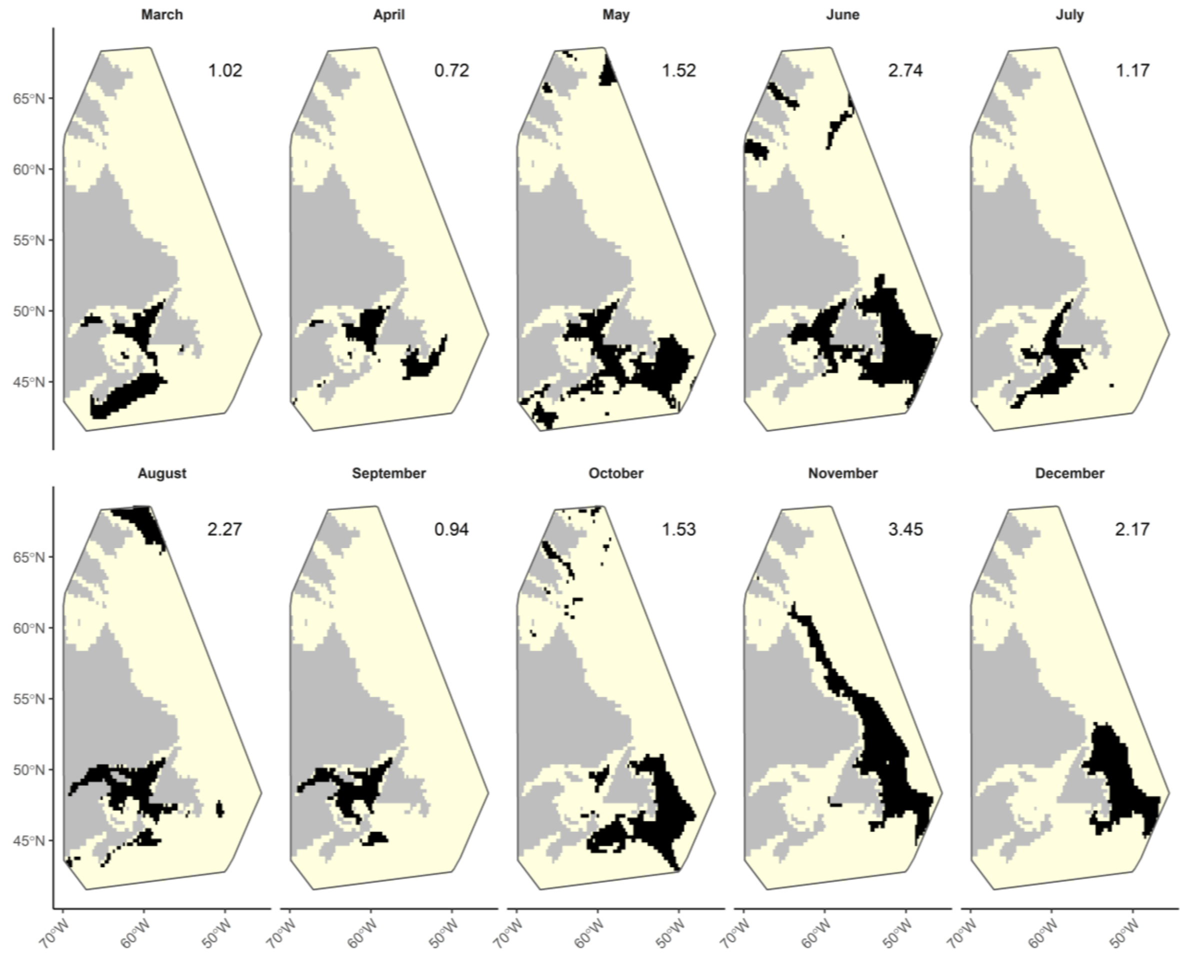

Figure 2.6*: Two-Dimensional Overview of the horizontal (x, y) average location of predicted suitable (black) and unsuitable (yellow) habitat for each modelled month, based on Maximum Kappa thresholds applied to Maxent model outputs. Suitable areas indicate the location of a suitable habitat cell, regardless of depth. The value on the top right indicates the percentage of cells in the spatial grid classified as suitable habitat.*

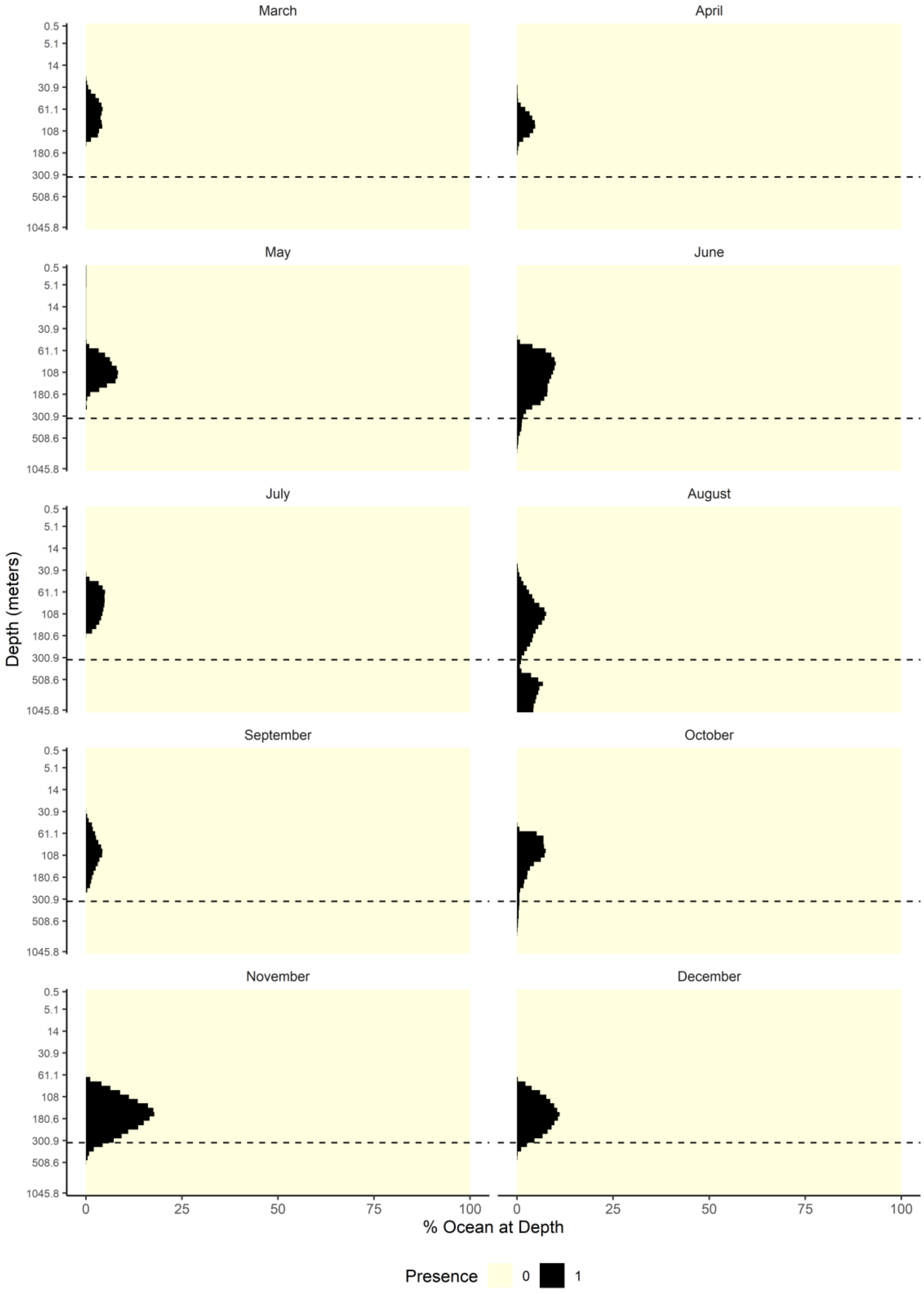

Figure 2.7*: The vertical average distribution of predicted suitable (black) and unsuitable (yellow) habitat relative to the amount of ocean available at each depth-layer for each modelled month, based on Maximum Kappa thresholds. Sea surface is represented at the top of the y-axis and deepest depth at the bottom. Note the greater ocean area at higher depths than lower depths due to increasing intrusion of the seafloor and that depth layers are not evenly spaced (see Appendix B.1). The dashed line represents the median seafloor depth for the study area (~313 meters).*

2.4: Discussion

For marine pelagic species that can move extensively horizontally and vertically throughout the water column, species distribution models should explicitly consider space in four dimensions – across depth and time as well as longitude and latitude. By coupling 17 years of presence data with "2.5-dimensional" oceanographic models, I quantified the spatial-temporal dynamics of relative habitat suitability throughout the water column across Atlantic Canada and the relative importance of modelled variables on a month-by-month basis.

The analysis indicates variable range and distribution of suitable habitat scores over depth and among monthly models. When grouping habitat suitability scores into suitable/not suitable habitat, I found suitable habitat in November showed a ~5-fold increase from the minimum estimated for April. I also observed depth changes with, for example, suitable habitat primarily located further west in shallower waters in March than in December. This pattern is consistent with observations of capelin moving eastwards and into deeper waters towards the end of the year (Carscadden and Nakashima, 1997). Although alternative thresholds may adopt a lower value for binning predictions into suitable/not suitable habitat (Nenzén & Araújo 2011), I expect the general distribution patterns to remain.

The binary maps also highlight months with notably different predicted distributions. Alongside the larger area in November that spreads northward, in May, June, August, and October, northern 'clusters' disconnected from the main distribution appeared. The OBIS database provides fewer capelin presences in the northern portion of the study area than further south (Figure 2.1). However, due to the nature of presence data, it is not clear if this pattern results from low levels of surveying, lack of reporting, or reflects genuine capelin absences. Nevertheless, the northern portion of the study area is not as extensively surveyed as the rest (e.g. DFO 2011), and thus potentially faces the highest risk of incorrect spatial prediction (Merow et al. 2013). This issue may also impact predictions at depths greater than

500 meters (Appendix B.2). Indeed, presence-only data prevents full assessment of the level of sampling effort involved, which may result in an environmental bias in the model. Furthermore, observational data also suffers from spatial biased (i.e. not collected from the entire study-region year-round), further compounding the risk of environmental bias and increasing the risk of under-prediction of the distribution of suitable habitat. Nevertheless, environmental conditions may also be suitable for capelin in the northern portion of the study area. While recognising the challenges of surveying this more remote area e.g. extensive sea ice during the winter months, increasing survey effort in the northern portion of the study area throughout the year may improve our understanding of capelin distribution, particularly in light of climate change and associated changes in oceanographic conditions (Lenoir et al. 2020).

Several studies suggested that including climate oscillation indices in distribution modelling could prove fruitful (Hermosilla et al. 2011, Roberts et al. 2019). The analysis indicated that the NAO and AMO indices play a minor role in the models. Although the models captured the temporal variability in the values of these indices, they do not capture their spatial influence on oceanographic conditions. Additionally, and with respect to the AMO, the study period is likely to be too short to capture significant variation in the index values because positive values dominated the period. Given that distributional changes in some marine species are correlated with climate oscillations (Roberts et al. 2019), determining how best to incorporate oscillations into distribution modelling warrants further investigation.

By producing monthly models, I was able to assess potential changes to capelin’s species-environment relationship via the relative permutation importance of modelled variables. Temperature is widely considered a key determinate of current and shifting marine fish distributions, including capelin (Rose 2005, Lenoir et al. 2020), though it also plays a small role in interannual variations in the distribution of some species (Thorson et al. 2017). I found temperature contributed the least to the March to May and December models. Alongside temperature, oxygen places substantial metabolic constraints on marine species distributions (Deutsch et al. 2015). This influence is most notable in the April and May models, in which dissolved oxygen became the most important predictor of capelin occurrence.

The changes in relative variable importance revealed in the models indicate potential variation in the capelin's realised niche relative to variations in conditions experienced in each month. For example, water temperatures are on average warmer in August than in March (Appendix B.10). With capelin being a cold-water species, warmer temperature is likely to be a more limiting variable (and thus have higher permutation importance) in August than March. Similarly, capelin tend to occupy a narrow salinity range (Rose, 2005), which may partially explain salinity's generally high permutation importance. Concerning the March model, in which salinity was the most important variable, a general freshening of water resulting from a combination of sea ice and lag effect of the Labrador Current, which is typically stronger during winter months, may also have played a key role (Han et al. 2008, Long et al. 2016). With regards to the increased importance of dissolved oxygen in May, this may be related to spring phytoplankton blooms. However, I note that the pattern is not repeated later in the year in relation to autumn blooms (Greene et al. 2008a), acknowledging that spring and autumn blooms may differ in intensity. By capturing changes in the relative importance of variables, particularly for small pelagics such as capelin whose distributions are closely tied to environmental conditions, monthly models have the potential to closely reflect temporal dynamics in species realised niches, improving our understanding and predictive ability regarding changing distributions under current and future conditions.

Distribution models require consideration of the relevant spatial and temporal scales at which species and oceanographic processes operate (Mannocci et al. 2017). The oceanographic data chosen to model distributions dictate the resolution of the models (monthly averaged 25° grid cell). While these models allowed me to encompass a long period of capelin data, their resolution may be too coarse, particularly during biologically important periods, such as during the spawning period when capelin physiology and behaviour changes (Rose 2005, Davoren et al. 2006b). I also note that the models do not distinguish between sub-populations in the region and thus ignores potential variation in sub-population responses to environmental correlates. Furthermore, the models presented in this study provide monthly average distributions, potentially masking interannual variation in conditions that determine distributions (Boyce et al. 2002). The continued development of finer spatial and temporal scale models, including those that resolve surface and subsurface dynamical features such as currents and eddies (Brodie et al. 2018), may create more refined distribution models, with their predictive output allowing for more efficient implementation of management measures (Lewison et al. 2015, Dunn et al. 2016), including nowcasting and forecasting of species distributions for pro-active management.

This study adds to the small albeit growing body of distribution models that embrace a “2.5-dimensional” approach and models that attempt to capture distribution changes on timescales more relevant to the dynamic nature of pelagic species. With survey effort spatially and temporally patchily distributed throughout the modelled space, the predicted distribution of suitable habitat offers new insights into the potential distribution of capelin – a forage species with substantial ecological importance in Atlantic Canada, and whose life-histories are sensitive to changing environmental conditions. By capturing species spatial-temporal dynamics over horizontal and vertical axes, and changes in the relative importance of modelled variables, such studies can enhance understanding and predictive modelling ability of pelagic species distributions under current and future conditions for pro-active ecosystem-based conservation and fisheries management.

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Chapter 3: Influence of the North Atlantic Oscillation on the distribution of a keystone pelagic fish

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Abstract

The spatial-temporal variability of mobile pelagic species presents a challenge for elucidating their ecology, interactions with other species, and ecosystem functions. This variability can be further complicated by cyclical-driven changes in distributions, such as those driven by large-scale climate oscillations like the North Atlantic Oscillation (NAO). Fish communities in the Northwest Atlantic have undergone substantial change over the past several decades, including changes to the ecology of keystone prey species. Using 17 years (1998 – 2014) of presence data and the species distribution model Maxent, I quantify changes in the horizontal (*x*, *y*) and vertical (*z*) monthly modelled distribution of suitable habitat for capelin (*Mallotus villosus*)—a migratory pelagic forage fish—in the Northwest Atlantic Ocean between positive and negative phases of the NAO and over the time-series as a whole, on a month-by-month basis. I hypothesised that shifts in the NAO would impact the distribution and range margins (e.g. size of suitable patches, northern bounding) of capelin over time. I found (1) substantial stability in predicted suitable habitat between the two NAO phases, (2) differences in the percentage of the study area predicted as suitable habitat largely arise from an expansion/contraction of existing patches of suitable habitat, and not from the appearance of new patches, and (3) over time, relative habitat suitability scores decline in six of the ten months modelled. Unlocking the spatial-temporal predictability and variability of pelagic species distributions may assist in dynamic and more traditional spatial management processes targeting pelagic species and interacting heterospecifics.

3.1: Introduction

Habitat loss and deterioration, climate change, invasive species, and pollution increasingly degrade the world's oceans (Halpern et al. 2015), with the overexploitation of wild marine populations in particular regarded as one of the most pervasive threats to marine biodiversity (Pauly & Palomares 2005a, McCauley et al. 2015). To protect and promote sustainable use of the ocean, the use of spatial management measures such as marine protected areas whose primary objectives relate to the conservation of biodiversity, and fisheries closures whose primary objectives focus on managing human interactions with commercially important species (Day et al. 2019) is growing. However, the application of spatial management measures remains challenging for migratory and other highly mobile species, in part because their spatial-temporal dynamics are not fully understood.

Large-scale climate oscillations, such as the El Niño Southern Oscillation (ENSO) and the Madden–Julian oscillation (MJO), influence oceanographic conditions globally and regionally (Webber et al. 2010, Roemmich & Gilson 2011). In the North Atlantic Ocean, fluctuations in oceanographic conditions relating to the North Atlantic Oscillation (NAO)—an oscillation in atmospheric surface pressure between the Icelandic Low, a semi-permanent low-pressure system between Iceland and southern Greenland in the North Atlantic/sub-Arctic, and the Azores High, a semi-permanent high-pressure system in the sub-tropical Atlantic (Visbeck et al. 2003)—has been associated with latitudinal and longitudinal distribution shifts in several marine species (Fisher et al. 2008, Greene et al. 2013, Roberts et al. 2019). The NAO oscillates between positive (when the pressure difference between the Icelandic Low and Azores High is large) and negative phases (when the pressure difference between the Icelandic Low and Azores High is small) on an irregular basis (Hall et al. 2017). Although the NAO is not currently predictable over long time scales (Domeisen et al. 2017), climate modelling suggests that, under current anthropogenic emission scenarios, the NAO will move towards a more positive trend (Rind et al. 2005, Gillett & Fyfe 2013).

Bio-logging technologies, species distribution modelling, oceanographic data availability, and oceanographic models are helping to reveal patterns and variations in pelagic species distributions (Maxwell et al. 2015, Hays et al. 2019, Andrews et al. 2020). Unlocking the spatial-temporal predictability and variability of pelagic species distribution patterns, particularly under changing oceanographic conditions, may assist in their management (Boerder et al. 2019, Pinsky et al. 2020). For example, models can inform dynamic management (management that changes in space and time in response to the shifting nature of the ocean and its users), and more static spatial management approaches such as time-area fishery closures that occur at a specific location, often at the same time every year (Lewison et al. 2015). They can also provide information relevant to population status (Link et al. 2011) and assist in separating natural fluctuations in distribution changes from longer-term trends (Fogarty et al. 2017). Furthermore, distribution shifts of keystone species such as forage fish—small, schooling, planktivorous species situated in the middle of marine food-webs—have ramifications for predator-prey and broader food-web relationships (Rose & O’Driscoll 2002, Cury et al. 2011, Pikitch et al. 2012).

Here, I quantify changes in the horizontal (*x*, *y*) and vertical (*z*) monthly modelled distribution of suitable habitat for capelin (*Mallotus villosus*) in Atlantic Canada under changing oceanographic conditions. Capelin is a small migratory forage fish that is considered a keystone species in the Atlantic Canadian Ocean food-web (Rose & O’Driscoll 2002). In terms of human consumption, capelin are targeted in recreational, indigenous, and commercial fisheries, and are considered critical for numerous predators such as Atlantic cod (*Gadus morhua*) and various seabird species (Buren et al. 2014a). Capelin distributions respond rapidly and directly to changing oceanographic conditions and indirectly through changes to planktonic prey abundance and distributions (Rose 2005, Carscadden et al. 2013a, Buren et al. 2014a, Villarino et al. 2015). Such rapid changes exhibited by forage fish (Peck et al. 2021) generally present challenges for relatively static approaches to managing human interactions with this ecologically important group. Potential distribution fluctuations across the region in relation to changing oceanographic conditions are not yet fully understood.

In Chapter 2, I included NAO index values into distribution models for capelin as a potential driver of habitat suitability. I found that the NAO had low permutation importance, potentially because including the NAO index values directly does not capture the variation spatial in oceanographic conditions experienced during the two phases. Here, I assess how differences in ocean conditions, as seen through the lens of NAO phases impact the distribution and range margins of capelin over time. I evaluate variation in the monthly horizontal (x, y) and vertical (z) distribution of suitable capelin habitat in Atlantic Canada using Maxent (Phillips et al. 2017) (1) between positive and negative winter NAO phases and (2) trends across the data time-series as a whole. On a month-by-month basis, I quantify variation in the horizontal (x, y) and vertical (z) distribution of suitable capelin habitat via boundings of predicted suitable habitat, percentage of the study area predicted as suitable, and suitable habitat patch number and size, between NAO phases and over the time-series. I also evaluate the stability of suitable habitat between phases and assess overall increasing and decreasing trends in the relative habitat suitability for each month. I discuss the use of species distribution models for detecting between-phase and time-series changes in distributions and implications for spatial management.

3.2: Materials and Methods

3.2.1: Study Region

The study region (hereafter “Atlantic Canadian region”) broadly extends from 40°N to 70°N. It includes waters lying up to the Canadian Exclusive Economic Zone (24 nautical miles from the low water line) and adjacent waters, including those on the Flemish Cap and the French territory of Saint Pierre and Miquelon (Appendix C.1).

The Atlantic Canadian region is temperate to sub-Arctic, dominated by the southward-moving Labrador Current bringing cold water from the Arctic, and the warmer, more saline Gulf Stream, which travels eastwards past the southern extents of the Scotian and Labrador Shelves. Responses of the region’s oceanographic climate to the NAO vary spatially, with winter NAO phases in particular influencing oceanographic conditions throughout the remainder of the year (Petrie 2007). For example, in years with positive NAO winter phases, Newfoundland and Labrador receive greater bouts of cold Arctic air brought in by stronger northwesterly winds, cooler sea temperatures, a larger, deeper cold intermediate layer, and heavier sea ice cover than in negative phases (Greene et al. 2013). Furthermore, positive NAO winters phases correlate more strongly with a weaker Labrador Current than in negative phases (Wang et al. 2016). As a result, Labrador Sea water can reach the Laurentian Channel in years with a positive NAO winter phase. In contrast, negative phases are correlated with an intensification of the Labrador Current allows penetration further south, even as far as the New York Bight (Marsh et al. 1999). Additionally, waters across most of the region, except the central and western Scotian shelf into the Gulf of Maine, are less saline and cooler during positive than negative phases (Petrie 2007). More broadly, climate-related changes to oceanographic conditions vary across the region. Generally, sea temperatures are warming, and ocean pH and sea ice cover levels are declining (Bernier et al. 2018). The specific study area (the area to which I limit the analyses) is defined by capelin presence data (see below).

3.2.2: Data: Environmental

I acquired temperature, salinity, oxygen, and chlorophyll data from the global numerical modelling products GLORYS V4.1 (CMEMS 2018a) and BIOMER V3.2 (CMEMS 2018b) for the years 1998 to 2014 inclusive. These variables were selected a priori (see Appendix C.2 for variable selection process). The models provide monthly average values for each oceanographic variable across 75 depth layers (0.5 meters to 5,902 meters at varying intervals –Appendix C.3) at a horizontal resolution of 0.25˚. Each depth layer is treated as a flat, two-dimensional slice, creating a “2.5D” ocean environment (Duffy & Chown 2017) in which I can apply common metrics to assess changes in distribution (see below). I converted all layers to a Canada Albers Equal Area Conic projection (25×25km). I gave each grid cell a unique identifier based on the longitude and latitude (*x*, y) location of each cell’s centroid, the depth layer the cell fell into (*z*), and the month and year (*t*). This set of grid cells is used to filter the presence points and create the background points for the distribution models (see below). I also obtained winter (December to February inclusive) NAO values (principle component based) from the National Center for Atmospheric Research (NCAR), calculated from the leading empirical orthogonal function sea level pressure anomalies between 20°-80°N, 90°W-40 °E (NCAR 2019). I calculated the NAO winter anomaly values using the 1981-2010 standard climatology (WMO 2017) and categorised them into positive and negative phases (Figure 3.1, Appendix C.4).

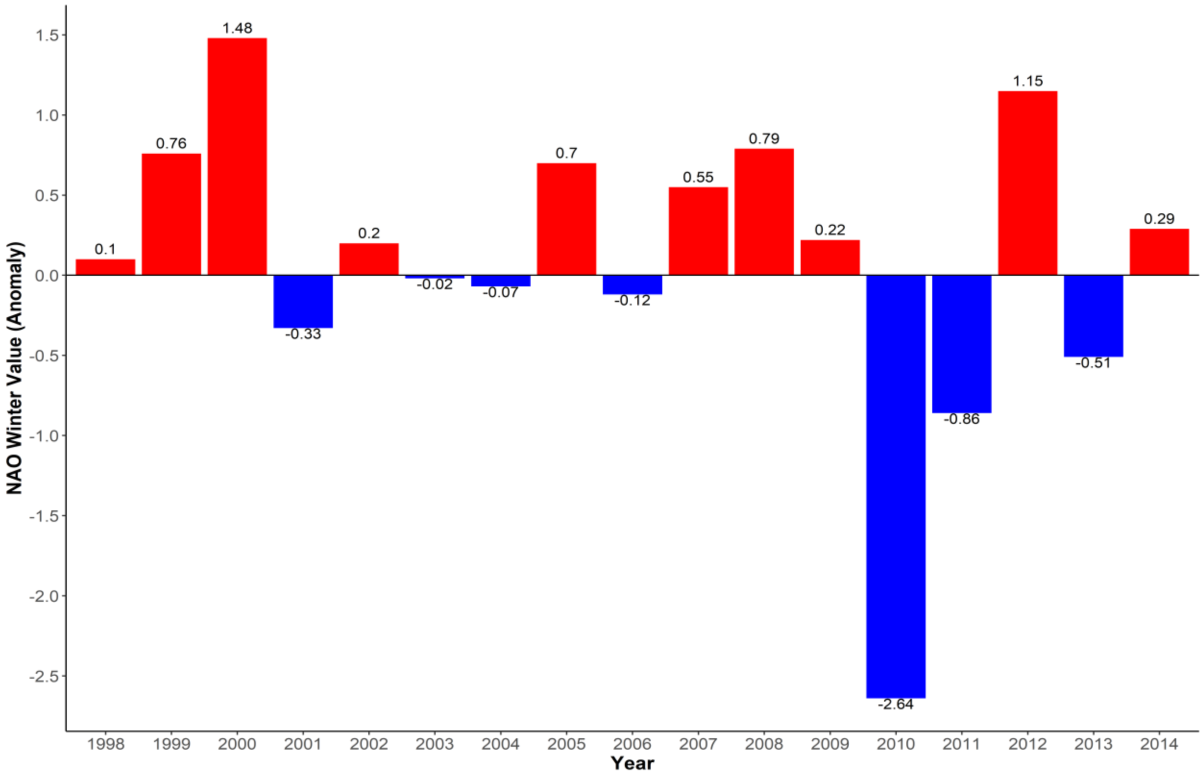

Figure 3.1: *NAO Winter anomaly values for the years 1998 to 2014 inclusive.*

3.2.3: Data: Species

I used capelin presence-only datasets for 1998 to 2014 inclusive, obtained from the Ocean Biogeographic Information System (OBIS, now known as the Ocean Biodiversity Information System) database (OBIS 2018). Organisations such as fishery management authorities and research institutions provide the datasets held in OBIS. At a minimum, submitted datasets contain a longitude-latitude location for observed species and an observation date; OBIS does not contain specific absence data. I retained presences that laid in or adjacent to the Canadian EEZ. Based on a minimum events per variable rule, which requires a minimum of five presences per predictor variable (Yalcin & Leroux 2018), I was unable to model February (10 unfiltered presences over three years). I also chose not to model January (154 unfiltered presences spread over four years) due to the low number of years represented by the presence data compared to the other months (ranging from 10 in August to 17 in September – Appendix C.4).

To prevent modelling outside of the capelin's potential horizontal (*x*, *y*) and vertical (*z*) geographic range, I used the capelin presence records to refine the study area—the area to which I restrict the analyses (Appendix C.1). The horizontal (*x*, *y*) boundaries were determined using a 100% minimum convex polygon (Syfert et al. 2014), whereas the vertical (*z*) boundary was limited to the deepest sampled oceanographic depth layer (Appendix C.3). The study area used the same 25×25km grid as the oceanographic data.

For the remaining months (March – December), I removed presences that lacked sampling depth information and whose locations fell outside the area covered by the oceanographic models (e.g. fell onto land or below the sea floor according to the oceanographic models). To avoid duplicating oceanographic conditions associated with capelin presences, I further reduced the presence data to only one presence per cell in the study area (Elith et al. 2006), leaving a total of 6,186 presence points across 10 months and 17 years. Because the sampling depth of the presences does not align perfectly with the depth layers provided in the oceanographic model, each presence was assigned to the depth layer nearest to sampling (Appendix C.3). I extracted oceanographic predictor variables to the presence points. I included surface values only for chlorophyll and the value at sampling depth-layer for temperature, salinity, and oxygen.

3.2.4: Modelling and Analysis

To assess the distributional changes between phases and across the time-series as a whole for each month, I (1) created a Maxent model for each month (all years included), (2) predicted habitat suitability for each month-year for which I have capelin data, (3) assessed distribution changes between the two NAO phases, and (4) applied a series of trend analyses (Figure 3.2). I now outline each of these steps.

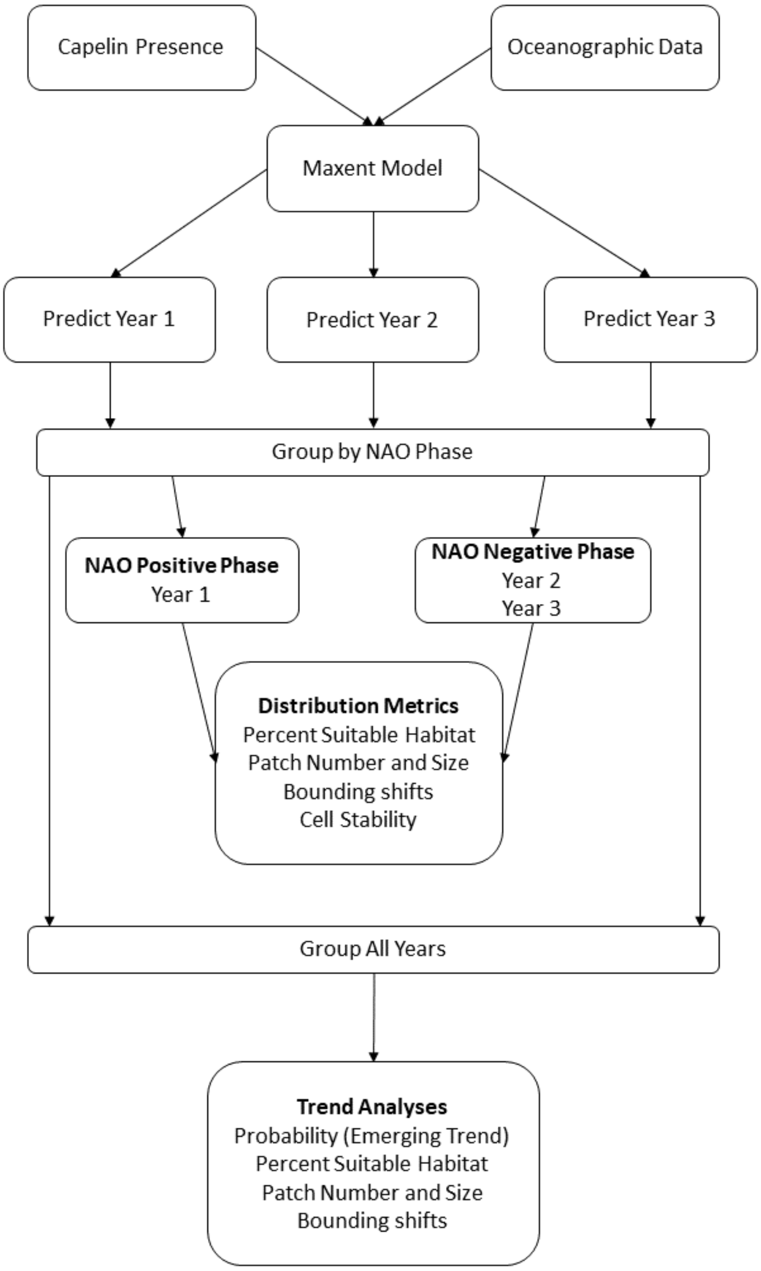

Figure 3.2*: Methods for modelling and distribution and trend metrics for a single month. The process was identical for each month. I fit Maxent models for capelin presence and environmental data for all years in one month (i.e. March 1999, March 2000, etc.). Then I predicted the distribution of capelin for each year of that month based on that year's environmental conditions. After grouping the prediction into NAO phases, I conducted two levels of analysis. First, I investigated patterns in distribution metrics and second, I conducted trend analysis. See text for full details on methods.*

3.2.4.1. Species distribution modelling

I used Maxent version 3.4.1 (Phillips et al. 2017, Appendix C.5) to model relative habitat suitability in the study area. Maxent predicts relative habitat suitability by comparing environmental conditions where the species of interest was present with conditions in the wider study area where the species might also occur (the background). Maxent is considered a robust model for presence-only data, such as that I have obtained from OBIS, and compares favourably to presence-absence-based options such as generalised linear models (GLMs), generalised additive models (GAMs), and boosted regression trees (BRTs) (Elith et al. 2006). To match the temporal dynamism in oceanographic variables and potential variation of capelin response to those changes, I built one Maxent model per month. The monthly approach follows similar approaches used by Alabia et al. (2016) and Wang et al. (2018) to model the distributions of marine pelagic species. I restrict model comparisons to within-month only because drawing comparisons between the output generated by models fit with different data points can be problematic (Guisan et al. 2017). For each model, I set the maximum number of iterations to 5000 (to allow entropy to be reached) and set regularisation (β) multiplier values to reduce overfitting. Regularisation values were selected using the lowest Akaike's Information Criterion adjusted for small sample size (AICc) score (Warren & Seifert 2011) from values ranging between 0.25 and 4, at 0.25 step intervals.

To provide each monthly Maxent model with background points, I extracted oceanographic variables to 10,000 background points per month, generated across the study area. As with the presence points, I limited the background points to one per unique grid cell. Oceanographic conditions in the same month can vary from one year to the next. To ensure I captured this variability, I weighted the number of background points generated by the number of presences recorded each year (Appendix C.4). For example, if 20 presences were recorded in 2001 and 80 in 2002, 20% of the background points and associated oceanographic conditions came from 2001, and 80% from 2002. Similarly, oceanographic conditions vary across the study area. To represent oceanographic conditions from the entire study area, I also weighted points by the number of cells in each Northwest Atlantic Fisheries Organization division (NAFO 2019) and the Hudson Strait, which falls outside the NAFO Convention Area (Andrews et al. 2020).

I used a 10-fold cross-validation, which splits the data into 10 folds, with each fold used to test the model and the other nine folds to train iteratively (Elith et al. 2011). I assessed the performance of each model using multiple metrics: testing and training area under the curve (AUC) scores (Phillips et al. 2017), true skill statistic (TSS) (Allouche et al. 2006), the continuous Boyce index (CBI) (Boyce et al. 2002), and the symmetric extremal dependence index (SEDI) based on a maximum Kappa threshold (Wunderlich et al. 2019) (for further details on the evaluation metrics, see Appendix C.6, A1 – A4).

I then used Maxent’s complementary log-log (cloglog) transformation to estimate relative habitat suitability throughout the study area (Phillips et al. 2017). Although I am modelling suitability across horizontal (x, y) and vertical (z) axes, Maxent predictions operate on flat (two-dimensional) surfaces. To overcome this constraint, for each oceanographic variable and each month-year time slice, I created one layer representing all of the depths by concatenating (joining together one after the other) the depth layers provided by the oceanographic models (Bentlage et al. 2013). I produced geographic predictions for each year-month time-slice for which capelin presence data were available. For example, if presence data were available for March 1999, 2000, and 2001, I produced geographic predictions for March 1999, 2000, and 2001 using the March model.

I carried out all modelling processes in R version 3.6.2 (R Core Team 2019) with the *Dismo* (Hijmans et al. 2017), EcoSpat (Broennimann et al. 2018), *enmSdm* (Smith 2019), and *Raster* (Hijmans 2019) packages.

3.2.4.2. Distribution changes between phases

The Maxent models provide predicted habitat suitability scores ranging from 0 (not suitable) to 1 (extremely suitable). To quantify distributions and ranges, it is common practice to use a threshold to identify predicted "suitable" and "unsuitable" habitat. To explore potential capelin habitat distribution changes between positive phases and negative phases, I used a Maximum Kappa threshold to identify suitable/unsuitable habitat. I chose this threshold for its resilience to prevalence, which cannot be accurately determined without genuine absences (Nenzén & Arajo, 2011). For each month, I used five common distribution metrics to assess changes between the positive and negative phases of the NAO—the percentage of the study area predicted as suitable habitat, the stability of suitable habitat, patch number and size (mean and maximum), and bounding location (mean of the five most northern, southern, western, eastern, shallowest, and deepest centroids) (Yalcin & Leroux 2017). Table 3.1 lists the patterns I expected and tested.

For each distribution metric except the stability metric, I report median values between the two NAO phases and compare differences using a two-sided Mann-Whitney U test on a month-by-month basis. An effect size less than 0.3 is corresponds to a small effect, 0.3 to <0.5 a moderate effect, and => 0.5 a large effect (for test details, see Appendix C.6.B1). In addition to this binary phase analysis, I considered the magnitude of the NAO value in each phase (i.e. continuous measures of the NAO value). I fit Generalized Linear Mixed Models (GLMM) with the distribution metric as the response variable, the Winter NAO value as the fixed effect, and monthly model as the random effect (for analysis details, see Appendix C.6.B2). To calculate the stability of suitable habitat between phases, I compared the number of times a suitable habitat cell was present in each month-phase group. Following hotspot detection rules (see section 3.2.4.3 *Time-series trend analysis* below), I considered a suitable habitat cell to be in a month-phase if it was present in 90% of the years in the month-phase grouping. Cells were categorised as (1) present in both positive and negative phases, (2) present in positive phases only, or (3) present in negative phases only. All analysis was executed using the R packages *SDMTools* (VanDerWal et al. 2019), *rstatix* (Kassambara 2020), *lme4* (Bates et al. 2020), and *MuMIn* (Bartoń 2020).

Table 3.1: *Description and expected patterns related to the distribution metrics used to assess variation between North Atlantic Oscillation (NAO) phases. All metrics were calculated individually for each month-year time slice.*

Distribution Metric	**Description**	**Expected patterns**	**Reasoning**	**Result**
Percentage of the study area classified as suitable habitat	The percentage of area classified as suitable habitat based on a Maxent model-derived threshold (Max Kappa) on all the individual depth layers. Reported percentages reflect the 'flat' area available on each individual depth layer.	A higher percentage of the study area classified as suitable habitat will characterise positive phases, particularly during the warmer months.	Capelin is a cold-water species (Rose 2005). As such, I expect that the colder conditions in NAO positive phases (Greene et al. 2013) will increase the availability of suitable habitat, particularly during the warmer months.	Although results generally aligned with expectations, I found no significant differences between NAO phases, except for May (a pattern contrary to expectation).
Number of Patches	The number of patches (a contiguous group of suitable habitat cells on an individual depth layer) found across all individual depth layers. A larger number of patches indicates higher fragmentation of suitable habitat relative to a lower number of patches. Because the depth layers are treated as flat surfaces, patches on adjacent depth layers are not considered contiguous.	The number of patches will not differ between the two NAO phases.	Spatially, oceanographic conditions primarily operate on a gradient, i.e. without abrupt boundaries (Talley et al. 2011). I do not expect the NAO to alter gradient patterns to the extent that they fragment suitable habitat.	I found no statistical difference in the number of patches between phases.
Patch Size (Mean and Maximum)	The mean and maximum patch* size in km^2 found	During positive phases, patch size will exceed patch size during	Species typically expand/contract their ranges at	Results for both the mean and maximum

	across all individual depth layers. *(a contiguous group of suitable habitat cells on an individual 'flat' depth layer. The minimum patch size is one cell, and as such not explored.)	negative phases, particularly during the warmer months.	the edges in response to changing oceanographic conditions. Core areas usually remain stable over time (e.g. Fisher et al. 2008). Due to the gradient-like quality of oceanographic conditions over space and predictions that the negative phase of the NAO will favour capelin (see above), I expect the same pattern for suitable habitat patches.	patch size were more mixed than expected, with no statistical support for expected patterns.
Habitat Stability	The persistence of a suitable habitat cell located on an individual depth-layer between the two NAO phases. A cell is considered to belong to a phase if it is present in 90% of the years in the month-phase grouping.	Suitable habitat cells will be mostly stable across phases. There will be more suitable habitat cells during positive phases only during the colder months and more in negative phases in the warmer months.	In line with the gradient-like nature of oceanographic conditions over space and the tendency of species to expand/contract ranges (see above), I expect to see strongest distributional changes on patch edges. Generally, I expect positive phases to be more favourable to capelin (see above).	Suitable habitat was generally stable between phases, and patterns in phase-only cells aligned with expectations.
Bounding variation	Horizontal (*x*, *y*) shifts in the mean of the five most northern, southern, western, eastern-most centroids, vertical (*z*) distribution shifts in the mean of the five shallowest and deepest most	Boundings will lie further south and on deeper depth layers during positive phases, particularly in the warmer months, and further north in negative phases than positive phases, particularly during cooler months.	I expect the cooler conditions of the positive phase to allow a more substantial intrusion of predicted suitable habitat in the south (where waters are typically warmer) and warmer conditions during negative	Results were more mixed than expected, with a statistical difference only in the eastern bounding in April. One result (eastern bounding in

	centroids. Horizontal shifts are provided in geographic coordinates (longitude, latitude, and vertical shifts on the depth layer).		phases to allow a more northerly intrusion (where conditions are generally cooler).	May) contradicted expectations.

3.2.4.3. Time-series trend analysis

To identify temporal trends in the relative habitat suitability scores across each month, I modelled distributions for March to December inclusive and conducted emerging hotspot analyses (ESRI 2020a) to identify statistically significant trends in suitability hotspots (high suitability scores) and cold spots (low suitability scores) over the time-series for which I had data. For example, the May analysis covers 1998 to 2011 inclusive and the September analysis covers 1998 to 2014. I used the emerging hotspot analysis tool in ArcGIS Pro (ESRI 2020b). IESRI (2020a) provides full details on the tool, but briefly, the tool measures trends by first assessing spatial clustering of values using the Getis-Ord Gi* statistic (Getis & Ord 1992) and then employs the Mann-Kendall trend statistic (Kendall & Gibbons 1990) to measure temporal trends across the time-series (for test details see B3 and B4 in Appendix C.6). Emerging hotspot analysis has been used to reveal several ecological temporal trends, including on the density of abalone (*Haliotis spp.*) (Young et al. 2020), forest loss (Ball et al. 2021), and cetacean strandings (Betty et al. 2020).

Cells in the study area were assigned one of 17 temporal state categories, including no pattern, persistent (a cell that has been a statistically significant hot/cold spot for 90% of the time-step intervals, with no discernible trend indicating an increase or decrease in the intensity of clustering over time), and sporadic (a cell that is an on-again then off-again hot/cold spots) (for an example output, see Appendix C.7). To avoid an unwieldy output, I focused on three temporal trend patterns: sporadic, intensifying, and diminishing (see Table 3.2 for trend definitions) and only considered those cells with a statistically significant trend. Because the analysis requires a minimum of 10 time-steps (years), I limited the analysis to overall trends in each month (i.e. no month-phase analysis). I note that March, August, October, and November are missing one year in their time series (Table C.4 in Appendix C.4).

Table 3.2*: Temporal states used in the emerging hotspot analysis to assess' habitat suitability score trends over the time series. Hotspots are cells with high habitat suitability values and cold spots with low habitat suitability values. Statistical significance is derived from the Mann-Kendall test executed in the analysis (ESRI 2020b).*

Emerging Hotspot Trend	**Description**
Sporadic Hotspot	A location (*x*, *y*, *z*) that is an on-again then off-again hotspot. Fewer than 90% of the years modelled have been statistically significant hotspots, and none of the years modelled have been statistically significant cold spots.
Intensifying Hotspot	A location (*x*, *y*, *z*) that has been a statistically significant hotspot for 90% of the years modelled, including the final (most recent) year. In addition, the intensity of clustering of high counts in each time step is increasing overall (i.e. habitat suitability scores are increasing), and that increase is statistically significant.
Diminishing Hotspot	A location (*x*, *y*, *z*) that has been a statistically significant hotspot for 90% of the years modelled, including the final (most recent) year. In addition, the intensity of clustering in each time step is decreasing overall (i.e. habitat suitability scores are decreasing), and that decrease is statistically significant.
Sporadic Cold Spot	A location (*x*, *y*, *z*) that is an on-again then off-again cold spot. Fewer than 90% of the years modelled have been statistically significant cold spots, and none of the time-step intervals have been statistically significant hotspots.
Intensifying Cold Spot	A location (*x*, *y*, *z*) that has been a statistically significant cold spot for 90% of the years modelled, including the final (most recent) year. In addition, the intensity of clustering of low counts in each time step is increasing overall (i.e. habitat suitability scores are decreasing), and that increase is statistically significant.
Diminishing Cold Spot	A location (*x*, *y*, *z*) that has been a statistically significant cold spot for 90% of the years modelled, including the final (most recent) year. In addition, the intensity of clustering of low counts in each time step is decreasing overall (i.e. habitat suitability scores are increasing), and that decrease is statistically significant.

I also employed the Mann-Kendall trend statistic (for test details see Appendix C.6,.B3) using the R Package *Kendall* (McLeod 2011) to evaluate trends across each month's time-series for the distribution metrics (1) percent of the study area predicted as suitable habitat; (2) shifts in the boundings (northern, southern, western, eastern, shallowest, and deepest); and (3) patch number and size (maximum and mean). To account for multiple comparisons, I applied a Bonferroni correction to detect statistical significance ($\alpha_{Bonferroni}$ = 0.05/10 distribution metrics = 0.005).

3.3: Results

3.3.1: Species Distribution Modelling

I ran one maxent model for each of the months from March to December (Figure 3.3). Overall, the models performed well (full details available in Table C.5 in Appendix C.5). Generally, the December model yielded the best performance (Test AUC 0.98, Training AUC 0.95, TSS 0.88, CBI 1, SEDI 0.89) and October the worst (Test AUC 0.91, Training AUC 0.90, TSS 0.70, CBI 0.99, SEDI 0.61).

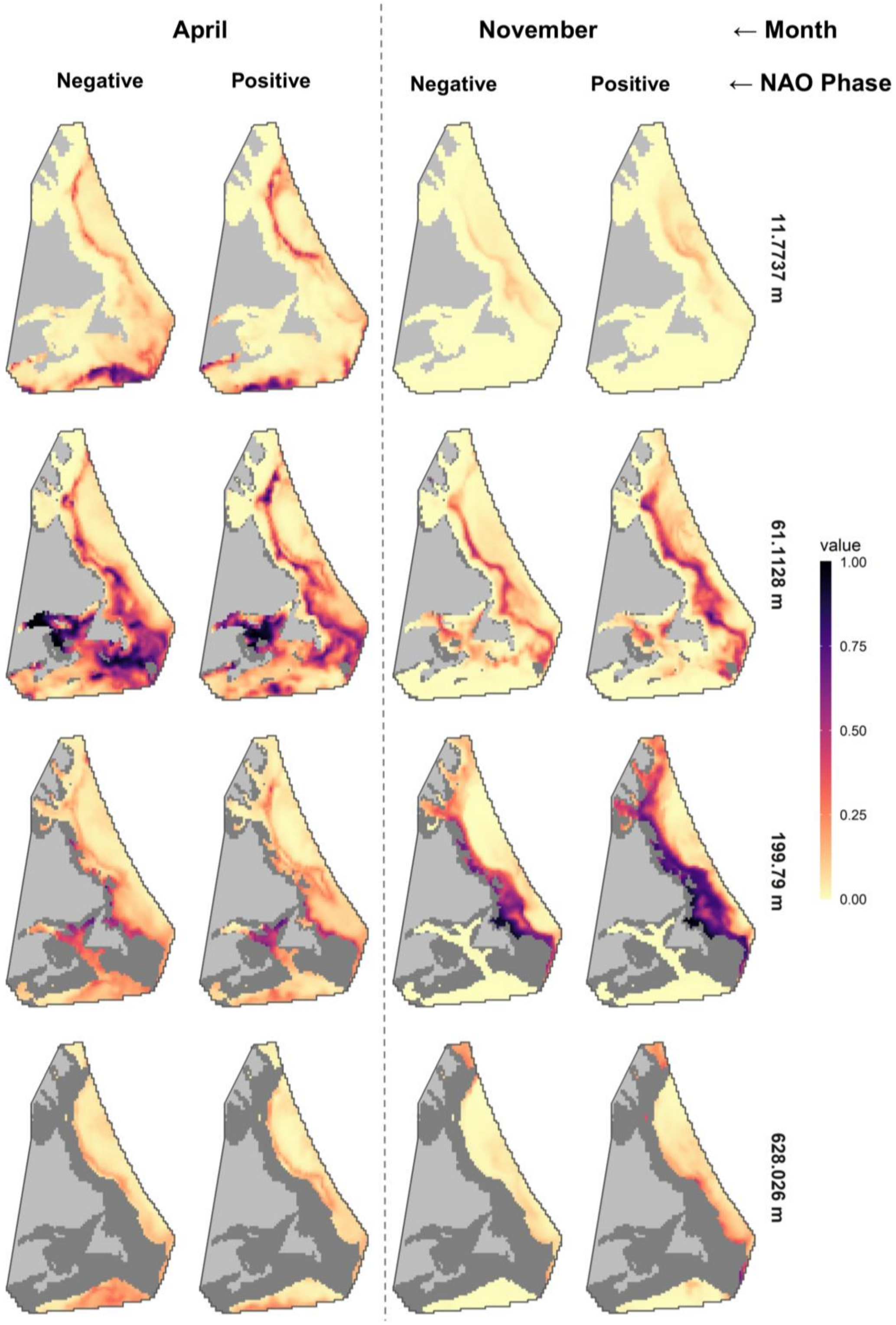

Figure 3.3*: Example of habitat suitability score output for the months of April and November between a year that experienced a positive phase of the NAO (2000) and a year that experienced a negative phase of the NAO (2010) across four depths levels. The year, month, and depths were arbitrarily chosen for illustrative purposes only. Colours represent the relative habitat suitability. Suitability ranges from 0 (lightest colours) to 1 (darkest colours), with values closer to 1 more suitable than those closer to 0.*

3.3.2: Distribution changes between phases

I assessed distribution changes between positive phases (e.g. generally cooler and less saline conditions in the study space) and negative phases (e.g. generally warmer and more saline conditions in the study space) of the NAO on an individual month-by-month basis using five commonly used metrics—the percentage of the study area classified as suitable habitat, the stability of suitable habitat, patch number and size (mean and maximum), and bounding location (northern, southern, western, eastern, shallowest, and deepest) (Table 3.1). I present boxplots for the distribution metrics for the months of April and November here (Figure 3.4) and boxplots and Mann-Whitney U effect size results for all months in Appendix C.8.

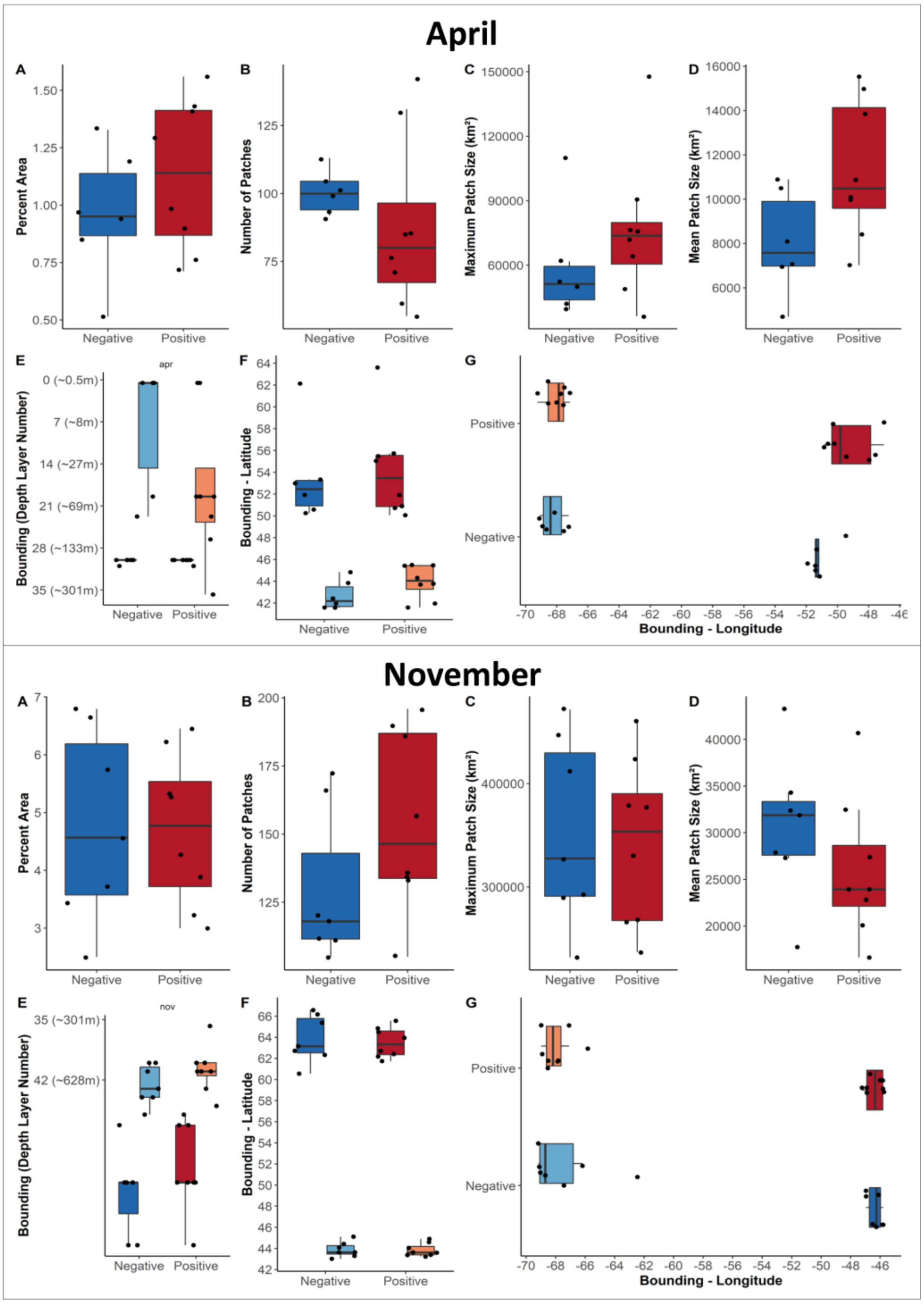

***Figure 3.4**: Distribution metrics for the months of April (top-panels) and November (bottom-panels) A: percent study area classified as suitable habitat, B: number of patches, C: maximum patch size (km^2), D: mean patch size (km^2), E: shallowest and deepest boundings, F: northern and southern boundings, and G: western and eastern boundings for negative (blue) and positive (red) NAO phases. Dots represent values for the individual years (14 years in April and 15 years in November). To prevent compression of the boxplots, depth boundings are given as the depth layer number, with the corresponding depth in meters indicated. The months were arbitrarily chosen for illustrative purposes only. Full boxplots for all months are available in Appendix C.8.*

I found substantial variation in the percentage of the study area predicted as suitable habitat within each month-phase grouping (Figures 3.3 and C.8.1). However, the effect size derived from the Mann-Whitney U test was only large for May, albeit with a large confidence interval (CI) range (effect size 0.66, CI range 0.25 – 0.84, Table C.8.1).

Analysis of suitable habitat stability between phases indicates the majority of cells classified as suitable habitat occurred in both positive and negative phases. The exceptions were with the April model, in which both the positive and negative phases were dominated by cells occurring only in the positive and negative phase, respectively, and June and October models, in which negative phases were dominated by cells occurring only in the negative phase (Table 3.3, Figure 3.5). When considering stability over depth, cells present only in either phase of the NAO typically occur at the same depths as those with cells present in both positive and negative phases. Exceptions include May, where cells appear at shallower depths in negative phases, and October when cells appear at deeper depths in negative phases.

Table 3.3*: Percentage of the suitable habitat cells classified as present in both negative and positive phases of the North Atlantic Oscillation (NAO), negative phases only, or positive phases only.*

		Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Negative Phase	Negative Only	39.20	60.58	42.24	55.10	27.64	3.89	47.42	84.55	14.16	2.93
	Both Phases	60.80	39.42	57.76	44.90	72.36	96.11	52.58	15.45	85.84	97.07
Positive Phase	Positive Only	26.85	66.78	24.28	6.41	24.55	7.71	18.28	3.43	15.50	42.26
	Both Phases	73.15	33.22	75.72	93.59	75.45	92.29	81.72	96.57	84.50	57.74

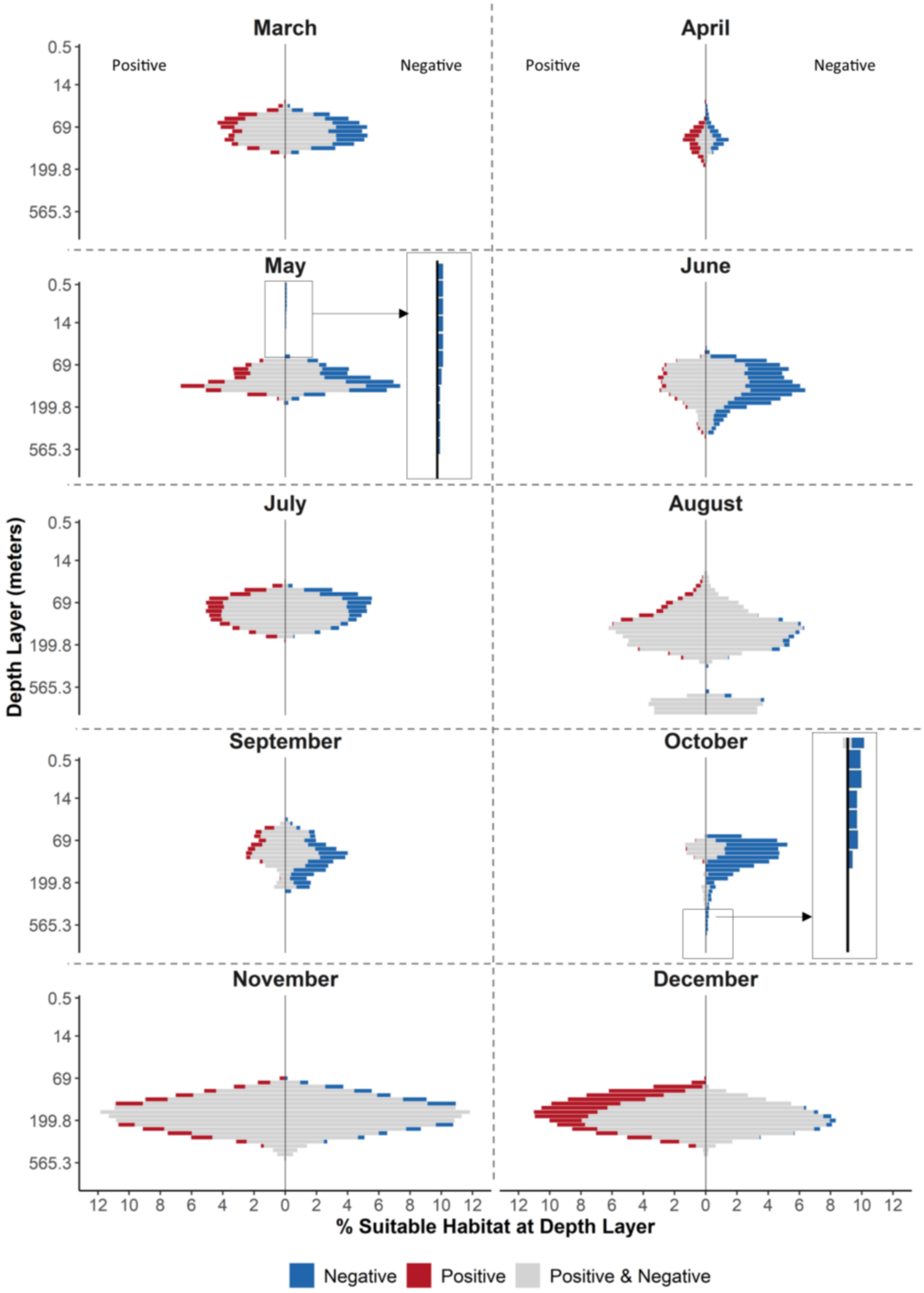

***Figure 3.5**: The vertical (z) distribution of predicted suitable habitat cells, relative to the amount of ocean available at each depth layer, for each modelled month-phase. Cells may be present in both negative and positive phases of the North Atlantic Oscillation (NAO), in negative phases only, or positive phases only. Note that there is a greater area of ocean at shallower depth layers than deeper due to increasing intrusion of the seafloor. Depth layers are not evenly spaced (for details on the depths, see Table C.3 in the Appendix).*

When considering patches, I detected some variation within and between phases. In terms of the median number of patches, August differed least between negative and positive phases, whereas May differed most (Figures 3.4 and C.8.2). The greatest median number of patches also occurred in May during both negative (219 patches) and positive (186 patches) phases, whereas August had the fewest (46 in both negative and positive phases). In terms of the size of patches (Figures 3.4, C.8.3, and C.8.4), the greatest variation in median maximum patch size between phases occurred in March (49,375 km^2 in the negative phase vs 98,125 km^2 in the positive) and the least in September (110,625 km^2 in negative phases vs 114,375 km^2 in positive phases). The greatest differences in median values for mean patch size occurred in December (28,266 km^2 cells in negative phases vs 42,770 km^2 in positive phases) and lowest in May (12,232 km^2 cells in negative phases vs 11,383 km^2 in positive phases).

Regarding boundings, across all months, I found little difference in the southern bounding location between negative and positive phases (Figures. 3.4 and C.8.5). The highest median latitudinal location of the southern bounding (most northerly) occurred in August during positive phases of the NAO (47.31°N), and lowest (most southerly) in May, also during positive phases (41.52°N). In terms of differences in location between positive and negative phases, the largest difference in the southern bounding location (a difference of 1.9° between the two phases) occurred in August, with the smallest difference (0°) in June. The median lowest latitudinal location of the northern bounding (most southerly) occurred in July during a positive NAO phase, and in both phases in March (50.67°N) and the highest (most northerly) location occurred in both phases in August (68.58°N). Comparing the median location of the northern bounding between phases, the greatest difference between positive and negative phases occurred in July (6.08° difference between the two phases), and the lowest in March and August (0° difference between the two phases). For the other months, I observed small median latitudinal differences between the two phases of the NAO. I also found little difference between the western bounding longitudinal location in all months (0° difference in May and August to 1.6° difference in December). (Figures 3.4 and C.8.6). The highest longitudinal location of the western bounding (most easterly) occurred in December during negative phases of the NAO (58.51°W) and the lowest (most westerly) during the positive phase in June (69.56°W). Similarly, the median eastern bounding longitudinal location differed little between NAO phases (ranging from 0° in August to 1.56° in April). The eastern bounding's highest longitudinal location (most easterly) occurred during a positive phase in June (45.86°W), and the lowest (most westerly) location occurred during both phases in August (57.51°W). With regards to the median value of the shallowest and deepest boundings (Figures 3.4 and C.8.7), little variation occurred between phases for each of the months, except for April and July, when the median shallowest bounding occurred at shallower depths in the negative than the positive phase, and September, October, and December when the deepest bounding occurred in deeper water in the positive phase. The Mann-Whitney U tests indicated three boundings with a large effect size – the deepest bounding in October (effect size 0.56, 95% CI range 0.19 – 0.83), the eastern-most bounding in April (effect size 0.69, 95% CI range 0.3 – 0.84**),** and the northern-most bounding in April (effect size 0.51, 95% CI range 0.06 – 0.84**) (**Tables C.8.5 – C.8.7 in Appendix C.8).

Across all distribution metrics (boundings, percent area, patch number and size), the GLMMs indicated that the fixed effect of NAO phase magnitude explained a small percentage of variation in the response variable (Marginal R^2 ranging between 0.000 and 0.003) but explained considerable variation between monthly models (Conditional R^2 ranging between 0.64 – 0.94) (Table 3.4).

Table 3.4*: Results of the GLMMs for each of the distribution metrics. For all models, the response variable was the metric, the fixed effect was the value of the North Atlantic Oscillation (NAO) winter anomaly, and the random effect was the monthly model. Fixed Effect Std Error = Fixed Effect Standard Error; Fixed Effect t-value = the Wald statistic;* R^2m *= marginal R squared values;* R^2c *= conditional R squared values.*

Distribution Metric	**Intercept Estimate**	**Fixed Effect Estimate**	**Fixed Effect Std Error**	**Fixed Effect *t*-value**	**R^2m**	**R^2c**
Percentage study area classified as suitable habitat	2.53	0.06	0.07	0.83	0.00	0.64
North Bounding	60.89	-0.47	0.31	-1.49	0.00	0.80
South Bounding	43.31	0.03	0.08	0.46	0.00	0.71
West Bounding	-67.72	-0.02	0.10	-0.18	0.00	0.87
East Bounding	-50.38	0.28	0.09	2.98	0.00	0.94
Shallowest Bounding	23.88	-0.26	0.87	-0.30	0.00	0.80
Deepest Bounding	483.26	-12.39	14.80	-0.84	0.00	0.74
Number of Patches	114.89	2.40	2.29	1.05	0.00	0.77
Maximum Patch Size (km^2)	174476.09	2335.50	5101.54	0.46	0.00	0.64
Mean Patch Size (km^2)	20635.60	166.99	591.82	0.28	0.00	0.64

3.3.3: Time-series trend analysis

I assessed trends over time in the distribution metrics percentage of the study area classified as suitable habitat, patch number, mean and maximum patch size, and location of the northern, southern, western, eastern, shallowest, and deepest boundings (Table 3.1), and in the relative habitat suitability values on a month-by-month basis. After applying Bonferroni corrections, the Mann-Kendall trend analysis of the distribution metrics revealed few statistically significant ($p < 0.005$) trends developing over time. Trends were detected in deepest bounding (October—decreasing), mean patch size (September—increasing), and number of patches (November—decreasing), and (Table 3.5).

Table 3.5*: Mann-Kendall trends for the distribution metrics that showed a statistically significant positive (where Kendall's tau statistic is a positive number) and negative (where Kendall's tau statistic is a negative number) trend. Tau values range from 0 to +1/-1 (positive/negative relationship), with scores of +1/-1 indicating a perfect relationship and 0 no relationship.*

Distribution Metric	Month	Kendall's tau statistic	p-value
Deepest bounding	October	-0.65	0.002
Mean patch size	September	0.51	0.004
Number of patches	November	-0.59	0.003

In terms of the emerging hotspot analysis looking at relative habitat suitability, the percentage of the study area that displayed a statistically significant up or down trend in suitability scores over the time series based on the chosen patterns (intensifying hot/cold spot, diminishing hot/cold spot, or sporadic hot/cold spot; see Table 3.2) varied from month to month (Figure 3.6 and Table 3.6), with the lowest percentage (4.3%) in December and the highest percentage (18.47%) in October. Decreasing trends dominated April, August, and October, increasing trends in November and December, and sporadic cold/hot spots in March, May, June, July, and September. The direction trends took were not the same for every depth layer. For example, in October, decreasing trends dominated the upper layers, whereas increasing trends became more prevalent at deeper depth layers. Decreasing trends typically dominated depth layers during March, April, May, July, and August, whereas increasing trends largely dominated June, September, October, November, and December.

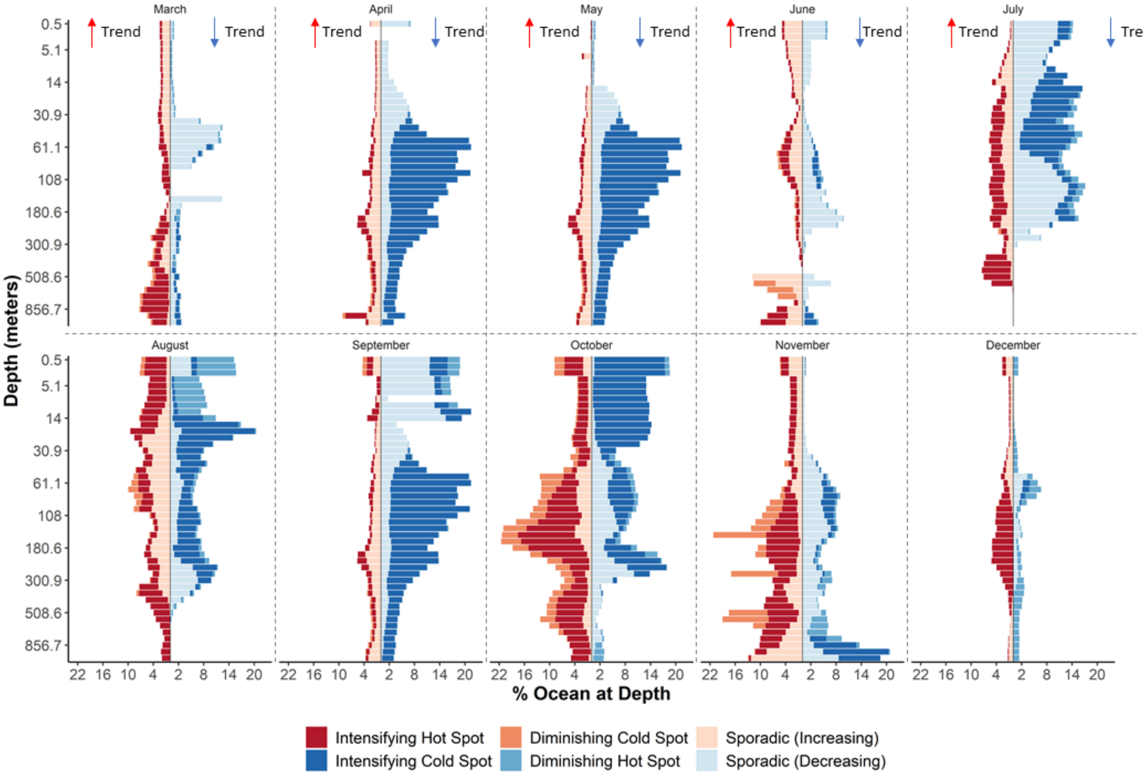

***Figure 3.6**: Habitat suitability trend by depth based on emerging hotspot analysis (ESRI 2020b) relative to the amount of ocean available at each depth layer. Note the greater area of ocean at shallower than deeper depths resulting from increasing intrusion of the seafloor. Depth layers are not evenly spaced. For details on the depth layers, see Appendix C.3. Red colours indicate an upward trend and blue a downward trend.*

***Table 3.6**: Percentage of the study area displaying a statistically significant increasing/decreasing trend in habitat suitability scores by pattern. Arrows indicate the direction of the trend (up ↑, down ↓, and up or down ↕).*

Month	Intensifying Hot Spot (↑)	Diminishing Cold Spot (↑)	Intensifying Cold Spot (↓)	Diminishing Hot Spot (↓)	Sporadic Cold Spot (↕)	Sporadic Hot Spot (↕)	Total
March	1.61	0.12	0.64	0.36	8.01	1.46	12.20
April	0.61	0.03	5.68	0.16	3.05	1.66	11.18
May	1.22	0.12	3.34	0.36	3.90	0.77	9.71
June	0.99	0.35	0.30	0.16	1.83	2.85	6.47
July	2.18	0.12	4.92	0.86	5.16	2.25	15.49
August	1.74	0.08	2.36	1.26	1.99	1.37	8.80
September	1.66	0.01	0.97	1.15	2.45	2.10	8.34
October	4.37	2.13	6.84	0.55	3.08	1.49	18.47
November	3.06	3.64	1.01	0.51	2.38	1.76	12.36
December	1.71	0.02	0.22	0.89	0.65	0.81	4.30

3.4: Discussion

Marine pelagic species distributions exhibit spatial variation both within and among years. Understanding the ecology of pelagic species, their ecosystem functions and interactions with other species, and for effective spatial management requires disentangling the drivers of these fluctuations. I assessed the variation in the modelled horizontal (*x*, *y*) and vertical (*z*) distribution of suitable habitat for a keystone forage fish (capelin) in Atlantic Canada over 17 years between positive and negative NAO phases and over the time series as a whole, and on a month-by-month basis. I observed (1) substantial stability in the cells with predicted suitable habitat between the two NAO phases, (2) differences in the percentage predicted as suitable habitat in the study area largely arises from an expansion/contraction of existing suitable habitat patches, and not the appearance of new patches, and (3) over time, the relative suitability of habitat declines in six of the ten months modelled. However, although I found some support for the hypothesis that NAO phase influences some components of capelin distribution, I found the influence generally weak, leaving us unable to attribute variability in distributions with differing oceanographic conditions experienced under different phases of the NAO.

In terms of habitat stability (Table 3.3, Figure 3.5), I found most suitable habitat cells remained stable across NAO phases, and that for the most part, single NAO phase cells appeared at the same depth layers as cells that appeared in both phases. From a management perspective, whereas one could conclude that distributions are stable enough to focus potential management actions on areas of suitable habitat that persist regardless of NAO phase, I caution that ignoring areas used only in one phase of the NAO or failing to account for a decrease suitable habitat patches in one locale (or increase in another) over time risks overlooking areas important for the species' persistence under changing conditions (Runge et al. 2016, D'Aloia et al. 2019).

Our study suggests that over time the deepest bounding is trending towards increasingly shallower depth layers in September and a deepening in October. Previous work assessing observed changes in the vertical (z) distribution using data from surveys conducted in May and September during the late 1980s to 2000 suggested that capelin favour deeper waters during these months (Mowbray 2002). Although this period covers a regime shift that impacted multiple fish species throughout the Atlantic Canadian region (Pedersen et al. 2020), this deepening apparently persisted into the early 2010s (Mowbray 2014). I note that September proved an interesting month in terms of trends in several metrics. Alongside the increasing (albeit weaker than October) increasing trend in deepest depth layer bounding, this study also suggests an increasing trend in mean and maximum patch size over time and a decreasing trend in the number of patches. The lack of significant increase or decrease in the percent of the study area classified as suitable habitat during this month suggests the loss of smaller patches over time. These patterns match the gradient-like nature of oceanographic conditions and previous work that indicates species ranges primarily expand/contract at the boundaries rather than fragment (Fisher et al. 2008, Talley et al. 2011). While the implications of variations in patch size and number are largely unknown for highly mobile and pelagic species like capelin, a smaller number of larger patches in one phase could indicate populations are more contracted in that phase. In contrast, a larger number of smaller patches in one phase could suggest that the population becomes more fragmentated in that phase. The impacts partly rely on the extent to which capelin habitat selection is based on density dependence, but could include some segments of the wider Atlantic Canadian population experiencing greater competition, predation risk, and direct/indirect fishing pressure in that phase in one phase than another (Kim et al. 2004, Worm & Tittensor 2011). Similar to other pelagic species, the role of density dependence and other factors in capelin habitat selection is largely unknown (Rose 2005).

Although the trend analysis of the distribution metrics showed few significant trends, I note that the emerging hotspot analysis on the predicted habitat suitability scores indicates that six out of the ten months modelled are experiencing a greater overall decline in relative habitat suitability scores. For those months, the decline spans the majority of depth layers and primarily impacts more ‘persistent’ (intensifying/diminishing) hot/cold spots. A continuation of these declining trends could have consequences for capelin abundance and distributions in Atlantic Canada (Rose 2005, Hollowed et al. 2013, Andrews et al. 2016). Indeed, previous work linked changing ocean conditions during the early 1990s to the collapse and distribution change of capelin in Newfoundland and Labrador (Pedersen et al. 2017). Although I cannot attribute the habitat suitability changes indicated in this study directly to climate change, I note the sensitivity of capelin distributions to changes in contemporary and predicted future oceanographic conditions (Rose 2005) and that the Northwest Atlantic Ocean has and is predicted to experience substantial changes in conditions (Bernier et al. 2018, Alexander et al. 2020).

Using environmental data derived from numerical ocean models, I modelled predicted distributions at multiple depth layers. However, SDMs and distribution analysis tools have primarily been designed for two-dimensional spaces that may over-simplify the three-dimensional habitat complexities experienced by pelagic species (Duffy & Chown 2017). Similarly, this study reports distribution changes on disparate depth layers, which I treat as two-dimensional. The development of modelling and analysis tools (e.g. patch measurements that include volume across multiple consecutive depth layers) that incorporate volume would be beneficial for assessing distribution changes of pelagic species that occur throughout the water column. I also note a generally weak understanding of the impact of changing suitable habitat patch size and number on migratory and other highly mobile species, despite the importance of assessing their response and vulnerability to changing conditions (McHenry et al. 2019).

The spatial and temporal resolution of the environmental data underlying distribution models influences predicted distributions, and by extension, distribution metrics. Although the extended time series of species and oceanographic data allowed me to explore variation between phases of the NAO, the resolution of the oceanographic data may mask fluctuations in oceanographic conditions and, by extension, predicted distribution changes (Saraux et al. 2014, Fernandez et al. 2018). Where possible, using finer spatial-temporal resolution data may elucidate distribution pattern changes. Such fine-scale data can be derived from Regional Ocean Modelling System (ROMS). For example, Abrahms et al. (2018) used daily 0.1° resolution data derived from a ROMS configured for the California Current Ecosystem to predict the year-round blue whale (*Balaenoptera musculus*) habitat suitability in the region. Temporally speaking, I was restricted to modelling for the months of March to December inclusive due to the low number of observations available in January and February. Although challenging, e.g. due to the spread of ice, obtaining observations during January and February would help fill this temporal gap and may be important given that oceanographic conditions may respond differently to climate change depending on the season (Alexander et al. 2020). Furthermore, the distribution metrics I used required conversion of predicted habitat suitability scores into a binary measure of suitable/not suitable habitat, which may further obscure variation between phases and trends across the time series. Experts continue to debate how to choose the ‘best’ threshold for defining the habitat suitability score at which a species will occur (Kou et al. 2014). From a management perspective, choosing a threshold may come down to the level of risk a manager is willing to take (Wilson et al. 2005). Although managers widely use the binary threshold approach for spatial planning, applying other approaches to evaluate distribution changes, such as fuzzy set logic (Kou et al. 2014), may prove useful.

Regarding the bounding (northern, southern, western, eastern, shallowest, and deepest) locations, I note that most bounds lay at the edge of this study area and thus may not fully capture bounding variation. Furthermore, whereas the winter NAO value can strongly influence ocean conditions in the Atlantic Canadian region, I note that its influence may take longer to permeate deeper waters. Longer-term influences on ocean variables may also lag over years and even decades (Visbeck et al. 2003). Additionally, distilling trend and between-phase analysis into meaningful ecological or managerial regions (e.g. in the Atlantic Canadian context, Federal Marine Bioregions (DFO 2009), NAFO subareas or divisions (NAFO 2019)) may aid in capturing spatial variation in oceanographic responses to the NAO and assist in spatial management planning. Although not available for this study, I also note that using abundance data rather than presence data may improve the accuracy of predicted habitat suitability and distribution changes and provide useful information on spatial population dynamics (Howard et al. 2014, Saraux et al. 2014). Having such abundance data could also allow explicit tests of how capelin density relates to habitat patch structure. Similarly, resolving dynamical ocean features such as fronts and eddies may also improve predictions (Abrahms et al. 2019). In addition, I suggest that including species interactions, such as predator-prey relationships, may also prove fruitful in capturing distribution changes under varying conditions. For example, the NAO indirectly influences capelin dynamics in the Barents Sea through cod and herring, both of which prey on capelin (Hjermann et al. 2004).

Increasingly, researchers use species distribution models such as Maxent to predict species distributions changes to improve spatial management and our understanding of species spatial ecology (Hannah 2008, Petitgas et al. 2010), particularly for species whose year-round distributions are not fully understood, and in light of climate change. Although species distribution models provide insights that we lack from direct observations, they assume that the underlying data accurately reflects the modelled species-environment relationship. However, species responses to changing environmental conditions can be complex and do not necessarily follow fixed, linear patterns over time or space (Montalto et al. 2016, Husson et al. 2020, Gilioli et al. 2021). We still lack clarity on the consistency of highly mobile species-environment relationships over space and time (Naujokaitis-Lewis & Fortin 2016, Andrews et al. 2020), and current and projected novel climates and communities (Williams & Jackson 2007a, Veloz et al. 2012b), combined with uncertainties in ocean-climate model projections (Payne et al. 2016), add further complications for distribution modelling and, in turn, for designing ‘future-proofed’ spatial management strategies that account for changing conditions.

Untangling the temporal ecology of species and determining how best to detect and measure changes over time represents an increasingly important area of research. By creating monthly models, I aimed to capture variation in spatial responses to changing oceanographic conditions, though note that this approach did not capture variation between NAO phases. Although I chose a monthly split, other temporal options exist. For example, some studies indicate that a species-environment relationship can differ in winter from spring (Lloret-Lloret et al. 2021). However, creating seasonally split models risks smoothing out little-studied or unknown variability in conditions and species responses important for distributions. Furthermore, seasonality can vary over time or space (Bintanja & van der Linden 2013, Kwiatkowski & Orr 2018, Dunstan et al. 2018). Quantifying variation in species and sub-population level responses to changing oceanographic conditions (e.g. between phases of the NAO, seasonally, interannually, over the time-series as a whole) may assist in building more accurate distribution models, improving the accuracy of their subsequent predictions under changing conditions, and, in turn, assist in reducing management uncertainty. Equally, climate change punctuates the importance of determining when and how to create temporally split models to predict species distributions and how those distributions may change over time.

This study used a modelling approach to assess spatial-temporal variability in the horizontal (x, y) and vertical (z) distributions of a mobile pelagic species, in this case, the forage fish capelin, between different ocean climates, in this case relating to the positive and negative phases of the NAO, and over time on an individual month-by-month basis. I demonstrate that although mobile pelagic species can vary in distribution, they can also exhibit a great deal of resilience. Incorporating fluctuations (or lack thereof) in distributions in cyclical or time-series trends into spatial management for mobile pelagics and, especially in the case of forage species, interacting heterospecifics may assist in developing more efficient and pro-active management approaches that seek to manage human interaction with species on ecologically-relevant spatial and temporal scales.

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Chapter 4: Incorporating the spatial-temporal distributions of prey availability into area-based management tools for marine ecosystems

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Abstract

Migratory and other highly mobile species rely on multiple locations throughout their life cycles. The dynamic nature of their distributions across space and time presents challenges, however, for identifying which areas they use and managing human activities that may hinder the survival of individuals and the persistence of populations. Given that prey availability often shapes the distribution and movement patterns of predatory migratory species, I suggest that capturing the spatial-temporal distributions of prey availability in distribution models for predators can assist in designing ecologically relevant area-based management tools (ABMTs). I propose a conceptual framework to predict and forecast potential seabird foraging spaces using available tools and data. The framework encompasses three stages: (1) understanding aspects of the ecology of seabirds and their prey related to prey availability, (2) modelling, forecasting, and evaluating foraging spaces, and (3) management applications, with specific consideration of ABMTs. Notably, the framework presents an iterative workflow for including new knowledge and data in the modelling and decision-making process to create ecologically relevant and adaptive ABMTs. I highlight that although we lack exhaustive data and the perfect knowledge to fully understand the spatial-temporal dynamics of predators and their prey, successfully counteracting biodiversity loss requires embracing modelling, adaptive tools, and management frameworks.

4.1: Introduction

From butterflies to birds to whales, migration has inspired scientific inquiry for millennia (Fryxell et al. 2011). Broadly, these studies demonstrate migration as a strategy to exploit (or avoid) spatial and often temporal variability in conditions and resources that aid (or hinder) persistence (Dingle & Drake 2007). Nevertheless, migratory and other highly mobile species are not necessarily adjusting to the nature, pace, and magnitude of human-driven changes to conditions (Simmonds & Isaac 2007, Winkler et al. 2014, Hays et al. 2016, Keogan et al. 2018). The most endangered of the avian taxa include seabirds, whose movements range from highly mobile residents (e.g. masked boobies *Sula dactylatra* (Roy et al. 2021)) to the species with the longest known migration (Arctic terns *Sterna paradisaea* (Egevang et al. 2010)). This taxonomic group has suffered an estimated 70% community-level population decline between 1950 – 2010, with the greatest declines seen in wide-ranging species (Paleczny et al. 2015). Although difficult to untangle from oceanographic influence and natural variation, several studies suggest that interaction with and competition for prey with fisheries can play a role in seabird decline (Grémillet et al. 2018, Dias et al. 2019, Hill et al. 2020, Free et al. 2021). Other sea-based threats include oil and gas extraction activities, and pollution on movement pathways routes, as well as climate-induced distribution changes of prey fish, particularly around colonies (Cristofari et al. 2018, Dias et al. 2019).

Several management tools are available to reduce human impacts on the ocean. In particular, managers are increasingly using area-based management tools (ABMTs), which regulate human activity in a specific area, to reach conservation and other management objectives (UN Environment 2018, De Santo 2018). Globally, ABMT coverage for conservation purposes remains low. For example, despite calls to protect at least 10% of the ocean with marine protected area networks (MPANs), which are specifically aimed at conserving biodiversity, and other effective ABMTs by 2020 (CBD 2010), as of the end of

2019, just 7.63% of the ocean was covered or proposed to be covered, by marine protected areas. Of those, less than half afforded high protection for the features they are supposed to support (Marine Conservation Institute 2021).

Nevertheless, international calls that set the new goal of 30% coverage by 2030 (G7 2021), ABMTs are set to increase in number and extent. However, ABMTs designed to protect highly mobile and migratory seabirds often fail to encompass the different locations needed for their survival (Maxwell et al. 2016). Notably, spatial protection for pelagic species typically lags well behind efforts for those species that remain close to the coast (Critchley et al. 2020), particularly for those who use the high seas, which lay beyond national jurisdiction (Beal et al. 2021).

The spatial ecology of highly mobile and migratory seabirds presents challenges for designing ABMTs that offer meaningful protection. Within a single population, seabirds use multiple areas for their survival and population persistence. Even during the breeding season, when birds typically become more spatially restricted, movements can span hundreds of kilometres (Birdlife International 2004). As with all predators, migratory seabird survival and population persistence often link strongly to prey availability throughout their migratory cycle, with declines in prey availability resulting from human activity or environmental changes implicated in seabird declines (Sydeman et al. 2017, Grémillet et al. 2018). Prey species such as small pelagic fish may respond to human pressure or environmental change via changes in their distribution, movement patterns, phenology, spawning location, and abundances (Kanamori et al. 2019, Santora et al. 2020, Sydeman et al. 2020, Fernandes et al. 2020). Given that the movement and distribution patterns of prey influence those of their predators (Wisz et al. 2013, Furey et al. 2018), changes to prey availability could induce changes in predator foraging space use (Fauchald et al. 2011, Ratcliffe et al. 2021). As such, explicitly considering the spatial-temporal distribution of prey availability could enhance

ABMTs such as protected area networks for highly mobile/migratory predators, including seabirds.

Here, I present a framework to predict and forecast potential seabird foraging spaces to aid in their identification for management. I begin by identifying aspects of prey fish availability that act as key components of seabird foraging spaces. Focusing on widely available tools, I then discuss modelling, forecasting, and analysing the spatial-temporal trends in foraging spaces, and discuss applying predicted foraging spaces to adaptive ABMT processes that can be used in conjunction with other management measures to reduce negative human impacts on seabirds throughout their migratory cycle.

4.2: The framework

Short-term spatial-temporal variability and longer-term shifts in space use challenge the development of ABMTs that capture foraging spaces used by seabirds throughout their migratory cycle. Novel climates (Veloz et al. 2012) present unique challenges to creating spatial management measures that are 'future-proofed' to changing prey and predator distributions.

Although several studies seek to elucidate seabird distributions based on oceanographic factors, this approach may be problematic for several reasons. First, because seabird distributions are likely driven by environmental factors that differ from their prey (Figure 4.1), environmental covariates may not be a good predictor of predator distributions. For example, Aragón et al. (2018) found that prey abundance distributions played a more significant role in the distribution of merlin (*Falco columbarius*) (a terrestrial raptor) than environmental covariates. Afán et al. (2021) demonstrated that chlorophyll concentrations, typically used as a proxy of prey for seabirds and other marine predators, is not necessarily a good predictor of Balearic shearwater (*Puffinus mauretanicus*) foraging areas, and Kane et al.

(2020) found chlorophyll concentrations were associated with Manx shearwater (*Puffinus puffinus*) at sea distributions in some colonies but not others. Second, the modelled statistical relationship of prey such as fish to covariates may vary over time and space. For example, Roberts et al. (2019) reported statistical relationships for seven commercial fish species in the South Atlantic Bight changed between phases of the North Atlantic Oscillation (NAO), and Muhling et al. (2020) found that relationships for Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in the California Current System altered with the occurrence of marine heatwaves.

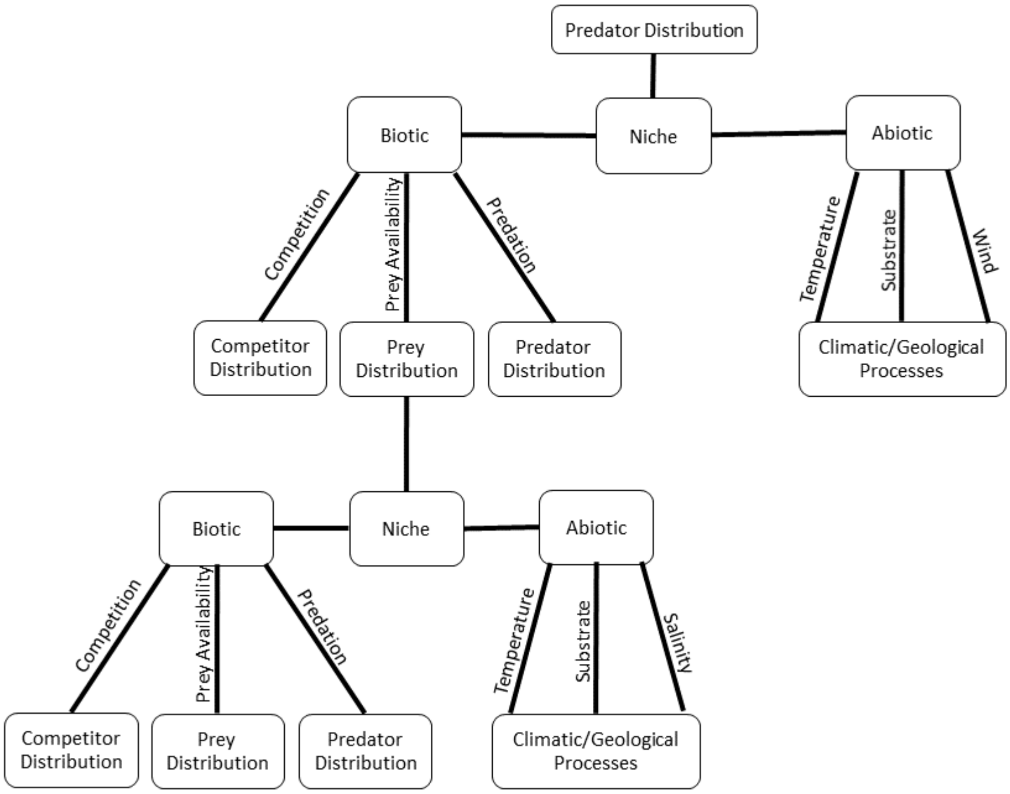

Figure 4.1*: The distribution of a predator is determined in part by the geographical location of its niche, which is comprised of abiotic and biotic factors, summarised here with examples of key drivers. Prey distribution is a significant component of prey availability. As with predators, prey distributions are governed by geospatial location and accessibility of the abiotic and biotic factors that make up its niche. Biotic and abiotic factors that govern the niche of a predator and prey may be entirely different (e.g. wind for the predator, salinity for the prey) or similar in type but quality (e.g. substrate for fish prey may refer to the availability of sandy seafloor, whereas for a seabird predator to availability of rocky outcrops). The biotic and abiotic factors that make up a niche may vary with phenology or migration stage/location for migratory species.*

The framework provides guidance for predicting and forecasting potential prey availability to equip decision-makers with the knowledge they need to create ecologically relevant and adaptive ABMTs. The framework has three components: (1) determining prey availability, (2) modelling, forecasting, and trend analysis, and (3) applications for ABMTs (Figure 4.2). The framework focuses only on foraging space use (i.e. does not consider seabird spaces whose primary use is unrelated to prey, such as rafting (Carter et al. 2016), moulting space (Petersen et al. 2008), or movement/migration pathways). Additionally, we do not consider the impact of seabird predation on local prey patch characteristics, the impacts of which vary between season and population (Gaston et al. 2007, Weber et al. 2021).

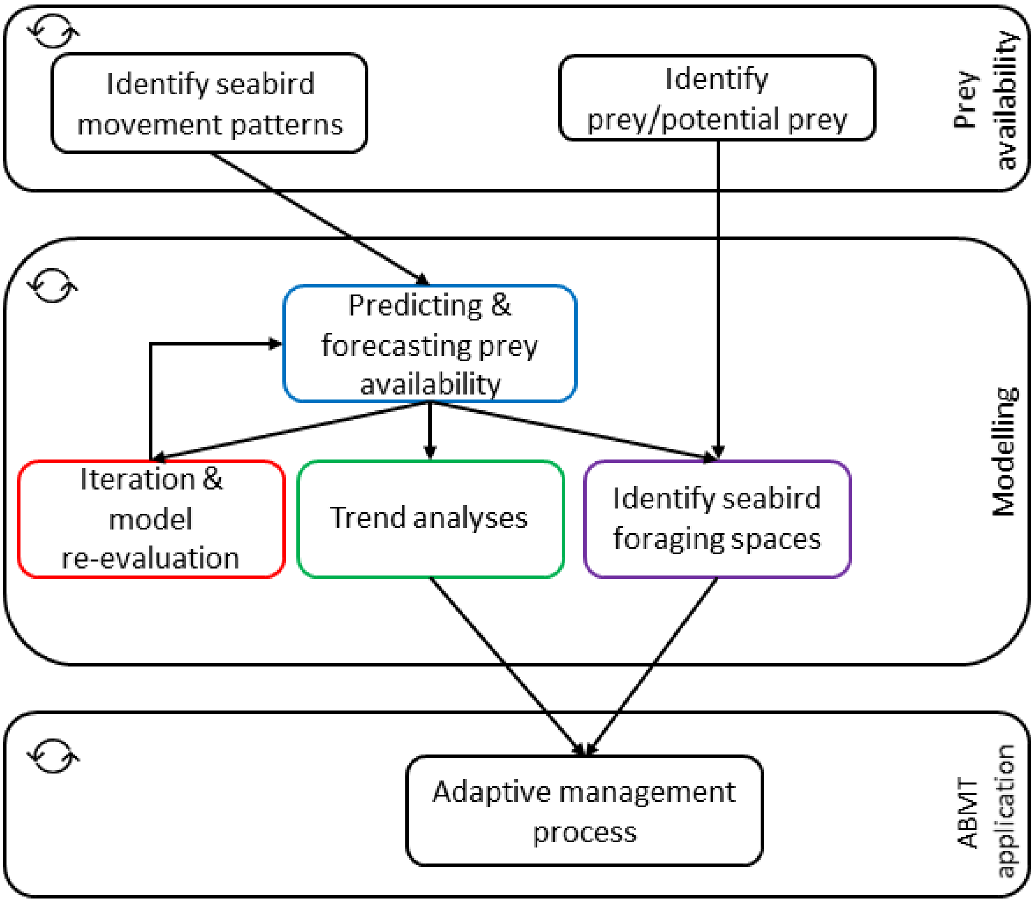

Figure 4.2: *The framework involves three stages covering prey availability (identifying seabird movement patterns and seabird prey/potential prey), modelling (predicting and forecasting prey availability, iteration and model re-evaluation, trend analyses, and identifying seabird foraging spaces), and adaptive management decision making. The elements in the modelling section are further broken down in Figures 4.6 (predicting and forecasting prey availability), 4.7 (Trend analyses), 4.8 (identifying seabird foraging spaces), and 4.10 (Iteration and model re-evaluation). All stages require iteration and feedback to (1) ensure both models and management are using the best and most recent available information possible and (2) to learn from, adapt, alter, and improve the process.*

4.3.1: Prey availability

Optimal foraging underlies resource tracking – how individuals move in response to spatially-temporally dynamic prey (Abrahms et al. 2021), with choice of foraging space based on the seabird’s ability to maximise energy intake and fitness. Although co-occurrence of predator and prey is a prerequisite to successful foraging, numerous studies identify prey availability as the primary driver of seabird foraging movements, migration movements, and distributions (Benoit-Bird et al. 2013, Waggitt et al. 2018, Hentati-Sundberg et al. 2021). Varying from species to species, prey availability is multifaceted, with prey spatial location and prey patch characteristics such as abundance, density, and prevalence as key elements of availability (Thiers et al. 2014, Boyd et al. 2015, Waggitt et al. 2018) (Figure 4.3). Seabirds trade-off each facet of prey availability to varying degrees depending on the conditions they face (Boyd et al. 2015, Amélineau et al. 2018), with populations of the same species or, in the case of differential migration/movement patterns, individuals of the same population potentially using different foraging spaces with very different returns on investment (Thiebot et al. 2013, Fayet et al. 2017).

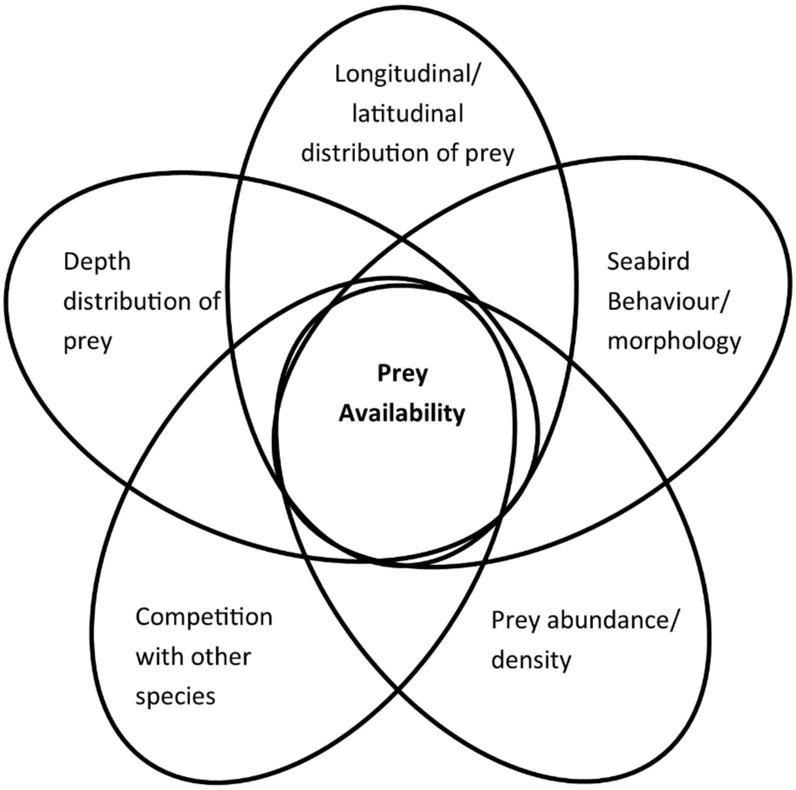

Figure 4.3*: Prey availability is comprised of multiple facets. Facets can vary over space and time and interact to make prey more or less available for a seabird. Facets may relate directly to the prey (e.g. prey abundance/density, the seabird (e.g. morphology) or to external factors (e.g. competition). Prey availability may be comprised of more or different facets than illustrated here.*

The abundance and distributions of seabird prey fish species typically tie closely to oceanographic conditions, with spatial-temporal dynamics arising from fluctuations in both ocean climate and climate change. For example, changes in the positioning of dynamic features that typically aggregate prey such as fronts, thermocline, or currents may redistribute prey further away from breeding grounds and/or into deeper waters (Durant et al. 2007, Péron et al. 2012), and more general trends in key oceanographic conditions such as temperature may result in a more wide-scale redistribution in response to natural fluctuations in oceanographic conditions (Fisher et al. 2008) or due to climate change (Schickele et al. 2021). In some cases, prey spatial patterns of migrations or aggregation formation for key life stages such as spawning may remain, though timings may vary (Davoren 2013, Murphy et al. 2018). Human fishing pressure may also impact prey species distributions by inducing phenotypic or genotypic changes (Coetzee et al. 2008, Hsieh et al. 2010, Frank et al. 2018) and alter local and regional abundances (Grémillet et al. 2018). The conditions determining prey distributions, patch characteristics, and threats may vary over seabird migration routes (Figure 4.4). The distributional response of seabirds to changing prey availability varies among species and populations (Box 1).

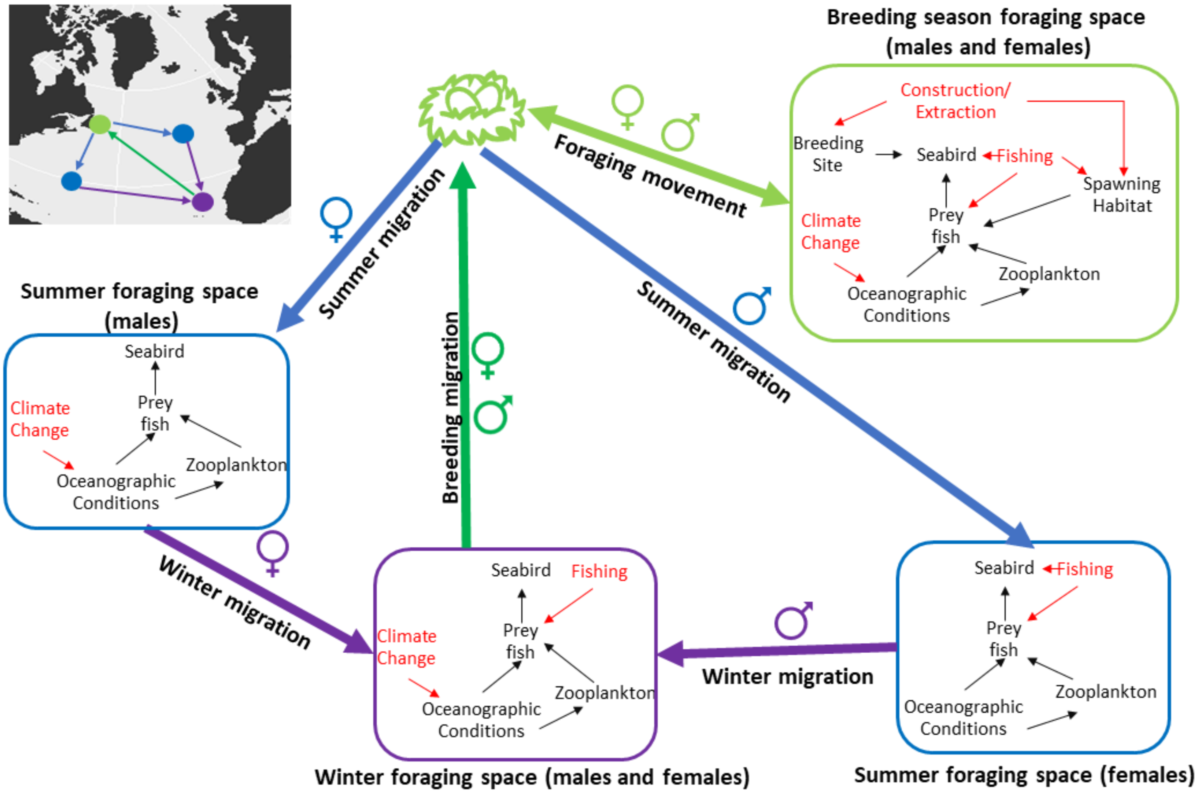

Figure 4.4*: Conceptual diagram showing the movement of a hypothetical seabird with differential (sex-based) summer migration and foraging space use. Foraging movements during the breeding season are bidirectional (parents making to-and-fro movements between the breeding site and prey – light green arrow and box), in contrast to unidirectional summer (blue), winter (purple), and breeding migrations (dark green). At each foraging space, prey distributions and patch characteristics may be driven by different biotic and abiotic factors and may be influenced by different threats (indicated in red).*

Box 1: Seabird responses to changing prey availability.
The distributional response of seabirds to changing prey availability likely varies among species and populations. For example, common guillemots (*Uria aalge*) delay breeding in response to late arrival of their key prey (Regular et al. 2008). Responding to fluctuating conditions, Cory's shearwaters (*Calonectris borealis*) switch foraging space in response to North Atlantic Oscillation (NAO)-driven changes to their prey (Avalos et al. 2017) during the breeding season whereas Peruvian boobies (*Sula variegata*) forage further when fishing removes more local prey patches (Bertrand et al. 2012). Outside the breeding season, common guillemots undertake dives that exceed their theoretical sustainable energy limits during late winters to access prey (Burke & Montevecchi 2018). Gentoo penguins (*Pygoscelis papua*) now use foraging spaces further from their resident colonies in response to changes in the distribution of their key prey (Ratcliffe et al. 2021), while Thin-billed prions (*Pachyptila belcheri*) and Wilson's storm-petrels (*Oceanites oceanicus*) shifted winter foraging movements polewards and northwards respectively (Quillfeldt et al. 2010). However, not all species or populations can avoid a spatial-temporal mismatch with changing prey availability. In the Barents Sea, for example, surface-feeding kittiwakes (*Rissa tridactyla*) have suffered much more from declines in prey than the pursuit diving common guillemot or Atlantic puffin (*Fratercula arctica*), with colonies at the edge of prey distributions fairing much worse than those located nearer more persistent prey patches (Barrett & Krasnov 1996).

4.3.1.1: Identifying seabird movement patterns

Seabird morphology and behaviours – particularly flight and fishing ability – can place some hard limitations on prey accessibility (Barrett & Krasnov 1996, Verberk et al. 2020). Both activities are energetically costly, with bird adaptations working to minimise or trade-off the costs of accessing prey.

The movements and migratory patterns of seabirds vary greatly (Table 4.1), with morphological adaptations in conjunction with environmental conditions that make long distances more efficient in some years and less so in others. For example, favourable winds may enable travel to more distant foraging spaces in some years by reducing the energetic cost of flight (Afán et al. 2021). In addition, different populations of the same species may vary in movement (Weimerskirch et al. 2017, Fayet et al. 2017), and differential migration - most commonly based on age or sex – may occur, resulting in different sub-groups in a population using entirely different spaces, or use of the same space at different times (Briedis & Bauer 2018). Regardless of distance potential, both long-distance and short-distance migrators may find their movements more constrained during some parts of their annual cycle than others. Most notably, the breeding season ties them to a terrestrial-based breeding site. During this period, seabirds exhibit central place foraging strategies, where they must complete to-and-from movements between their nest and foraging space in sufficient time and with adequate prey supply to ensure the survival of chicks and themselves (Weber et al. 2021). Although species vary in their energetic requirements for survival and breeding success (Hentati-Sundberg et al. 2021), the increase in energetic demands during the breeding season means the profitability of a foraging space with the same level of prey availability may be greater outside the breeding season than inside.

In terms of fishing, seabirds can be broadly categorised as surface feeders, plunge divers, and pursuit divers, with each mechanism placing different depth limitations on prey accessibility (Table 4.1). Pursuit divers, which actively pursue their prey underwater, can reach considerable depths, with the deepest dive recorded from emperor penguins (*Aptenodytes forsteri*) (565 meters) (Wienecke et al. 2007). However, most pursuit divers apparently never reach such depths. For example, studies report diving depths up to ~68 meters for sooty shearwaters (*Puffinus griseus*) (Shaffer et al. 2006) and up to 180 meters for common guillemots (*Uria aalge*) (Piatt & Nettleship 1985). Plunge divers, such as Cabot's tern (*Thalasseus acuflavidus*) and northern gannets (*Morus bassanus*), have been recorded at depths of up to two and 34 meters, respectively (Brierley & Fernandes 2001, Tavares et al. 2017). Although generally not efficient swimmers, some plunge divers include an active swimming phase (Cox et al. 2016). Surface feeders, whether foraging while flying or swimming (e.g. fairy prions *Pachyptila turtur*), typically target prey at or near the sea surface.

Data sources

Seabird tracking data can provide high-resolution population-specific details on migration patterns and foraging movements during the breeding seasons and, depending on the tracking device, diving depths at specific foraging spaces (Chimienti et al. 2017). To account for differential migration or foraging strategies, ideally tracking data would be demographically representative (e.g. male and female; adults, immature, and juvenile) and cover the entire annual cycle of the birds. Furthermore, data from multiple years would help elucidate changing spatial-temporal patterns or variations associated with different environmental conditions. However, ethical, economic, and practical considerations limit the feasibility of gathering tracking data (Bernard et al. 2021), limiting tracking information on population-specific movements. High-resolution, population-specific data used in conjunction with (or replaced by) more generalised data sources may prove useful in elucidating movement and depth limitations. These sources could include tracking data from other seabird populations, observations, range maps, and foraging radii for the breeding season (Grecian et al. 2012, Critchley et al. 2020). Regardless of data source, in the absence of compelling population-level data demonstrating the existence (or lack thereof) of differential migration and foraging strategies, I advise caution in assuming that demographically restricted data represents the seabird population as a whole, and that data collected in the breeding season applies to the non-breeding season and vice versa. Movement, range, and diving data may reside in accessible databases such as Movebank (Wikelski et al. 2021) or the Seabird Tracking Database (Birdlife International 2021b), as well as in private collections such as those held by academics, government departments, NGOs, and peer-reviewed and grey literature. I also note alternative observation data sources exist, including bycatch location information (Lewison et al. 2014).

***Table 4.1**: Examples of the movements and diets of seabirds from different orders and families obtained from peer-reviewed publications and seabird databases.*

Family	**Scientific name**	**Common name**	**Biogeographic Realm**	**Foraging style**	**Foraging trip movement from colony during breeding season**	**Movement outside breeding season**	**Diving depth**	**Primary prey group**	**References**
Spheniscidae	*Aptenodytes forsteri*	Emperor penguin	Southern Ocean	Pursuit diving	565 km (females during incubation) 125km (males during chick rearing)	Juveniles: 2579 ± 2385 km	565 m	Pelagic fish, cephalopods, krill	Wienecke & Robertson 1997, Wienecke et al. 2007, Thiebot et al. 2013, Birdlife International 2021a
Procellariidae	*Ardenna grisea*	Sooty sheerwater	NE Atlantic, Mediterranean, Mid-tropical North Pacific Ocean, South-east Pacific, Tropical W Atlantic, Mid-South Tropical Pacific, Offshore	Pursuit diving	393.0 ± 22.1 km	64,037 ± 9,779 km	68.2 m	Pelagic fish and cephalopods	Shaffer et al. 2006, Bonnet-Lebrun et al. 2020, Birdlife International 2021a

			& NW North Atlantic, Offshore Indian Ocean, Argentina, Chile, S Africa						
Diomedeidae	*Diomedea dabbenena*	Tristan Albatross	Offshore Indian Ocean, Offshore South Atlantic, Southern Africa	Surface feeder (suspected)	Avg. 940 km during incubation, avg. 380 km during chick-rearing	5000 km	Unknow. Assumed to be upper surface waters.	Pelagic fish and cephalopods	Birdlife International 2004, 2021a, Bond et al. 2021
Hydrobatidae	*Hydrobates pelagicus*	European storm petrel	NE Atlantic, Arctic Europe, Mediterranean, offshore North Atlantic, Offshore South Atlantic, Tropical East Atlantic, Southern Africa	Surface feeder	387 km	>10,000 km	5.6 m	Pelagic fish, cephalopods, crustaceans	Wernham et al. 2002, Albores-Barajas et al. 2011, Birdlife International 2021a, Bolton 2021
Oceanitidae	*Oceanites oceanicus*	Wilson's storm petrel	NE Atlantic, SE Pacific, Tropical West Atlantic, Tropical Indo-Pacific and Coastal Indian, Sub-tropical Australia and	Surface feeder	Est. 500 km	Unknown, but thought to be >1,000 km (probably much greater)	<1 m	Pelagic fish, crustaceans	Croxall et al. 1988, Gladbach et al. 2007, Birdlife International 2021a

			Coral Sea, Mid-South Tropical Pacific, Tasman Sea into SW Pacific, Offshore Indian Ocean, Offshore South Atlantic, Offshore mid-eastern Pacific, Tropical East Atlantic, Argentina, Chile, Southern Australia, Southern Africa, New Zealand, Southern Ocean						
Alcidae	*Uria aalge*	Common guillemot	NE Atlantic, Arctic Europe, North Pacific, Tropical West Atlantic, Offshore North Atlantic, Offshore West Pacific	Pursuit diving	100 km	1,200 km	180 m	Pelagic fish	Piatt & Nettleship 1985, Davoren & Anderson 2003, McFarlane Tranquilla et al. 2014, Birdlife International 2021a

Laridae	*Sterna paradisaea*	Arctic tern	Artic Europe, Arctic, Southern Ocean	Surface feeder	30 km	70,900 km (59,500–81,600 km)	0.5 m	Pelagic fish, crustaceans	Egevang et al. 2010, Thaxter et al. 2012, Birdlife International 2021a
Pelecanidae	*Pelecanus thagus*	Peruvian pelican	Southeast Pacific, Tropical Eastern Pacific, Chile	Plunge diving and surface feeding	83 km	Unknown	2 m	Pelagic fish	Zavalaga et al. 2011, Birdlife International 2021a
Sulidae	*Morus bassanus*	Northern gannet	NE Atlantic, Arctic Europe, Mediterranean, North Atlantic boreal and sub-Arctic from Canada to Greenland Sea, Tropical West Atlantic, Offshore North Atlantic, Offshore South Atlantic	Plunge diving	590 km	33,600 km	34 m	Pelagic fish	Brierley & Fernandes 2001, Thaxter et al. 2012, Garthe et al. 2016, Birdlife International 2021a
Anatidae	*Polysticta stelleri*	Steller's Eider	Arctic, North Pacific	Surface feeder, Pursuit diving	Coastally restricted. Often breeds several km	>5,000 km	6.8 m	Molluscs, crustaceans, other invertebrates	Petersen et al. 2008, Heggøy et al. 2019, Birdlife

					inland and forages in fresh, saline, or brackish water, as well as in tidal flats				International 2021a

4.3.1.2: Identifying prey/potential prey.

Effective modelling of prey availability requires knowledge of which prey species to model. Some seabirds may target a few ‘preferred prey’ species (specialists), in contrast to others that may target multiple prey species more opportunistically (generalists). For example, whereas fishes primarily comprise the diets of greater crested terns (*Thalasseus bergii*) in the Western Cape, South Africa during breeding, the prey came from at least 47 different families (Gaglio et al. 2018). On the other end of the scale, red-legged kittiwake (*Rissa brevirostris*) in the Bering Sea feed almost exclusively on lanternfish (*Myctophidae*) (Kokubun et al. 2015). Furthermore, seabird diets may vary among populations, with ontogeny, over migratory stage, and breeding status (Karnovsky et al. 2008, Campioni et al. 2016, Paiva et al. 2016, Botha & Pistorius 2018) (Figure 4.5). Although all seabirds can engage in prey switching, they typically prefer higher quality prey than alternative sources. As such, prey switching typically occurs with reduced prey availability. Prey switching has been implicated in the declining condition of individual seabirds and populations (Grémillet et al. 2008, Divoky et al. 2015, Reynolds et al. 2019).

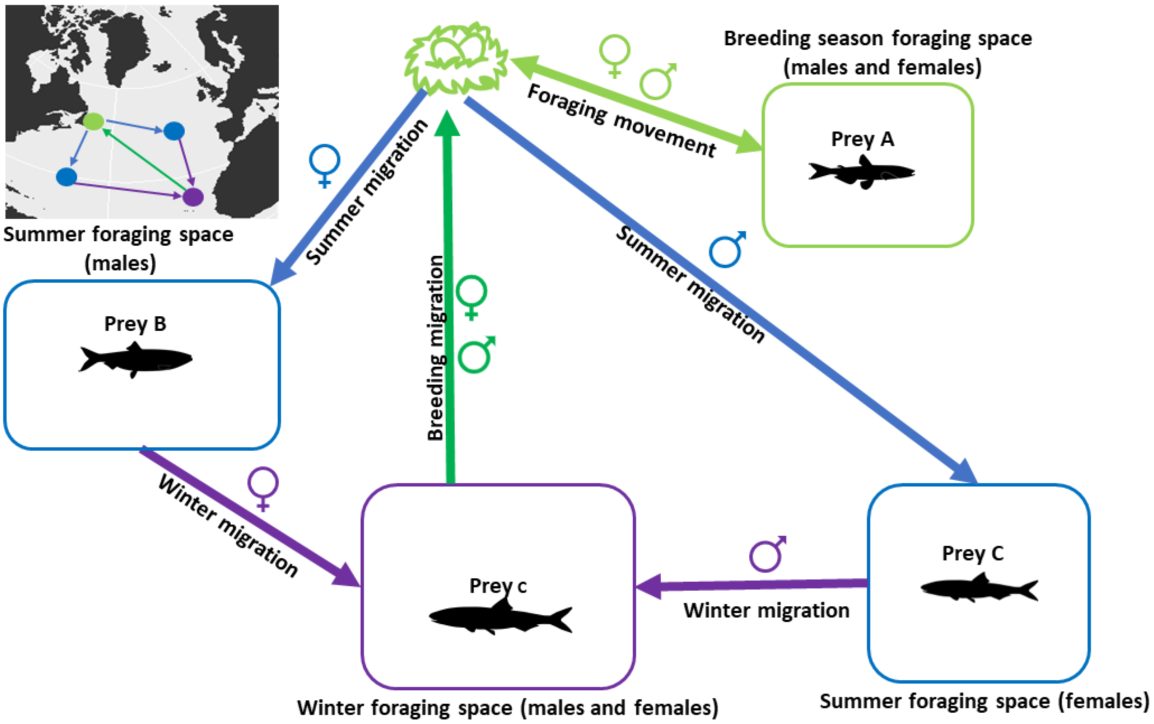

Figure 4.5: *A particular prey species may be targeted in one or several spatially discrete foraging spaces used throughout the migration cycle. In this conceptual diagram, females exploit two prey species – prey 'A' during the breeding season (light green) and prey 'C' at spatially separate summer (blue) and winter (purple) foraging spaces. In contrast, males exploit three prey species (prey 'A' during the breeding season (light green), prey 'B' in their summer (blue) foraging space, and prey 'C' in their winter (purple) foraging space).*

Data sources

Obtaining population-specific prey data can be challenging, particularly outside of the seabird's breeding season. Combining data from multiple sources may help infer prey or potential prey throughout the bird's migration or possible demographic variation in prey species. Alongside peer-review publications, grey literature, and privately-held databases, several direct and indirect sources can offer dietary data, including stomach sampling of live or dead birds, excrement and pellet sampling, eDNA sampling (direct, e.g. from faeces and indirect, e.g. from passive sampling at known foraging hotspots/with tracking data), and observations and photo-sampling (Barrett et al. 2007, Gaglio et al. 2018, Cavallo et al. 2020, Bessey et al. 2021). Although they cannot provide the same level of detail, stable isotope and fatty acid analysis can help determine the tropic level of prey and, when used in conjunction with other information sources, including potential prey ranges and seabird tracking, can help to infer prey species (Paiva et al. 2016, Zango et al. 2019).

4.3.2: Modelling

Distribution models are a family of quantitative tools that use species occurrence records with abiotic and biotic data to predict characteristics such as probability of occurrence or abundance in geographical space of single species (species distribution models) or communities (community distribution models) (Guisan et al. 2017, Norberg et al. 2019). Distribution models can predict three key attributes of seabird prey availability – longitudinal and latitudinal (x, y) distribution of prey patches, vertical distribution (z) of prey patches, and a measure of prey patch characteristics. Combining model predictions with seabird movement patterns can identify historic and forecast future potential geographic location foraging spaces, and assess trends in the spatial-temporal variability of prey availability. Together, these outputs can assist decision-makers in prioritising when and where best to implement

ABMTs, as well as inform types of management actions. Box 4.2 provides a glossary of key modelling terms.

Box 4.2: Glossary of modelling terms

Community distribution model (CDM): Statistical models or the amalgamation of multiple SDMs to predict the geographic distribution of communities.

Covariates: The biotic or abiotic factors included in a distribution model to predict species (SDM) or community (CDM) distribution.

Distribution model predictions: Prediction of the geographic distributions of a species/community across the same time and space as used to create the distribution model.

Distribution model forecasts: Prediction of the geographic distributions of a species/community at a future point in time.

Hindcast: Prediction of the geographic distribution a species/community in the past. Historical covariates do not necessarily cover the same temporal extent as species data used to create the underlying distribution model.

Resolution: The smallest distance (spatial resolution) or period (temporal resolution) between two measurements. Finer-scale resolutions capture more detail than coarser-scale resolutions.

Spatial extent: The area (longitude, latitude, depth) boundaries that encompass the area of interest.

Species distribution model (SDM): Statistical models that predict the geographic distribution of a single species.

Box 4.2: Glossary of modelling terms (cont.)

Species presence/absence data: Data listing the date/time and location where a species has been observed (presence) or where it has not been observed despite survey effort at that location (absence).

Temporal extent: The duration or range of the period of interest (e.g., the years 1998 – 2020 or the months January to March).

Trend analysis: The assessment and quantification of changes in patterns over time. Also known as time-series analysis.

4.3.2.1: Predicting and forecasting prey availability

Multiple distribution models that can be used to predict prey availability exist, including regression-based techniques (e.g. Multivariate Adaptive Regression Splines -MARS, Generalized Linear Model - GLM), machine learning (e.g. Maximum Entropy – Maxent, Gaussian processes - GP), and mechanistic models (e.g. Global Repositioning Dynamics of Diadromous fish Distribution – GR3D) (Rougier et al. 2014, Golding & Purse 2016, Guisan et al. 2017). Models can be run alone, or multiple models can be run together to produce averaged predictions (ensemble modelling) (Hao et al. 2020). Choice of distribution model(s) depends on several factors, including types and quality of data available, model assumptions, and modelling objective. Several existing publications compare and contrast the various distribution modelling options available and best practices (Elith et al. 2006, Franklin 2010, Evans et al. 2015, Guillera-Arroita et al. 2015), discuss community modelling (Ferrier & Guisan 2006, Nieto-Lugilde et al. 2018, Norberg et al. 2019), and assess the quality and suitability of model and data options (Sofaer et al. 2019).

At a minimum, modelling prey availability requires (1) data on the prey species (presence or presence/absence records with date and location of observation) and (2) abiotic and biotic covariates that cover the spatial-temporal extent of the species data and area where distribution predictions are required if it extends beyond the species observations (see Petitpierre et al. 2017 and Werkowska et al. 2017 for discussion on model transferability). However, certain data attributes could result in better model predictions (Table 4.2). For example, prey species data containing abundance/density information allows models to predict prey patch characteristics such as density that may be important to seabirds (Franklin 2010). Demographic data may prove useful where the prey species exhibits ontogenetic habitat shifts for more targeted distribution modelling (Vasconcelos et al. 2014). Distribution models can include physiological information, potentially combined with demographic data (Evans et al. 2015). Samples from multiple months over many years can help ascertain model transferability over time and if and when the statistical species relationship to modelled covariates changes or fluctuates (Radosavljevic & Anderson 2014, Roberts et al. 2019, Muhling et al. 2020). Sampling depth information can be used in conjunction with depth-stratified covariate (predictor) datasets such as those derived from ocean models to link samples to more proximal covariate values and offer depth-stratified predictions (Andrews et al. 2020). The spatial and temporal resolution of covariates should, as far as possible, reflect the dynamics of the covariate processes, the spatial-temporal ecology of the species being modelled and scales of predator-prey interactions, and the predictive skill of the model (Fauchald et al. 2000, Mannocci et al. 2017, Manzoor et al. 2018), which likely includes both short-term and long-term climatological conditions (Brodie et al. 2021). This information is particularly important for highly mobile and migratory prey whose distributions can change rapidly with changing conditions.

Forecasting prey availability requires covariates to be forecastable at the desired spatial resolution (e.g. 1 km^2 vs 10 km^2) and temporal resolution (e.g. one week vs one month) (Jacox et al. 2020, Brodie et al. 2021). Regular forecasting (i.e. making predictions into the future as and when temporally novel forecasted covariates become available) (Figure 4.6) could create opportunities for adaptive and dynamic management that responds rapidly to variations in the spatial-temporal distributions of potential seabird foraging spaces (Dietze et al. 2018). The temporal scale at which forecasts should be made will be dictated somewhat by the temporal availability of the covariate data, though ideally should be at a scale that is actionable by management. In the absence of forecastable covariates, model outputs are restricted to predicting contemporary and historic prey availability/distributions (i.e. temporally matches the covariate data used to generate the distribution model; Figure 4.6). Uncertainty that arises throughout the modelling, prediction, and forecasting process should be quantified and reported (Box 3).

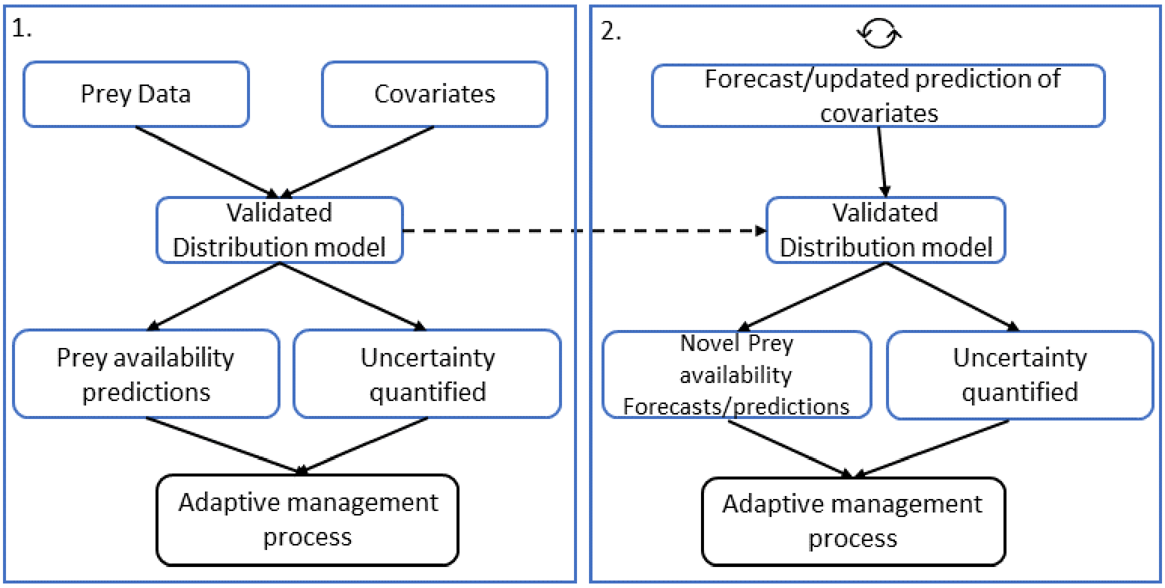

Figure 4.6: *Predicting and forecasting prey availability requires (1) the construction of a validated distribution model, which can then be used to make predictions (i.e. using novel albeit historic covariate data) or forecasts (e.g. using covariate forecasts) where available (2). Both the initial distribution model and future update outputs should include spatial predictions, with uncertainty in those predictions/forecasts quantified where possible for incorporation into an adaptive management process. Novel prey availability forecasts/predictions should be generated as and when novel covariate forecasts/updated predictions become available and rapidly fed into the adaptive management process for application on the ground.*

Box 3: Uncertainty

All models carry some level of uncertainty. Identifying and quantifying uncertainty is important for improving models and for decision makers to accurately assess the quality of the model output, as well as potential outcomes of actions they may implement and risks of inaction based on those outputs (Beale & Lennon 2012, Sofaer et al. 2019). Uncertainty may arise from numerous sources such as foraging radius estimates used to determine the maximum distance seabirds travel during the breeding season, in the covariates used to model prey availability, seabird use of foraging spaces identified by the process, and choice of distribution model. Forecasting introduces additional sources of uncertainty including those arising from the underlying algorithms, processing errors, the initial conditions and data input into the model, how parameters change and interact in the model, and the drivers that create change, and sensitivity of the system to change (Dietze 2017). Forecast skill may also deteriorate with lead time adding a temporal element to uncertainty, though as with other sources of uncertainty can be improved with model development (Meehl et al. 2014, Stern & Davidson 2015). Accounting for uncertainty throughout the modelling and forecasting process is important to identify where improvements can be made and where models foraging space predictions may be particularly reliable/unreliable (Sofaer et al. 2019, White et al. 2019). Furthermore, key sources of uncertainty may also be targeted as areas for additional or improved empirical data collection.

Table 4.2*: Key considerations for species and covariate (predictor) data for predicting prey availability. Better Solutions allow more detailed prey availability predictions to be run than good solutions.*

Consideration		**Good Solution**	**Better Solution**
Prey species data	Sampling type	Presence/presence absence	Abundance/density
	Sampling location	Longitude and latitude location of sampling	Longitude, latitude, and depth location of sampling
	Temporal resolution	Seasonal covering a few years	Multiple months over many years spanning different 'ocean climates', particularly for highly mobile/migratory prey species
	Demographic data	No demographic information on prey sampled	Age or sex of the prey sampled
	Physiological information	No physiological information on prey species	Physiological information on prey species available
Covariates (predictor) variables	Spatial-temporal attributes	Extent covers the time and location over which prey species data were acquired (and the area/time where/when distribution predictions are desired if outside the extent of the species data). Spatial and/or temporal resolution may be coarse	The spatial and temporal resolution of the data match the dynamics in the ecology of the prey and covariates themselves, with the extent offering sufficient spatial-temporal coverage of the species data (and any area/time outside of the species data that distribution predictions are required).
	Depth dimensions	Values available at a single depth	Values available at multiple depths
	Forecastability	Cannot currently be forecasted	Can be forecast at temporal scales relevant management and the ecology of the prey species

4.3.2.2: Trend analyses

Trend analyses (analysis of spatial patterns over time) of the predictions and forecasts produced by distribution models can be used to provide temporal information of the changing state of predicted prey availability for adaptive management planning (sensu Walters 1986) (Figure 4.7). Trends may reveal, among other attributes, areas where prey patches persist (or are forecast to persist), over time, where patch characteristics fluctuate with oceanographic conditions, or where patches show a declining/increasing trend. Trend analysis requires predictions or forecasts from multiple periods (e.g. the same month over multiple years), and can be run at multiple temporal scales, with the minimum scale being that of the underlying prediction. For example, if a prediction is made monthly, inter-month and inter-annual temporal trends can be analysed. Several options exist for analysing trends in predicted distributions and patch characteristics available. For example, emerging hotspot analyses (ESRI 2020) can reveal spatial-temporal trends in predicted habitat suitability (Andrews et al. in review) and density (Young et al. 2020). Mann-Kendall trend statistics (Kendall & Gibbons 1990) can be used in conjunction with landscape metrics to assess trends in spatial attributes of prey patches (Hesselbarth et al. 2019), including temporal changes in movement patterns of highly mobile and migratory species in response to fluctuations in conditions as well as longer-term trends. Although, to the best of my knowledge, no tool for analysing patches in three dimensions exists, depth-specific information can still be garnered (e.g. by analysing predicted distributions and/or abundances on depth layers provided by ocean models (Andrews et al. in review).

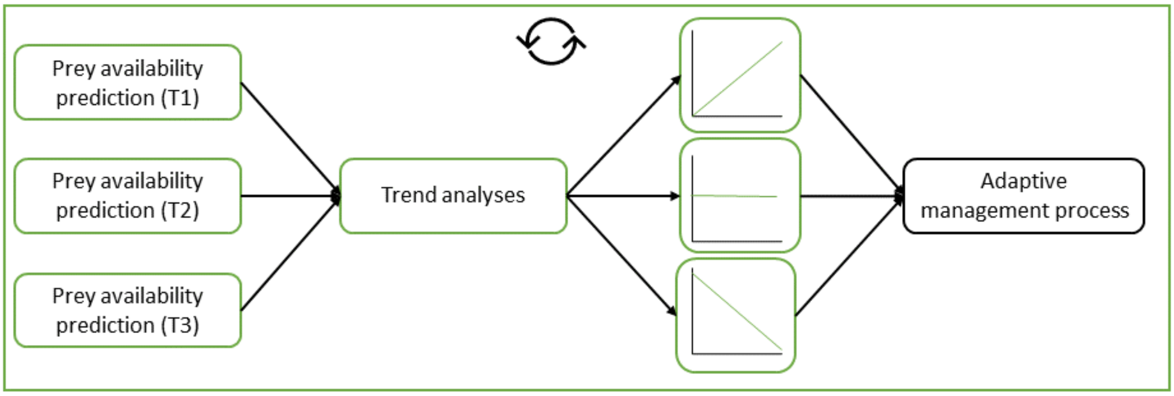

Figure 4.7: *Trend analyses such as Mann-Kendal trend statistics and emerging hotspot analysis can be used to detect spatial-temporal changes in key attributes of prey availability which should be fed into an adaptive management process. Trends should be re-analysed as and when new prey availability predictions become available and fed into the adaptive management process.*

4.3.2.3: Identifying seabird foraging spaces

To provide guidance on potential seabird foraging spaces, predicted or forecasted prey availability must be used in conjunction with seabird movement information (Figure 4.8).

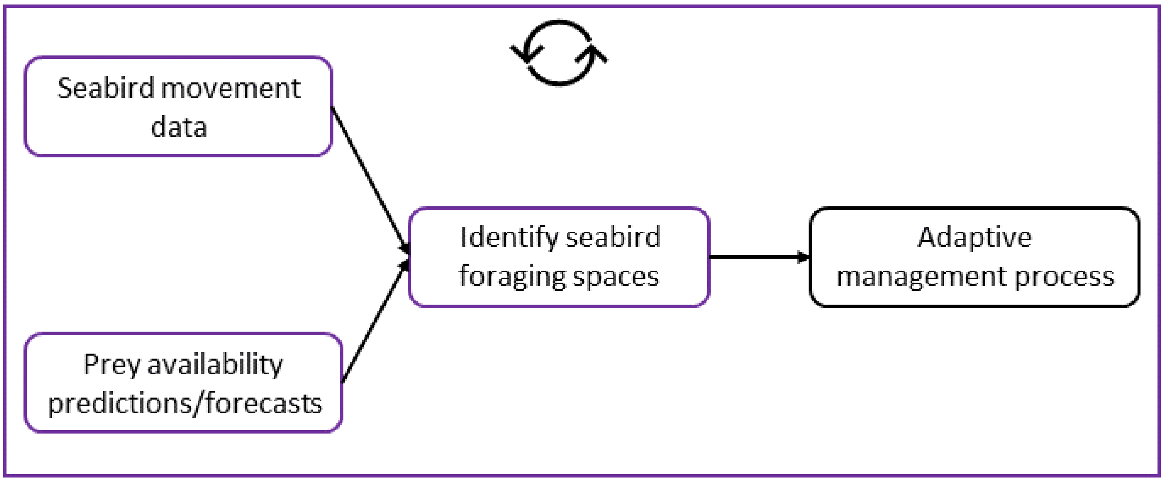

Figure 4.8: *Potential seabird foraging spaces are identified by refining prey availability predictions/forecasts with seabird movement data. Seabird foraging space identification should occur as and when new/updated seabird movement and prey availability predictions/forecasts are available, with updates rapidly fed into the management process for adaptive ABMT implementation.*

Specifically, refinement of prey availability into potential foraging spaces should consider three characteristics (1) seabird ranges (movement across longitudinal and latitude), (2) the depth seabirds can reach, and (3) prey patch characteristic metrics (e.g. predicted abundance, probability of presence) and spatial location (i.e. the distribution). Ideally, all three attributes would be used to identify potential foraging spaces. However, I note that using seabird range movements with either depth or prey patch characteristics can still provide useful information on prey availability necessary for adaptive management planning around potential seabird foraging spaces (Figure 4.9). In the absence of seabird depth information, I still encourage generating predictions, forecasts, and trend analysis on the depth distribution of prey for two reasons (1) seabird depth data may become available later, in which case historic predictions can be used to create more refined trend analyses, and (2) depth distribution predictions and trends provide insights into the spatial ecology of the prey species, which may assist current or future management decisions. Uncertainty surrounding seabird range and depth information should be characterised and reported where possible.

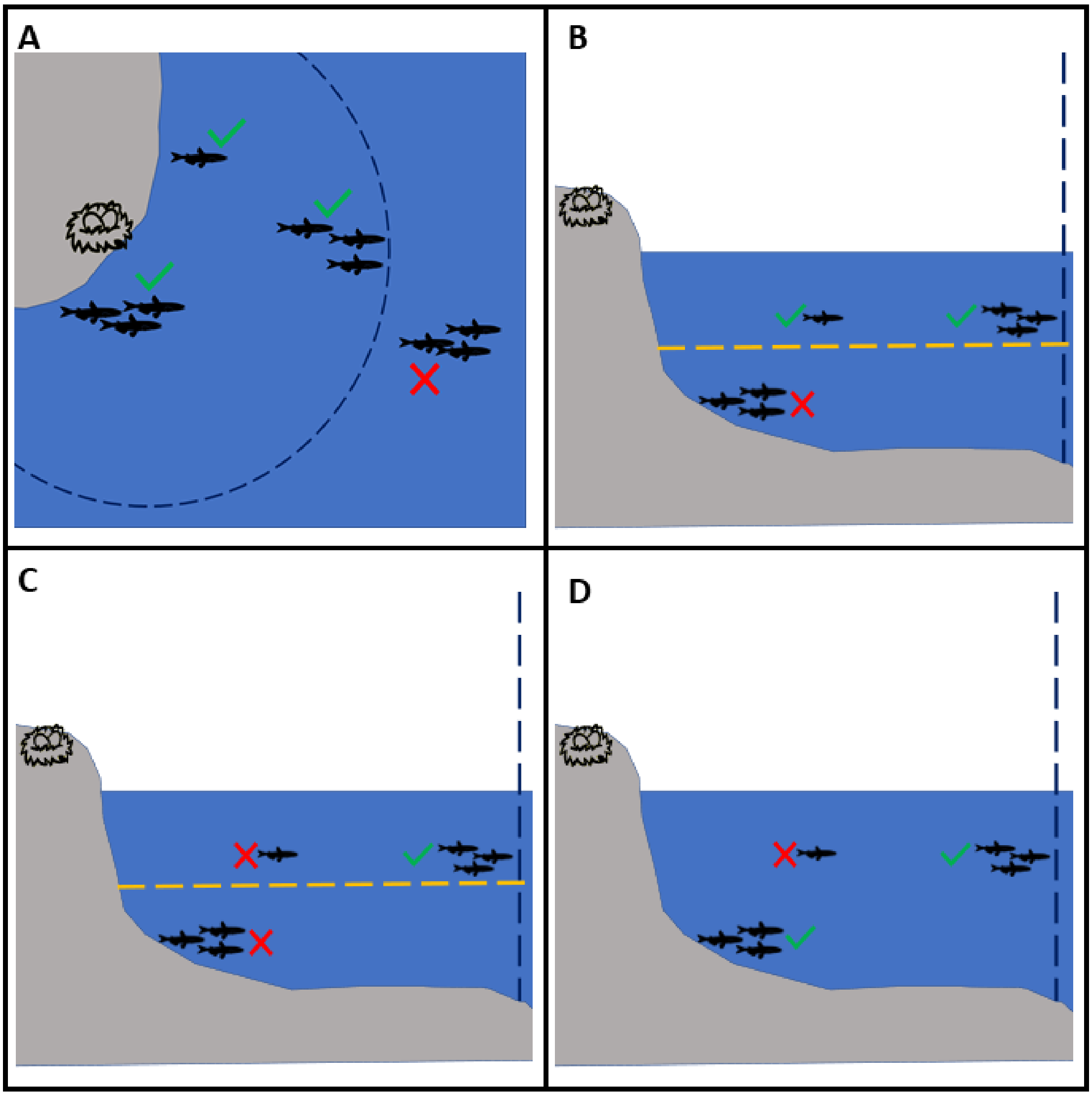

Figure 4.9: *Models of prey availability can be refined to indicate potential foraging spaces based on seabird horizontal movements, depth capabilities, and prey patch characteristics such as abundance or probability of occurrence. As illustrated in this conceptual diagram of seabird foraging movements during the breeding season, the level of refinement depends on the combination of attributes used. In A, foraging spaces are defined based on foraging radius estimates only, excluding (red cross) only one of the four potential prey patches. In B, adding depth limit estimates, refining which prey patches are most likely to be used as foraging spaces. In C, including the abundance of prey (assuming that, all things being equal, seabirds will preferentially exploit the prey patch with the highest abundance) further refines foraging space identification. In D, abundance information remains, but depth limit estimates are not available. The uncertainty produced by the various combination of attributes should be weighed up when applying predicted foraging spaces to management.*

Seabird tracking data and at-sea observations can provide insights into the spatial response of seabirds to predicted and forecasted changing prey availability. For example, despite clear links between prey density or abundance at large spatial scales and seabird population persistence and fitness (Cury et al. 2011, Barbraud et al. 2018), the minimal level of density or abundance required for seabirds to consider exploiting that prey patch is less clear. More directly, tracking and at-sea observations of seabirds can provide precise information to identify likely foraging spaces that seabirds from specific populations will exploit than those identified from more general range or foraging radii estimates.

4.3.2.4: Iteration and model re-evaluation

Distribution models are built on species data and covariates that are mostly using data from the past or having only one time period (i.e. a snapshot). Resulting predictions projected into the past, present, or future geographic space, assumes a species relationship with modelled covariates remains constant throughout its range and over time (Trainor & Schmitz 2014). Relying on fixed models could be problematic if the prey's statistical relationship to modelled covariates varies and/or if the "rules" for species assemblies and/or interactions change (Hof et al. 2012, Brown & Carnaval 2019). Furthermore, distribution models that perform well on historic data do not necessarily forecast well (Becker et al. 2019). Instead, a model process that iteratively assimilates new data sources, assesses whether the model remains fit for purpose (i.e. reflects how the modelled species is currently reacting to current conditions), and reassesses model performance based on novel data sources may more accurately reflect the dynamic nature of prey availability. Dietze et al. (2018) and White et al. (2019) offered best practices for iterative ecological forecasting, and Dietze et al. (2021) offered guidance on output and metadata standards.

Model iteration (Figure 4.10) should primarily occur for one of three reasons: (1) temporally novel prey data becomes available, (2) temporally novel prey and covariate data spanning the same timeframe becomes available, or (3) a novel covariate becomes available. To ensure that the model and outputs are still fit for purpose, temporally novel prey data should be used to validate any forecasts/predictions previously produced that overlap with the timeframe of the new prey data. Poor validation results may indicate that the distribution model needs to be revisited or that the modelled species-environment relationship is not static. If models are still fit for purpose, the prey data should be incorporated into the model for future predictions/forecasts. Where temporally novel prey and covariate data spanning the same timeframe becomes available, the underlying model should be rebuilt and validated to incorporate the novel data. Any previous prey availability predictions, forecasts (now hindcasts), and trend analyses should be regenerated for continuity and comparability between model outputs.

Similarly, introducing novel covariates may result in better models, and thus better predictions/forecasts of prey availability, make little difference, or reduce the model's skill. New models should be built to include the new covariate, validated, and assessed against the existing model. If the model is improved with the new covariate, the new model should replace the existing model. Again, any previously generated predictions, forecasts (now hindcasts), and trend analyses should be regenerated.

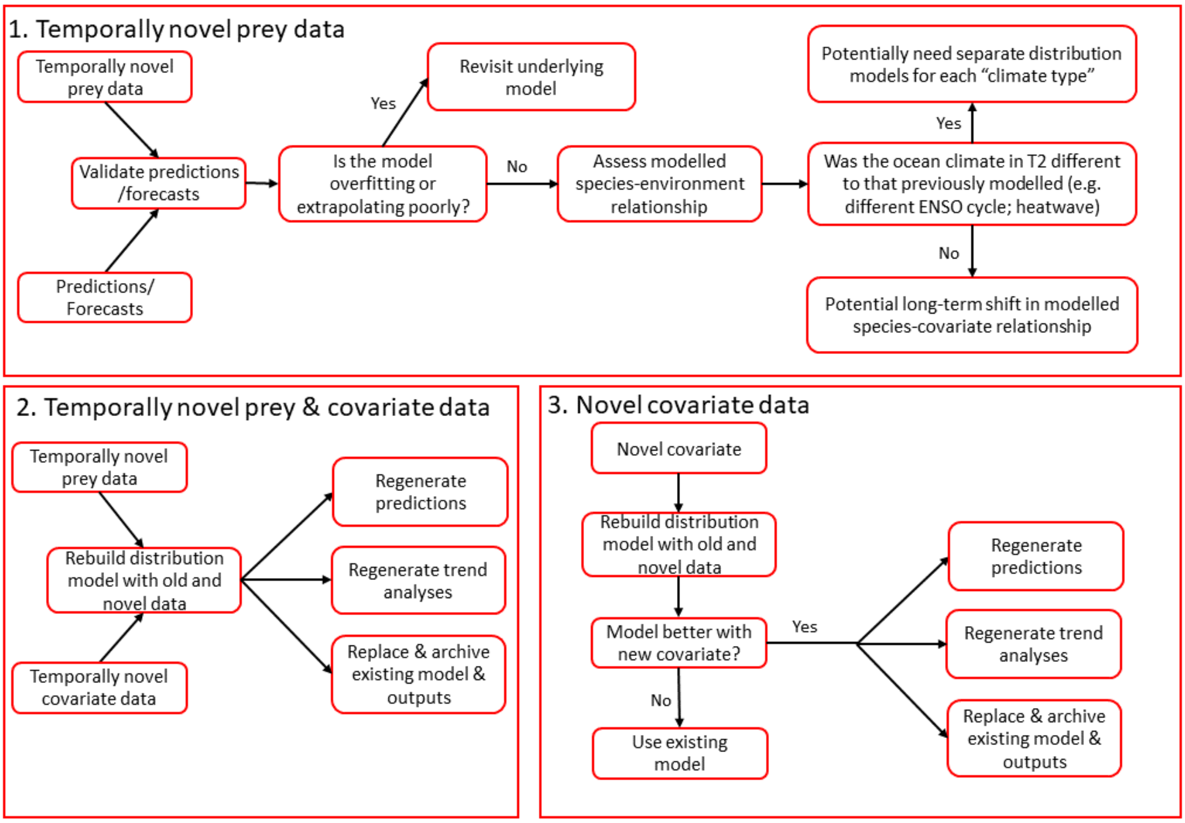

***Figure 4.10**: Model iteration & re-evaluation should occur when (1) temporally novel prey data becomes available, (2) temporally novel prey and covariate data become available, and (3) a novel covariate data source becomes available.*

4.3.3: Area-based management tool application

Area-based management tools (ABMTs) apply management measures to a specific area to achieve desired goals or objectives. ABMTs encompass a highly diverse group of strategies that can be spatially and temporally static (e.g. an area subject to permanent fishery closure) or dynamic (e.g. an area may only be closed to fisheries at certain times) and may or may not be sectoral specific (e.g. fishery gear restrictions). ABMTs have been implemented in areas around seabird colonies to reduce negative interactions with fisheries, including time-area closures in South Africa for African penguins (*Spheniscus demersus*) (Sherley et al. 2018). More recently, MPAs and MPANs are increasingly gaining traction as effective management tools to minimise human impacts on biodiversity (Ortuño Crespo et al. 2020) (Box 4). The long-term conservation of highly mobile and migratory species requires the incorporation of spatial-temporal dynamics throughout their life cycle (Runge et al. 2016), and ecologically relevant MPANs composed of static (i.e. traditional MPAs) and/or dynamic areas (i.e. varies in time and/or space) (D'Aloia et al. 2019, Dunn et al. 2019, Ortuño Crespo et al. 2020) offer the potential to reduce current and emerging human interactions with seabirds and their prey at their various foraging spaces. I note that any given prey species patch is likely to be utilised by other marine predators (McGowan et al. 2013, Davies et al. 2021). As such, MPANs established for the conservation of foraging spaces identified for one seabird population may have biodiversity benefits beyond the population or species of seabird targeted for protection.

Forecasting and assessing trends in the characteristics of potential seabird foraging spaces (e.g. spatial patterns, abundance or probability of presence) provides key information that decision-makers can use to design and maintain ecologically relevant MPANs that pro-actively reduce manageable risks to seabirds. For example, fisheries management can help ensure sufficient prey availability in the region, whereas restricting fishing activity at key foraging spaces can buffer against more localised depletion that may place particular pressure on seabird populations and reduce the chance of negative interactions such as bycatch (Bertrand et al. 2012, Dias 2017, Sherley et al. 2018). Indeed, failure to protect the most 'important' foraging spaces (e.g. those with high prey availability) to avoid conflict with human activity and, as a result favour less 'important' foraging spaces (e.g. those with low prey availability) for protection will likely yield suboptimal benefits for the seabirds and reduce cost-efficiency (McGowan et al. 2013). Furthermore, information derived from models and forecasts of foraging spaces can assist in identifying those populations at greater risk. For example, seabirds that forage at the edge of prey's distribution ranges may encounter lower prey concentrations and be more susceptible to changing oceanographic conditions than those located in the centre of the prey’s distributional range. This effect may be particularly pronounced at the trailing edge of the prey’s range or in locations with reduced prey habitat quality (Robinson et al. 2015, Waldock et al. 2019).

Box 4: MPA Networks

Marine protected areas (MPAs) are a type of ABMT designed to meet objectives related to the conservation of biodiversity (Day et al. 2019). The extent to which MPAs can assist in achieving conservation objectives depends on a number of factors including their location, what activities they restrict and enforcement of the rules, and consideration of the ecology of the species, habitats, or ecosystems they aim to assist in their design (Edgar et al. 2014). For example, while fisheries management tools aimed at reducing fishing pressure on essential prey may help ensure prey is regionally abundant, MPAs and other ABMTs can specifically buffer against depletion at key foraging spaces (Bertrand et al. 2012, Barbraud et al. 2018, Dahood et al. 2020).

MPAs are typically placed inside exclusive economic zones (EEZs), though awareness of the need for placement in areas beyond national jurisdiction (ABNJ) (Ortuño Crespo et al. 2020). MPAs in both EEZs and ABNJs could prove beneficial for a wide range of migratory species whose movements may take them into the EEZs of different jurisdictions and into the high seas.

The use of MPAs for migratory species has been criticized for being too small relative to the home range (Botsford et al. 2003). Furthermore, the spatial scale of migratory species distributions may make MPAs – and particularly MPAs that prohibit extraction - that cover their entire range politically unpalatable (Hooker et al. 2011). For this reason, large scale MPAs largely occur in the more remote areas of the ocean where human use is fairly low (Leenhardt et al. 2013). Like their smaller-scale counterparts, large MPAs are not necessarily in the places needed to ensure species or habitat conservation objectives are reached (Stevenson et al. 2020).

Since migratory and other highly mobile species typically only use a portion of their potential range during any given stage in their annual cycle (Merkel et al. 2021), rather than attempting to implement large-scale MPAs, MPA Networks - “a collection of individual MPAs or reserves operating cooperatively and synergistically, at various spatial scales and with a range of protection levels that are designed to meet objectives that a single reserve cannot achieve” may provide sufficient protection (IUCN World Commission on Protected Areas 2008). In particular, networks composed of static (i.e. traditional MPAs) and/or dynamic (i.e. varies in time and/or space) areas targeted to manage human activity at ecologically relevant spatial and temporal scales may prove valuable (D’Aloia et al. 2019, Dunn et al. 2019).

Modelled outputs can also help guide decisions on human activities and whether they should be allowed within an MPANs for seabirds. For example, a proposed tidal energy installation in a foraging space may currently lie below the depth that seabirds typically dive to; however, if prey distribution trends into deeper depths towards the installation, the risk of seabird-installation interaction increases as the birds follow their prey. Alternatively, the installation may influence prey population characteristics important for prey availability (Scott et al. 2014). Similarly, changes in prey availability may result in predator redistributions into fishing areas, creating conflict between seabird and fisheries for prey and potentially increasing the risk of seabird bycatch mortality (Hobday et al. 2015, Ratcliffe et al. 2021) unless effectively managed. Managers already utilise forecasts of species distributions to pro-actively manage fisheries to reduce bycatch of several species, including tuna and sea turtles (Hobday & Hartmann 2006, Howell et al. 2015).

Whether an activity can be managed dynamically or not depends partly on the nature of the activity and the spatial-temporal dynamics of prey and seabirds. For example, restricting fishing activities from just one particular locale while seabirds exploit that space may prove sufficient. In contrast, activities that fundamentally alter features that create prey spawning aggregations require more permanent restrictions. Equally important, while more static approaches may be suitable for foraging spaces that exhibit spatial stability across varying ocean conditions (e.g. Sherley et al. 2018), MPAs that remain fixed in space may not prove effective for foraging spaces that spatially fluctuate in response to cyclical phases in oceanographic conditions (for example) or are shifting in response to climate change, even if the management of activities within include a temporal component (e.g. fishing excluded during the months when seabirds exploit the space) (Figure 4.11).

Managers face several challenges in implementing ABMTs for seabirds. For example, competition with human users, particularly for existing or future industrial uses (e.g. fishing, oil and gas) for space, may make their designation politically unpalatable (Jones et al. 2016). More specific to MPANs, the designation of areas typically occurs on an ad-hoc basis rather than as a single effort to build a connected network (Roff 2014). Fragmented planning may arise from the planning process (e.g. designation on individual areas occurs as and when sufficient scientific evidence and political backing aligns), or due to the involvement of different management bodies (e.g. from different jurisdictions, cover different ecological realms), each with different priorities and different capabilities (Giakoumi et al. 2018). Regardless of the cause, an ad-hoc approach may result in a network that does not cover the full migratory cycle of seabirds, even if the data are available to make a network possible.

Nevertheless, lack of ability to create a fully connected network should not hamper efforts to implement individual ABMTs in areas that have been identified as important. Efforts to implement adaptive management measures may be hampered if predictions or forecasts cannot be produced and distributed to decision-makers and then integrated into management practice on a timely basis. This may be a particularly acute problem for highly dynamic ABMTs. Management bodies may need to implement new processes to ensure the regular production and integration of outputs (Welch et al. 2018). Other challenges relate to monitoring and enforcement capabilities and engagement of stakeholders in the planning process (De Santo, 2018). It is important to note that the use of MPANs and other ABMTs does not negate the need for other management measures, such as fisheries management to manage prey extraction over the wider region e.g. biomass cut-off, or bycatch reduction measures e.g. changing hook type on long-lines (Cury et al. 2011, Hobday et al. 2015, Koehn et al. 2021).

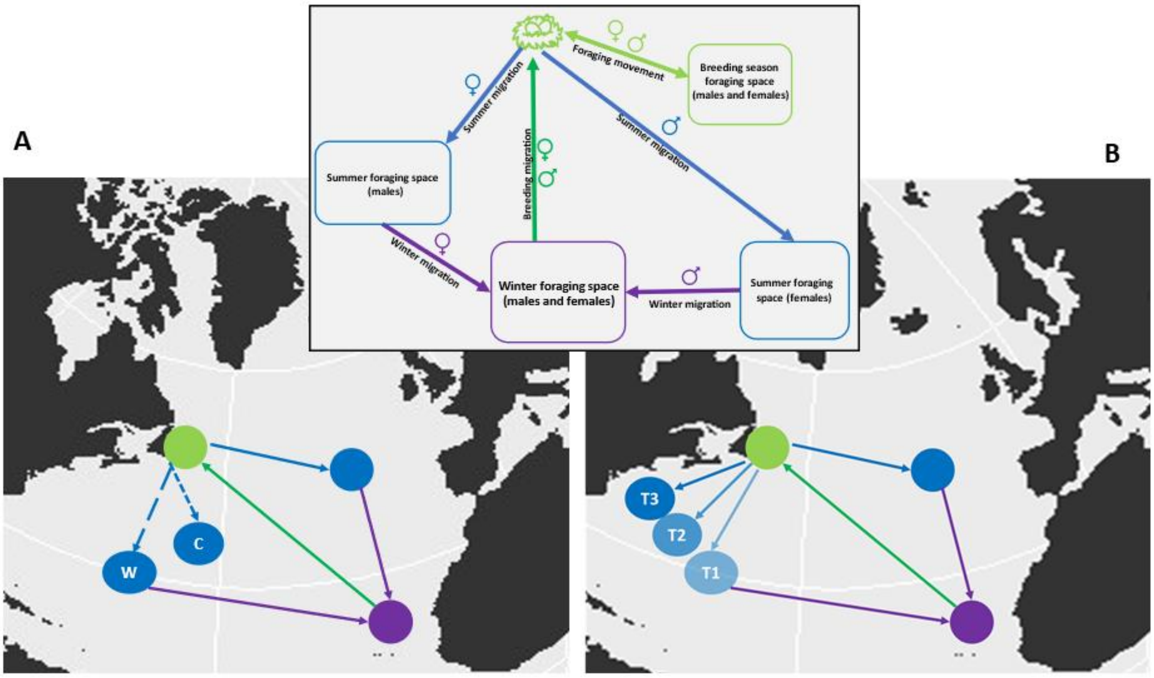

***Figure 4.11**: Ecologically coherent MPANs for migratory species should encompass the foraging spaces used throughout the migratory cycle and account for potential shifts in foraging spaces. In this conceptual diagram, the summer foraging space (left blue) used by males may vary spatially depending on prevailing oceanographic conditions (e.g. further west in warm (W) years than in cold (C) years) (A) or are shifting northwest wards (T1 – T3) with climate change (B). In both cases, decision-makers need to ensure the MPA at those migration stages are spatially (and potentially temporally) dynamic.*

4.4: Conclusion

Although we lack the comprehensive knowledge needed to know precisely how species will respond to changing ocean conditions, in an era of biodiversity decline as a direct result of human activities (Halpern et al. 2015) and where nations strive to expand area-based management of the ocean (G7 2021), the importance of using the best available knowledge to identify areas that could be important for population persistence has never been greater (Schmitz et al. 2015, Queirós et al. 2016). I present a conceptual framework to help researchers and decision-makers identify potential foraging spaces for seabirds for inclusion in ABMTs such as MPANs and identify patterns and trends that may alter the spatial and temporal distribution of those foraging spaces. Crucially this framework enables the integration of new data that can support adaptive management processes.

The framework can be used with seabird and prey data varying in quality and quantity and use existing distribution models to forecast potential foraging spaces and analyse spatial and temporal trends important for designing and adapting MPANs to the changing spatial needs of species. Nevertheless, our framework offers a starting point. I support calls to develop automated dynamic and iterative forecasting tools (Dietze et al. 2018, White et al. 2019). In particular, I encourage the development of iterative tools that incorporate community dynamics and key species interactions, such as predator-prey interactions that shape spatial-temporal dynamics of marine species and population persistence (Pedersen et al. 2017). I also recognise the significant effort and logistical challenges in acquiring seabird movement and prey data for such models. I suggest that new data acquisition should focus on threatened, data-poor seabird species inhabiting poorly surveyed regions (Mott & Clarke 2018, Bernard et al. 2021) and their prey. I also encourage researchers and other data-collection agents to embrace the open data movement and share available data in discoverable and accessible repositories. Finally, I call upon decision-makers to embrace uncertainty, adaptive tools, and management frameworks to create rapid measures for the conservation of biodiversity with the best available information, rather than wait for complete knowledge that will never come.

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Chapter 5: Summary

Shaped by biotic and abiotic factors, adaptation and evolution, the abundance, distributions, and very existences of species have waxed and waned through millennia (Peterson & Lieberman 2012), but only in the last three centuries has one species has emerged as a dominant threat to biodiversity on a global scale (Vitousek 1997, Waters et al. 2016). As unabated human exploitation and alteration of the World continue to impact biodiversity negatively and, by extension, humans, so do calls to halt damaging activities and restore species, communities, and ecosystems (Secretariat of the Convention on Biological Diversity 2020, WWF 2020, World Economic Forum 2021).

Although science alone cannot solve the biodiversity crisis, it can provide vital knowledge that can inform the development, implementation, and maintenance of effective solutions. To ensure ecological relevancy, area-based management tools (ABMTs) that seek to manage human activities in geographic spaces require quantifiable measurements on species distributions and their responses to changing biotic and abiotic conditions. However, the logistical and financial complications of monitoring and surveying in the ocean challenge efforts to obtain direct observations of marine species distributions (Costello et al. 2010). The spatial ecology of migratory species and other highly mobile species further complicates the situation. Where one migratory species occurs today may differ greatly from where it will occur next month, and where it occurs in one month may differ from where it will occur in that same month the following year. For pelagic species, such spatial-temporal variations may occur over horizontal (longitude, latitude) and vertical (depth) axes. Furthermore, with species interacting and co-depending on each other to varying degrees, the spatial-temporal response of one species may directly or indirectly influence the spatial-temporal dynamics of another species significantly (Rayfield et al. 2009, Furey et al. 2018).

My thesis sought to (1) determine the intra-annual (average monthly) distribution of a keystone pelagic fish (capelin) in Atlantic Canada across horizontal (longitude and latitude) and vertical (depth) axes, (2) quantify the stability of the predicted fishes' distributions across varying ocean climates (e.g. phases of the NAO) and over time across the three spatial axes, and (3) provide guidance for explicitly incorporating predicted prey distributions into processes for determining and managing the foraging spaces of top predators (seabirds). Briefly, I:

1) Documented substantial differences in modelled probabilities of presence across horizontal (longitude and latitude) and vertical (depth) axes from one monthly-model to the next. Differences included expansion and contractions and shifts in the northern, southern, western, and eastern edges of predicted ranges. In addition, by using individual monthly models, I revealed variation in the statistical species-environment relationship of capelin to modelled covariates. Of particular note was the changing importance of temperature, which due to the ectothermic nature of many marine species and their tendency to reside in temperature close to their upper thermal limit (Pinsky et al. 2019), is typically seen as the primary driver of marine species distributions. In this study, the April and May models listed temperature as the least important modelled covariate.
2) Determined broad similarity in modelled distribution patterns between different ocean climates on a month-by-month basis, as represented by positive and negative phases of the North Atlantic Oscillation, and over the 17-year study period in which I modelled predictions as a whole (1998 – 2014). In agreement with other studies that explored shifts in species distributions, changes in modelled patterns primarily resulted from expansion and contraction of presence patches over longitude and latitude, and to a lesser extent, depth. Furthermore, in six out of the ten months I

modelled, the predicted habitat suitability scores tended to decline over the 17-year study period. These declines occurred across all depth layers.

3) Proposed a framework for modelling and forecasting the spatial-temporal dynamics of prey availability with the purpose of identifying potential seabird foraging spaces. The framework encompasses three broad steps for understanding aspects of (i) seabird and prey ecology related to prey availability, (ii) modelling, forecasting, and evaluating foraging spaces, and (iii) applying potential foraging spaces to adaptive decision-making processes. I highlight the importance of considering the different conditions faced by seabirds and their prey, how physiological and behavioural constraints can influence the availability of prey, and how prey availability can change over space and time. To allow this framework to be operationalised, I designed it to take advantage of existing tools and predator and prey data of varying quality (e.g. foraging radius of seabirds).

Ecological research often focuses on understanding, quantifying, and predicting species distributions (Ebach 2015). With climate and other human-driven changes, this focus is arguably more important now than at any other time in scientific history. Ecological niche theory, and in particular Hutchinsonian niche theory, underlies the study of species distributions. This concept contrasts the fundamental niche – the suite of abiotic conditions that allow for a species to persist (the *n*-dimensional hypervolume), and the realised niche, which tempers the fundamental niche with biotic conditions with positive and negative interactions with other species (Hutchinson 1957). The fundamental niche can exist in environmental space or geographic space, but because the realised niche relies on the location of interacting species, it can only occur in geographic space (Colwell & Rangel 2009). Together with movement/dispersal potential (Soberón 2010), the realised niche determines the geographic distribution of a species.

Species distribution modelling, which projects species realised niches across geographic space, is a relatively young field, particularly in its application to the marine environment (Guisan et al. 2017, Robinson et al. 2017). Although some distribution models seek to explicitly incorporate dispersal (Monsimet et al. 2020) and biotic interactions (Norberg et al. 2019), most distribution models focus on abiotic determinants of distributions, primarily because abiotic covariate data are more readily available than biotic or dispersal data (Elith & Leathwick 2009). However, in recent decades, observed and modelled oceanographic covariate data from subsurface waters have become available (England & Oke 2002, Assis et al. 2018), and crucially at ecologically relevant temporal scales (Becker et al. 2016, Mannocci et al. 2017). My thesis forms part of a growing body of research harnessing the availability of modelled oceanographic data to understand and predict the spatial-temporal dynamics of highly mobile species across three-dimensional ocean space and incorporate species interactions into processes that identify potential candidates for ABMTs such as marine protected areas that seek to manage human activities that degrade species, communities, and ecosystems. This work is also timely, with the launch of the UN Decade of Ocean Science for Sustainable Development (Ocean Decade) highlighting a greater need for modelling changes, making predictions, interdependence and connectivity between ecosystems, observation and monitoring, and open data, among others (Claudet et al. 2020).

With prey availability playing a key role in the movement and distributions of predators (Wisz et al. 2013, Furey et al. 2018, Ratcliffe et al. 2021), increasing knowledge of biotic factors - specifically those relating to prey availability – and understanding their role in predator space choice is an essential step for the development of distribution modelling and by extension for providing robust information for ABMT development. However, several challenges remain in incorporating prey availability into distribution modelling. Perhaps most important for migratory species modelling under changing conditions, distribution models (including community distribution models) typically take a static perspective, assuming unchanging species relationships to covariates over space and time (Trainor & Schmitz 2014). Food-web theory makes similar assumptions, typically assuming fixed predator-prey interactions across space and time (e.g. a puffin will always eat capelin, regardless of the location or timing of the puffin within its migratory cycle) (Cohen et al. 2003, Blanchet et al. 2020, but see Koen-Alonso (2007)). However, this static perspective does not play out in real-world scenarios. For example, in the case of seabirds, diet may change in response to the spatial-temporal dynamics of suitable prey (e.g. migrating prey arriving near a seabird colony, with ontogeny (e.g. immature individuals consuming different prey than mature individuals), or with spatial location/migratory stage (e.g. wintering location vs summer location) (Karnovsky et al. 2008, Kowalczyk et al. 2015, Campioni et al. 2016).

Nevertheless, researchers increasingly seek to include predator-prey and other trophic interactions in ecological models. For example, Gravel et al. (2011) expanded the Theory of Island Biogeography to include trophic interactions for metacommunity modelling, with improved predictions of species richness. More empirically, Olivier et al. (2019) took advantage of long-term surveys to model temporal changes in community composition and food-web structure in the German Bight. In terms of distribution modelling, Thorson et al. (2016) developed a spatial dynamic factor analysis to model spatial-temporal shifts of communities, and Trainor & Schmitz (2014) developed a trophic interaction distribution model to explicitly model the accessibility of snowshoe hare (*Lepus americanus*) to Canada lynx (*Lynx canadensis*). My fourth chapter extends this development with a framework to capture the spatial-temporal dynamics of prey, the spatial-temporal dynamics of the predator, and the predator’s spatial and/or dietary response to changing prey availability over time and space. Future work should continue developing methods to capture the spatial-temporal dynamics of predators and prey, including incorporating iterative frameworks for assimilating new knowledge and data.

Researchers increasingly recognise the interconnected nature of marine species, communities, and ecosystems (Carr et al. 2017). In essence, what happens in one location can have ramifications elsewhere. As such, managers increasingly recognise the importance of developing MPA networks (MPANs) that incorporate ecological spatial connectivity – “processes by which genes, organisms [individuals], populations, species, nutrients and/or energy move among spatially distinct habitats, populations, communities or ecosystems” (Marine Protected Area Federal Advisory Committee 2017) as vital. In the ocean, considerable attention has focused on genetic connectivity – the movement of genes among subpopulations within a metapopulation, and population connectivity – the movement of individuals among spatially discrete subpopulations within a metapopulation, facilitated via dispersive propagules such as egg, larvae, spores, and fruits (Gaylord et al. 2006, Planes et al. 2009, Mari et al. 2020). Migratory connectivity (the geographic linking of individuals or populations between different stages of the annual cycle), spatial-temporal connectivity (the appearance and disappearance of reachable habitat patches over time), and meta-ecosystem connectivity (the flow of matter, energy, and information between different and spatially distinct ecosystems) (Loreau et al. 2003, Marra et al. 2010, Martensen et al. 2017) has received less attention. Although this thesis contributes to the understanding of migratory and spatial-temporal connectivity, I have also considered meta-ecosystem connectivity in a collaborative study completed during my PhD (Peller, Andrews et al. 2020) (see Appendix D.1 for the abstract). Here, we demonstrated that non-living resource-flows such as algal detritus couple temperate coastal benthic ecosystems of different types and that connectedness between ecosystems occur at much smaller spatial scales than larval connectivity. In light of the domination of connectivity by propagules in the literature, the latter finding is particularly important for the development of ecologically coherent and connected MPANs. Equally, the development of MPANs could benefit from considering migratory species that can connect, interact, and alter similar and different communities/ecosystems over substantially larger scales (Varpe et al. 2005, Kremen et al. 2007, Semmens et al. 2011).

Throughout this thesis, I have identified multiple knowledge and methodological gaps which, if filled, could improve the modelling of migratory and other highly mobile species and provide more robust guidance for ABMT development and management. For example, in Chapter Two, I highlighted how species statistical relationships to modelled covariates might vary over relatively short timescales. However, if and when statistical relationships may change or how rapidly those changes may occur remains unclear. Future work should focus on determining when, where, and why fluctuations in statistical relationships may occur. In Chapter Three, I highlighted that although existing patch metrics that quantify species distributions and patches can provide useful ecological information and reveal changes over time, their use is limited to flat, two-dimensional surfaces. To improve outputs for pelagic species that occupy three-dimensional space, future work should focus on developing tools that incorporate volume into measurement calculations and analysis. In Chapter Four, I highlighted that data availability is an important component in developing robust models, and how the lack of information on the spatial-temporal dynamics of seabirds and their responses to prey availability outside the breeding season in particular hampers efforts to develop ecologically relevant ABMTs such as MPANs that consider space use across migratory cycles. Future work should include the continued development and maintenance of and contribution to accessible data repositories. Such repositories include Movebank (Wikelski et al. 2021), which provides movement data on multiple terrestrial and aquatic species, the Ocean Biodiversity Information System (OBIS 2018), which provides observational data on marine species, and Mangel (Poisot et al. 2016), which provides ecological interactions data. While these and other shortcomings may present scientific uncertainty, they should not be used as a justification for failing to act swiftly to adapt, mitigate, or prevent threats to species, communities, or ecosystems (the Precautionary Principle (Read & O'Riordan 2017)). Indeed, with the accelerating decline of biodiversity and degradation of ecosystems and the services they provide, reconciling "*the need to know versus the need to act*" (Ardron et al. 2008) has never been more critical.

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Appendices

Appendix A: Atlantic Canadian Capelin: A primer

A.1: Forage Fish

Situated in the middle of the food-web throughout their life-cycle, forage fish transfer energy from low-trophic levels (i.e. zooplankton) to higher trophic levels (e.g. predatory fishes, seabirds, and mammals) (Cury et al. 2000, Alder et al. 2008). With short lifespans, fast growth, and high reproductive rates, oceanic conditions strongly influence forage fish abundance. Boom-bust population cycles and redistributions have been linked to large-scale climate forcing such as the Atlantic Multidecadal Oscillation and Pacific Decadal Oscillation, as well as more general changes to the oceanographic climate and prey availability (Peterson & Schwing 2003, Hedd et al. 2006, Ayón et al. 2008, Groger et al. 2010, Buchheister et al. 2016, Checkley et al. 2017). Whilst forage fish fluctuations in abundance and distributions have occurred prior to large-scale industrial fishing (McClatchie et al. 2017), overfishing can exacerbate collapses and potentially reduce recovery rates (Coetzee et al. 2008, Essington et al. 2015, Greene et al. 2015), with impacts on the wider ecosystem and fisheries that target forage fish predators (Pikitch et al. 2012, Koehn et al. 2017) (though see Hilborn et al.(2017) and rebuttal (Pikitch et al. 2018)).

A.2: Capelin in Atlantic Canada

Atlantic Canadian waters are home to several forage species. Amongst the most wide-ranging species is the capelin (*Mallotus villosus*). Capelin are exclusively found in the northern hemisphere, adopting a circumpolar distribution in the Pacific and Arctic Ocean, the Barents, White, and Norwegian Seas, and the North Atlantic (Rose 2005). Atlantic Canadian capelin and the neighbouring West Greenland-Barents Sea capelin originated from the Pacific, dispersing through the Canadian Arctic around 2 and 1.6 million years ago (Dodson et al. 2007). Today, four genetically distinct populations exist – two in the Pacific, one around West Greenland, and one in the Northeast Atlantic around Atlantic Canada (Præbel et al. 2008).

Particularly in Newfoundland and Labrador waters, capelin are regarded as a "lynchpin" species for their critical role in what is essentially a wasp-waist ecosystem (Rice 1995, Bakun 2006, Cowan 2017). Alongside humans, notable predators include Hudson Bay beluga whales (*Delphinapterus leucas*) (Kelley et al. 2010), cod (*Gadus morhua*) (Rose & O'Driscoll 2002), harp seals (*Pagophilus groenlandicus*) (Sergeant 1973). Genetic analysis has revealed at least seven sub-populations of capelin occupy Atlantic Canadian waters (Kenchington et al. 2015), though it is unclear to what degree the sub-populations mix (Carscadden 1976, DFO 2018b) (but see Nakashima (1992). Atlantic Canadian capelin are currently managed as four units, separated into NAFO divisions 2J + 3KL (since 1993), 3NO, 3Ps, and 4RST (Figure A.1).

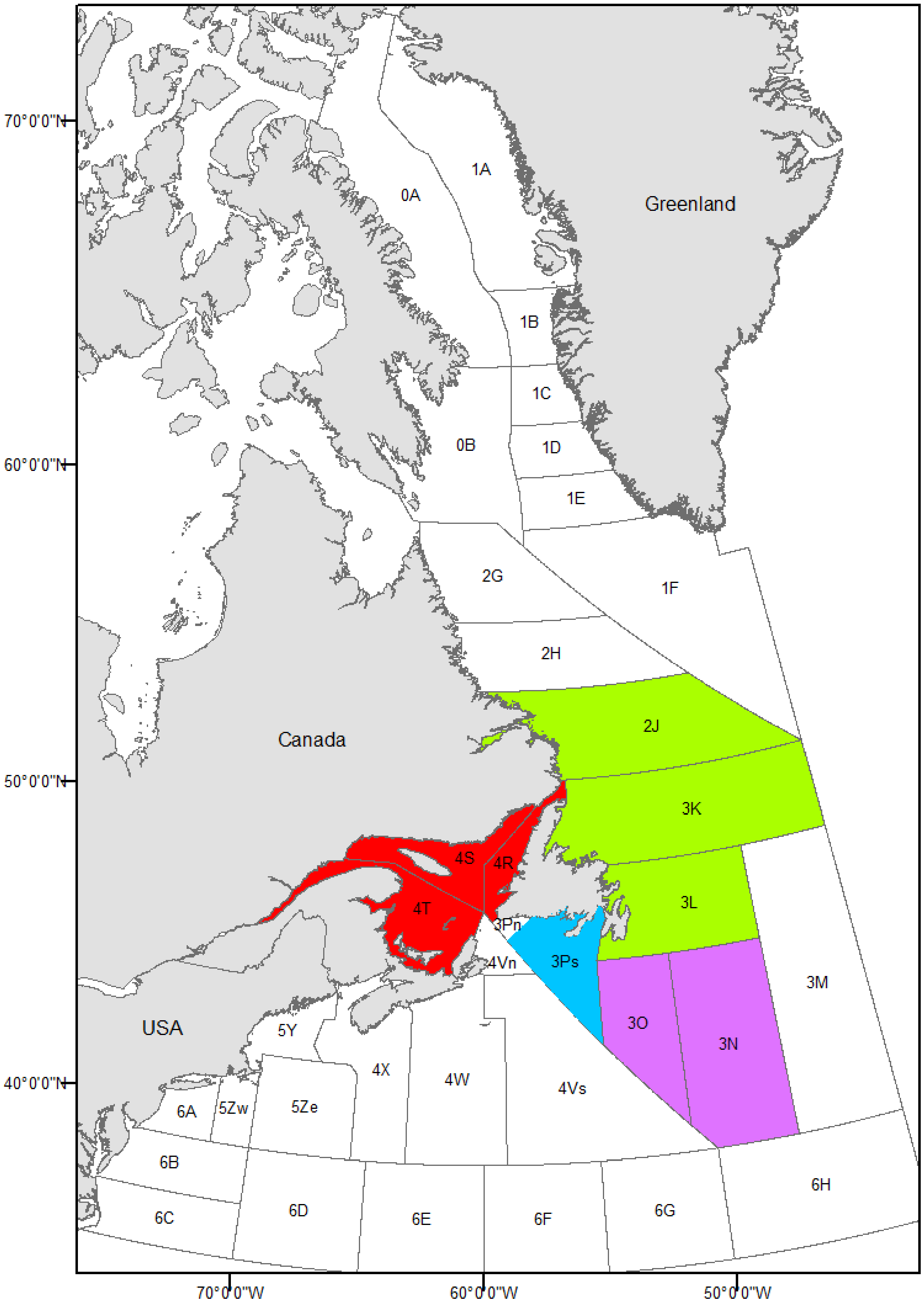

Figure A.1:Capelin in Atlantic Canadian waters are currently managed as four separate units; 4RST (red). 3Ps (blue), 3NO (purple), and 2J3KL (green).

A.3: Capelin Ecology

Capelin is a migratory pelagic species with distributions closely tied to oceanographic conditions. Capelin are typically found in waters with salinity ranges between 33 and 35 PSU (Practical Salinity Unit) and in temperatures no warmer than six °C (Rose 2005), while a lack of antifreeze protein prevents them from surviving waters colder than -1.9 °C (Raymond & Hassel 2000). Colder sea temperatures and increasing ice coverage has seen Newfoundland and Labrador capelin shift their distributions in large numbers southwards into the Bay of Fundy, whilst temperature increases of 2 - 4˚ Celsius are thought to be sufficient to cause capelin to shift distributions up to 18˚ latitude north (Dunbar 1983, Rose 2005). Distribution shifts in relation to temperature have also been detected in the Barents and Icelandic Seas (Pálsson et al. 2012, Stergiou 1991). Capelin in 2J3KL during the fall tend to take on more northerly distributions when at higher abundance (Carscadden et al. 2013a, DFO 2018a, Buren et al. 2019).

Capelin are zooplantivores, with the exact species consumed varying depending on availability. In spring on the Grand Banks, copepods, juvenile fish (including juvenile capelin), and euphausiids form the bulk of adult capelin diets (Gerasimova 1994), whilst the diet of capelin in Labrador waters in autumn are dominated by amphipods and copepods (Chan & Carscadden 1973, Dalpadado & Mowbray 2013). During the winter months, capelin are not thought to feed (Winters 1970). Alongside temperature, the availability of zooplankton is strongly linked to growth. For example, warmer conditions with high zooplankton biomass, particularly of key prey such as *Calanus* copepods, appear to promote faster growth (Gerasimova 1994, Hedeholm et al. 2012, Obradovich et al. 2014).

Migration of mature capelin from their wintering grounds primarily located near the edge of the continental shelf and the Grand Banks and occasionally deep waters closer to the coast (Winters 1970), to inshore areas of Newfoundland and Labrador and to the Southeast

Shoal typically takes place early spring (Carscadden et al. 1989). The exact timing varies from one year to the next, though it appears to be primarily regulated by temperature, with colder years seeing later spawning (Shackell et al. 1994a, Regular et al. 2009, Murphy et al. 2021). In NAFO division 3L during the springs of 1985 – 1990, immature capelin were found further north than their mature counterparts. However, surveys during the spring of 1991 and 1992 failed to find any mature capelin in the southern portion of 3L (Shackell et al. 1994b), possibly due to a delay in maturation and consequent delay in pre-spawning migration from more northern areas to the southern part of 3L resulting from colder sea temperatures. In the Gulf of St Lawrence, some capelin are thought to migrate to spawning areas on the Scotian Shelf (Kenchington et al. 2015). Alongside migrations towards coastal Newfoundland, Grand Banks Capelin also migrate to the Southeast Shoal (Gerasimova 1994). Some capelin are known to overwinter inshore, such as in Trinity Bay (Winters 1970).

Historically, spawning in Newfoundland and Labrador occurred in June and July (Carscadden & Nakashima 1997) and in the Gulf of St Lawrence between April and July (DFO 2018b). Since the regime shift in the 1990s, Newfoundland and Labrador spawning occurred later in July (Murphy et al. 2018b). In some areas, such as in the territory of the Southern Inuit of NunatuKavut, capelin spawning appears to be more sporadic (DFO 2018a).

Capelin are aggregating bottom spawners, selecting both beach and inshore demersal areas along the coast of Nunavut, Newfoundland and Labrador, and throughout the Gulf of St Lawrence (Nakashima & Wheeler 2002, Lazartigues et al. 2016, McNicholl et al. 2018), as well as offshore demersal area on the Southeast Shoal and Western Bank (Carscadden et al. 1989, Reiss et al. 2000). Generally, capelin at lower latitudes spawn earlier than those at higher latitudes (Narayanan et al. 1995) and earlier in the west than the east (Bailey et al. 1977, DFO 2018b).

It is not clear if most capelin are natal spawners, but it has become apparent that capelin do not necessarily exhibit site fidelity, with some individuals showing flexibility in choice of spawning location (Davoren 2013c, Crook et al. 2017). Capelin appear to exhibit both facultative and obligate spawning behaviours. Where a spawning ground is found to be unsuitable (e.g. due to temperature), some males may not spawn, whilst others take on extensive movements to locate an appropriate site based on temperature (e.g. select for deeper water sites in warm-water years), as well as physical characteristics of the substrate (Davoren et al. 2007, Davoren 2013c). Nevertheless, otolith chemistry analysis differs between beach and deep-water spawners, suggesting population structure arising from different behavioural contingents within Atlantic Canadian capelin (Davoren 2013c, Cayuela et al. 2020).

Once capelin arrives near their spawning grounds, they remain in deep-water (>200 meters) 'staging areas', where gonadal development is completed. With temperature exhibiting a strong positive relationship with gonad development, the length of time spent in the staging area can vary (Davoren et al. 2006a). After gonadal development is complete, capelin form sex-specific schools. In the case of beach spawners, males move into the intertidal area of beaches, whilst females remain in deeper waters until they are ready to spawn (Nakashima & Borstad 1997). Both larger males (>17 cm) and larger females (> 15 cm) tend to arrive at spawning grounds before their smaller counterparts (Vandeperre & Methven 2007, Maxner et al. 2016). Males are typically semelparous breeders, typically dying shortly after multiple spawning bursts within a short period. Females have a higher post-spawning survival rate than males and can spawn for two or more years (Nakashima 1992, Christiansen et al. 2008).

There are several notable differences between beach and demersal spawning. Beach spawning events are shorter and earlier than those occurring on demersal sites (Penton et al.

2012). Spawning on demersal grounds occurs at lower, often more stable temperatures than on beaches and typically at higher salinity (Penton et al. 2012, Purchase 2017, DFO 2018b). Combined with warmer temperatures, earlier spawning at beaches results in the larvae from beach spawners hatching approximately one month earlier than their demersal counterparts (Davoren et al. 2014). After hatching, capelin larvae quickly assume shoaling behaviour (Morgan et al. 1994) and exhibit diel vertical migration (Frank & Carscadden 1989), though they typically remain in the top 20 meters of the ocean where they feed on small zooplankton. In some locations, notably in coastal embayment's, larvae may be entrained near their natal spawning ground or for up to several months before migrating to nursery areas (Frank & Carscadden 1989). Elsewhere larvae may be swept further from their natal spawning grounds and eventually becoming entrained elsewhere (Taggart & Leggett 1987). For example, capelin larvae are noted to be present in high abundance in the lower St Lawrence estuary (Jacquaz et al. 1977, de Lafontaine 1990), the Saguenay Fjord (Sirois et al. 2009, Lazartigues et al. 2016), and the Southeast Shoal (Carscadden et al. 1989).

The offshore banks of 2J3KL appear to be important nursery areas for capelin (Gerasimova 1994, Carscadden & Nakashima 1997), as does the lower St Lawrence estuary and the mouth of Saguenay Fjord (Bailey et al. 1977, de Lafontaine 1990). Once larvae reach the nursery areas and have passed their first winter, they typically undergo metamorphosis into the juvenile form (Frank & Leggett 1990). The juvenile capelin remains in mixed-sex shoals until they reach sexual maturity (around 2 – 3 years old) (McNicholl et al. 2018). Nursery residents on the northern Grand Banks migrate north during the summer and autumn (Carscadden et al. 2013a).

A.4: 1990s regime shift and capelin

Following decades of high levels of fishery exploitation, the North Atlantic experienced a significant shift in ocean climate in the 1990s, during which sea temperatures and salinity dropped significantly (Greene et al. 2008b). Combined with high exploitation levels, this regime shift saw several marine species – notably groundfish – decline rapidly in abundance across Atlantic Canada's water (Bakanev 1992, Pedersen et al. 2017b). Capelin also experienced a decline in abundance, shifted their distribution, and changed migration patterns, notably more towards the northern Grand Banks, Flemish Cap, eastern Scotian Shelf, and Hudson Bay, as well as into deeper waters, began maturing at younger ages (from 3 – 4 years old to 2) and smaller sizes, and spawning later (Frank et al. 1996, 2016, Carscadden & Nakashima 1997, Mowbray 2002, Gaston et al. 2003, DFO 2018a b). Furthermore, larvae are spawning later, creating a potential mismatch between conditions that aid their survival, such as onshore winds (Frank & Lettett 1982, Murphy et al. 2018a). Mismatches may also prevalent between spawning timing and prey availability, which is mediated by the spring bloom (Buren et al. 2014b, Mullowney et al. 2016).

Whilst directed fishery pressure is not thought to have been a major factor in these changes (Carscadden et al. 2001), there are concerns that current exploitation levels may be impacting capelin recovery (WWF Canada 2016). Indeed, whilst similar oceanographic conditions were experienced in Icelandic and the Barents Seas in the 1990s, and capelin exhibited similar biological responses, their population have subsequently recovered. Atlantic Canadian populations have not shown the same level of recovery despite favourable oceanographic conditions (Carscadden et al. 2013b, DFO 2018a). The reasons for poor recovery are not fully understood but are thought to include timing mismatches between peak larval emergence and onshore wind events and the spring bloom – and thus the availability of prey - due to changes in sea ice dynamics (Buren et al. 2014).

A.5: Capelin fisheries in Atlantic Canada

During the 1970s, the commercial capelin fishery shifted from a primarily small, domestic fishery operating with traps to one accommodating a directed large offshore fishery, composed of domestic and foreign fleets. Catches peaked in the late 1970s at 246k tons (Carscadden & Nakashima 1997). Following a rapid decline in stocks likely caused by overfishing and poor recruitment, the 3NO offshore fishery closed between 1979 and 1986, and reopened between 1987 and 1992 under quota (ICNAF 1979 197, NAFO 1994b). The offshore fishery closed again in 1993 and has not reopened. The 3L offshore fishery permanently closed in 1979, whilst the 2J3KL continued until 1992.

With the large offshore foreign fishery in decline, the small inshore fishery of 2J3KL and 4RST, which remains today, began primarily targeting roe-bearing capelin for Japanese markets. This smaller domestic fishery peaked between 1988 and 1990 at 80k tons, however by the early 1990s, landings declined to 30k tons. The decline in inshore landings at this time occurred at the same time as a decline in abundance. The inshore fisheries operating in the Gulf of St Lawrence and Estuary (4RST) are dominated by catches purse seine, "tuck" seine (a type of modified beach seine designed to catch capelin in deeper waters), and trap and weir fisheries from the west coast of Newfoundland. The fishery is managed under a Total Allowable Catch (TAC). Although capelin are regularly caught as bycatch in shrimp fisheries, the catches are not officially counted in the management statistics (DFO 2018c), though more recently has been considered in stock assessments (H. Murphy 2021, pers. comm) . In 2J3KL, purse and tuck seines also dominate the catch, though traps and beach seines are also used and managed under a TAC. Today capelin from 2J3KL and 4RST still go to the Japanese roe market, though there is a growing Chinese market for female capelin. Males, which were historically dumped or used as fertiliser are now sold to the USA and China as feed in marine parks or aquaculture operations (DFO 2018a b).

Alongside cultural significance, capelin in Labrador also form part of a subsistence food fishery for southern Inuit (WWF Canada 2018). Throughout Newfoundland, Labrador, and the Gulf of St Lawrence, capelin also form the basis of a recreational fishery that primarily targets beach spawning capelin (DFO 2018c).

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Appendix B: Appendices for Chapter 2: Modelling the spatial-temporal distributions and associated determining factors of a keystone pelagic fish.

B.1: Numerical models and depth- layers used to model and predict probability of capelin occurrence.

The numerical modelling product GLORYS V4.1 is a reanalysis product provided by MERCATOR Ocean and made available by the E.U. Copernicus Marine Environment Monitoring Service (CMEMS 2018a). GLORYS is based on the NEMO Ocean modelling platform. Among others, model configuration includes horizontal pressure gradients represented by a free surface formulation which filters out high-frequency gravity waves, advection tracers delineated with a total variance diminishing advection scheme, and a reanalysis system which uses the LIM2 thermodynamic sea-ice model and driven at the surface by the ERA-Interim reanalysis products. For further details, I refer the reader to the product sheet available from Copernicus Marine Environment Monitoring Service. The performance of previous versions of GLORYS has been tested against in-situ measurements from the region and was found to have a good predictive skill (e.g. Wang and Greenan, 2013; Murillo et al. 2016).

The numerical modelling product BIOMER V3.2 is a non-assimilative hindcast product provided by MERCATOR Ocean and made available by the E.U. Copernicus Marine Environment Monitoring Service (CMEMS 2018b). BIOMER is based on the PISCES product, which forms part of the NEMO Ocean modelling platform. Among others, model configuration includes atmospheric forcing fields from the ERA-Interim reanalysis product and offline forcing of physical processes from NEMO. For further details, I refer the reader to the product sheet available from Copernicus Marine Environment Monitoring Service. The underlying PISCES product has been used in studies exploring biogeochemical processes in the region (e.g. Quéré et al. 2005; Moreau et al. 2016).

The GLORYS and BIOMER ocean models are not truly 3-dimensional. Instead, they represent the global ocean as a series of depth layers (Table B.2). I used the depth-layer closest to the sampling depth to delineate oceanographic conditions at the sampling location. For example, if a sample came from a depth of 127 meters, I used conditions from the depth-layer representing conditions at 133.08 meters as this layer is closer than the one representing 120 meters (Table B1.1).

Table B1.1: *The Minimum Convex Polygon (MCP) encompasses 47 depth layers derived from the GLORYS* (CMEMS 2018) *and BIOMER* (CMEMS & Paul 2018) *ocean models. Depth values have been rounded to two decimal points.*

Layer No	Depth (meters)	Layer No	Depth (meters)
1	0.51	24	97.04
2	1.56	25	108.03
3	2.67	26	120.00
4	3.86	28	133.08
5	5.14	29	163.17
6	6.54	30	180.55
7	8.09	31	199.79
8	9.82	32	221.14
9	11.77	33	244.89
10	13.99	34	271.36
11	16.53	35	300.89
12	19.43	36	333.86
13	22.76	37	370.69
14	26.56	38	411.79
15	30.87	39	457.63
16	35.74	40	508.64
17	41.18	41	565.29
18	47.21	42	628.03
19	53.85	43	697.26
20	61.11	44	773.39
21	69.02	45	856.68
22	77.61	46	947.45
23	86.93	47	1045.85

B.2: Capelin presence points from the OBIS database.

The Ocean Biodiversity Information System (OBIS) is an open-access aggregation database of global ocean species presence points, crowdsourced from “national projects, programmes, institutes or organisations, National Ocean Data Centers or regional or international projects, programmes and institutions or organisations that carry out data management functions.” At the time of writing (2020), the database contains over 59 million species presence points covering over 131,000 species. OBIS is a “living” database with both historical and more contemporaneous species observations added by data provides on ad hoc basis. Species data is obtained from the OBIS database as a series of presences with associated location information. The data providers can include additional information such as the date, the age/size of the presences, and abundance, but their inclusion varies from one provider to the next.

I downloaded capelin presence data from the year 1998 to 2015. I removed duplicates and presences missing depth/date information, and those for which I could not append environmental data. I also removed the year 2015 as there were only ten presences for the entire year. To prevent over-sampling cells, I reduced the number of presence points to one per spatial-temporal grid cell. A total of 6,350 presence points remained (Table B.2.1, Figure B.2.2).

Table B.2.1: *Number of presences available for modelling per month. Duplicates and points missing depth/date/environmental data have been removed, and presences have been reduced to one per environmental cell. Note January was not modelled due to the low number of years, and February was not modelled due to the low number of presence points.*

	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
1998	0	0	0	36	53	103	20	0	28	53	120	8
1999	0	0	44	19	45	110	23	0	48	6	91	40
2000	0	0	40	24	45	96	19	0	51	24	112	54
2001	0	5	22	31	53	73	13	0	26	17	65	90
2002	0	0	32	42	59	89	17	0	68	28	48	59
2003	38	0	22	38	67	97	17	0	17	27	42	69
2004	73	0	0	29	58	96	25	24	39	15	75	71
2005	12	4	28	13	39	85	32	45	36	39	94	26
2006	31	1	46	11	2	103	22	47	33	48	78	47
2007	0	0	18	27	36	79	58	50	47	24	76	50
2008	0	0	26	18	54	105	12	54	39	24	92	39
2009	0	0	10	34	106	43	8	0	40	21	109	24
2010	0	0	15	18	48	102	25	7	57	48	101	27
2011	0	0	0	30	71	82	11	7	34	42	72	34
2012	0	0	0	0	0	0	6	9	39	0	0	0
2013	0	0	0	0	0	0	25	3	30	3	1	0
2014	0	0	0	0	0	0	0	6	61	3	0	0
Total	154	10	303	370	736	1263	333	252	693	422	1176	638

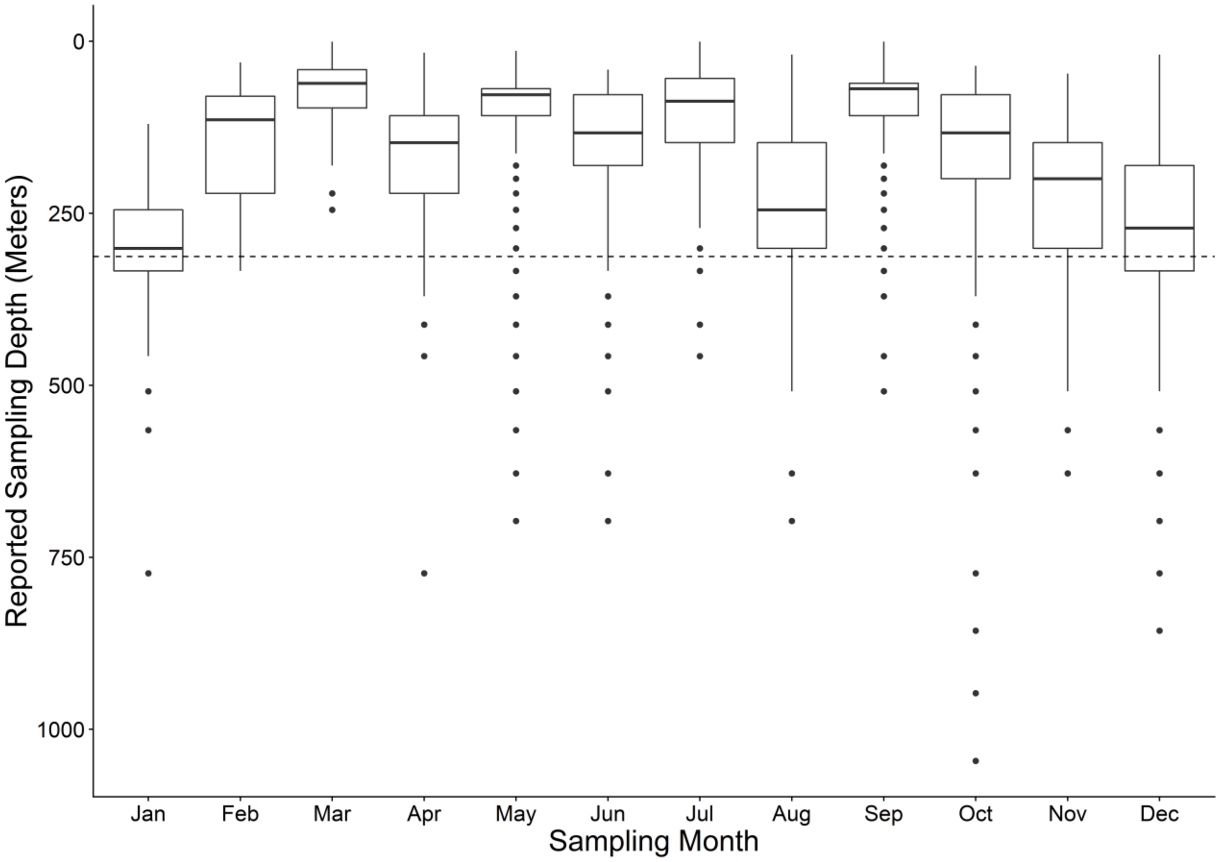

***Figure B.2.2**: The distribution of presence data over depth available for modelling. The dashed line indicates the median depth of the study area (~313 meters). Duplicates and points missing depth/environmental data have been removed, and presences have been reduced to one per environmental cell. Note January was not modelled due to the low number of years, and February was not modelled due to the low number of presence points. The dashed line indicated the median depth of the seafloor in the study region (~313 meters).*

B.3: Gear type categories identified in the OBIS metadata.

***Table B.3**: Gear type information may be provided by data contributors when submitting their datasets to the Ocean Biogeographic Information System (OBIS) database. There is no reporting standard for gear type and as such, details provided by contributors varied between datasets. I did not include gear type in the models due to insufficient gear information and concerns that some reporting may have led to incorrect gear type classification. The gear type classification presented here is for the 'cleaned' presence dataset, i.e. the presences that remained after those that lacked oceanographic information at depth, were duplicate entries in the OBIS database, or appeared in the same spatial-temporal cell were removed.*

Gear Type	**Frequency**
Bottom trawl "Alfredo-3"	3
Bottom trawl "Campelen-14"	35
Bottom trawl "Campelen-1800"	4736
Bottom trawl "Campelen-21"	31
Bottom trawl "Cosmos-2600"	32
Bottom trawl "Western IIA"	675
Bottom trawl (unknown)	606
Vertical plankton tow	17
Not specified	215

B.4: Brief background on Maxent.

Maxent (Phillips et al. 2006) is a widely-used presence-background model based on the maximum entropy principle – that subject to prior knowledge, the probability distribution which best describes the data is that with maximum entropy (i.e. the least informative distribution). By comparing known presences with the background environment, Maxent’s output indicates the extent to which the model fits presence data more or less than it would if the presences had a uniform distribution. Maxent performs well compared to presence-only and the arguably more robust presence-absence based models such as generalised linear models (GLMs) and generalised additive models (GAMs), including with small sample sizes when regularisation (β) multiplier values are tuned to the model (Elith et al. 2006, Pearson et al. 2007).

B.5: Selecting the number of background points to use in each monthly model.

Although as a general rule Maxent performance does not substantially improve with more than 10,000 background points, some studies involving large study areas such as ours have found using a much larger number of background points that more fully capture the variation in conditions across a species range results in better performing models (Guevara et al. 2018). To determine the optimal number of background points while still allowing for efficient computational processing time, I compared the distribution of each oceanographic variable collected from 10,000, 20,000, 50,000, 100,000, and 190,000 randomly generated points from three different periods – February 1999, June 2014, and October 2007 (Figures B.5.1, B.5.2, and B.5.3). As there was little difference between the distributions, in the interests of efficiency, I opted to generate 10,000 background points per model. Only one background point per spatial-temporal grid cell was permitted to prevent over-representation of oceanographic conditions (Elith et al. 2006).

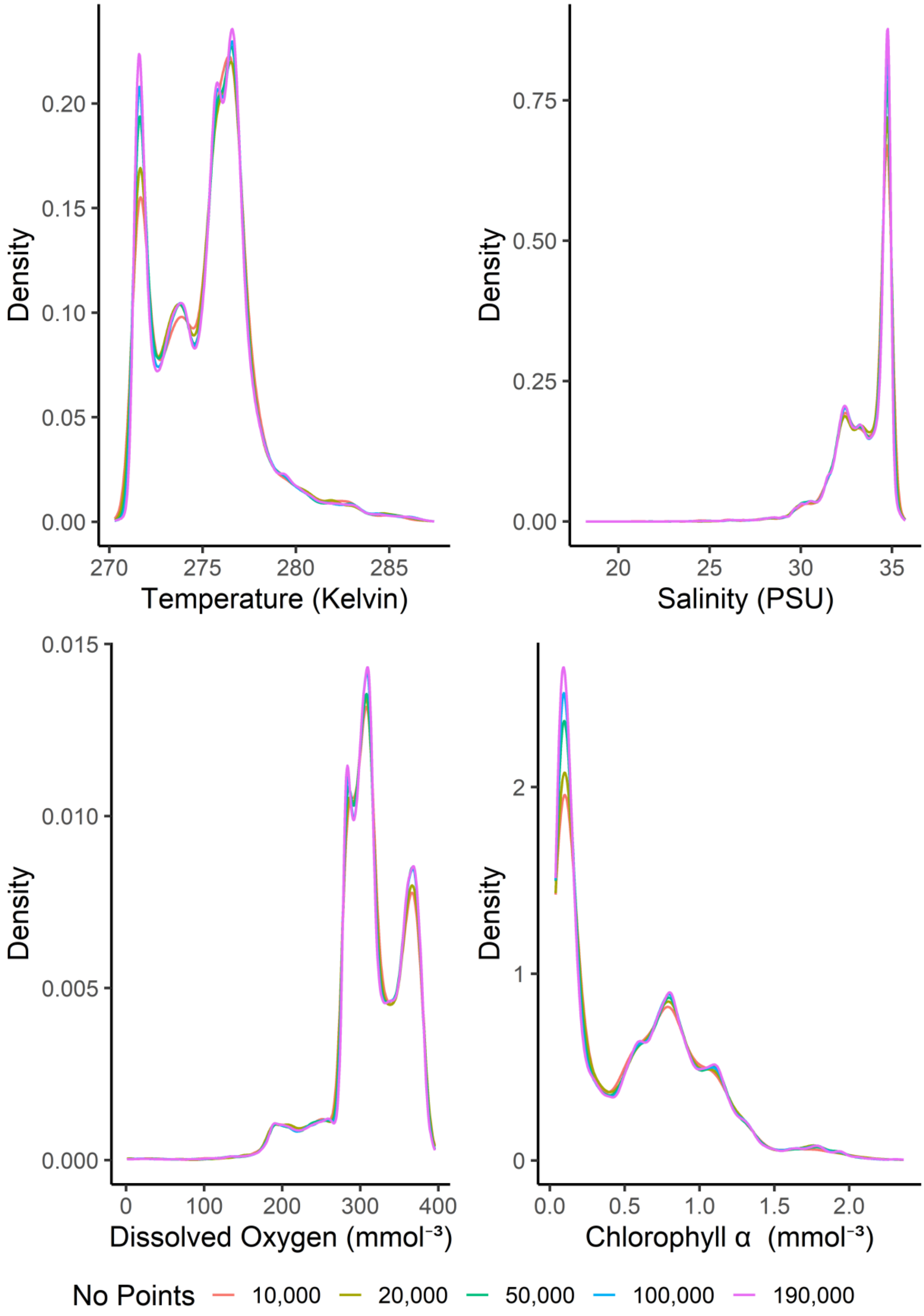

Figure B.5.1: Distribution of each oceanographic variable collected from 10,000, 20,000, 50,000, 100,000, and 190,000 randomly generated points during February 1992.

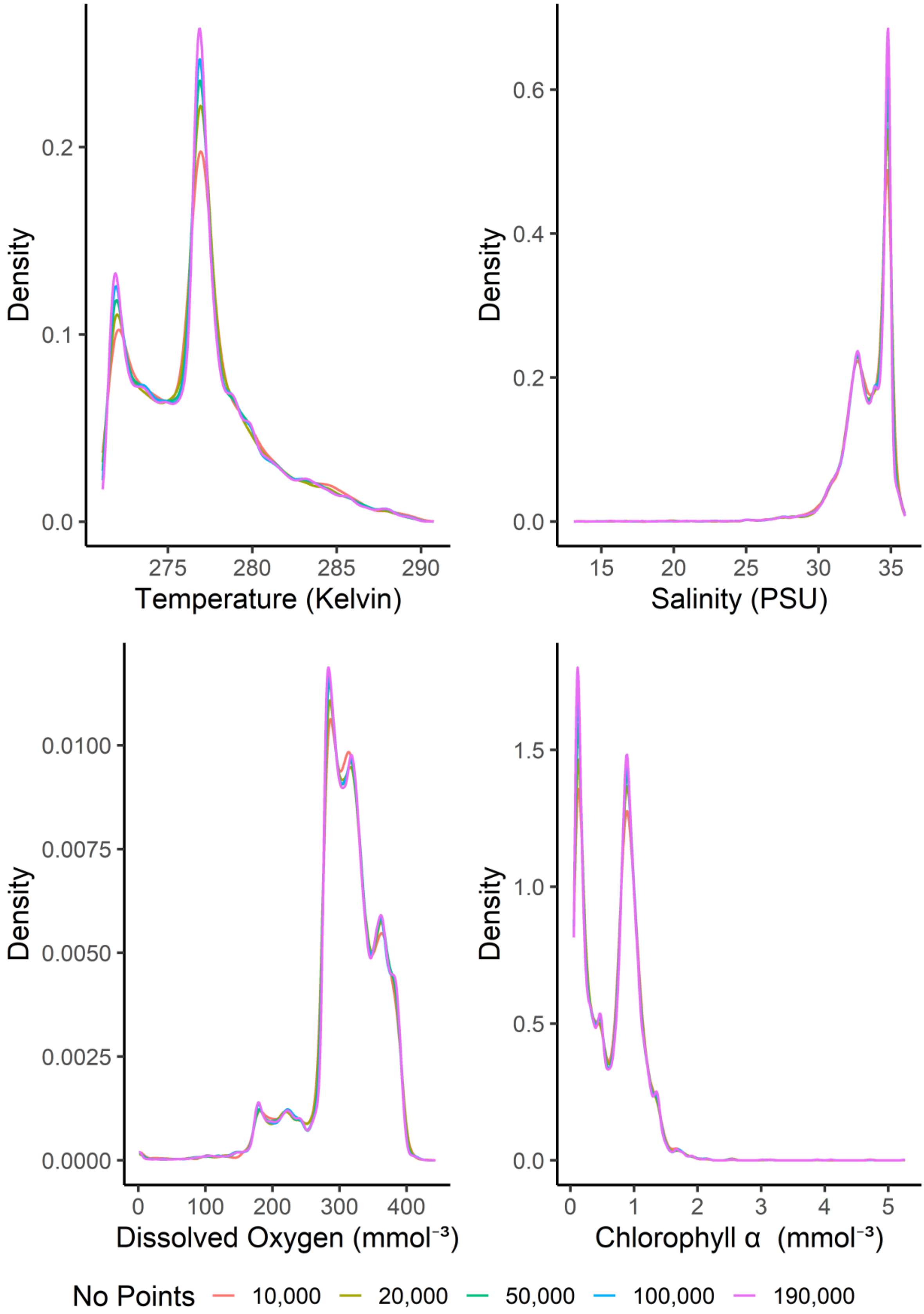

Figure B.5.2: Distribution of each oceanographic variable collected from 10,000, 20,000, 50,000, 100,000, and 190,000 randomly generated points during June 2004.

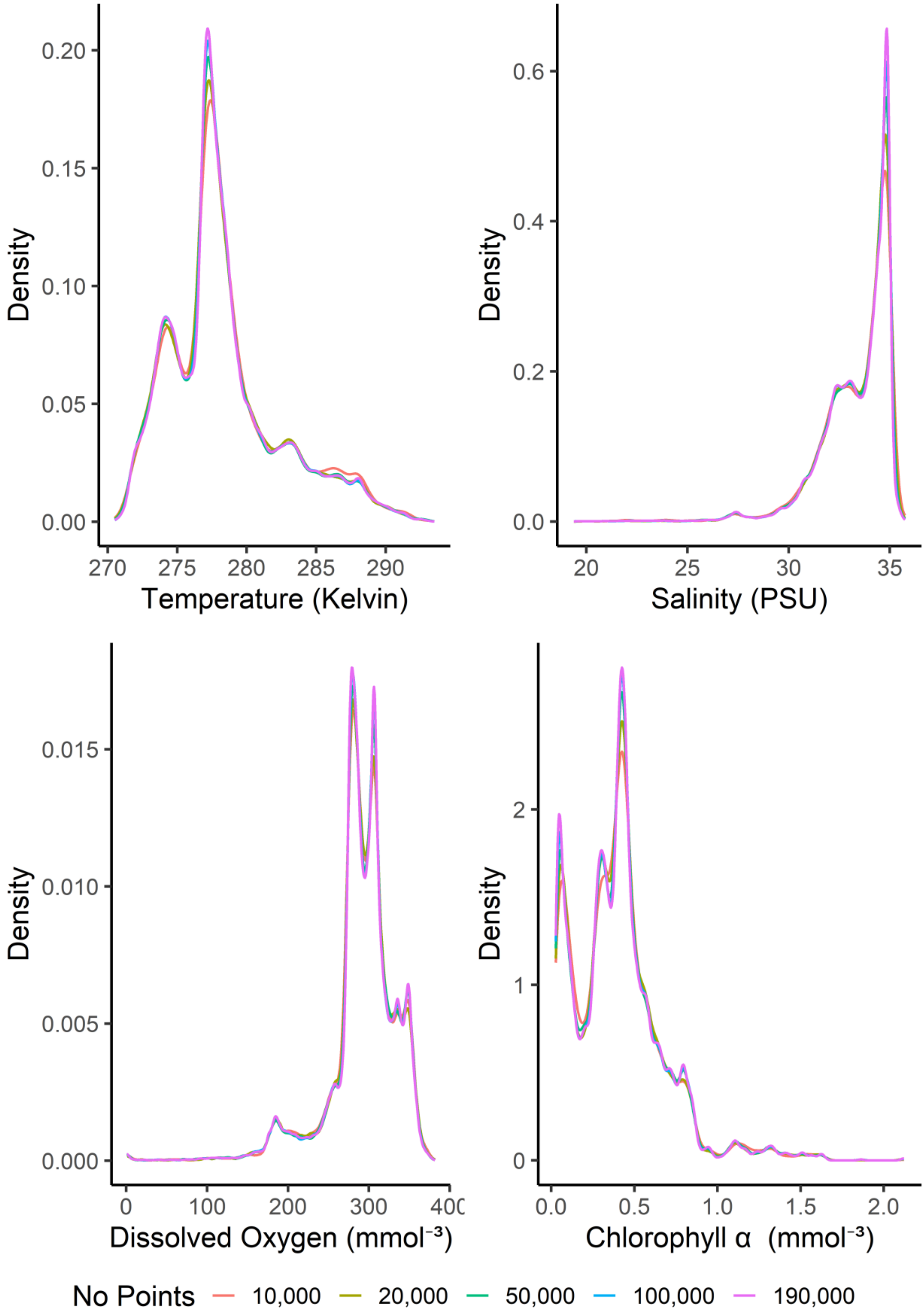

Figure B.5.3: Distribution of each oceanographic variable collected from 10,000, 20,000, 50,000, 100,000, and 190,000 randomly generated points during October 2007.

B.6: NAFO division with percentage weighting for background point creation.

To ensure that I sufficiently captured conditions across the capelin's range, I also weighted points by the number of spatial grid cells represented in each Northwest Atlantic Fisheries Organization (NAFO) division and the area of the Hudson Strait represented in the MCP (Figure B.6).

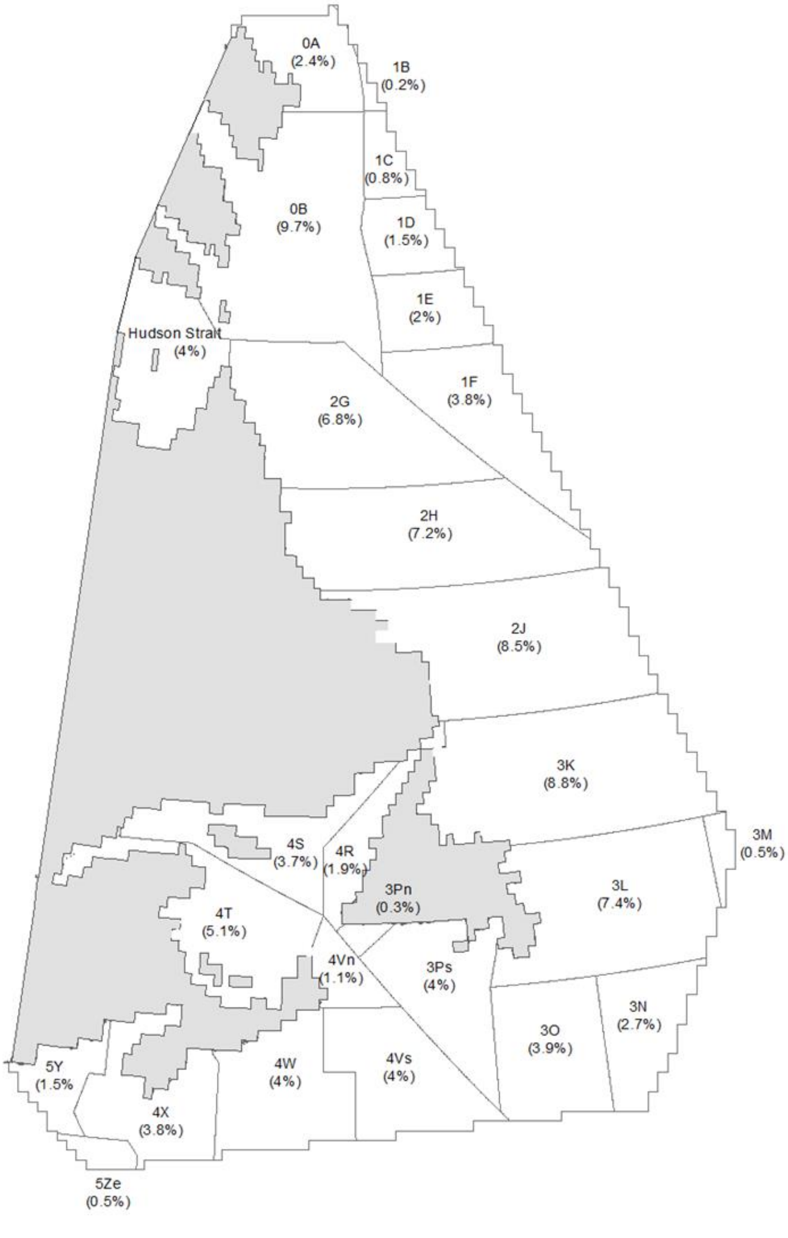

Figure B.6: NAFO divisions and percentage of spatial grid cells within each division. Map created in ESRI ArcMap 10.5.

B.7: Variable Selection: Spearman Correlation and VIF.

To minimise the impact of collinearity, I selected variables for each monthly model a-priori using Spearman correlation coefficient and variance inflation factor (VIF) (Dormann et al. 2013). I removed variables with correlation coefficients above 0.7 (Table B.7.1) and VIF values above five (Table B.7.2), giving variable retention preference to oceanographic variables closest to sampling depth as, due to proximity, they likely have a more direct impact on species occurrence than more distal values.

Table B.7.1: Spearman correlation coefficients for all variables indicating highly (> 0.7 / < -0.7) and moderately (> 0.5 / < -0.5 correlated variables.

Variable1	**Variable2**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
AMO (sampling month)	AMO (previous winter)	-0.97	1	-	-	-	-	-	-	-	-	-	-
AMO (sampling month)	AMO (previous month)	1	0.85	0.64	0.69	0.82	0.87	0.89	0.94	0.92	0.73	0.94	0.71
AMO (sampling month)	NAO (sampling month)	-0.78	-0.85	0.53	-	-0.65	-	-	-	-	-	-	-
AMO (sampling month)	NAO (previous winter)	-0.54	1	-0.64	-	-	-	-	-	-	-	-	-
AMO (sampling month)	NAO (previous month)	0.73	1	-	-	-0.59	-0.62	-	0.57	-	-0.54	-	-
AMO (previous winter)	AMO (previous month)	-0.97	0.85	-	-	-	-	-	-	-	-	-	-
AMO (previous winter)	NAO (sampling month)	0.86	-0.85	-	-	-	-	-	-	-	-	-	-
AMO (previous winter)	NAO (previous winter)	-	-1	-	-	-	-	-	-	-	-	-	-
AMO (previous winter)	NAO (previous month)	-0.55	1	-	-	-	-	-	-	-	0.54	-	-

AMO (previous month)	NAO (sampling month)	-0.78	-1	-	-	0.5	-	-	-	-	-	-	-
AMO (previous month)	NAO (previous winter)	-0.54	-0.85	-0.7	-	-0.57	-	-	-	-	-	-	-
AMO (previous month)	NAO (previous month)	0.73	0.85	-	-	-	-0.56	-	-	-	-	-	-
NAO (sampling month)	NAO (previous winter)	0.55	0.85	-	-	-	-	-	-	-	-	-	-
NAO (sampling month)	NAO (previous month)	-	-0.85	-	-	-	-	0.55	-	-	-	-	-
NAO (previous winter)	NAO (previous month)	-0.86	-1	-	-0.53	-	-	-	-	0.51	-	-	-
Chl (surface)	Chl (depth)	0.51	0.5	-	-	-	-	-	-	-	-	-	-
Chl (surface)	Temp (surface)	-	-	-	-	-0.55	-0.76	-0.69	-0.66	-0.72	-0.77	-	-
Chl (surface)	Temp (depth)	-	-	-	-	-	-0.57	-	-	-	-0.54	-	-
Chl (surface)	O2 (surface)	-	-	-	-	0.52	0.8	0.74	0.68	0.76	0.82	0.52	-
Chl (surface)	O2 (depth)	-	-	-	-	-	-	-	-	-	0.51	-	-
Chl (surface)	Salinity (surface)	-0.52	-	-	-	-	-	-	-	-	-	-	-
Chl (depth)	O2 (depth)	0.66	0.69	0.72	0.76	0.77	0.79	0.72	0.67	0.64	0.67	0.64	0.6
Chl (depth)	Salinity (depth)	-0.72	-0.7	-0.67	-0.63	-0.56	-0.62	-0.59	-0.55	-0.56	-0.64	-0.72	0.73
Mixed Layer Depth	Sea Surface Height	-0.82	-0.73	-0.71	-0.72	-0.73	-0.74	-0.7	-0.65	-0.71	-0.77	-0.77	-0.78
Mixed Layer Depth	O2 (surface)	-0.65	-0.62	-0.61	-0.57	-	-	-	-	-	-	-	-0.5
Mixed Layer Depth	Salinity (surface)	0.86	0.76	-0.78	0.81	0.81	0.84	0.75	0.73	0.83	0.86	0.86	0.85
Mixed Layer Depth	Salinity (depth)	0.65	0.57	0.56	0.6	0.57	0.59	0.53	0.5	0.58	0.62	0.64	0.65
Mixed Layer Depth	Bottom depth	-0.65	-0.59	-0.59	-0.6	-0.59	-0.61	-0.6	-059	-0.66	-0.67	-0.67	-0.66

Sea Surface Height	O2 (surface)	0.70	0.79	0.74	0.71	-	-	-	-	-	-	-	-
Sea Surface Height	Salinity (surface)	-0.95	-0.96	-0.94	-0.93	-0.92	-0.89	-0.88	-0.88	-0.85	-0.9	-0.91	-0.93
Sea Surface Height	Salinity (depth)	-0.76	-0.79	-0.75	-0.77	-0.74	-0.7	-0.67	-0.63	-0.6	-0.66	-0.7	-0.74
Sea Surface Height	Bottom depth	0.74	0.78	0.75	0.76	0.75	0.75	0.71	0.70	0.68	0.71	0.73	0.75
Temp (surface)	Temp (depth)	0.89	0.85	0.84	0.86	0.82	0.73	0.63	0.54	0.63	0.71	0.84	0.89
Temp (surface)	O2 (surface)	-0.80	-0.74	-0.68	-0.68	-0.84	-0.95	-0.96	-0.97	-0.97	-0.97	-0.94	-0.86
Temp (surface)	O2 (depth)	-0.56	-0.53	-0.51	-0.5	-	-0.52	-0.54	-0.55	-0.62	-0.66	-0.64	-0.59
Temp (surface)	Salinity (depth)	-	0.5	0.5	-	-	-	-	-	-	-	-	-
Temp (surface)	Bottom depth	-0.53	-0.59	-0.56	-	-	-	-	-	-	-	-	-
Temp (depth)	O2 (surface)	-0.76	-0.67	-0.64	-0.69	-0.81	-0.75	-0.65	0.57	-0.65	-0.72	-0.83	-0.84
Temp (depth)	O2 (depth)	-0.73	-0.79	-0.78	-0.73	-0.61	-0.5	-0.52	-0.51	-0.55	-0.53	-0.57	-0.66
Temp (depth)	Salinity (depth)	0.58	0.64	0.67	0.6	-	-	-	-	-	-	-	-
Temp (depth)	Bottom depth	-0.52	-0.58	-0.56	-0.54	-	-	-	-	-	-	-	-
O2 (surface)	O2 (depth)	0.63	0.6	0.59	0.59	0.62	0.57	0.59	0.6	0.65	0.7	0.7	0.68
O2 (surface)	Salinity (surface)	-0.68	-0.78	-0.79	-0.75	-	-	-	-	-	-	-	-
O2 (surface)	Salinity (depth)	-0.66	-0.74	-0.73	-0.69	-	-	-	-	-	-	-	-
O2 (surface)	Bottom depth	0.66	0.77	0.77	0.73	0.51	-	-	-	-	-	-	0.5
O2 (depth)	Salinity (depth)	-0.75	-0.77	-0.78	-0.77	-0.7	-0.62	-	-	-	-	0.6	-0.68
O2 (depth)	Bottom depth	0.53	0.57	0.57	0.56	-	-	-	-	-	-	-	-

Salinity (surface)	Salinity (depth)	0.78	0.8	0.78	0.81	0.78	0.76	0.73	0.72	0.73	0.74	0.77	0.78
Salinity (surface)	Bottom depth	-0.75	-0.77	-0.77	-0.78	-0.79	-0.79	-0.75	-0.77	-0.78	-0.77	-0.79	-0.78
Salinity (depth)	Bottom depth	-0.76	-0.77	-0.76	-0.77	-0.76	-0.76	-0.74	-0.72	-0.72	-0.74	-0.75	-0.76

B.7.2: Variables used in final models with VIF scores. Note January and February models were not run due to the low number of presence points/sampling years.

	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
Temp (depth)	2.17	2.64	2.26	1.86	1.74	1.50	1.54	1.54	1.43	1.50	1.60	1.52
Salinity (depth)	2.55	2.22	1.98	1.56	1.38	1.27	1.33	1.32	1.19	1.27	1.49	1.87
O2 (depth)	2.46	2.38	2.27	2.09	1.79	1.54	1.52	1.32	1.22	1.54	1.73	2.18
Chl (surface)	1.74	1.57	1.30	1.09	1.38	1.42	1.21	1.14	1.21	1.42	1.31	1.44
NAO (sample month)	1.32	1.01	1.44	3.30	1.67	1.18	2.93	1.38	2.02	1.18	1.36	1.84
NAO (previous month)	-	-	1.43	1.69	4.31	1.39	2.50	1.71	1.75	1.39	1.21	1.37
NAO (previous winter)	1.32	-	1.52	4.10	3.69	1.06	1.64	1.34	1.64	1.06	1.07	1.53
AMO (sample month)	-	-	1.44	2.27	2.51	1.53	1.30	1.66	1.20	1.53	1.63	1.25
AMO (previous winter)	-	-	1.09	1.24	1.16	1.06	1.60	1.16	1.73	1.06	1.69	1.30

B.8: Model performance metrics.

I used four metrics to quantify the performance of the models (Table B.8). Testing and training area under the curve (AUC) scores are derived from receiver operator characteristic (ROC) analysis (Equation 1). The AUC is independent of threshold (Phillips et al. 2006), indicates the probability that a randomly chosen presence location ranks higher in suitability than a randomly chosen background point. Values range from 0 to 1. Values closer to 1 indicate the discriminatory power is good, whereas values close to and less than 0.5 indicate discriminatory power is poor (Fielding & Bell 1997).

$$AUC = \frac{1}{n_A * n_N} \sum_{1}^{n_A} \sum_{1}^{n_N} S(TP, FP)$$

Equation 1: Both the testing and training AUC scores are calculated in the same manner but test different subsections of the data (testing and training datasets, respectively). n_A = *number of presences;* n_N = *number of absences;* TP = *number of true presences predicted by the model;* FP = *number of false presences predicted by the model. The value of* S *is conditional: If* $TP > FP, S = 1$; *If* $TP = FP, S = 0.5$; *If* $TP < FP, S = 0$. (Vida 1993).

The true skill statistic (TSS) is related to the widely used Cohens Kappa statistic which indicates the extent to which observed and predicted values are higher than expected by chance (Allouche et al. 2006) (Equation 2). Values range from -1 to +1, with scores of +1 indicating perfect agreement and scores of 0 and less indicating values are no better than chance.

$$Sensitivity = \frac{TP}{TP + FA}$$

$$Specificity = \frac{TA}{FP + TA}$$

$$TSS = sensitivity + specificity - 1$$

Equation 2: TSS if a function of sensitivity (the probability of a model correctly predicting a presence) and specificity (the probability of a model correctly predicting an absence). TP *= the number presences accurately predicted;* FP *= the number of presences falsely predicted (type 1 error);* TA *= the number of absences accurately predicted; FA = the number of absences falsely predicted (type 2 error).*

Both the AUC and TSS measures were developed for presence-absence, not presence-background/presence-only modelling. In presence-absence models, the AUC assesses how well the model can discriminate between presences and absences. In presence-background models, the AUC uses background points instead of absences which is problematic because background points may contain presences and absences. The TSS relies on prevalence which can only be accurately estimated with true absence data. Nevertheless, these metrics are widely used for models such as Maxent, primarily due to the lack of alternatives (Merow et al. 2013). One such alternative, however, is the Continuous Boyce Index (CBI) (Boyce et al. 2002) (Equation 3), which measures the degree to which model predictions differ from random over a moving window. It is independent of threshold and prevalence and is considered a robust measurement for presence-background and presence-only models. As with the TSS, CBI values range from -1 to +1, with scores of +1 indicating perfect agreement and scores of 0 and less indicating values are no better than chance and poor model performance.

$$P_i = \frac{p_i}{\sum_{j=1}^{b} p_j}$$

$$E_i = \frac{a_i}{\sum_{j=1}^{b} a_j}$$

$$F_i = \frac{P_i}{E_i}$$

Equation 3: The Continuous Boyce Index. Distribution ranges are subdivided into b bins. For each bin (i), both the predicted frequency of presence points (P_i) and the expected frequency of presence points if they were randomly distributed in the window (E_i) are calculated, and then used to create a predicted-to-expected ratio (F_i). p_i = number of presence points predicted to fall into the distribution bin i; $\sum p_j$ = the total number of presence points; a_i = the number of grid cells belonging to distribution class i; $\sum a_j$ = the total number of cells.

The AUC and TSS scores were obtained from the R package Dismo (Hijmans et al. 2017), while the CBI was obtained with the R package enmSdm (Smith 2019). For each month, each metric was calculated separately for each temporal fold and then averaged to produce average predictive performances.

Table B.8: Performance metrics for each of the monthly models. The mean represents the values obtained for all temporal fold, whereas the minimum and maximum values represent the highest and lowest scoring temporal fold. For the TSS and CBI, values range from -1 to +1, with scores of +1 indicating perfect agreement, and scores of -1 indicating completely imperfect agreement. Scores of 0 indicate values are no better than chance. For the train and test AUC, values arrange from 0 – 1 with scores of 1 indicating perfect agreement, and scores of 0 completely imperfect agreement.

		Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Train AUC	**Mean**	0.95	0.95	0.91	0.91	0.93	0.93	0.94	0.92	0.92	0.95
	Max	0.96	0.96	0.93	0.92	0.93	0.94	0.94	0.92	0.93	0.96
	Min	0.94	0.94	0.90	0.91	0.92	0.93	0.94	0.90	0.92	0.95
Test AUC	**Mean**	0.95	0.93	0.92	0.96	0.92	0.99	0.95	0.89	0.96	0.97
	Max	0.98	0.99	0.98	0.98	0.98	0.87	0.99	0.97	1.00	0.99
	Min	0.87	0.84	0.78	0.94	0.69	0.63	0.74	0.67	0.93	0.93
TSS	**Mean**	0.83	0.79	0.75	0.81	0.77	0.74	0.85	0.72	0.87	0.89
	Max	0.94	0.97	0.98	0.85	0.94	0.95	0.93	0.94	1.00	0.96
	Min	0.71	0.53*	0.50*	0.75	0.33**	0.43***	0.55****	0.37*****	0.73	0.80
CBI	**Mean**	0.99	0.98	1.00	1.00	0.96	0.97	1.00	0.99	1.00	1.00
	Max	1.00	1.00	1.00	1.00	0.99	0.99	1.00	1.00	1.00	1.00
	Min	0.98	0.95	0.99	1.00	0.94	0.90	0.99	0.99	1.00	0.99

* One-fold out of fourteen had a TSS < 0.6

** Two folds out of sixteen had a TSS <0.6

*** Two folds out of eleven had a TSS <0.6

**** One-fold out of eighteen had a TSS <0.6

***** One-fold out of sixteen had a TSS <0.6

B.9: Concatenating depth layers into raster grid for prediction.

Species distribution models, including Maxent, are operationalised on two-dimensional surfaces. To predict the estimated probability of presence across the 2.5D space as a whole (i.e. across all depth layers), I concatenated each of the oceanographic variable depth layers into a continuous grid, in which each depth layer and its associated environmental values are retained. Concatenation is achieved by transforming the coordinates to incorporate a depth indicator, and then joining individual layers using shell scripting to create a continuous grid (see Bentlage et al. 2013 for full methods). These concatenated grids were used for predicting the estimated probability of presence of capelin (Figure B.9).

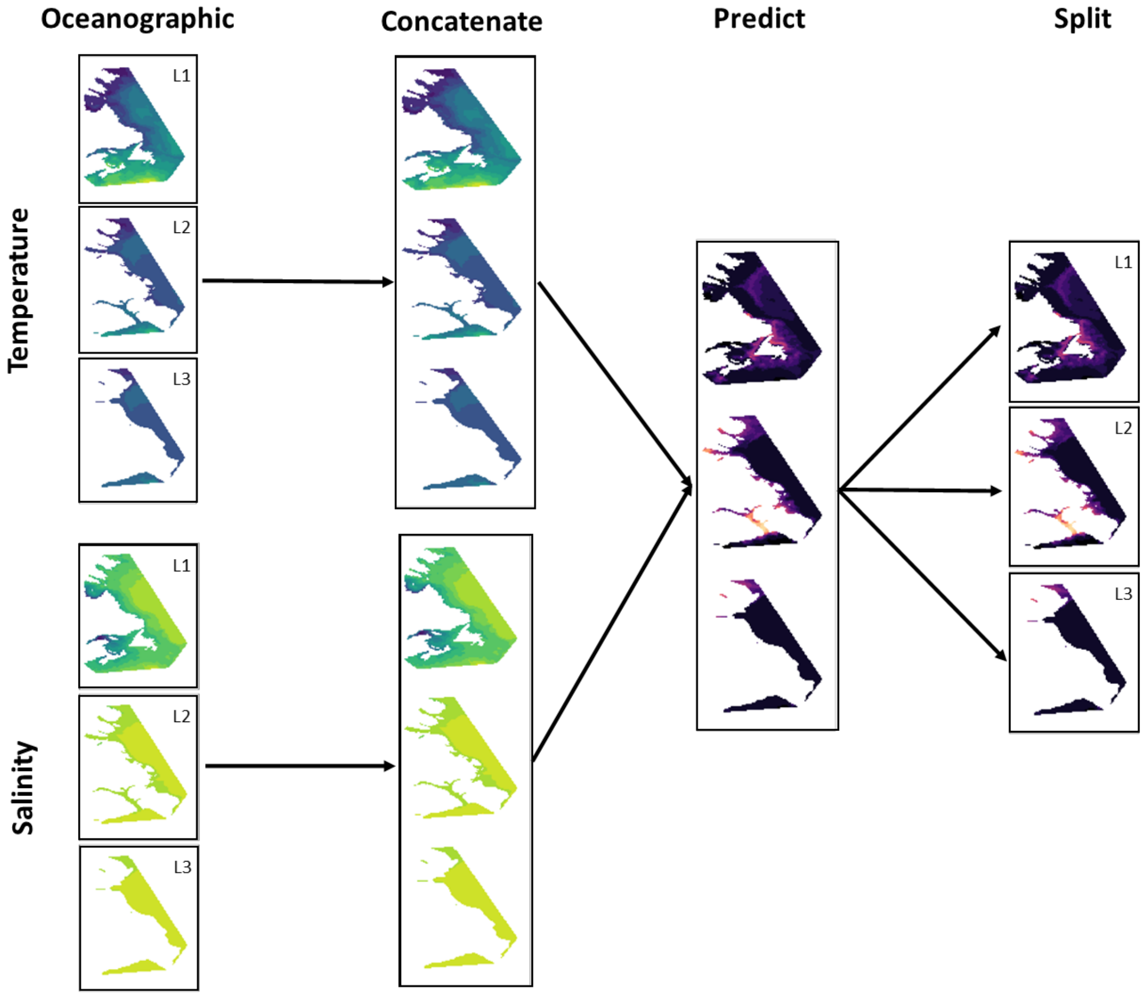

Figure B.9: *Example of concatenating multiple depth layers into a continuous grid for prediction purposes. In this example, separate temperature depth layers (L1, L2, and L3) for July 2004 are concatenated into a continuous 'temperature grid'. Separate salinity depth layers (L1, L2, L3) for July 2004 are concatenated into a continuous 'salinity grid'. These continuous grids are used for prediction. The resulting prediction can then be split back into individual depth layers (L1, L2, L3). The year, month, depths, and oceanographic variables have been arbitrarily chosen for illustrative purposes only.*

B.10: Variation in environmental correlates.

The background points provide an overview of environmental conditions across the MCP area used in the models (Table B.10). Across all months, median chlorophyll concentration values ranged from 0.25 mmol.m^{-3} (August) to 1.1 mmol.m^{-3} (May), with the smallest range in August (1.65 mmol.m^{-3}) and the largest range in July (4.53 mmol.m^{-3})). Median dissolved oxygen values ranged from 289.81 mmol.m^{-3} (September) to 321.71 mmol.m^{-3} (May) (smallest range in October (380.98 mmol.m^{-3}), with the largest range in July (446.14 mmol.m^{-3})). The median salinity value was lowest in August (33.41 PSU) and highest in March (33.71 PSU) (smallest range in December (14.63 PSU), with the largest range in June (22.26 PSU)). Temperature ranged from a Median of 27.11 kelvin (March) to 277.67 kelvin (August) (smallest range in April (15.63 kelvin), largest range in August (25.88 kelvin)). Median AMO values during ‘sampling month’ ranged from 0.09 (April and May) to 0.14 (March, July, and August), while NAO values ranged from -0.75 (March) to 0.29 (May). The NAO median values from the previous month were lowest in July (-0.23) and highest in March (0.95). Median AMO winter values ranged from 0.09 (April and May) to 0.14 (March, July, and August) while NAO winter values ranged from -0.18 (July, August, September) to 0.37 (March). Table B.10 shows the maximum, minimum, range, mean, and median values of all environmental variables (oceanographic and climate oscillations) from the background points used in each of the monthly models.

Figure B.10 provides a visual representation of the range and distribution of the oceanographic variables used in the model (chlorophyll, dissolved oxygen, salinity, and temperature) across three months (March, June, and December) in the year 1998 at a single depth layer (11.8 meters).

***Table B.10**: Summary data of the environmental correlates associated with the background points used in each monthly model.*

	Chlorophyll Concentration at surface (mmol.m^{-3})					**Dissolved Oxygen at sampling depth (mmol.m^{-3})**				
Month	**Min**	**Max**	**Mean**	**Median**	**Range**	**Min**	**Max**	**Mean**	**Median**	**Range**
3	0.02	2.54	0.72	0.73	2.52	1.01	396.47	313.53	314.48	395.46
4	0.02	2.85	0.94	0.94	2.83	1.01	405.01	315.08	318.06	403.99
5	0.09	2.99	0.99	1.1	2.9	1.00	417.36	312.46	321.71	416.36
6	0.05	3.42	0.73	0.79	3.37	1.00	418.55	305.63	309.86	417.55
7	0.03	4.56	0.39	0.36	4.53	1.00	447.13	297.81	297.8	446.14
8	0.03	1.68	0.26	0.25	1.65	0.99	402.95	290.45	290.48	401.96
9	0.03	2.69	0.29	0.26	2.66	0.99	394.89	287.48	289.81	393.9
10	0.03	2.37	0.37	0.35	2.34	0.94	381.93	289.12	292.27	380.98
11	0.04	2.52	0.4	0.36	2.48	0.96	386.5	295.34	300.9	385.53
12	0.09	2.22	0.39	0.37	2.13	0.95	390.24	301.35	306.65	389.29
	Salinity Concentration at sampling depth (PSU)					**Temperature at sampling depth (kelvin)**				
Month	**Min**	**Max**	**Mean**	**Median**	**Range**	**Min**	**Max**	**Mean**	**Median**	**Range**
3	20.25	35.69	33.33	33.71	15.44	270.68	286.76	275.05	275.11	16.07
4	15.92	35.69	33.3	33.69	19.77	270.99	286.62	275.25	275.39	15.63
5	14.15	35.76	33.23	33.55	21.61	270.82	287.69	275.91	276.32	16.87
6	13.49	35.75	33.11	33.54	22.26	270.73	291.46	277.06	276.86	20.73
7	14.46	35.95	33.04	33.51	21.49	270.38	293.83	278.32	277.21	23.45
8	16.69	35.84	32.95	33.41	19.15	270.77	296.66	279.52	277.67	25.88
9	16.57	36	33.01	33.43	19.44	270.67	296.14	279.3	277.65	25.47
10	17.97	35.92	33.02	33.48	17.95	270.72	295.86	278.57	277.54	25.14
11	19.38	35.93	33.06	33.48	16.55	270.69	290.06	277.46	277.18	19.37
12	21.2	35.83	33.17	33.58	14.63	270.54	289.79	276.48	276.61	19.25
	AMO from previous winter					**AMO from sampling month**				
Month	**Min**	**Max**	**Mean**	**Median**	**Range**	**Min**	**Max**	**Mean**	**Median**	**Range**
3	-0.09	0.21	0.11	0.14	0.31	-0.16	0.29	0.11	0.1	0.45
4	-0.09	0.21	0.06	0.09	0.31	-0.13	0.43	0.1	0.08	0.56
5	-0.09	0.21	0.07	0.09	0.31	-0.06	0.46	0.13	0.15	0.52

6	-0.09	0.21	0.08	0.13	0.31	-0.12	0.49	0.21	0.2	0.61
7	-0.09	0.21	0.09	0.14	0.31	-0.07	0.49	0.24	0.21	0.55
8	-0.07	0.21	0.11	0.14	0.28	0.06	0.53	0.28	0.32	0.47
9	-0.09	0.21	0.08	0.13	0.31	0.06	0.45	0.25	0.24	0.4
10	-0.09	0.21	0.06	0.1	0.31	-0.04	0.43	0.23	0.24	0.47
11	-0.09	0.21	0.08	0.1	0.31	-0.07	0.32	0.12	0.14	0.39
12	-0.09	0.21	0.07	0.1	0.31	-0.13	0.28	0.11	0.17	0.41
	NAO from previous winter					**NAO from sampling month**				
Month	**Min**	**Max**	**Mean**	**Median**	**Range**	**Min**	**Max**	**Mean**	**Median**	**Range**
3	-0.69	1.66	0.35	0.37	2.35	-2.32	1.78	-0.46	-0.75	4.10
4	-3.03	1.66	0.06	0.12	4.69	-1.29	2.31	0.13	0.27	3.60
5	-3.03	1.66	0.04	0.12	4.69	-1.33	1.49	0.30	0.29	2.82
6	-3.03	1.66	0.06	0.03	4.69	-1.25	1.03	-0.15	-0.23	2.28
7	-3.03	1.66	0.08	-0.18	4.69	-1.05	0.46	-0.07	0.02	1.51
8	-3.03	1.47	-0.08	-0.18	4.50	-0.97	0.79	-0.20	-0.09	1.76
9	-3.03	1.66	-0.06	-0.18	4.69	-1.89	1.00	-0.02	0.10	2.89
10	-3.03	1.66	-0.07	0.12	4.69	-1.89	1.20	-0.33	-0.58	3.09
11	-3.03	1.66	0.12	0.12	4.69	-1.64	1.57	0.01	0.16	3.21
12	-3.03	1.66	0.22	0.12	4.69	-3.63	2.60	-0.14	-0.14	6.23

	NAO from the month previous to sampling				
Month	**Min**	**Max**	**Mean**	**Median**	**Range**
3	-3.98	2.86	0.28	0.95	6.84
4	-2.32	1.78	0.18	0.58	4.10
5	-1.29	2.31	0.09	0.27	3.60
6	-1.33	1.49	0.13	0.27	2.82
7	-1.25	1.03	-0.22	-0.23	2.28
8	-1.24	0.40	-0.10	-0.12	1.64
9	-0.97	0.79	-0.17	-0.21	1.76
10	-1.89	1.00	-0.22	0.05	2.89
11	-1.89	1.2	-0.21	-0.08	3.09
12	-1.64	1.21	0.16	0.28	2.85

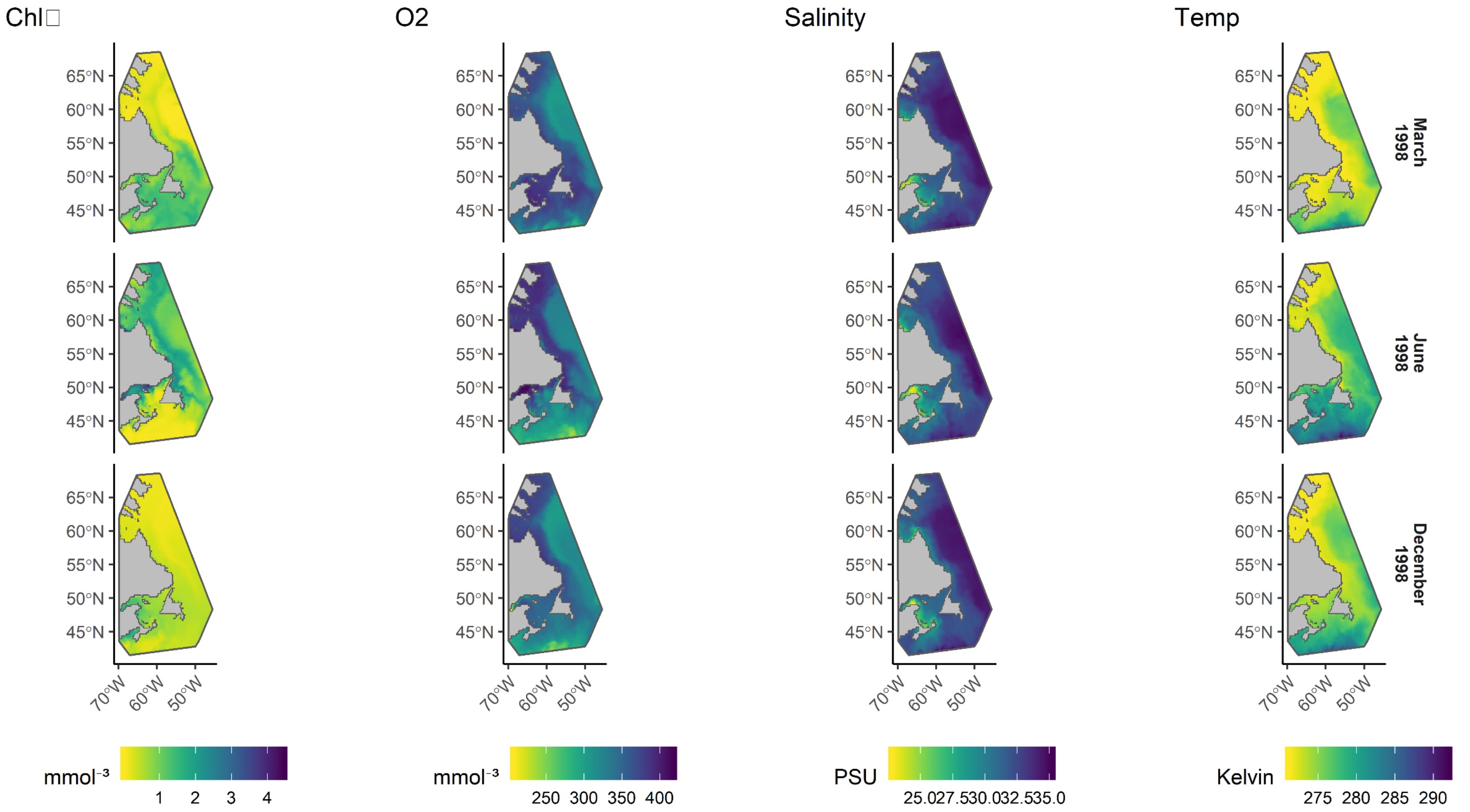

Figure B.10: Modelled oceanographic conditions at 11.8 meters during March, June, and December 1998. The year, month, and depths have been arbitrarily chosen for illustrative purposes only.

B.11: References

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Appendix C: Appendices for Chapter 3: Influence of the North Atlantic Oscillation on the distribution of a keystone pelagic fish

C.1: Study Region and Study Area

The broader study region lies in the Northwest Atlantic, broadly covering waters lying up to the Canadian Exclusive Economic Zone (24 nautical miles from the low water line) and adjacent waters, including those on the Flemish Cap and the French territory of Saint Pierre and Miquelon. The study area (where I limit the analysis to) is defined by a minimum convex polygon derived from the capelin occurrences I obtained from the OBIS database (Syfert et al. 2014, OBIS 2018) (Figure C.1).

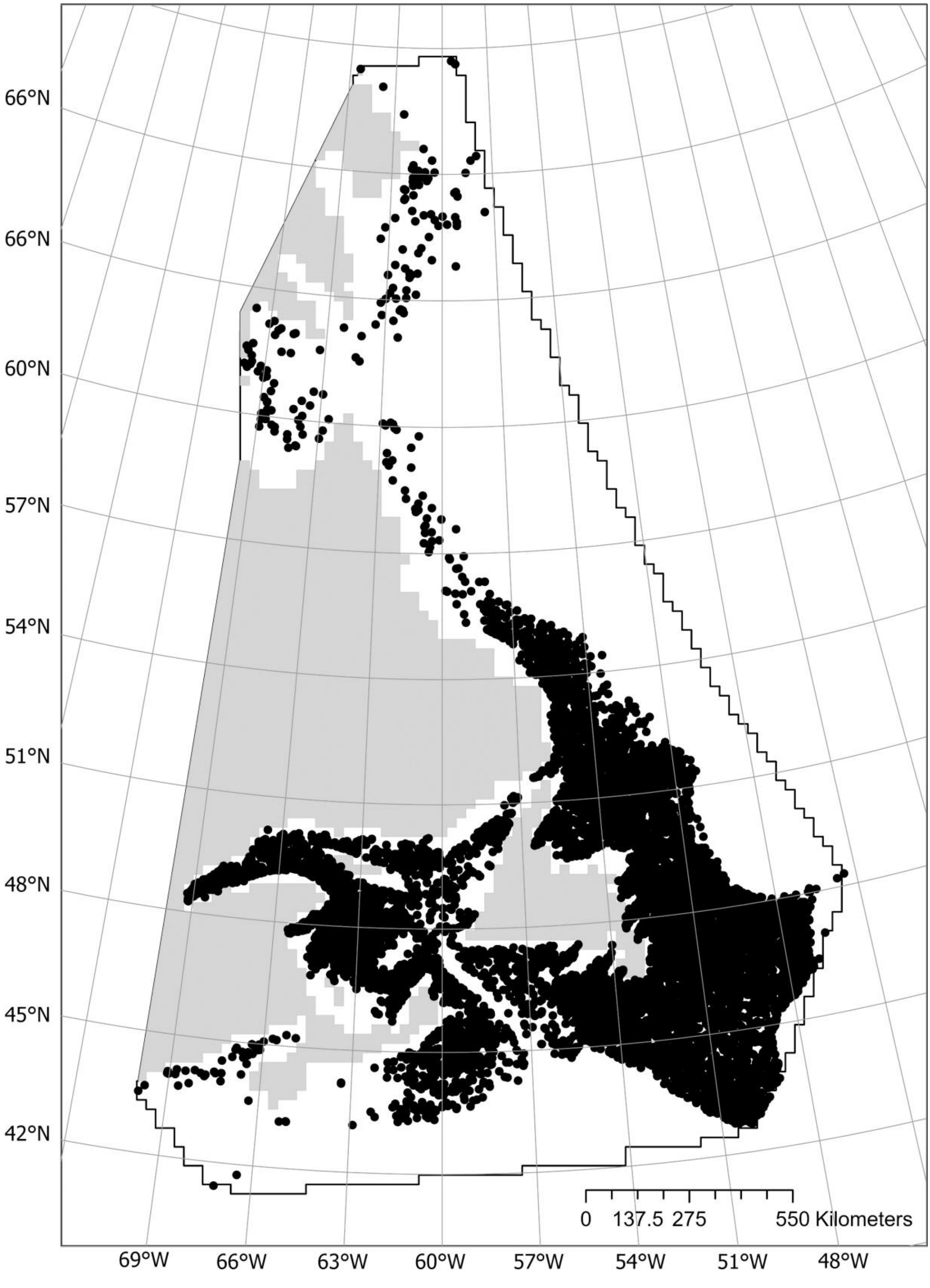


***Figure C.1**: The study area was delineated using a Minimum Convex Polygon (MCP – solid line) based on the capelin presence data obtained from OBIS (dots). The map is displayed in a Canada Albers Equal Area Conic projection.*

C.2: Variable selection

To minimise impacts of collinearity of predictors variables in the models, I selected the oceanographic variables temperature, salinity, oxygen from the depth layer closest to the sampling depth reported in the OBIS database/at the depth layer the background point was generated at, and chlorophyll from the surface a-priori from a larger group of variables. I explain the process below.

For the presence/background points, I extracted chlorophyll, density mixed layer depth, oxygen, salinity, sea surface height, temperature, and bottom depth variables from the GLORYS and BIOMER ocean models (CMEMS 2018, CMEMS & Paul 2018). Although with the notable exception of temperature (Rose 2005), these variables have not been widely tested for association with capelin, they are commonly associated with pelagic fish distributions (e.g. Becker et al. 2016, Schickele et al. 2020). I extracted both values at the sea surface and at sampling depth, except for bottom depth. Sea surface height and density mixed layer depth as these variables are single-layer values only.

To check for collinearity, I used two tests – the Spearman correlation coefficient and the variance inflation factor (VIF) (Dormann et al. 2013). I removed variables with a correlation coefficient greater than 0. 7 (Table C.2.1) and VIF values above five (Table C.2.2) as they are considered to have high collinearity. I gave preference to variables at depth as the direct impact of a variable likely diminishes in strength with distance.

***Table C.2.1**: Spearman correlation coefficients for the oceanographic variables indicating highly (> 0.7 / < -0.7) and moderately (> 0.5 / < -0.5) correlated variables. For each variable, I tested values at the surface (surface), and at sampling depth (depth).*

Variable 1	Variable 2	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Chlorophyll (surface)	Temperature (surface)	-	-	-0.55	-0.76	-0.69	-0.66	-0.72	-0.77	-	-
Chlorophyll (surface)	Temperature (depth)	-	-	-	-0.57	-	-	-	-0.54	-	-
Chlorophyll (surface)	Oxygen (surface)	-	-	0.52	0.8	0.74	0.68	0.76	0.82	0.52	-
Chlorophyll (surface)	Oxygen (depth)	-	-	-	-	-	-	-	0.51	-	-
Chlorophyll (depth)	Oxygen (depth)	0.72	0.76	0.77	0.79	0.72	0.67	0.64	0.67	0.64	0.6
Chlorophyll (depth)	Salinity (depth)	-0.67	-0.63	-0.56	-0.62	-0.59	-0.55	-0.56	-0.64	-0.72	0.73
Mixed Layer Depth	Sea Surface Height	-0.71	-0.72	-0.73	-0.74	-0.7	-0.65	-0.71	-0.77	-0.77	-0.78
Mixed Layer Depth	Oxygen (surface)	-0.61	-0.57	-	-	-	-	-	-	-	-0.5
Mixed Layer Depth	Salinity (surface)	-0.78	0.81	0.81	0.84	0.75	0.73	0.83	0.86	0.86	0.85
Mixed Layer Depth	Salinity (depth)	0.56	0.6	0.57	0.59	0.53	0.5	0.58	0.62	0.64	0.65
Mixed Layer Depth	Bottom depth	-0.59	-0.6	-0.59	-0.61	-0.6	-059	-0.66	-0.67	-0.67	-0.66
Sea Surface Height	Oxygen (surface)	0.74	0.71	-	-	-	-	-	-	-	-
Sea Surface Height	Salinity (surface)	-0.94	-0.93	-0.92	-0.89	-0.88	-0.88	-0.85	-0.9	-0.91	-0.93
Sea Surface Height	Salinity (depth)	-0.75	-0.77	-0.74	-0.7	-0.67	-0.63	-0.6	-0.66	-0.7	-0.74
Sea Surface Height	Bottom depth	0.75	0.76	0.75	0.75	0.71	0.70	0.68	0.71	0.73	0.75
Temperature (surface)	Temperature (depth)	0.84	0.86	0.82	0.73	0.63	0.54	0.63	0.71	0.84	0.89
Temperature (surface)	Oxygen (surface)	-0.68	-0.68	-0.84	-0.95	-0.96	-0.97	-0.97	-0.97	-0.94	-0.86

Temperature (surface)	Oxygen (depth)	-0.51	-0.5	-	-0.52	-0.54	-0.55	-0.62	-0.66	-0.64	-0.59
Temperature (surface)	Salinity (depth)	0.5	-	-	-	-	-	-	-	-	-
Temperature (surface)	Bottom depth	-0.56	-	-	-	-	-	-	-	-	-
Temperature (depth)	Oxygen (surface)	-0.64	-0.69	-0.81	-0.75	-0.65	0.57	-0.65	-0.72	-0.83	-0.84
Temperature (depth)	Oxygen (depth)	-0.78	-0.73	-0.61	-0.5	-0.52	-0.51	-0.55	-0.53	-0.57	-0.66
Temperature (depth)	Salinity (depth)	0.67	0.6	-	-	-	-	-	-	-	-
Temperature (depth)	Bottom depth	-0.56	-0.54	-	-	-	-	-	-	-	-
Oxygen (surface)	Oxygen (depth)	0.59	0.59	0.62	0.57	0.59	0.6	0.65	0.7	0.7	0.68
Oxygen (surface)	Salinity (surface)	-0.79	-0.75	-	-	-	-	-	-	-	-
Oxygen (surface)	Salinity (depth)	-0.73	-0.69	-	-	-	-	-	-	-	-
Oxygen (surface)	Bottom depth	0.77	0.73	0.51	-	-	-	-	-	-	0.5
Oxygen (depth)	Salinity (depth)	-0.78	-0.77	-0.7	-0.62	-	-	-	-	0.6	-0.68
Oxygen (depth)	Bottom depth	0.57	0.56	-	-	-	-	-	-	-	-
Salinity (surface)	Salinity (depth)	0.78	0.81	0.78	0.76	0.73	0.72	0.73	0.74	0.77	0.78
Salinity (surface)	Bottom depth	-0.77	-0.78	-0.79	-0.79	-0.75	-0.77	-0.78	-0.77	-0.79	-0.78
Salinity (depth)	Bottom depth	-0.76	-0.77	-0.76	-0.76	-0.74	-0.72	-0.72	-0.74	-0.75	-0.76

Table C.2.2: *VIF Scores for the variables used in the final Maxent models.*

	Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
Temperature (depth)	2.26	1.86	1.74	1.50	1.54	1.54	1.43	1.50	1.60	1.52
Salinity (depth)	1.98	1.56	1.38	1.27	1.33	1.32	1.19	1.27	1.49	1.87
Oxygen (depth)	2.27	2.09	1.79	1.54	1.52	1.32	1.22	1.54	1.73	2.18
Chlorophyll (surface)	1.30	1.09	1.38	1.42	1.21	1.14	1.21	1.42	1.31	1.44

C.3: Numerical Model Depth layers

The numerical ocean modelling products GLORYS V4.1 and BIOMER V3.2 provide global oceanographic data across 75 depth levels, 47 of which fall within the study area. Depth levels are not evenly spaced, nor do they precisely match the species presence data's sampling depth. For each presence point, I appended oceanographic data from the level closest to the sampling. For example, if a sample came from a depth of 44 meters, I used conditions from the depth-layer representing conditions at 41.18 meters as this layer is closer than the one representing 47.21 meters (Table C.3).

Table C.3*: The Minimum Convex Polygon (MCP) encompasses 47 depth layers derived from the GLORYS* (CMEMS 2018a) *and BIOMER* (CMEMS 2018b) *ocean models. Depth values are rounded to two decimal points.*

Layer No	Depth (meters)	Layer No	Depth (meters)
1	0.51	24	97.04
2	1.56	25	108.03
3	2.67	26	120.00
4	3.86	28	133.08
5	5.14	29	163.17
6	6.54	30	180.55
7	8.09	31	199.79
8	9.82	32	221.14
9	11.77	33	244.89
10	13.99	34	271.36
11	16.53	35	300.89
12	19.43	36	333.86
13	22.76	37	370.69
14	26.56	38	411.79
15	30.87	39	457.63
16	35.74	40	508.64
17	41.18	41	565.29
18	47.21	42	628.03
19	53.85	43	697.26
20	61.11	44	773.39
21	69.02	45	856.68
22	77.61	46	947.45
23	86.93	47	1045.85

C.4: North Atlantic Oscillation (NAO)

The North Atlantic Oscillation is an oscillation in atmospheric surface pressure between the Icelandic Low (a semi-permanent low-pressure system between Iceland and southern Greenland in the North Atlantic/sub-Arctic) and the Azores High (a semi-permanent high-pressure system in the sub-tropical Atlantic) (Visbeck et al. 2003). In the western Atlantic, including waters in and around the study region, winter NAO phases influence oceanographic conditions throughout the remainder of the year (Petrie 2007, Figure C.4.1)).

I obtained winter (December to February inclusive) North Atlantic Oscillation values (PC-based) from the National Center for Atmospheric Research (NCAR), calculated from the leading empirical orthogonal function sea level pressure anomalies between 20°-80°N, 90°W-40 °E (NCAR 2019). I categorised a year as belonging to the positive or negative phase based on the winter anomaly values (1981- 2010 standard climatology (WMO 2017) (Figure XXX)). Positive years dominate the time series (ten out of the seventeen years) (Table C.4).

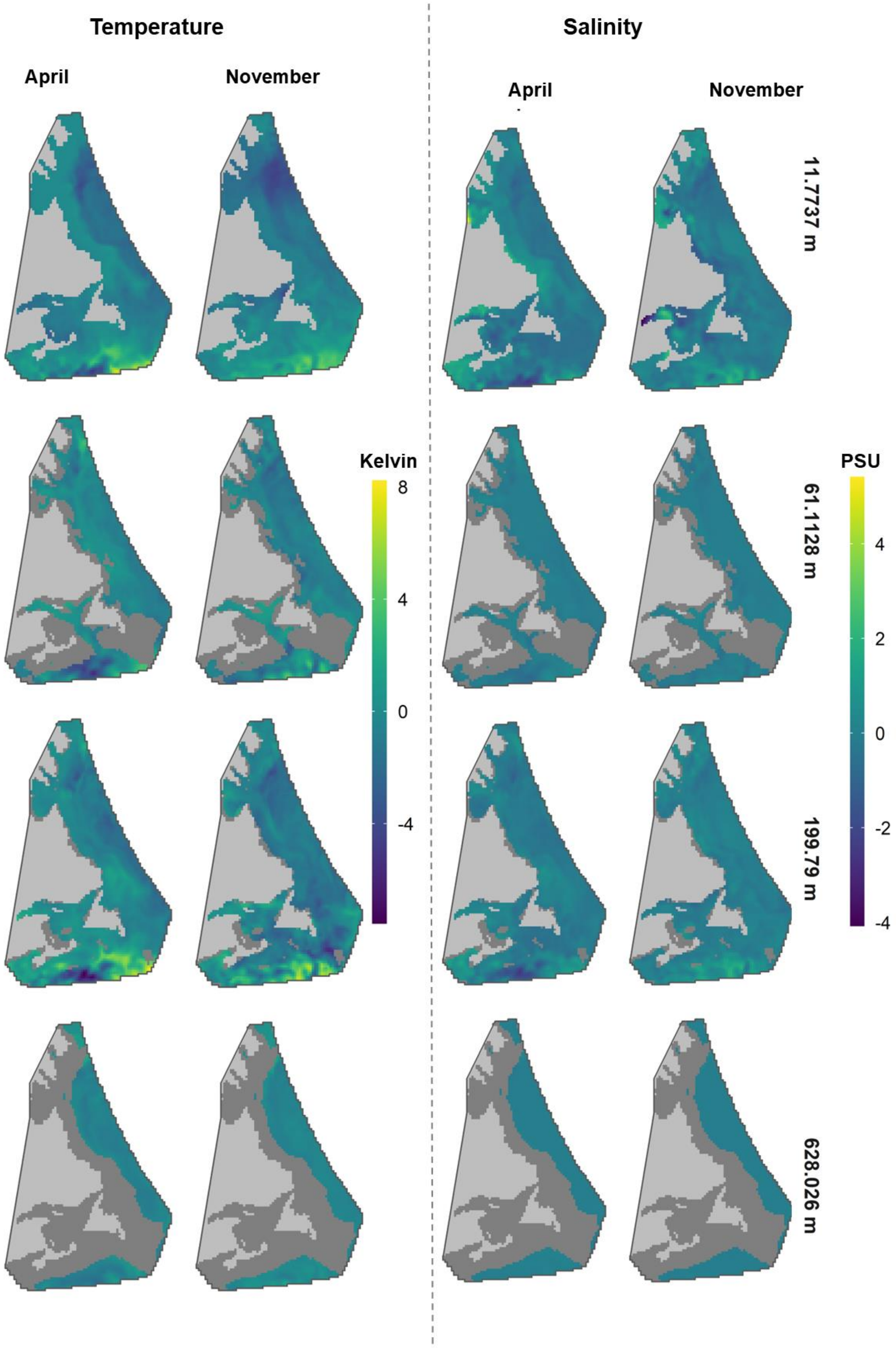
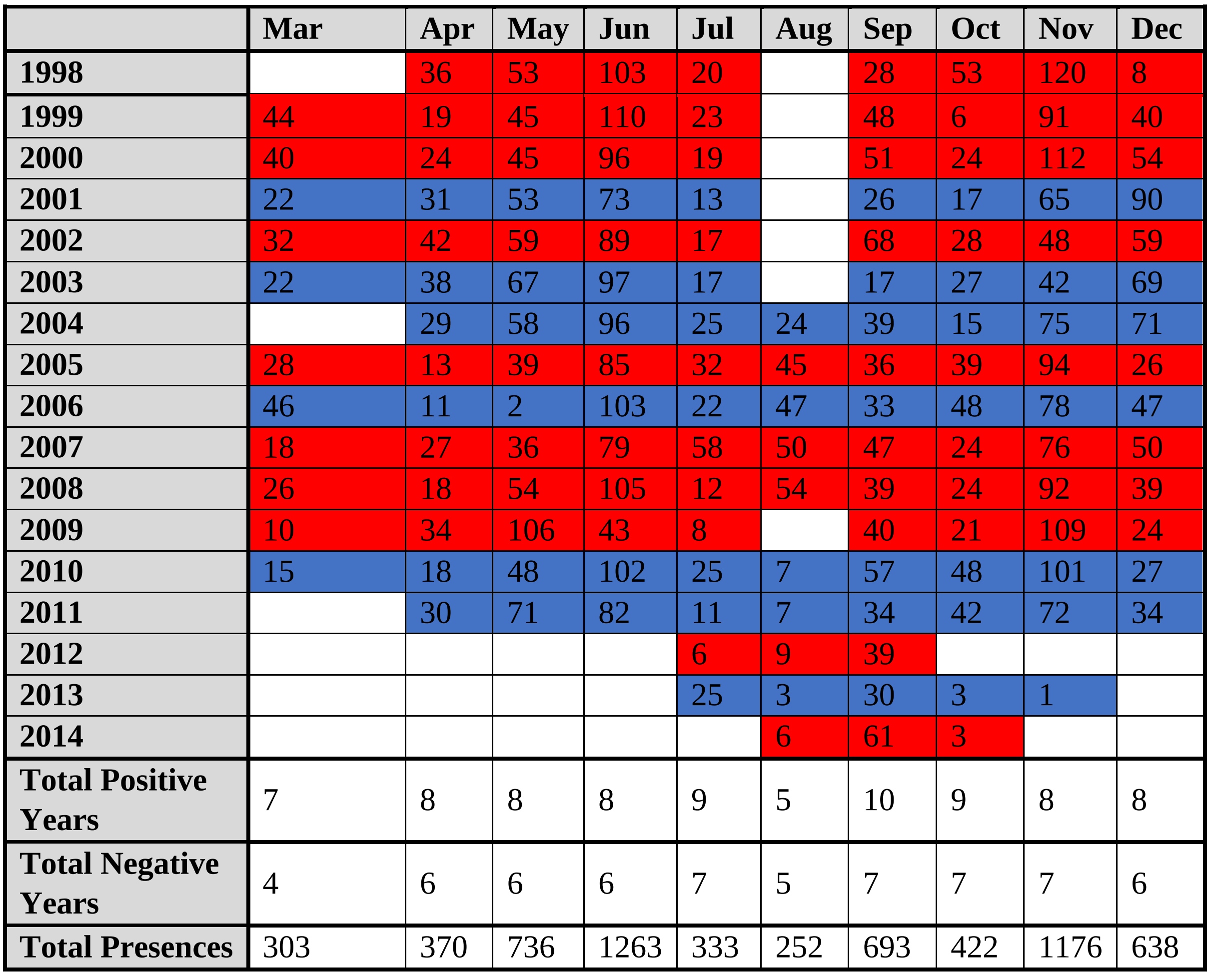


Figure C.4.1: *Difference in temperature and salinity between a year which experienced a positive winter NAO phase (2000) and a year which experienced a negative winter NAO phase (2010) across four depths levels. The year, month, depths, and variables have been arbitrarily chosen for illustrative purposes only. Differences are calculated by subtracting values in the 2010 from those in 2000.*

Table C.4*: Number of years falling into the NAO winter anomaly positive phase (red) and negative phase (blue) and presences per year for each month modelled. Years are only counted if there is presence data for those years as I do not consider years for which I have no data in the models or analysis.*



	Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
1998		36	53	103	20		28	53	120	8
1999	44	19	45	110	23		48	6	91	40
2000	40	24	45	96	19		51	24	112	54
2001	22	31	53	73	13		26	17	65	90
2002	32	42	59	89	17		68	28	48	59
2003	22	38	67	97	17		17	27	42	69
2004		29	58	96	25	24	39	15	75	71
2005	28	13	39	85	32	45	36	39	94	26
2006	46	11	2	103	22	47	33	48	78	47
2007	18	27	36	79	58	50	47	24	76	50
2008	26	18	54	105	12	54	39	24	92	39
2009	10	34	106	43	8		40	21	109	24
2010	15	18	48	102	25	7	57	48	101	27
2011		30	71	82	11	7	34	42	72	34
2012					6	9	39			
2013					25	3	30	3	1	
2014						6	61	3		
Total Positive Years	7	8	8	8	9	5	10	9	8	8
Total Negative Years	4	6	6	6	7	5	7	7	7	6
Total Presences	303	370	736	1263	333	252	693	422	1176	638

C.5: Maxent Model

Overview

The Maxent species distribution model is a machine learning model that compares environmental conditions associated with georeferenced species presences with georeferenced points from the wider study area (background points) to predict distributions (Phillips et al. 2006). The model is based on the maximum entropy principle—that subject to prior knowledge, the probability distribution which best describes the data is that with maximum entropy (i.e. the least informative distribution). Maxent is among the most widely used species distribution model and is particularly suited to datasets for which true absences are not known. It performs well compared to models that can utilise absence data such as generalised linear models (GLMs) and generalised additive models (GAMs) (Elith et al. 2006). Several studies have explored how best to build a Maxent model for users unique circumstances. For the interested reader alongside Elith et al. 2006 and Phillips et al. 2006, I recommend Merow et al. 2013, Feng et al. 2017, and Phillips et al. 2017 as good entry points.

Results

Overall, each of the monthly Maxent models performed well (Table C.5). The December model performed the best overall, and the October model the least.

Table C.5: *Evaluation metrics for each of the monthly models, reported to two decimal places. AUC - Area Under the Curve; TSS - True Skill Statistic; CBI – Continuous Boyce Index; SEDI - Symmetric Extremal Dependence Index.*

Month	Test AUC	Training AUC	TSS	CBI	SEDI
March	0.96	0.94	0.81	0.99	0.81
April	0.95	0.93	0.78	0.98	0.77
May	0.92	0.89	0.70	1	0.75
June	0.96	0.91	0.81	1	0.88
July	0.93	0.91	0.70	0.97	0.75
August	0.93	0.92	0.73	0.97	0.78
September	0.97	0.94	0.87	1	0.89
October	0.91	0.90	0.70	0.99	0.61
November	0.96	0.91	0.83	1	0.89
December	0.98	0.95	0.88	1	0.89

Maxent models provide information on the permutation importance of each variable used in the model. I found that generally, temperature was most important, except in April and May when oxygen dominated, and in December when chlorophyll dominated (Figure C.5). I refer the reader to Andrews et al. 2020 for further discussion on the variable importance patterns.

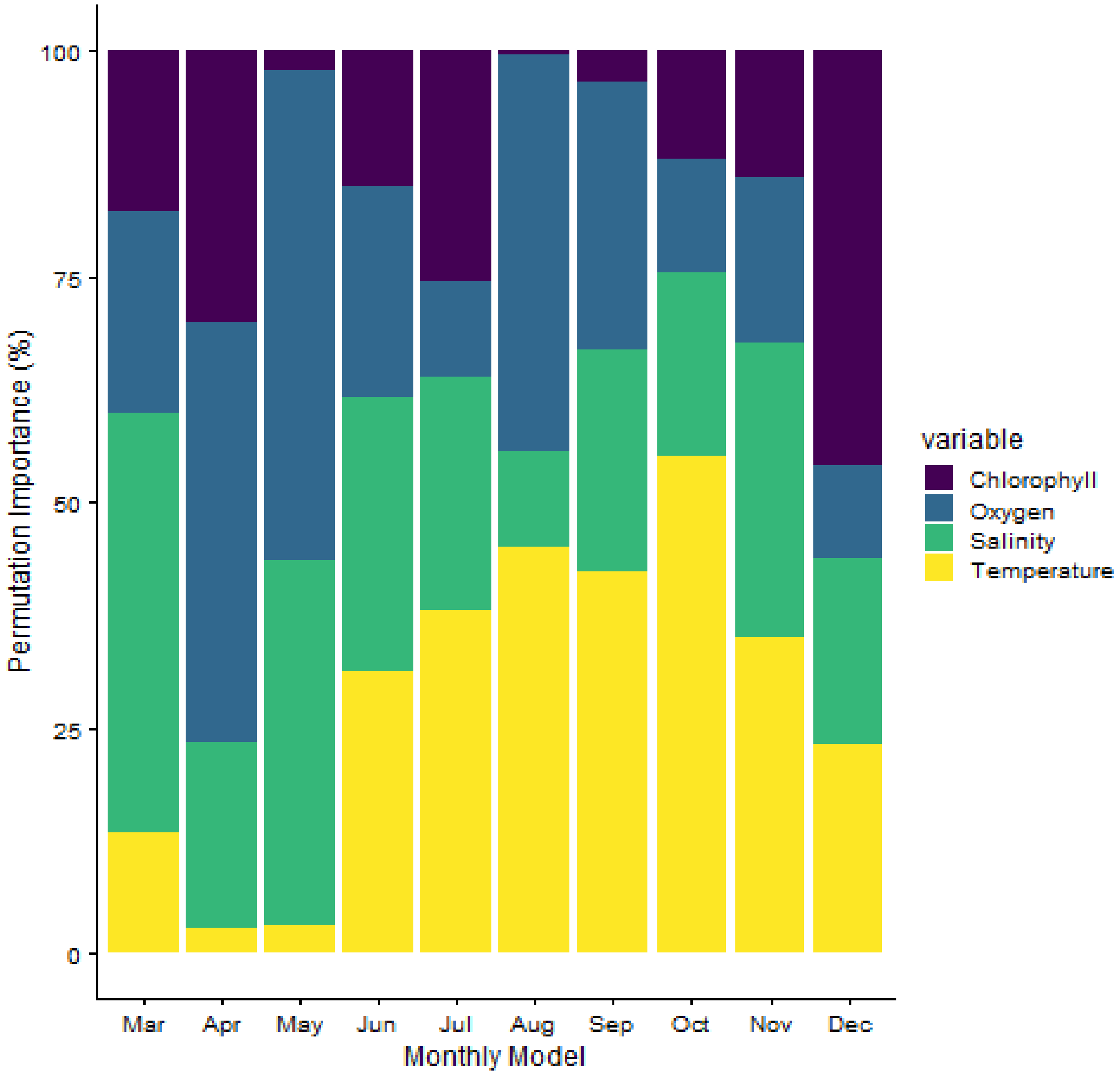


Figure C.5*: Permutation importance for each of the monthly Maxent models.*

C.6: Metrics

A: Species Distribution Model Evaluation Metrics

To evaluate each of the monthly model's performance, I used five metrics – Testing AUC, Training AUC, True Skill Statistic, Continuous Boyce Index, and Symmetric Extremal Dependence Index. I used the following R packages to calculate the performance metrics:

- AUC test and training, and TSS: Dismo (Hijmans et al. 2017).
- CBI and SEDI: enmSdm (Smith 2019).

C.6.A1: Testing and Training AUC

Testing and training Area Under the Curve (AUC) indicates the probability that a randomly chosen presence location ranks higher in suitability than a randomly chosen background point. Scores are derived from receiver operator characteristic (ROC) analysis and are independent of threshold (Phillips et al. 2006). Values range from 0 to 1. Values closer to 1 indicate the discriminatory power is good, whereas values close to and less than 0.5 indicate discriminatory power is poor (Fielding & Bell 1997).

$$AUC = \frac{1}{n_A * n_N} \sum_{1}^{n_A} \sum_{1}^{n_N} S(TP, FP)$$

Equation C.6.A1: Area Under the Curve (AUC) scores. Both the testing and training AUC scores are calculated in the same manner but test different subsections of the data (testing and training datasets, respectively). n_A *= number of presences;* n_N *= number of absences;* TP *= number of true presences predicted by the model;* FP *= number of false presences predicted by the model. The value of* S *is conditional: If* $TP > FP, S = 1$*; If* $TP = FP, S = 0.5$*; If* $TP < FP, S = 0$*. (Vida 1993).*

C.6.A2: True Skills Statistic

The true skill statistic (TSS) indicates the extent to which observed and predicted values are higher than expected by chance (Allouche et al. 2006). It is a function of sensitivity (the probability of a model correctly predicting a presence) and specificity (the probability of a model correctly predicting an absence). Values range from -1 to +1, with scores of +1 indicating perfect agreement, zero indicating no better than chance, and less than zero indicating performance is worse than chance.

$$Sensitivity = \frac{TP}{TP + FA}$$

$$Specificity = \frac{TA}{FP + TA}$$

$$TSS = sensitivity + specificity - 1$$

Equation C.6.A2: The true skill statistic (TSS), where TP = the number of presences accurately predicted; FP = the number of presences falsely predicted (type 1 error); TA = the number of absences accurately predicted; FA = the number of absences falsely predicted (type 2 error).

C.6.A3: Continuous Boyce Index

The Continuous Boyce Index (CBI) (Boyce et al. 2002) indicates the degree to which model predictions differ from random over a moving window. It is independent of threshold and prevalence. Values range from -1 to +1, with scores of +1 indicating perfect agreement, zero indicating no better than chance, and less than zero indicating performance is worse than chance.

$$P_i = \frac{p_i}{\sum_{j=1}^{b} p_j}$$

$$E_i = \frac{a_i}{\sum_{j=1}^{b} a_j}$$

$$F_i = \frac{P_i}{E_i}$$

Equation C.6.A3: The Continuous Boyce Index (CBI), where distribution ranges are subdivided into b bins. For each bin (i), both the predicted frequency of presence points (P_i) and the expected frequency of presence points if they were randomly distributed in the window (E_i) are calculated and then used to create a predicted-to-expected ratio (F_i). p_i = number of presence points predicted to fall into the distribution bin i; $\sum p_j$ = the total number of presence points; a_i = the number of grid cells belonging to distribution class i; $\sum a_j$ = the total number of cells.

C.6.A4: Symmetric Extremal Dependence Index (SEDI)

The Symmetric Extremal Dependence Index (SEDI) (Wunderlich et al. 2019) is a threshold-independent metric that benefits from reduced sensitivity to prevalence. Since it employs a low-confidence error-weighting to the background points, it is particularly suited to presence-background models. Values range from -1 to +1, with scores of +1 indicating perfect agreement, zero indicating no better than chance, and less than zero indicating performance is worse than chance.

$$SEDI = \frac{\log(F) - \log(H) - \log(1-F) + \log(1-H)}{\log(F) + \log(H) + \log(1-F) + \log(1-H)}$$

Equation C.6.A4: The Symmetric Extremal Dependence Index (SEDI), where H = sensitivity (hit rate); F = false positive rate.

B: Distribution metrics

I used two statistical tests to quantify differences in distributions between the two phases – the Mann-Whitney *U* test and Generalised Linear Mixed Model (GLMM), and one test (the Mann-Kendall trend test) to quantify any trends in the metrics time series. I used the following R packages to run the tests:

- Mann-Whitney U Test: rstatix (Kassambara 2020).
- Generalised Linear Mixed Model: lme4 (Bates et al. 2020) and MuMIn (Bartoń 2020).
- Mann-Kendall Trend test: Kendall (McLeod 2011).

The emerging hotspot analysis (ESRI 2020b) employs the Getis-Ord Gi* statistic and the Mann-Kendall Trend test.

C.6.B1: Mann-Whitney U Test

The Mann-Whitney *U* test is a non-parametric test that assesses if the median of two groups are equal. It is suitable for small sample sizes and independent samples. The effect size is calculated as $Z/\sqrt{N}$, with *Z* being the standardised U score and *N* corresponding to the total sample size. Effects sizes less than 0.3 are considered to have a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect.

$$U_1 = R_1 - \frac{n_1(n_1+1)}{2}$$
$$U_2 = R_2 - \frac{n_2(n_2+1)}{2}$$

Equation C.6.B1: The Mann-Whitney U test, where R = Sum of ranks; n = sample size.

C.6.B2: Generalised Linear Mixed Model

The Generalised Linear Mixed Model (GLMM) is an extension of the linear model that includes fixed and random effects.

$$Y_{si} = (\beta_0 + S_{0s}) + \beta_1 X_i + e_{si}$$

Equation C.6.B2: Generalized Linear Mixed Model, where Y = response variable (the distribution metric); S = subject (the month-model), i = item; β_0 *= intercept;* β_1 *= slope;* X_i *= independent variable (the NAO value);* e_{si} *= observation-level error.*

C.6.B3: Mann-Kendall Trend Test

The Mann-Kendall Trend test (Kendall & Gibbons 1990) is a rank correlation test between ranked observations and their order in a time-series. For a time series, the test statistic (*S*) is given by

$$S = \sum_{i<j} a_{ij}$$

where

$$a_{ij} = \operatorname{sign}\left(x_j - x_i\right) = \operatorname{sign}\left(R_j - R_i\right) = \begin{cases} 1 & x_i < x_j \\ 0 & x_i = x_j \\ -1 & x_i > x_j \end{cases}$$

Equation C.6.B3: The Mann-Kendall Trend test, where R_i *and* R_j *= ranks of observations or observations* x_i *and* x_j*. Values range from 0 to +1/-1 (positive/negative relationship), with scores of +1/-1 indicating a perfect relationship and 0 no relationship.*

C.6.B4: Getis-Ord Gi statistic*

The Getis-Ord Gi* statistic (Getis & Ord 1992) determines where features with low or high values spatially cluster within the context of its neighbouring features.

$$G_i^* = \frac{\sum_{j=1}^{n} w_{i,j} x_j - \bar{X} \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\frac{\left[n \sum_{j=1}^{n} w_{i,j}^2 - \left(\sum_{j=1}^{n} w_{i,j} \right)^2 \right]}{n-1}}}$$

and

$$\bar{X} = \frac{\sum_{j=1}^{n} x_j}{n}$$

$$S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - (\bar{X})^2}$$

Equation C.6.B4: The Getis-Ord Gi statistic, where* x_j *is the attribute value for feature* j, $w_{i,j}$ *is the spatial weight between feature* i *and* j *is equal to the total number of features.*

C.7: Emerging Trend Analysis

The emerging hotspot analysis (ESRI 2020b) identifies statistically significant trends in habitat hotspots (high habitat suitability scores) and cold spots (low habitat suitability scores) over the time series for which there is data. Cells in the study area are assigned one of seventeen temporal state categories (Figure C.7). To avoid the output becoming unwieldy, I only considered those areas with a statistically significant trend and focused on three temporal trend patterns: sporadic, intensifying, and diminishing.

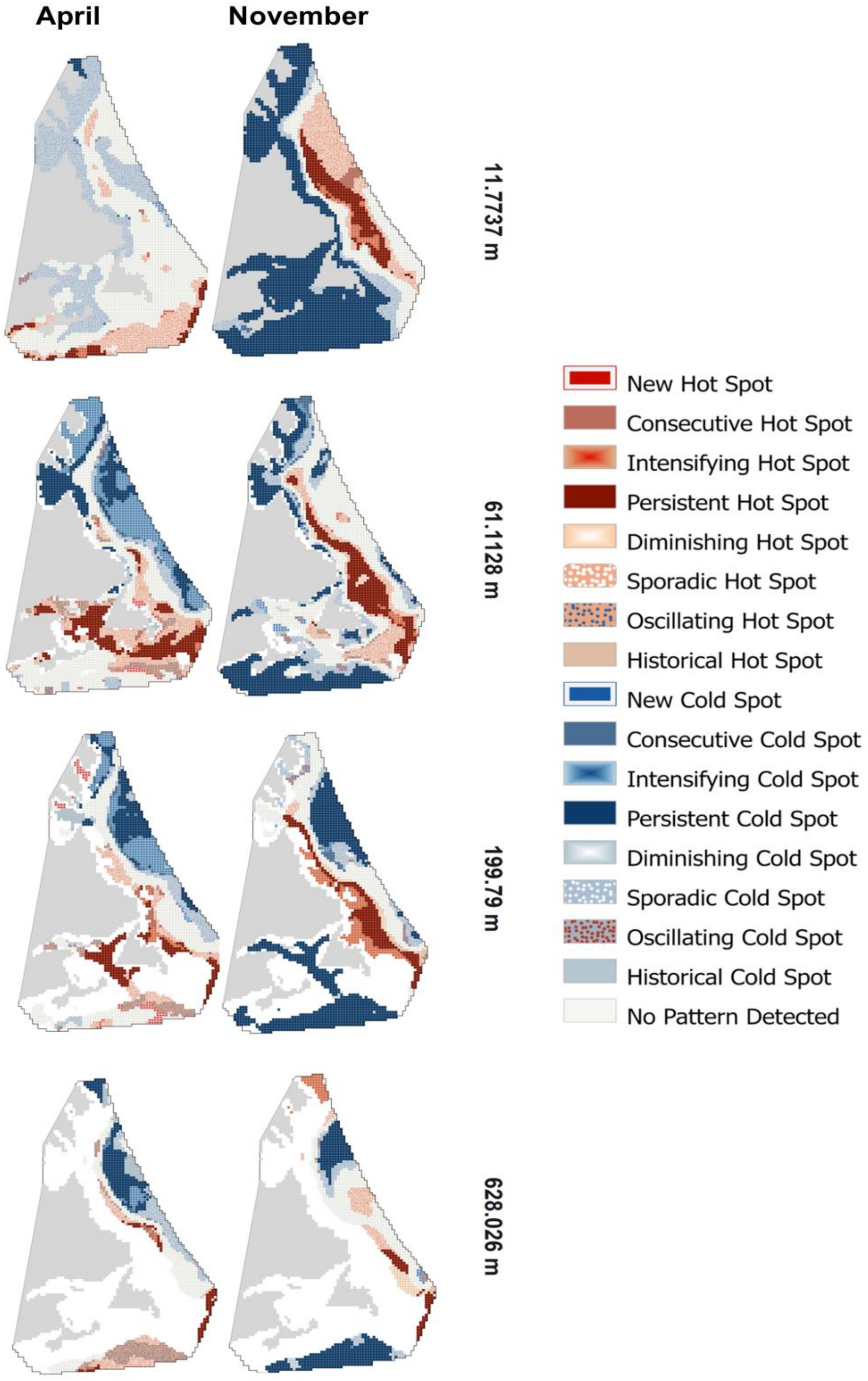


Figure C.7*: Example of the emerging hotspot analysis for April and November across four depths levels. The month and depths have been arbitrarily chosen for illustrative purposes only.*

C.8: Distribution Metric Boxplots & Mann-Whitney Effect Sizes

I assessed distribution changes between the positive and negative phase of the NAO using five commonly used metrics – the percentage of the study area predicted as suitable habitat (Figure C.8.1 and Table C.8.1), the stability of suitable habitat cells (Figure 3.4 and Table 3.3 in the main text), suitable habitat patch number (Figure C.8.2 and Table C.8.2) and size (mean – Figure C.8.3 and Table C.8.3, and maximum - Figure C.8.4 and Table C.8.4), and bounding location (northern/southern – Figure C.8.5 and Table C.8.5, western/eastern – Figure C.8.6 and Table C.8.6, shallowest/deepest – Figure C.8.7 and Table C.8.7).

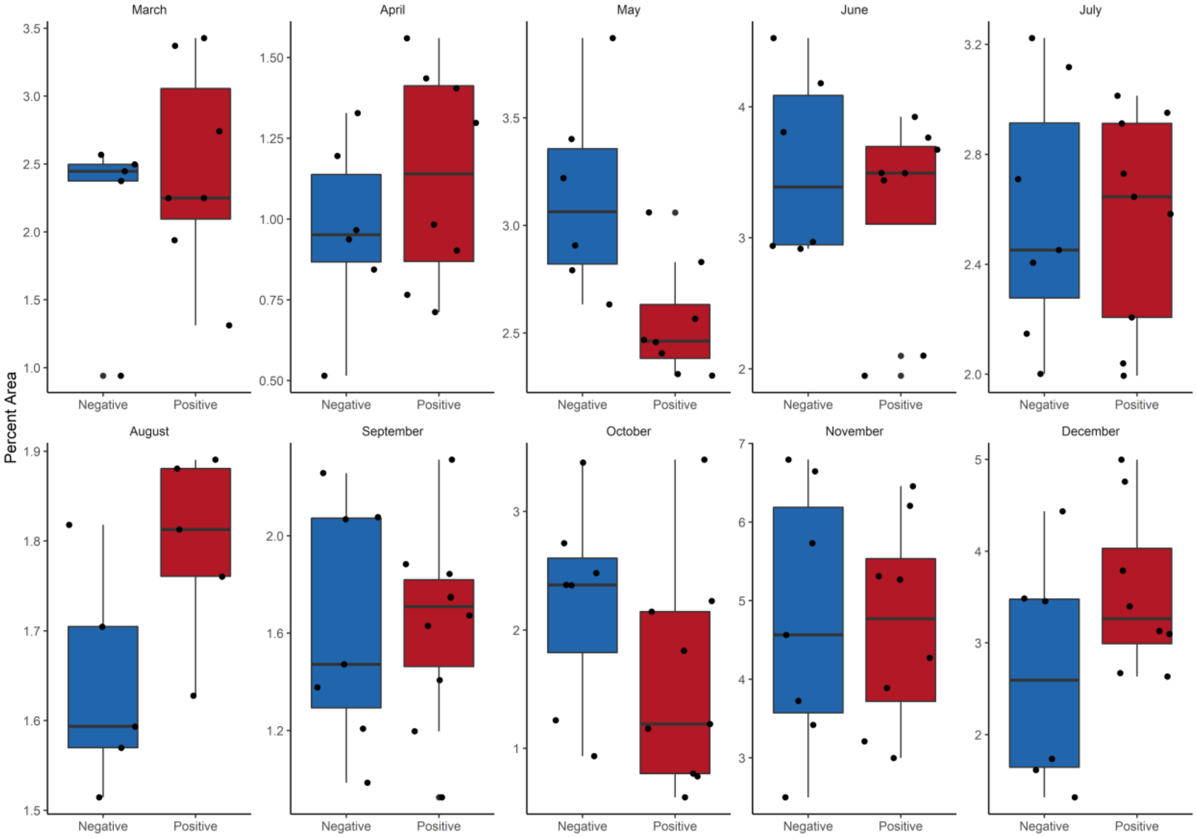


Figure C.8.1: *The percentage of the study area predicted as suitable habitat in the negative and positive phases of the NAO for each month. Dots indicate the value for individual years.*

Table C.8.1*: Mann-Whitney effect sizes for the percentage of the study area predicted as suitable habitat in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect.*

Month	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
March	0.07	Small	0 – 0.66
April	0.24	Small	0.02 – 0.67
May	0.66	Large	0.25 – 0.84
June	0.17	Small	0 – 0.67
July	0.17	Small	0 – 0.69
August	0.17	Small	0 – 0.69
September	0.00	Small	0 – 0.61
October	0.44	Moderate	0.04 – 0.82
November	0.06	Small	0 – 0.62
December	0.28	Small	0.02 – 0.71

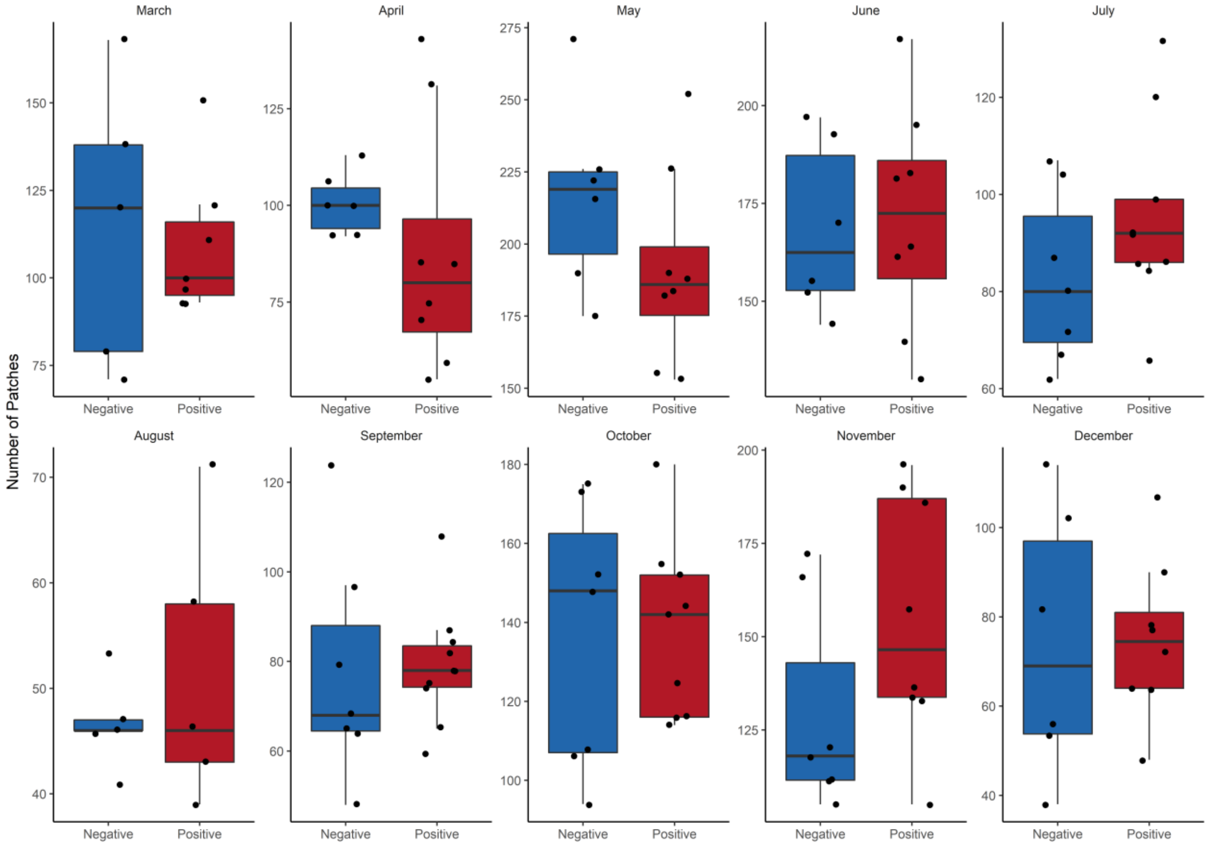


Figure C.8.2*: Number of suitable habitat patches per month by NAO phase. Points represent the value for each year modelled.*

***Table C.8.2**: Mann-Whitney effect sizes for the number of suitable habitat patches in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect.*

Month	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
March	0.02	Small	0 - 0.74
April	0.42	Moderate	0 - 0.85
May	0.35	Moderate	0.02 - 0.77
June	0.03	Small	0 - 0.61
July	0.28	Small	0.01 - 0.71
August	0.03	Small	0 - 0.76
September	0.13	Small	0.01 - 0.64
October	0.40	Moderate	0.03 - 0.8
November	0.03	Small	0 - 0.63
December	0.42	Moderate	0 - 0.85

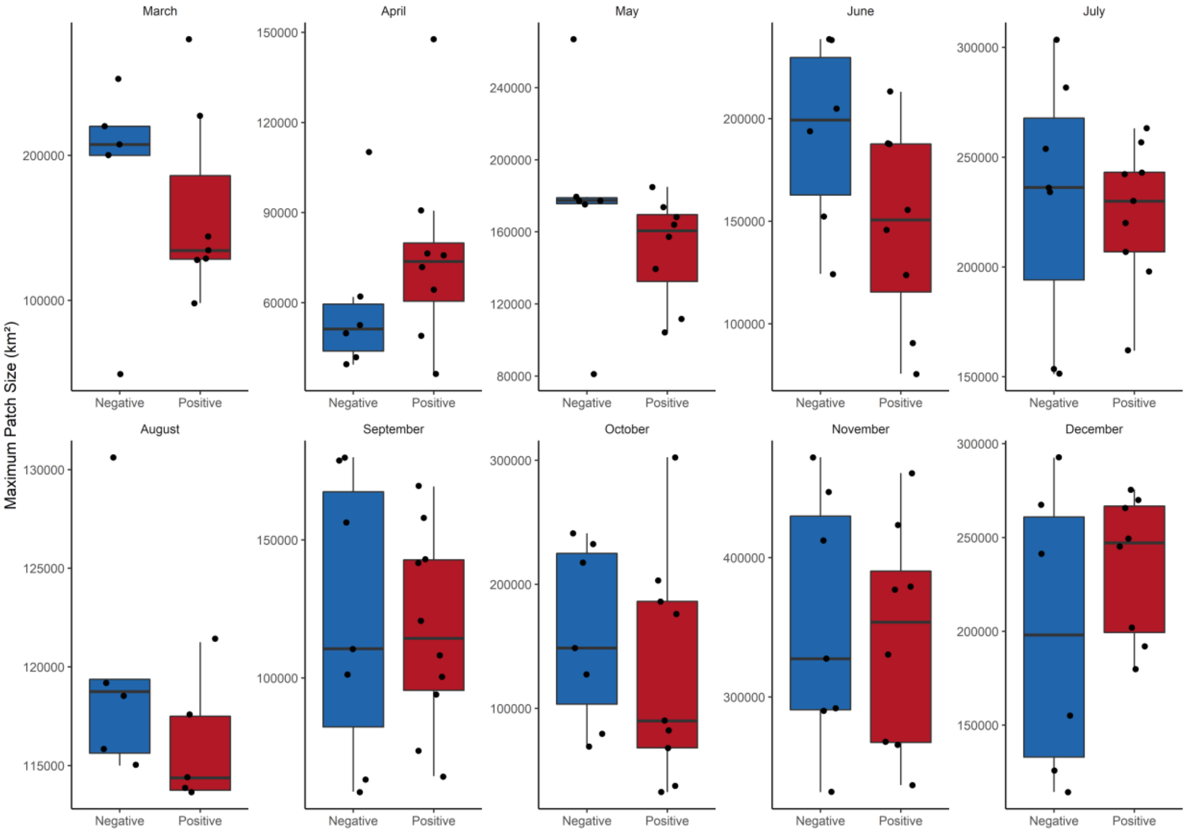


***Figure C.8.3**: Maximum size of patches per month by phase. Points represent values in each year modelled.*

***Table C.8.3**: Mann-Whitney effect sizes for the maximum patch size in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect.*

Month	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
March	0.16	Small	0 - 0.79
April	0.31	Moderate	0.02 - 0.81
May	0.41	Moderate	0.02 - 0.84
June	0.45	Moderate	0.03 - 0.81
July	0.09	Small	0.01 - 0.65
August	0.09	Small	0.01 - 0.65
September	0.05	Small	0 - 0.6
October	0.22	Small	0 - 0.68
November	0.06	Small	0 - 0.61
December	0.24	Small	0 - 0.73

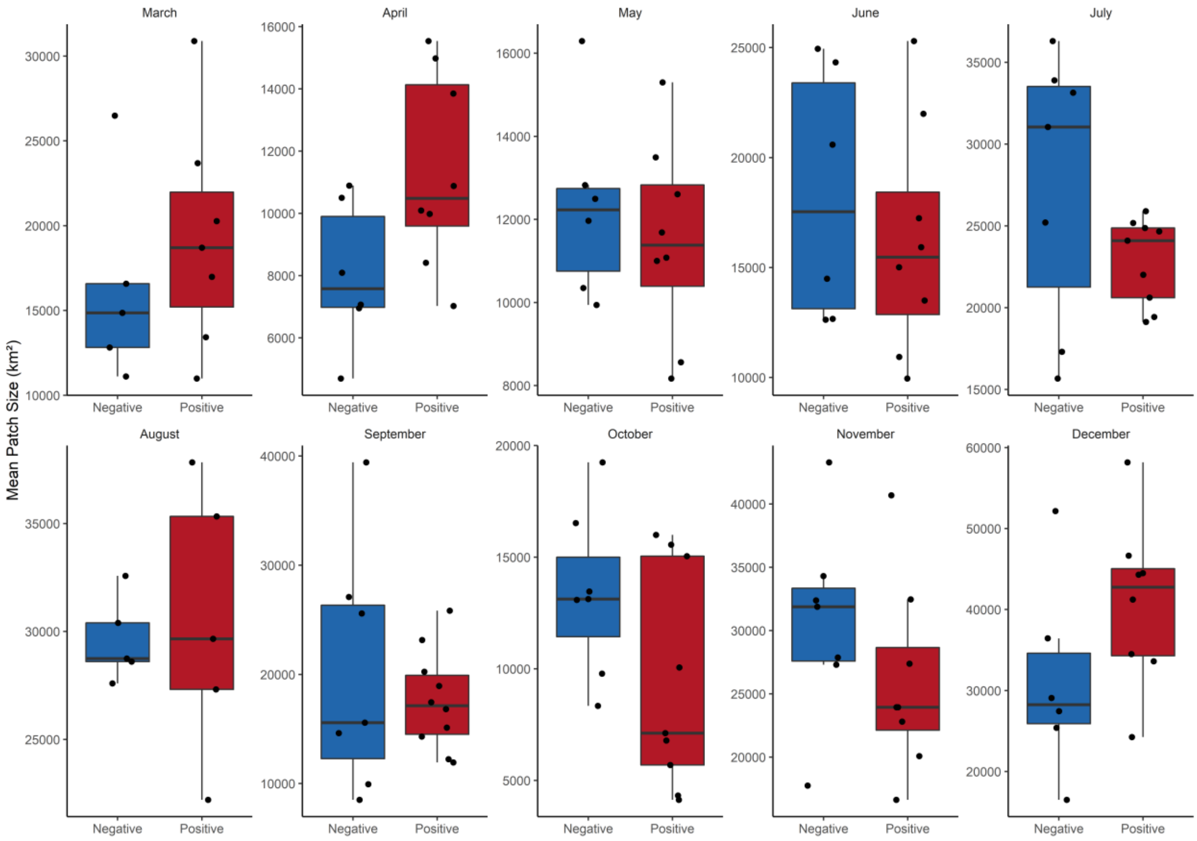


***Figure C.8.4**: Mean size of patches per month by phase. Points represent values in each year modelled.*

Table C.8.4: *Mann-Whitney effect sizes for the mean patch size in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect.*

Month	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
March	0.26	Small	0.0006 - 0.8
April	0.45	Moderate	0.07 - 0.81
May	0.14	Small	0 - 0.6
June	0.10	Small	0 - 0.63
July	0.33	Moderate	0 - 0.82
August	0.03	Small	0 - 0.83
September	0.02	Small	0 - 0.67
October	0.38	Moderate	0.01 - 0.76
November	0.33	Moderate	0.03 - 0.74
December	0.38	Moderate	0.02 - 0.81

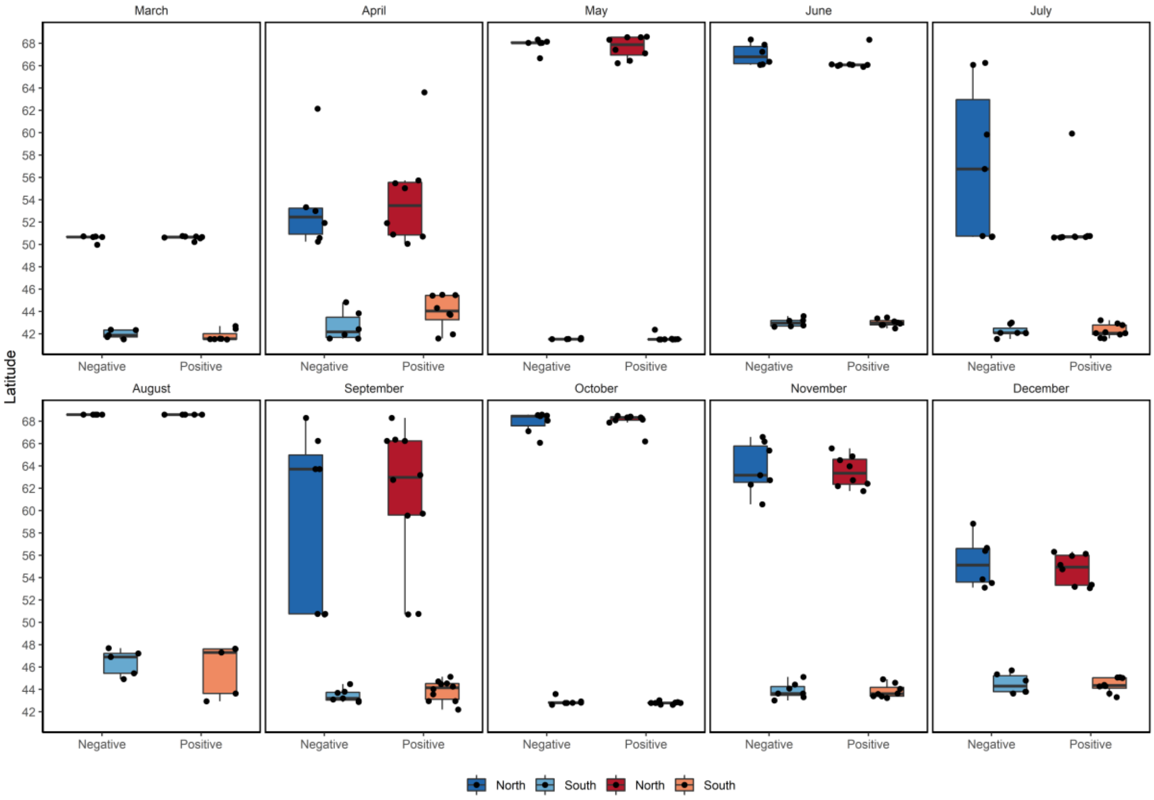


Figure C.8.5: *Location of the northern and southern bounding for each month by phase. Points represent values for each year modelled.*

Table C.8.5*: Mann-Whitney effect sizes for the northern and southern boundings in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect. NA = no difference in the values.*

Metric	**Month**	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
Northern Bounding	March	0.02	Small	0 - 0.64
	April	0.10	Small	0 - 0.63
	May	0.03	Small	0 - 0.61
	June	0.51	Large	0.06 - 0.84
	July	0.47	Moderate	0.04 - 0.78
	August	NA	NA	NA
	September	0.05	Small	0 - 0.56
	October	0.17	Small	0 - 0.7
	November	0.15	Small	0 - 0.66
	December	0.24	Small	00.73
Southern Bounding	March	0.16	Small	0 - 0.79
	April	0.40	Moderate	0.02 - 0.77
	May	0.31	Moderate	0.02 - 0.75
	June	0.03	Small	0.02 - 0.66
	July	0.07	Small	0 - 0.57
	August	0.03	Small	0 - 0.77
	September	0.26	Small	0.02 - 0.67
	October	0.18	Small	0.01 - 0.64
	November	0.06	Small	0.02 - 0.61
	December	0.09	Small	0.02 - 0.63

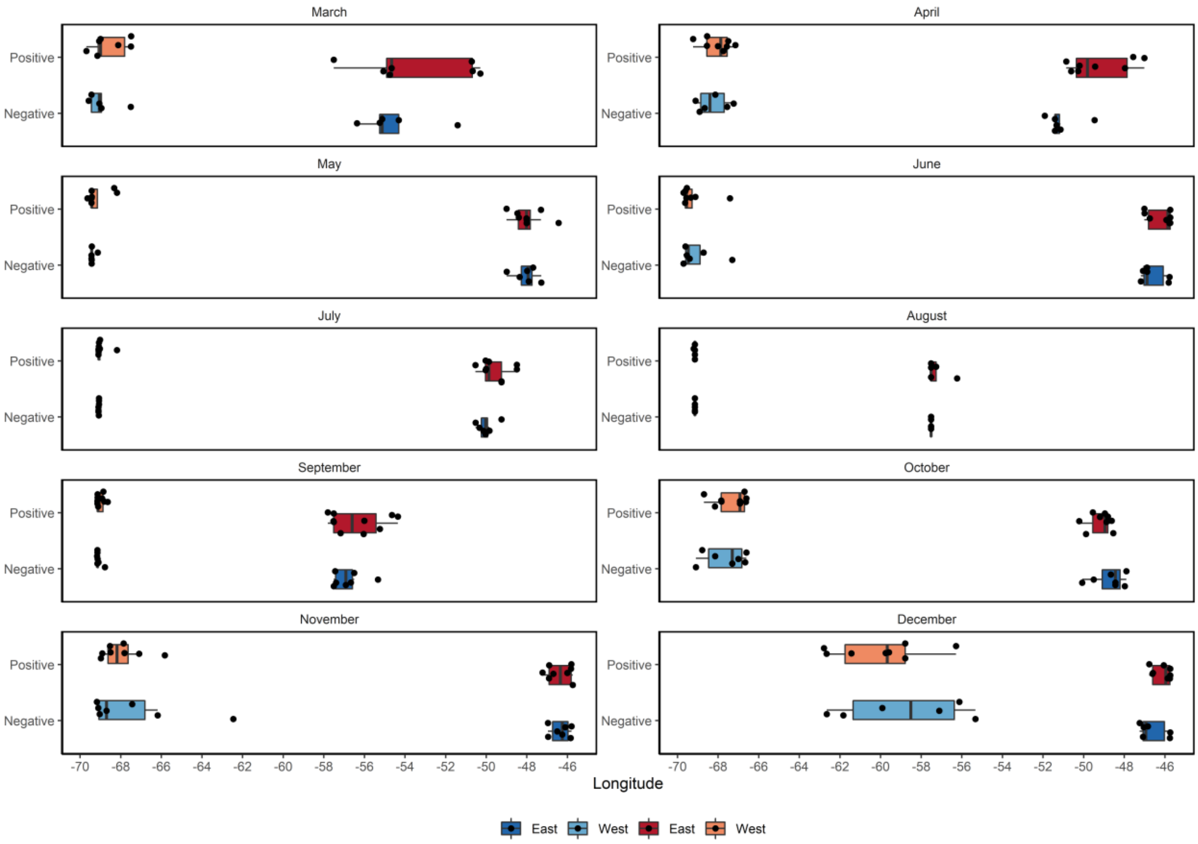


Figure C.8.6*: Location of the western and eastern bounding for each month by phase. Points represent values for each year modelled.*

Table C.8.6*: Mann-Whitney effect sizes for the western and eastern boundings in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect. NA = no difference in the values*.

Metric	**Month**	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
Western Bounding	March	0.16	Small	0 - 0.66
	April	0.17	Small	0 - 0.68
	May	0.02	Small	0 - 0.58
	June	0.14	Small	0 - 0.67
	July	0.24	Small	0.01 - 0.66
	August	NA	NA	NA
	September	0.33	Moderate	0.02 - 0.71
	October	0.16	Small	0.01 - 0.63
	November	0.15	Small	0 - 0.69
	December	0.21	Small	0 - 0.69
Eastern Bounding	March	0.30	Moderate	0 - 0.8
	April	0.69	Large	0.3 - 0.84
	May	0.17	Small	0.02 - 0.67
	June	0.38	Moderate	0.02 - 0.77
	July	0.39	Moderate	0.03 - 0.77
	August	NA	NA	NA
	September	0.04	Small	0 - 0.52
	October	0.41	Moderate	0.04 - 0.79
	November	0.06	Small	0 - 0.56
	December	0.40	Moderate	0.02 - 0.84

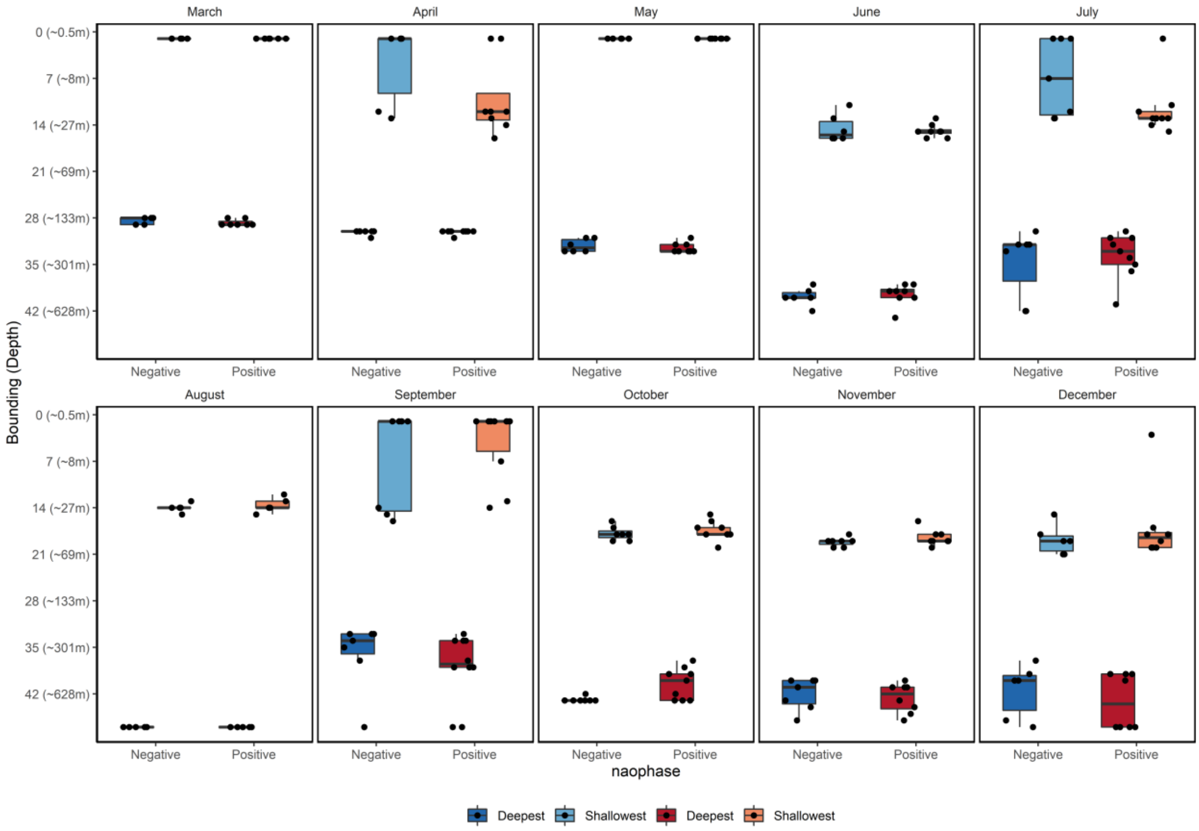


Figure C.8.7*: Location of the shallowest and deepest bounding for each month by phase. Points represent values for each year modelled. To avoid compression of the boxplots, the y-axis uses the depth layer number, with the corresponding depth in meters indicated.*

Table C.8.7*: Mann-Whitney effect sizes for the shallowest and deepest boundings in the negative and positive phases of the NAO for each month. Effect size magnitudes less than 0.3 are considered to be a small effect, 0.3 – <0.5 a moderate effect, and => 0.5 a large effect. NA = no difference in the values.*

Metric	**Month**	**Effect Size**	**Magnitude**	**Confidence Interval (95%)**
Shallowest Bounding	March	NA	NA	NA
	April	0.40	Moderate	0.04 - 0.78
	May	NA	NA	NA
	June	0.05	Small	0.02 - 0.66
	July	0.45	Moderate	0.04 - 0.78
	August	0.18	Small	0 - 0.72
	September	0.24	Small	0.01 - 0.68
	October	0.19	Small	0.01 - 0.65
	November	0.29	Small	0.02 - 0.68
	December	0.18	Small	0.02 - 0.69
Deepest Bounding	March	NA	NA	NA
	April	0.06	Small	0 - 0.53
	May	0.17	Small	0 - 0.7
	June	0.20	Small	0.02 - 0.65
	July	0.05	Small	0 - 0.59
	August	NA	NA	NA
	September	0.33	Moderate	0.01 - 0.73
	October	0.56	Large	0.19 - 0.83
	November	0.20	Small	0 - 0.66
	December	0.20	Small	0.02 - 0.69

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Appendix D: Abstract for Peller T, Andrews S, Leroux SJ, Guichard F (2020)

Peller T, Andrews S, Leroux SJ, Guichard F (2020) From Marine Metacommunities to Meta-ecosystems: Examining the Nature, Scale and Significance of Resource Flows in Benthic Marine Environments. Ecosystems. https://doi.org/10.1007/s10021-020-00580-x

The metacommunity framework has been readily applied to coastal benthic marine environments to examine how larval dispersal affects the dynamics of patchily distributed communities. Transitioning to a meta-ecosystem perspective requires knowledge of interactions between living and non-living compartments occurring across scales in these environments. Here, we synthesize and analyze evidence of non-living resource flows in coastal benthic marine environments. Our objectives are to establish the types of benthic ecosystems that are coupled by resource flows, the spatial scale and directionality of the couplings, and the magnitude of resulting subsidization of recipient organisms. We find that resource flows commonly couple different types of coastal benthic ecosystems and can occur bidirectionally between ecosystems. Our quantitative synthesis yields a frequency distribution of resource flow distance, which suggests they frequently couple ecosystems across smaller distances than larval dispersal and that the probability of resource flows coupling benthic ecosystems decreases exponentially with distance between ecosystems. The magnitude of subsidization of recipient organisms also decreases with distance from the source of the resource flow. Our findings reveal that considering ecosystem heterogeneity and the respective scales of different types of spatial flows will be an important component of extending the marine metacommunity framework to metaecosystems. We propose an avenue for integrating ecosystem heterogeneity into meta-ecosystem theory, based upon general differences in functioning across coupled ecosystems revealed by our synthesis, and we argue for the development of a hierarchical meta-ecosystem theory.