

Drivers of variation in the predator-prey interaction between cod and capelin in the Barents Sea



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Thesis for the degree of Philosophiae Doctor (PhD)
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Scientific environment

The work in this thesis was carried out from 2015 to 2019 at the Institute of Marine Research, Ecosystem processes research group, and at the University of Bergen, Theoretical ecology group. The candidate also visited the College of Earth, Ocean, and Atmospheric Sciences at Oregon State University, and the Department of Ecology and Environmental Science at Umeå University. The work was funded by the Research Council of Norway through the project CODFUN (grant number 243676/E40).



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Summary

Cod (*Gadus morhua*) and capelin (*Mallotus villosus*) are commercially important species with key roles in the Barents Sea ecosystem. Cod is a major predator on capelin, and fluctuations in the capelin stock has influenced growth and reproduction of cod. Cod-capelin population dynamics are central to the fisheries management of capelin and play an important role in ecosystem models and assessments. The cod-capelin interaction has mainly been studied at population level, but variation at smaller scales can have a large influence on population-level processes. In this thesis, I aimed to quantify and explain spatial and temporal variation in the cod-capelin interaction at different scales, with a focus on spatial overlap and consumption. The work combines theoretical modelling with statistical analyses of survey data collected over 12 years in late summer and winter.

In **Paper 1**, we develop optimal foraging models to study individual-level mechanisms of cod prey selection and show that capelin is the most profitable of cod's many prey species. Under assumptions of active prey search and homogeneous prey distributions, the models predict selective feeding on capelin at a rate that is limited by cod's digestion rather than prey encounter. However, a comparison with field data revealed that cod's feeding on capelin varies considerably between individuals. In **Paper 2**, we analyse cod-capelin spatial distributions with spatially explicit statistical models and identify the main overlap areas in late summer and winter. We find that cod has a weak aggregative response to capelin in both seasons, and that increasing population sizes and water temperatures have influenced a northward shift in the late summer overlap area. In **Paper 3**, we use statistical models to analyse cod stomach data from the overlap area in late summer. We find that a large proportion of the population-level diet is capelin, but individual consumption is highly variable. Variation in capelin density alone cannot explain variation in cod feeding since cod's functional response to capelin quickly reaches saturation. In contrast, the vertical distribution of capelin strongly influences variation in cod feeding, especially at the Great and Central banks where the main feeding interaction takes place during daylight.

List of Publications

- Fall, J., Fiksen, Ø. (*In prep*). No room for dessert: a mechanistic model of prey selection in gut-limited predatory fish. (*Submitted to Fish and Fisheries, in review*)
- Fall, J., Ciannelli, L., Skaret, G. & Johannesen, E (2018). Seasonal dynamics of spatial distributions and overlap between Northeast Arctic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) in the Barents Sea. PLOS ONE 13(10): e0205921. doi: 10.1371/journal.pone.0205921
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1. Introduction

1.1 Variation in nature

Variation is a defining characteristic of natural systems. In time and space, between and within individuals, variation facilitates coexistence (Costa-Pereira et al. 2018), influences the rise and fall of populations (Schreiber et al. 2011), and ultimately forms the foundation of evolution by natural selection (Darwin 1859). Variation exists in all aspects of an animal's life, but in ecological research, our need to understand the dynamics of entire populations have required simplification of individual complexity (Bolnick et al. 2011). For example, in the field of population dynamics where a central challenge is to explain the persistence of species, many classic models assume that all individuals respond equally to their environment (Murdoch et al. 2003).

All animals are connected to other animals through consumer-resource interactions such as parasitism, grazing, and predation. When these interactions vary between individuals, habitats, or subpopulations, the overall consumer-resource dynamics derived from assumptions of individual similarity may not be true to nature (Chesson 1984, Englund and Leonardsson 2008, Bolnick et al. 2011). Individual variation may increase the resilience of populations to environmental change and promote ecosystem stability, suggesting that management systems may benefit from measures that promote diversity in genetic, behavioural and physiological traits (Ward et al. 2016).

The environments in which animals live vary as well. On the ocean floor, predators and prey interact among stones, seamounts, mud and crevasses that offer hiding places or attract predators to fertile hunting grounds. But the aquatic habitat does not end here; some animals spend their entire lives in the water column. At first glance, this habitat appears homogeneous, but it is often spatially structured by water currents, fronts and aggregations of planktonic organisms (Pittman et al. 2011). Prey species in the water column rely on clever methods of predator avoidance, such as

migrating deeper into darker environments during the day, aggregating in large groups, or camouflaging themselves with colour, transparency or counter-shading (Pitcher and Parrish 1993, Verity and Smetacek 1996). In temperate and polar regions, aquatic animals are exposed to seasonal changes in temperature, salinity, light, or ice-cover. Many animals also migrate over large distances during their lifetime to breed or to find better feeding grounds (Fauchald et al. 2006, Rasmussen et al. 2007). Thus, marine habitats are three-dimensional, dynamic environments where variation in predator-prey interactions and physical properties occur over a vast range of spatial and temporal scales.

Estimates of predator-prey interaction strength has become increasingly important for several fields of research, including ecosystem modelling (Metcalf et al. 2008, Pedersen et al. 2008), climate impacts on species and communities (Vucic-Pestic et al. 2011, Killen et al. 2013), and multispecies and ecosystem approaches to fisheries management (Bogstad and Gjørseter 2001, Ward et al. 2016, Deroba 2018). Therefore, a central task in ecology is to identify and quantify drivers of variation in predator-prey interactions.

1.2 Three perspectives on predator-prey interactions

1.2.1 Foraging theory: the behavioural responses of individuals to their environment

“...no animal, of course, has faultless judgement.” (Emlen, 1966)

Most animals have a favourite prey, one that they would always try to capture and eat if they come across it. But what if this prey is rare or other prey becomes more abundant? Which potential prey should be ignored at an encounter? These are core question in diet theory and was the very start of foraging theory (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Werner and Hall 1974, Charnov 1976). Foraging theory is a branch of behavioural ecology that aims to

explain and predict the outcome of consumer-resource interactions from mechanisms underlying the predation process.

A central assumption in traditional foraging theory, also called Optimal Foraging Theory (OFT), is that predators possess the necessary information and abilities to behave optimally when feeding, something, the theory postulates, that is favoured by natural selection. OFT is based on cost-benefit analyses derived from the field of economy. The profitability of prey is quantified in terms of potential energy gain per unit handling time, i.e., the time cost of pursuing, attacking and consuming a prey, and it is predicted that prey should be ignored at encounter if the predator would gain more energy from searching for and capturing better prey. Early OFT models successfully predicted the diet of a variety of species, including fish, e.g., bluegill (*Lepomis macrochirus*, Centrarchidae) (Werner et al. 1981). However, there are many examples where OFT has failed to explain diets, notably for the three-spined stickleback (*Gasterosteus aculeatus*, Gasterosteidae) (Gill 2003, and references therein), and the prey size selection of many piscivorous fish (Juanes 1994).

A major limitation of simple optimality models is that natural selection works on several, often conflicting, traits and that selection pressure is variable in space and time, producing a diversity of phenotypes for a particular trait (Rosen et al. 2007, Giske et al. 2014). In addition, the assumption that a predator has perfect knowledge of its environment is rarely met, leading to suboptimal decisions (Andersen et al. 2016). This means that diets may vary between individuals that have different abilities to detect or handle specific prey, have different trade-offs between foraging and other needs, such as avoiding predators, or have different physiological requirements for specific nutrients (Araújo et al. 2011). The assumption that prey handling time limits feeding rate has also come into question, since many predators are limited by digestion rather than handling (Giske and Salvanes 1995, Hirakawa 1997, Jeschke et al. 2002). If the processing ability of the gut limits ingestion rate, predators could benefit from selecting prey that give high energy return per unit digestion time rather than handling time (Verlinden and Wiley 1989, Gill and Hart 1998).

While foraging has remained a central topic in ecology, the field has evolved from optimality towards individual- and trait-based models where environmental stochasticity, predator state and behavioural feedback loops affect decision-making (Kristiansen et al. 2009, Railsback and Harvey 2013). Nevertheless, OFT was a major step forward in ecology, and its predictions still have value for understanding the basic decisions that foraging animals make, which form the foundation for food web structure and function (Beckerman et al. 2006).

1.2.2 Spatial ecology: environmental constraints on species distributions and overlap

“Spatial patterns within a natural community, generated by a variety of extrinsic and intrinsic factors, clearly influence apparent and emergent aspects of that assemblage.” (Levin and Paine, 1974)

The field of spatial ecology studies the dynamic nature of animal distributions that arise from the numerous physical and biological trade-offs in animals and their interactions with other species. Compared to foraging theory, spatial ecology is a comparatively new field of study, especially in the marine environment (Taylor et al. 2002, Pittman et al. 2011, Bartolino et al. 2017). The field is rooted in older theories like the Ideal Free Distribution, which proposed that animals distribute to match their resources so that more productive habitats have more consumers than habitats with fewer resources (Fretwell and Lucas 1969). This theory assumes that the resource is unable to move in response to increased predation risk. In nature, many predators and prey are mobile and responsive, actively pursuing prey and avoiding being eaten.

Across the ocean landscape, or “seascape”, predator and prey overlap is affected by the presence of competing species, the location of suitable breeding areas, and variation in the physical environment that influence animal physiology. Any factor that affects prey or predator fitness can work as spatial anchor for the predator-prey interaction, restricting the spatial distribution of one or both species. In turn, this may influence the outcome of the behavioural response race, where predators try to

capture prey and prey try to avoid being eaten (Sih 2005). For example, if prey has a wider temperature tolerance than the predator, it may find refuge in habitats that the predator does not enter (Rose and Leggett 1990, Ciannelli and Bailey 2005). Prey generally has a higher incentive of winning the behavioural response race than the predator, since the alternative outcome means the end of its life (Dawkins and Krebs 1979). However, if predators are rare, prey may be more inclined to occupy habitats with higher predation risk, and if a successful meal is the only thing standing between a predator and certain death, predators and prey will be more evenly matched (Sih 2005).

Since the variation and complexity of ecological systems generally increase with increasing spatial scale (Englund and Cooper 2003), the patterns and processes that are detectable in studies depend on the spatial scale at which we view the system (Wiens 1989). The spatial scale also influences our perception of a predator-prey interaction (Sih 2005); at large spatial scales, predator and prey densities are often positively correlated and spatial anchors may stabilise species distributions over time. In other words, the predator overlaps with its prey and, in Sih's terminology, wins the behavioural response race. Zooming in on the interaction, we may discover that the spatial coherence of predator and prey gets weaker with decreasing scale, possibly because the predator has less to lose if it misses a feeding opportunity when another is close by. At scales approaching the individual feeding process, prey and predator densities will be negatively correlated if prey are successfully avoiding predators (Hammond et al. 2007), but also if predators deplete prey patches (Barraquand and Murrell 2013).

Thus, a main focus in spatial ecology is to understand drivers behind variation in species distributions and overlap, and its implications for ecological dynamics.

1.2.3 Predator-prey population dynamics: the rise and fall of populations

“The growth rate of a predator population depends not only on what individuals eat, but also on how they convert consumed prey into new predators.” (Abrams and Ginsburg, 2000)

Population dynamics describes changes in species abundance over time and relates the change to biological and physical processes. A population is said to reach equilibrium when its growth rate is balanced out by processes that prevent further increases in growth, such as density-dependent reductions in survival or reproductive output (Eberhardt 2002). The dynamics may be stable, meaning that once a population has reached equilibrium, it will return or oscillate around it after a perturbation (e.g., environmental change). In contrast, unstable dynamics occur when a perturbation causes the population to move away from its equilibrium (Murdoch et al. 2003).

Population dynamics models predict that the dynamics of a tightly linked predator-prey pair will oscillate, for example as a result of time lags between changes in the prey population and responses of the predator population (Murdoch et al. 2003). However, the oscillations may be dampened by density-dependence in growth and other vital rates, which tend to have stabilising effects on predator-prey interactions. Spatial heterogeneity, generalist feeding strategies, and individual diet variation may also contribute to decoupling and stabilising of predator-prey population dynamics (Murdoch et al. 2003, Gibert and DeLong 2015).

Predator-prey population dynamics can be described with the functional and numerical responses. The functional response is the average predator's consumption of prey in relation to prey density (Holling 1959), or in relation to the ratio of prey and predator densities (Abrams and Ginzburg 2000). Three basic forms of the response are described. In the type I functional response, consumption increases linearly with prey density, while in type II, consumption first increases linearly before

decelerating towards an asymptote as the predator reaches saturation due to handling or digestion limitation. The type III functional response describes the concept of prey switching, where the predator starts consuming prey above a density threshold. The numerical response is the change in predator density with prey density and can be divided into a demographic and an aggregative response (Solomon 1949, Readshaw 1973). The demographic response is the change in predator survival or reproductive output in response to changing prey density, while the aggregative response is the aggregation of predators in high-density prey patches (i.e., a positive spatial association).

Most population dynamics models assume that predator and prey individuals respond equally to each other, and that the response of the average individual therefore is representative of the population response. More recent developments in the field includes the use of individual-based models for evaluating sources of observed variability at population level (e.g., Hermann et al. 2001, Ospina-Alvarez et al. 2015, Radchuk et al. 2016), recognising that individual variation is a common feature of natural systems that can have substantial effects on estimates of population-level interaction strength (Gibert et al. 2015).

1.3 The predator-prey interaction between cod and capelin

Atlantic cod (*Gadus morhua*, hereafter cod) is a predatory fish endemic to the North Atlantic. Cod exhibits flexible behavior in terms of feeding, migration, reproduction, and social interaction, and its responses to environmental change vary both at the population and individual level (Meager et al. 2017). As a species, cod is a generalist feeder, with a diet reflecting local prey availability (Meager et al. 2017). In northern ecosystems with few species and strong trophic links, abundant cod populations can have profound effects on ecosystem structure and function (Link et al. 2009). For the three northernmost cod populations, the Northeast Arctic, Icelandic and Northern cod, the high-energy capelin (*Mallotus villosus*) is an important prey (Link et al. 2009). Capelin is a small pelagic fish that is a major forage species also for sea birds and marine mammals (Carscadden and Vilhjálmsson 2002). Due to high predation

pressure, a short lifespan, and climatic fluctuations, capelin populations fluctuate widely in abundance (Orlova et al. 2010, Carscadden et al. 2013).

This thesis is concerned with the interaction between cod and capelin in the Barents Sea. At present, this cod population (Northeast Arctic) is the largest in the world, supporting valuable fisheries on both immatures and spawners (Rose 2019). Barents Sea capelin is also fished, and mainly processed into fishmeal and oil. Cod is the most important predator on capelin after the larval stage (Dolgov 2002), and capelin makes up 10-60% of the cod population's diet depending on season and capelin abundance (Johannesen et al. 2016a). The cod and capelin populations are not only affected by each other, but also by fishing, environmental change, and the dynamics of other species (e.g., Hjermann et al. 2004, Ingvaldsen and Gjørseter 2013, Kjesbu et al. 2014, Gjørseter et al. 2015b). The capelin population has gone through several collapses and recoveries in the past decades, a pattern that is related to heavy predation on capelin larvae by strong year-classes of juvenile herring (*Clupea harengus*) in combination with high adult mortality from cod and harp seals (*Pagophilus groenlandicus*) (Gjørseter 1998, Stige et al. 2010, Gjørseter et al. 2015b, Solvang et al. 2018). Fluctuations in capelin abundance has in turn influenced the condition, growth, and reproduction of its predators, including cod (e.g., Marshall et al. 2000, Gjørseter et al. 2009).

After the 1980s capelin collapse caused ripple effects across several trophic levels, multispecies considerations were introduced in the fisheries management of capelin (Gjørseter et al. 2002). Specifically, estimates of mortality due to predation from cod was included in the assessment. The consumption of capelin by cod is estimated based on extensive stomach sampling of cod from different seasons, and assumptions about spatial overlap between the species (Bogstad and Gjørseter 2001, Tjelmeland 2005). It has long been recognised that the aggregated consumption estimate could be improved by including information about spatial and temporal variation in the cod-capelin interaction (Bogstad and Gjørseter 2001), but so far, the interaction has mainly been studied at population level (but see Strand and Huse 2007, Johannesen et al. 2012b).

1.4 The Barents Sea ecosystem

1.4.1 Area description

Beyond the northern coasts of Norway and Russia, the continental shelf stretches all the way to 81°N before plummeting into the Arctic Ocean. This shelf, bordered by Svalbard and the shelf edge in the west and Novaya Zemlya in the east, is the Barents Sea. Its northern parts are dominated by Arctic water masses, while Atlantic water flows in from the Norwegian Sea in the south-west (Fig. 1). The two water masses meet at the Polar front, forming strong temperature and salinity gradients. The northern Barents Sea is seasonally ice-covered, with maximum ice extent in April and minimum in September (Jakobsen and Ozhigin 2011). Seasonal changes in light conditions are also profound in the Arctic, ranging from polar night when the sun never rises to midnight sun when it does not set.

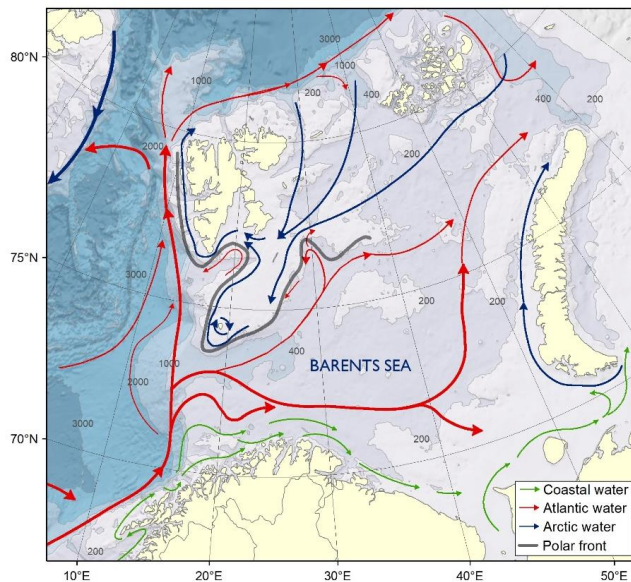


Figure 1: Main currents and bathymetry of the Barents Sea. Map created by Gjertsen and Ingvaldsen / Havforskningsinstituttet.

The seasonal variation in physical conditions is reflected in the biology; in late spring, phytoplankton bloom in the wake of the receding ice, in turn providing ample food for the zooplankton community that is dominated by copepods (*Copepoda*) and krill (*Euphausiacea*). The zooplankton support populations of planktivorous fish

throughout the summer feeding season, such as the resident capelin and polar cod (*Boreogadus saida*), and juvenile Norwegian spring-spawning herring that use the Barents Sea as a nursery area. At higher trophic levels, predatory fish and marine mammals take advantage of the increased production. The large gadoids cod, haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) are important predators on the pelagic fish together with marine mammals and sea birds (Olsen et al. 2010, Durant et al. 2014). When winter approaches and the area cools again, mobile animals move south to the ice-free areas of the Barents Sea, overwinter under the ice, or embark on long migrations to warmer oceans (Jakobsen and Ozhigin 2011). Both cod and capelin undertake long spawning and feeding migrations (Fig. 2). During winter and early spring, capelin migrate to the northern coasts of Norway

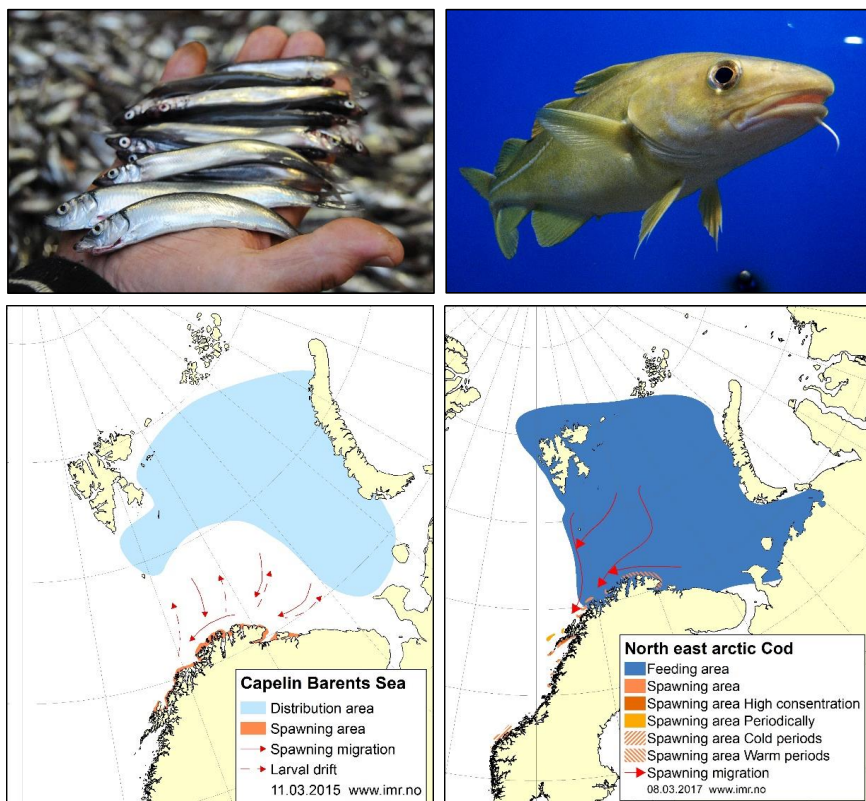


Figure 2: Distributions of capelin and cod in the Barents Sea. Maps by Horneland, Skulstad, and Gjertsen / Havforskningsinstituttet. Capelin image: Nøttestad / Havforskningsinstituttet. Cod image: *Portrait of Cod*. Linnman, 2011.

and Russia where the matures spawn in March-April. Capelin is short-lived, and most individuals die after their first spawning (Gjørseter 1998). Around the same time, mature cod migrate to their spawning grounds around the Lofoten islands in the Norwegian Sea, while immatures remain inside the Barents Sea (Bergstad et al. 1987). When summer comes, young and maturing capelin migrate northwards again to feed, reaching their northernmost distribution in September-October (Gjørseter 1998). The cod population is distributed over most of the Barents Sea shelf at this time of year, with high concentrations in the northern capelin distribution area and in the southeast (Bergstad et al. 1987).

The Arctic Barents Sea is currently undergoing one of the most rapid climatic changes on record (Lind et al. 2018), which has resulted higher water temperatures, reduced ice cover, and changes in the spatial distributions and interactions of many species (Johannesen et al. 2012a, Orlova et al. 2013, Kjesbu et al. 2014, Fossheim et al. 2015). To predict how the cod-capelin interaction and larger Barents Sea ecosystem may respond to further environmental change, it is urgent to know more about drivers of variation in trophic interaction strength.

1.4.2 Monitoring the ecosystem

Norway and Russia have a long history of scientific cooperation in the Barents Sea and have performed joint monitoring surveys since the 1960s (Eriksen et al. 2017). In 2003, several of the summer/autumn surveys were merged into one ecosystem survey that collects synoptic data on the abiotic environment and the distribution and abundance of species from several trophic levels. The primary goal of this survey is to measure the adult component of the capelin population for stock assessment, but the ecosystem data have also provided valuable insights on species distributions, interactions, and changes in the ecosystem (e.g., Fossheim et al. 2015, Johannesen et al. 2016b). In winter, another joint survey has run since 1981 with the goal of measuring the stocks of cod and haddock. This survey collects data on fewer ecosystem components than the ecosystem survey, but have been used to study trophic interactions of target (e.g., Johansen 2003, Johannesen et al. 2016a) and non-

target species (Fauchald and Erikstad 2002). Both surveys collect detailed information on the stomach contents of cod and other species.

2. Aim of the thesis and research questions

The aim of this thesis was to quantify and explain spatial and temporal variation in the cod-capelin interaction at different scales, with a focus on spatial overlap and consumption. The work explores the interaction from the perspectives of foraging theory, spatial ecology and population dynamics and covers spatial scales ranging from whole organism to seascape, temporal scales from seconds to a decade, and organisational scales from individuals to populations (Fig. 3).

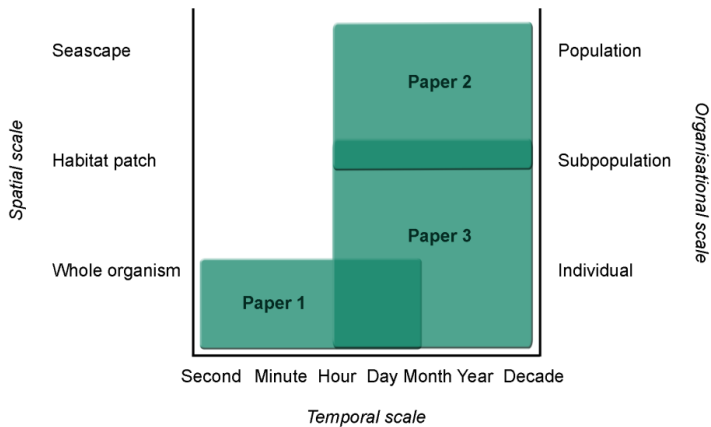


Figure 3: Range of spatial, temporal, and organisational scales at which aspects of the cod-capelin interaction was studied in the three papers of this thesis. Adapted from Horodysky et al. (2015).

In Paper 1 (**P1**), we developed optimal foraging models to study individual-level mechanisms of cod prey selection. The models incorporate limitations on feeding rate due to slow digestion, and consequences of this limitation for prey selection. The acts of searching for, ingesting and digesting prey occur on scales from seconds to days, and we study stable-state diets on the scale of months under the premise of energy maximisation. In relation to the cod-capelin interaction, the paper focuses on the following questions:

- ❖ *What is the relative profitability of capelin in relation to other prey?*

- ❖ *What is the optimal diet composition of cod from different models of prey selection?*
- ❖ *How is the optimal diet affected by capelin density?*
- ❖ *Do the optimal and observed diets differ, and if so, why?*

In Paper 2 (**P2**), cod and capelin species distributions were analysed with statistical models in relation to population sizes and environmental variables. Based on the distribution models, spatial overlap between the species was identified and quantified. The study is concerned with population level distributions based on two 12-year time series of monitoring data, one from late summer and one from winter. Variation in species densities was studied at a spatial mesoscale within the distribution areas (seascape, ~65 km), and variation between years, seasons, sampling days, and time of day was also considered. The research questions for this study were:

- ❖ *How does mesoscale variation in cod and capelin densities relate to abiotic and biotic factors?*
- ❖ *How does the spatial overlap between cod and capelin vary in space, between years, and between seasons?*
- ❖ *What factors drive variation in the overlap?*

Finally, in Paper 3 (**P3**), cod stomach data collected in the overlap area were analysed with statistical models to study biological and physical drivers of variation in cod's feeding on capelin. Here we zoomed in from population level to the part of the cod population that can potentially interact with capelin, looking at local (habitat patch, ~2 km) scale drivers of variation in individual cod feeding. Specifically, the following question was asked:

- ❖ *How is cod's consumption of capelin, the individual diet breadth, and the between-individual diet variation affected by the local biological and physical environment?*

3. Integrating perspectives from foraging theory, spatial ecology and population dynamics: what have we learned about the cod-capelin interaction?

3.1 The optimal diet for cod: is capelin a preferred prey?

Capelin has little competition as the most profitable prey for cod, as it has a higher caloric content and is digested faster than other prey species (**P1**). The average capelin density in the northern Barents Sea appears to be high enough for cod to feed on this prey only (**P1**), but the amount of capelin eaten varies widely between individuals and the average cod eats less capelin than predicted from the foraging models (**P1**, **P3**). This is not surprising since the availability of capelin varies in time and space (**P2**, **P3**), while the foraging model depicts an idealised environment where prey encounter rates are constant, and cod is assumed to engage in active prey search. The cod population feeds on a variety of other prey species (Dolgov et al. 2011, Johannesen et al. 2016a), but capelin nevertheless dominated the diets of most cod that had managed to feed on this prey in the overlap area (Fig. 4 a). The capelin-feeders also had a higher total consumption than those feeding on other prey (Fig 4 b). The “all or nothing” consumption of capelin likely reflects a stochastic prey encounter process with a schooling prey, and was also found in cod feeding on

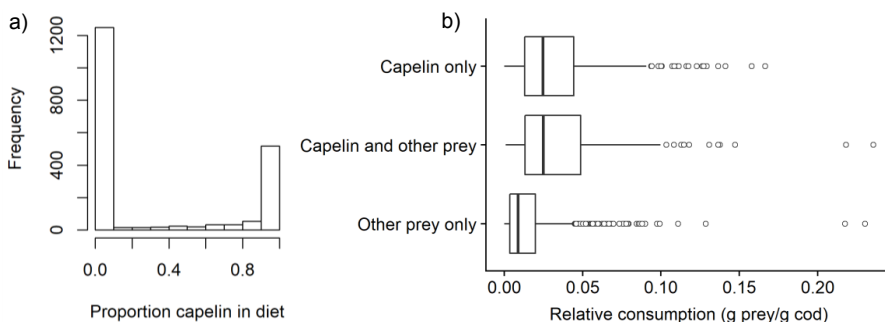


Figure 4: a) Capelin weight proportion of the total stomach contents in cod sampled in the cod-capelin overlap area. b) Relative prey consumption in cod feeding on capelin only, capelin and other prey, and other prey only. The plots are based on raw data from **P3**.

capelin off eastern Iceland (Magnússon and Aspelund 1997). Strand and Huse (2007) modelled the presence of capelin as a stochastic process and found that when capelin schools were present, cod became satiated within the first hours of feeding. Variation in feeding opportunity is therefore a strong candidate for explaining variation in cod's feeding on capelin. Before discussing this further (section 3.3), I will consider another, non-exclusive, explanation. What if a pure capelin diet is not optimal for cod?

An energy-maximizing predator should favour prey with high fat content, such as capelin, since fat contains more energy than proteins and carbohydrates. But like humans, fish cannot synthesise all other important nutritional compounds from fat and needs a more balanced diet. Laboratory experiments have demonstrated selective foraging for nutrients across several animal taxa, including fish (Kohl et al. 2015). For example, rainbow trout (*Oncorhynchus mykiss*) offered food pellets containing either high protein, high fat or high starch selected a combination similar to the estimated nutrient requirements of salmonids (Yamamoto et al. 2001). The relative importance of different nutrients may also vary throughout the year and with maturity stage. In the Øresund strait, cod feed on migrant herring and on resident shore crab *Carcinus maenas*. Analysis of prey nutritional composition revealed that the lipid-rich and energetically most profitable herring was low in arachidonic acid (ARA), a specific fatty acid linked to increased egg quantity, quality and survival (Røjbek et al. 2014, van Deurs et al. 2016). The optimal diet for maturing cod in this population is therefore a combination of both prey species (van Deurs et al. *submitted*). Interestingly, capelin is also low in ARA (Jangaard 1974). While no difference has been found between the total prey consumption of male and female Barents Sea cod in late summer or winter (Michalsen et al. 2008), sex-specific prey selection has not been studied in detail. For immature cod, ensuring a high protein intake may be more important, since they require a higher proportion of protein in the diet to maximise growth rate (Árnason et al. 2010). Further research in this direction may be worthwhile and feasible; some information on cod nutritional requirements is available from laboratory experiments (e.g., Jobling 1988, dos Santos et al. 1993,

Darias et al. 2011), prey nutritional composition can be examined experimentally or collected from the literature (e.g., Jangaard 1974, Percy and Fife 1981), and theoretical models that consider constraints on diet imposed by nutritional requirements can be developed, for example based on stochastic dynamic programming (Clark and Mangel 2000).

3.2 Cod's aggregative response to capelin is weak

The cod-capelin interaction can be described by the numerical and functional responses. In this work I consider the aggregative part of the numerical response that describes the spatial correlation between cod and capelin densities, and the functional response that is cod's consumption of capelin in relation to capelin density. The functional response is discussed in section 3.3.1.

Due to the scale dependence of predator-prey correlations across space (Rose and Leggett 1990, Sih 2005), cod's aggregative response to capelin may differ between spatial scales. In this thesis, I studied large-scale distributions and overlap in the entire Barents Sea (**P2**), identified the main overlap area (**P2**), and studied effects of the local environment on cod feeding within the overlap area (**P3**). Capelin densities were computed at two different scales based on the same raw data: in **P2**, densities were interpolated in a radius of approximately 65 km around the trawl stations, and the association between cod and capelin densities was evaluated at this mesoscale in species distribution models and with an overlap index. In **P3**, I used data from acoustic transects that overlapped with the trawl hauls to compare cod consumption with cod and capelin densities in the local environment. Cod's aggregative response to capelin can therefore be compared at three spatial scales, two of which have the same extent but different grain (i.e., resolution, Englund and Cooper 2003): the entire Barents Sea (Fig. 5 a), the overlap area (Fig. 5 b), and the overlap area with increased resolution (Fig. 5 c).

Cod is distributed over a much larger area than capelin in late summer (**P2**), which means that a part of the cod population does not interact with capelin at this time of

year. This does not imply that the aggregative response must be weak; cod could occur in higher densities in the overlap area than outside of it. However, while there is a positive correlation between cod and capelin densities across the Barents Sea, it is

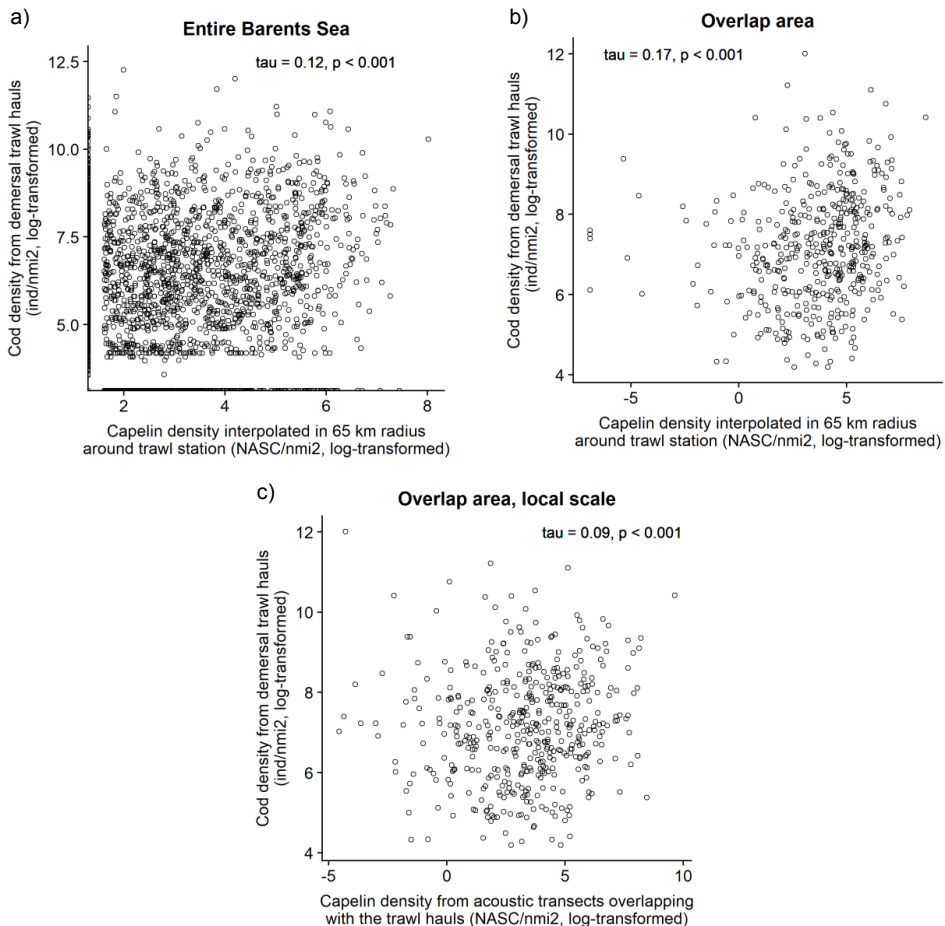


Figure 5: Aggregative response of cod to capelin in late summer at three spatial scales. a) Entire Barents Sea (**P2**). Cod density measured in demersal trawl hauls versus capelin density interpolated around the trawl stations. Points along the axes represent zero values; at 42% of the stations with cod, zero or very low (NASC < 5) capelin density was registered, while only 8 % of the stations with capelin had no cod. b) Overlap area (**P2**). Cod density measured in demersal trawl hauls versus capelin density interpolated around the trawl stations. 13 extremely low values of capelin density were set to 0.001 (-6.9 on log scale) for better visual representation. c) Local scale in overlap area (**P3**). Cod density from demersal trawl hauls versus capelin density from overlapping acoustic transects. Tau is the value of Kendall's rank correlation coefficient for the correlation between cod and capelin densities.

weak (**P2**, Fig. 5 a), and high cod densities are also found in areas where there is little or no capelin. Zooming in on the overlap area, correlations are still weak but slightly stronger at the coarser spatial resolution compared to the finer resolution (Figs 5 b and c). Cod's aggregative response to capelin was thus weak at all three scales considered here.

Four potential explanations for the weak aggregative response are considered in this synthesis: 1) cod's diverse diet results in weak associations with single prey species (section 3.1, 3.4.1), 2) cod gets satiated at low capelin density and therefore have no extra benefit of distributing ideally with respect to capelin density (section 3.1, 3.3.1, **P1**), 3) the proximity of capelin to cod is more important than capelin density (section 3.3, **P3**), and 4) local capelin densities are reduced due to predator avoidance or prey depletion (section 3.3.3).

3.3 A three-dimensional spatial game

3.3.1 The cod-capelin functional response: is capelin density important in the overlap area?

In the late summer overlap area, half of the prey mass consumed by cod was capelin, but just over a third of cod individuals had fed on this prey (**P3**). This means that the proportion of capelin in the population-level diet is not always representative of individual diets, as indicated by the smaller data set analysed in **P1** (see also section 3.4.4). Capelin depth distribution had a stronger effect on individual consumption than capelin density, and the empirical functional response quickly reached saturation (**P3**). This implies that vertically integrated capelin density at the standard sampling scale of ~2 km (1 nautical mile) is not a good indicator of capelin availability to cod. Capelin density varied in time and space at the local scale studied, and there is therefore good reason to believe that significant variation exists at smaller scales as well. Could variation in capelin density within the sampling scale explain the rapid saturation of the functional response?

Cod's feeding on capelin varied in space and over the diel cycle, with the highest consumption on banks during daylight when capelin was distributed closer to the

seafloor (**P3**, and below). Capelin distribution is patchier during light hours (Skaret et al. *submitted*), indicating schooling or shoaling behaviour. With a patchy distribution, capelin may not be homogeneously distributed over the 2 km acoustical transect. If so, we may associate cod with capelin densities that differ from those experienced by cod during feeding. This may in turn contribute to a weak empirical functional response and possibly reduce prey density at saturation (Rindorf and Gislason 2005). The vertical distribution of capelin is probably less variable at this small spatial scale because it is influenced by light level (Dalpadado and Mowbray 2013), which is unlikely to vary as much during the 15 min it takes for the research vessel to tow a standard trawl haul.

It is also possible that variations in capelin density within the overlap area is truly of little importance to cod. In the Northwest Atlantic, Horne and Schneider (1994) found no spatial association between cod and capelin at scales from 20 m to 10 km, and proposed a bioenergetic explanation. Due to the high abundance of capelin, a cod swimming through the capelin spawning area would encounter enough capelin over time to satisfy its energetic requirements without aggregating in high density patches. In the Barents Sea, the median capelin density in the cod-capelin overlap area appears to be high enough to satiate cod (**P1**, **P3**), and we found no significant effect of the interaction between capelin depth distribution and capelin density on capelin consumption in **P3**. That is, when capelin was close to the seafloor where cod resides, there was no additional effect of capelin density on consumption. While the evidence is not conclusive, it appears that capelin accessibility (vertical distribution) and detectability (light level) are more important for feeding success than local capelin density within the overlap area.

3.3.2 Capelin diel vertical migrations affect cod's feeding opportunity

The vertical distribution of capelin changed during the diel cycle, with a tendency for deeper distributions during the day (Fig. 6). Cod consumed more capelin during daylight at the Great and Central banks (100-200 m depth, **P3**, Fig. 7 a), where

capelin was distributed closer to the seafloor throughout the diel cycle (Fig. 6, Fig. 7 b).

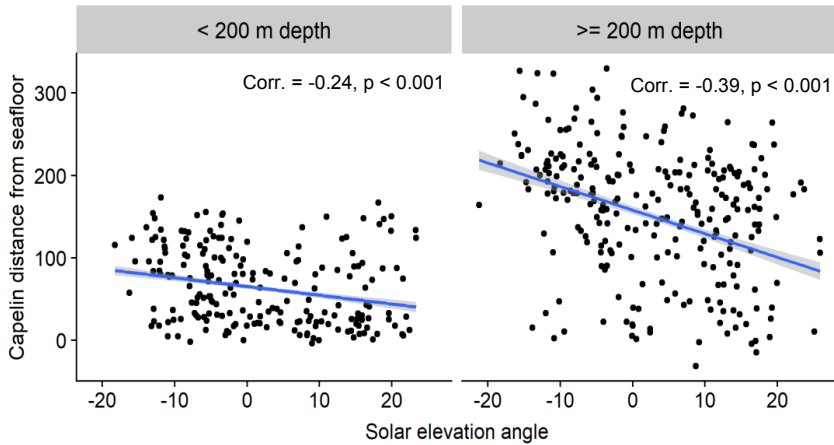


Figure 6: The weighted median depth of capelin acoustic backscatter decreases with increasing light level. The correlation was stronger in deeper areas (GLM, intercept: 72.2, std. error = 1.94, $p < 0.001$. Δ Depth ≥ 200 m: 88.9, std. error = 2.68, $p < 0.001$). Corr. is the value of Pearson's correlation coefficient. Across all depths, the correlation was -0.23 ($p < 0.001$).

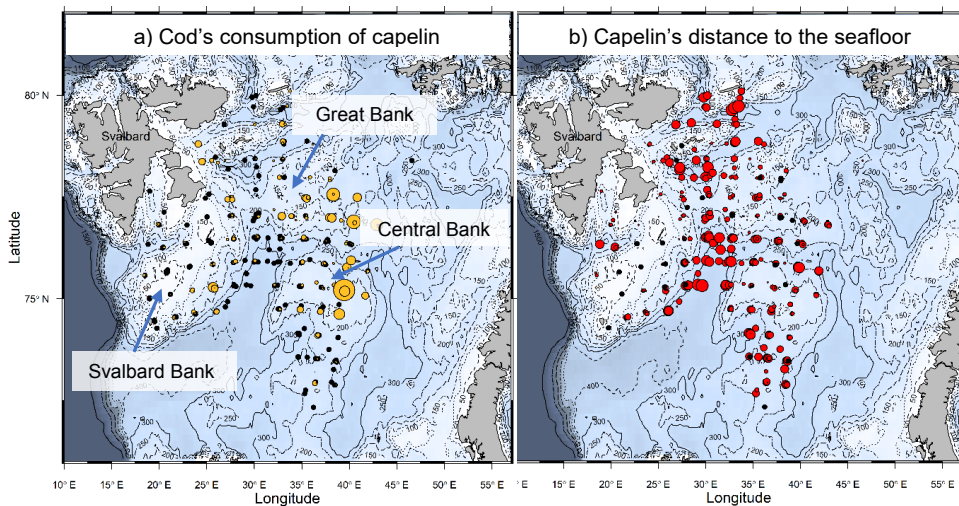


Figure 7: a) Observed consumption of capelin by cod in the overlap area 2004-2015. The size of the golden circles is proportional to the mean consumption of capelin by cod at the sampling station. Black circles represent sampled stations where no cod had fed on capelin. b) Distance from the weighted median depth of the capelin acoustic registrations to the seafloor, where the size of the red circles is proportional to the distance and black circles indicate distances < 10 m from the seafloor. Both day and night stations are shown.

A fine-scale study on cod feeding at the Great Bank in early autumn found that cod's feeding on pelagic fish peaked in the hours after dawn (Skaret et al. *submitted*). Cod's slow digestion may limit our ability to detect finer temporal changes in cod feeding in the data analysed here (**P3**), but daylight feeding on banks is in agreement with the fine-scale study. Because vertical movements are energetically costly for cod (Strand and Huse 2007, van der Kooij et al. 2007), the shallower depths at banks imply a reduced energetic cost of feeding on pelagic prey. Further, light is attenuated with depth in the water column, which means that the light level at the seafloor is higher in shallow areas (Lorenzen 1972). As cod is mainly a visual predator (Meager et al. 2017), a higher light level on banks compared to the deep may increase feeding success. However, cod can detect prey by vision in very low light conditions (Meager et al. 2010), and it may be the closeness of capelin to the seafloor that is the main reason for the high feeding success at the Great and Central banks of the Barents Sea.

A less intuitive pattern emerged in deeper areas, where consumption was somewhat higher at night than during the day (**P3**). Since cod needs several days to digest a capelin meal (**P1**, **P3**), could it be that cod caught in the deep have fed in shallow areas and moved to deeper waters to digest? This could be advantageous in two ways, depending on food availability. In an *in situ* experiment in Iceland, cod that was regularly fed capelin moved to warmer areas to digest, optimising their growth rate, while unfed cod with much lower prey consumption occupied colder areas, presumably to conserve energy by reducing metabolic rates (Björnsson 2018). However, in our study, the mean temperature was similar at the deep and shallow stations (0.8 vs 0.6°C), giving little scope for metabolic regulation. We must therefore look elsewhere to explain the apparent feeding on capelin at night.

Schooling in prey is an antipredator response thought to reduce predation risk for individual prey (Pitcher and Parrish 1993). As the sun goes down and prey detection by visual predators is reduced, capelin disperse in the water column (Skaret et al. *submitted*). If cod is able to detect capelin by vision in low light or in darkness using other senses, such as olfaction or the lateral line organ (Løkkeborg 1998, Strand and Huse 2007), it may exploit dispersed capelin at night. Cod in the deep need to ascend

farther from the bottom to feed on capelin than cod on banks – especially at night – but easier capture of capelin may give energetic benefits despite the longer vertical migration distance. The extent and duration of vertical migrations are highly variable in cod (Pálsson and Thorsteinsson 2003, Hobson et al. 2007, Neuenfeldt et al. 2009). In a tagging experiment in the Barents Sea, some cod made vertical ascents exceeding 100 m at the 2 h temporal resolution of the tag (Godø and Michalsen 2000), which may reflect prey search behaviour (Strand and Huse 2007). In the Northwest Atlantic, cod matched the diel vertical migrations of capelin in October and February, feeding mainly at twilight and at night (Turuk 1973), while in the North Sea, tagged cod were more active at night in late summer (Righton et al. 2001). In the Barents Sea, cod also feed on capelin during winter when the sun does not rise above the horizon (Johannesen et al. 2016a). To understand the mechanisms behind the apparent feeding on capelin at night, diel investigations in deeper areas are needed.

So far, I have considered cod and capelin's three-dimensional spatial game mainly from the perspective of cod. But why does capelin descend so close to the seafloor during daylight if this increases predation risk?

3.3.3 Bottom topography influences species interactions across several trophic levels

Capelin feed on copepods and krill (Dalpadado and Mowbray 2013), organisms that also perform diel vertical migrations as a trade-off between growth and predation risk (Pearre 2003). Descending into deeper waters during the day is an effective strategy to escape predators hunting by vision. But on banks, shallow depths constrain the vertical migrations of large zooplankton, trapping them close to the bottom where there is enough light for visual detection by pelagic fish (Aarflot et al. 2018). This suggests that the near-bottom bank habitat is a profitable feeding ground also for capelin. However, at the banks, capelin face predation risk not only from cod but also from whales (Skern-Mauritzen et al. 2011), dolphins (Fall and Skern-Mauritzen 2014), and seabirds that occur in high numbers in the region (Barrett et al. 2002). It therefore seems plausible that capelin face a trade-off between feeding and avoiding predators attacking from below and above. In response, risk-averse individuals may

distribute outside of the banks at the cost of reduced feeding opportunity, while others face the risk of descending into the cod habitat for a good meal. This trade-off may explain why cod is more strongly associated with the bank areas than capelin (**P2**).

This observation resembles the “leapfrog effect” (Sih 1998): when prey actively avoids the predator or when prey is locally depleted, stronger correlations may occur between the predator and the resource of its prey than with the prey itself. We have not examined the association between cod and capelin’s zooplankton prey but find a similar effect one “leap” further; the cod predator is more strongly associated with the topographic constraint on the prey resource distribution than it is with its prey (**P2**). This may result from local depletion of capelin on banks, capelin escaping predation by distributing outside of the bank areas, or a combination of the two.

In summary, the main feeding interaction between cod and capelin occurred at the Great and Central banks at 100-200 m depth, and the consumption increased when capelin was distributed closer to the seafloor during daylight. At the shallower and warmer Svalbard bank, cod fed less on capelin, had a higher diet breadth, and higher between-individual diet variation (see discussion in **P3**). In deeper areas, the diet breadth was more variable and cod consumption was higher at night than during the day (**P3**, Fig. 7).

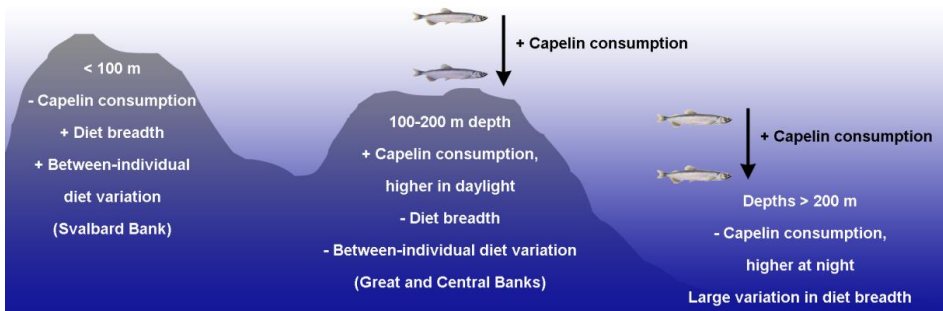


Figure 7: Schematic illustration of the influence of bottom topography on cod's feeding on capelin.

3.4 Implications for cod-capelin population dynamics

3.4.1 Individual diet variation in a generalist species

Generalist populations such as the cod often have weak functional responses to single prey species (Murdoch et al. 2002), more stable population diets over time (Durant et al. 2014), and high between-individual diet variation (Bolnick et al. 2007). The latter may be caused by trait variation, such as individual differences in prey capture ability or nutrient requirements, or by variations in prey availability over the species distribution area (Araújo et al. 2011). Around 200 prey species have been identified in the Barents Sea cod population (Dolgov et al. 2011), but in **P3** we found that most cod had fed on less than three prey species. Even though the snapshot stomach data probably underestimate individual diet breadth, it seems unlikely that each cod has access to or the ability to feed on all species in the population diet.

In **P3**, I computed the proportional similarity index for individual cod, a measure of similarity between individual and population-level diets (Schoener 1968, Feinsinger et al. 1981, Bolnick et al. 2002). I compared the individual diet with the average diet of the individual's size group instead of the entire population to minimise effects of cod size on diet variation. Diet similarity was generally low even after adjusting for the null expectation (see **P3**), indicating a high level of between-individual diet variation. In addition, many response-covariate relationships in **P3** had wide confidence bands, suggesting variation in individual responses to the same level of an environmental variable. Unfortunately, effects of environmental heterogeneity on diet similarity could not be fully separated from true individual variation (i.e., variation in diet between similar cod from the same environment) since only one individual per 5 cm length class was sampled at each station. Nevertheless, individuals in size groups with higher group diet breadths had diets that were more different from each other (Fig. 8). This indicates that diversification of cod's population-level diet occurs through individual cod including different prey species in their diet instead of all cod broadening their niche. The generalist nature of this cod population therefore appears to result from between-individual diet variation, which may be a contributing factor to the weak empirical functional response of cod to capelin. In future work, it is

possible to analyse older data material containing multiple samples per length class to elucidate if diets also vary between similarly-sized fish from the same environment.

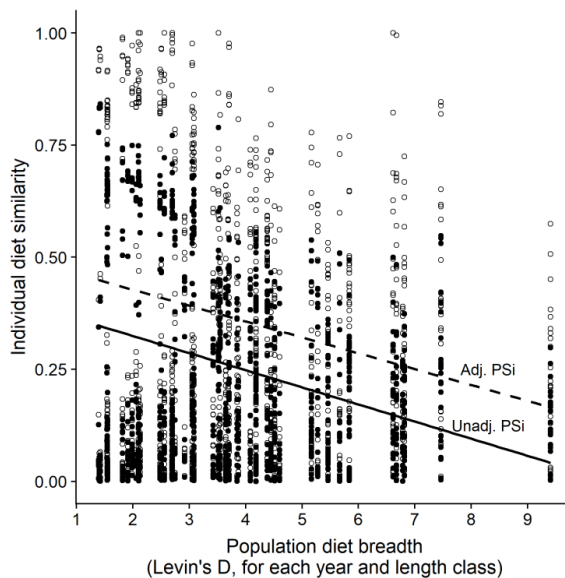


Figure 8: Relationship between population diet breadth (Levin's D , c.f. individual diet breadth in **P3**) and individual diet similarity (Proportional similarity index, PS_i), showing that individual cod diets are more similar to the average diet of its size group when the group diet contains fewer prey species. The unfilled circles and dashed regression line show values of diet similarity adjusted after the null expectation for each individual fish if they randomly sample the group diet (see **P3** for details), and the filled circles and solid line show unadjusted values. The relationships were significant for both unadjusted and adjusted diet similarity (GLM_{unadj}: est. = -0.03, std. error = 0.003, $p < 0.001$. GLM_{adj}: est. = -0.03, std. error = 0.002, $p < 0.001$).

3.4.2 Horizontal overlap is a poor indicator of interaction strength

The weak aggregational and functional responses of cod to capelin and the importance of capelin vertical distribution for feeding imply that a horizontal overlap does not always equal a vertical overlap and subsequent feeding opportunity for cod. More generally, correlation indices between species densities may be poor indicators of interaction strength when environmental heterogeneity constrains or facilitates a predator-prey interaction (**P2**, **P3**), or when the predator's feeding rate is more constrained by gut processing than prey encounter rate (**P1**). A look at the relationship between the estimated overlap and consumption in the late summer

overlap area confirms that the correlation is weak, both at the large scale from **P2** (Fig. 9 a) and at the smaller scale studied in **P3** (Fig. 9 b). Scaling up even further to look at annual correlations between mean consumption and mean overlap in the overlap area, the correlation is no longer significant (Kendall's rank correlation coefficient $\tau = -0.33$, $p > 0.05$).

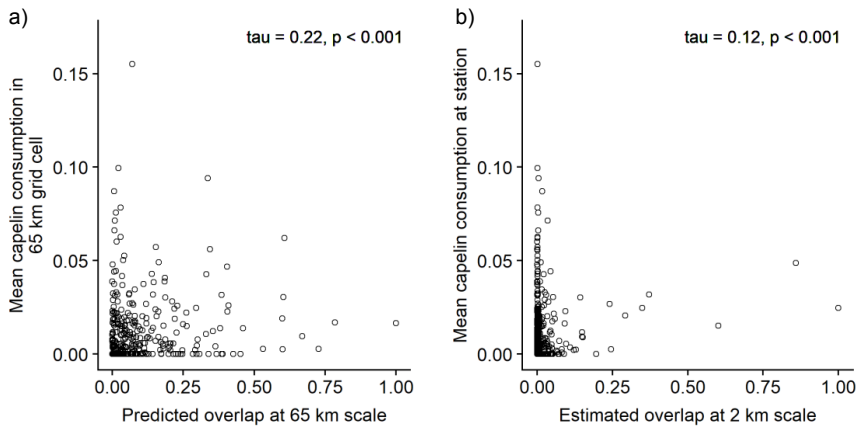


Figure 9: Cod-capelin overlap versus capelin consumption at two spatial scales in the overlap area. a) predicted overlap from **P2** (recalculated within the overlap area) versus the mean consumption of cod caught at stations within the 65 km grid cell, b) overlap estimated at the 2 km scale versus the mean consumption of cod caught at the same station. Consumption was calculated on data from **P3**. The overlap index from **P2** was used; overlap ranges from 0 to 1 where 1 means that the highest cod and capelin densities from a given year were measured at the same location.

Predator-prey overlap is nevertheless useful for identifying the general areas where species may interact, and to follow changes in these areas over time. The late summer overlap area shifted northeastward during the 2004–2015 study years, which was related to increased temperature and a large cod population (**P2**). This change resulted in spatial overlap with the previously less exploited (by cod) northern- and easternmost distribution areas of the capelin population, and an overall increase in the overlap between immature cod and capelin (**P2**). This has led to a higher capelin consumption in late summer compared to earlier periods when cod did not distribute in these areas, but also to increased consumption of polar cod and other Arctic fishes (ICES 2017b). Therefore, changes in the spatial overlap with capelin alone does not

give a full picture of recent changes in cod feeding. In future work, it may be informative to consider the relationship between capelin consumption and overlap with alternative prey species.

3.5 Implications for fisheries management

3.5.1 A brief history of the cod-capelin stock dynamics

Cod predation is a major source of natural mortality for the capelin population and is included in the capelin stock assessment (Bogstad and Gjørseter 2001). Although many studies have demonstrated the importance of capelin for the cod stock (e.g., Hjermann et al. 2007, Gjørseter et al. 2009, Solvang et al. 2018), capelin abundance is not taken into account in the cod assessment (ICES 2017a). However, cannibalism is accounted for in the cod assessment (ICES 2017a). In some periods, cannibalism has increased, and cod growth has decreased at low capelin stock levels (below). The cod assessment therefore has an indirect link to capelin.

The capelin stock has collapsed and recovered three times since the 1970s, with varying effects on the cod population. During the first collapse in the 1980s, cod experienced acute food shortage that led to a 50 % reduction in weight at age of 3-5 year old cod (Gjørseter et al. 2009). In turn, this resulted in increased fishing mortality since the quota is given in tonnes, which put additional pressure on the stock. By the end of the 1980s, cod catches were very low (Hjermann et al. 2007). A cod stomach sampling programme was initiated in 1984, which confirmed that cod consumed large quantities of capelin (Gjørseter et al. 2002). This spurred work on including estimates of natural mortality from cod in the capelin stock assessment. An increase in cod stock biomass in the 1990s led to higher fishing quotas, but they were set too high, and the cod stock declined again when the capelin population collapsed for the second time in the late 1990s (Hyllen 2002). This time, cannibalism on cod juveniles increased dramatically (Gjørseter et al. 2009). A period of smaller cod fishing quotas followed, but there was a large problem with illegal fishing in international waters that slowed down recovery (Hjermann et al. 2007). The capelin collapsed once again in 2003, but this had less severe effects on the cod population as

it managed to feed more on alternative prey (mainly herring and polar cod, Gjøsæter et al. 2009). A new harvest control rule came into full effect in 2007 (Stokke 2009), around the time that the capelin stock recovered from its third collapse. After this point, the combined effects of reduced fishing pressure and a favourable climate has led to recovery and growth of the cod stock (Kjesbu et al. 2014). The age-structure of the population has been nearly restored to preindustrial fishing levels (Kjesbu et al. 2014), resulting in higher abundance of large individuals that on average feed less on capelin (Dolgov et al. 2011). The large cod population has expanded its late summer feeding area further into the Arctic waters of the northeastern Barents Sea, where it is feeding increasingly on Arctic species in addition to capelin (P2, Kjesbu et al. 2014, ICES 2017b). This appears to have increased between-individual diet variation in cod and weakened the interactions between cod and single prey species. All these factors probably contribute to the decoupling between cod growth and the size of the capelin stock seen in recent years (Gjøsæter et al. 2009, Kjesbu et al. 2014, Johannesen et al. 2016a).

3.5.2 Estimation of the capelin spawning stock

The main capelin fishery takes place on the spawning grounds of the southern Barents Sea in January-April (Gjøsæter 1998), but the capelin stock size is estimated from data collected in the late summer ecosystem survey. Several attempts have been made to measure the maturing stock just before the fishery, but so far, this has not reduced uncertainty compared to the projections based on autumn data (e.g., Eriksen et al. 2009). This is mainly because capelin is less available for acoustic estimation in winter. Scientists and fishers have reported that the vertical distribution of capelin changes during the spawning migration, suggesting that capelin migrate close to the surface offshore but descend to the bottom closer to the spawning grounds along the coast. Echo sounding equipment have blind zones both at the surface and along the bottom (Totland et al. 2009), and capelin may be completely undetectable when they spawn on the seafloor (Bogetveit et al. 2008). To study capelin distribution in winter, we therefore used data from demersal trawl hauls in addition to acoustics from the winter survey (P2).

Capelin was found both at the seafloor and in the water column. The spatial distribution patterns of capelin based on acoustics and demersal trawl were different; the highest acoustic densities were detected in the northern part of the distribution area, while high demersal trawl densities were also detected in the central and southern parts. Capelin caught in demersal trawls were on average larger in the south than in the north. This gives some support for a vertical distribution shift as maturing capelin migrate to the coast. Our results suggest that the demersal trawl and acoustics partly sample different components of the capelin stock throughout the winter survey period, and that these two methods may need to be combined to estimate the maturing component. Further research on this topic would benefit from a thorough analysis of capelin vertical distribution in winter. This knowledge is essential for determining which gear or combination of gears is most appropriate for sampling, and for assessing when capelin is most available for estimation. Vertically resolved acoustic data from the winter survey may be used to model changes in vertical distribution across time and space. It may also be possible to look at changes in the relative proportions of capelin detected in the demersal trawl and with acoustics. If capelin vertical distribution can be predicted from environmental conditions or other factors, we would be one step closer to knowing where and when to survey the maturing capelin stock.

3.5.3 Estimation of prey consumption by cod

Because it is technically difficult to measure the capelin spawning stock close to spawning, fisheries scientists rely on projections of natural mortality to estimate the proportion of capelin spawners that survive the autumn and winter months. Explicit estimates of cod consumption are included as part of the natural mortality. This thesis gives new insight into cod and capelin winter distributions and overlap that may assist future improvements of the consumption estimate. In addition, the results on autumn feeding highlight an import bias that may result from averaging consumption across individuals.

Implications of winter overlap for estimation of capelin consumption

In the estimate of capelin consumption by cod, it is assumed that cod and capelin overlap completely during a certain amount of time (Tjelmeland 2005). Cod predation is thus treated as a homogeneous process in space. This may be a reasonable approximation within a limited spatial and temporal scale, since cod has been observed to aggregate in the capelin spawning area and feed almost exclusively on capelin (Bogetveit et al. 2008). However, we found a weak overlap between cod and capelin in winter (**P2**). The incomplete sampling of capelin by both acoustics and demersal trawl probably contribute to this result (see discussion in **P2**), and overlap is likely underestimated at the nearshore spawning grounds that are not covered well by the winter survey. Even so, the spatial distribution of capelin estimated from survey data largely reflected what is known about capelin distribution in winter, with smaller individuals found in the north and larger maturing capelin found farther south (**P2**). The cod-capelin overlap varied in space also in the northern and central areas where the capelin density estimates may be more reliable. It therefore seems reasonable to assume that cod's opportunity to feed on capelin varies in space as well.

A central assumption in the assessment is that only immature cod feed on mature capelin in winter (Bogstad and Gjørseter 2001). This is because mature cod are underway on their own spawning migration out of the Barents Sea at this time (Bergstad et al. 1987), and because large cod generally feed less on capelin (Dolgov et al. 2011). Interestingly, mature cod had the highest overlap with capelin, and this overlap increased over the study period (**P2**). The overlap may simply reflect that mature cod and capelin occur in the same area during their respective migrations. But stomach contents have revealed that mature cod do consume capelin during this time (Michalsen et al. 2008, Gjørseter et al. 2015a, Johannesen et al. 2016a). Considering the present high abundance of mature cod and the increased winter overlap with capelin, further investigations into mature cod feeding in winter is warranted (see also Gjørseter et al. 2015a). The assumption that immature cod feed only on mature capelin may also need to be revised, as suggested by Bogstad and Gjørseter (2001). Our separation of capelin into immature and mature components is somewhat uncertain (see discussion in **P2**), but the length distribution in demersal trawl hauls

indicated that immature cod overlap with immature capelin in the northern winter distribution area. This is in line with previous work that has found an important role for immature capelin in the diet of immature cod in winter (Bogstad and Gjørseter 2001).

Jensen's Inequality: the effect of averaging individual stomachs

Individual variation in nonlinear processes that affect consumption rate may bias estimates based on averaging due to a mechanism called “Jensen’s Inequality” (Ruel and Ayres 1999). This happens because non-linearities shift the average individual consumption rate away from the consumption rate of an average individual. These two measures appear similar, but the first is calculated by taking the average of individual consumption rates, while the second is the consumption rate based on the average ingested prey mass. In a type II functional response, the consumption rate at prey density N depends non-linearly on the predator’s attack rate a (also called search efficiency or search volume) and prey handling time h (Equation 1).

$$f(N) = aN/(1 + ahN) \quad (1)$$

Specifically, the relationship between consumption rate and attack rate is convex; the consumption increases with increasing attack rate until it reaches a plateau (Fig. 10). Conversely, handling time is in the denominator of the functional response equation, which means that the relationship between consumption rate and handling time is concave. Therefore, individual variation in attack rate may result in an average

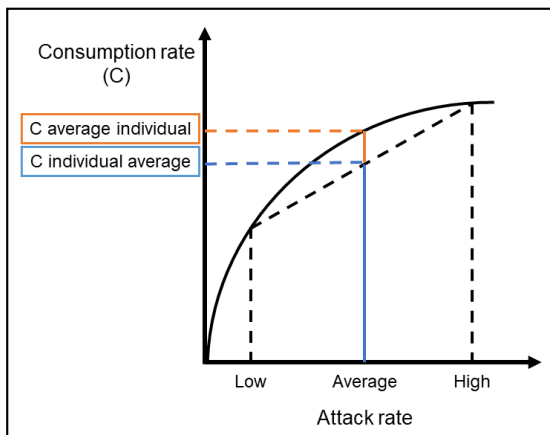


Figure 10: Illustration of Jensen’s Inequality, redrawn from Bolnick et al. (2011). Consumption rate is a convex function of attack rate, and variation in individual attack rates therefore result in the average individual consumption rate (blue line) being lower than the consumption rate evaluated at the average individual attack rate (orange line).

feeding rate that is lower than the feeding rate of the average individual (Fig. 10), whereas the opposite is true for variation in handling time (Bolnick et al. 2011).

As we have seen throughout this synthesis, cod's consumption of capelin in late summer varies widely between individuals, which suggests strong variation in the attack rate for a given prey density. The attack rate, in this context more aptly named search volume, depends on the swimming speed of cod, and on the distance at which cod can detect prey (Beauchamp et al. 1999). The detection distance is in turn influenced by environmental conditions, such as light level and turbidity (Turesson and Brönmark 2007, Meager et al. 2010). The observed variation in attack rate may therefore result from changes in light level that affect capelin vertical distribution and cod visual range. Variations in swimming speed may also contribute to variations in attack rate, especially if cod acts as a sit-and-pursue predator on the banks instead of engaging in active search for prey.

A simple evaluation of the importance of Jensen's inequality for estimates of capelin consumption in late summer can be done based on the stomach data from **P3**. First, I calculate the daily consumption rate of each individual using the stomach evacuation model for Atlantic cod by Temming and Herrmann (2003), where consumption rate depends on the mass of the predator, the mass prey consumed, ambient temperature, and a prey-specific digestibility constant. Next, I compare this to the consumption rate of an average individual, calculated using the average mass of the sampled cod, the average water temperature at the sampling stations, and the average capelin mass in cod stomachs. This gives an average individual consumption rate of 3.6 g/day, while the consumption rate for the average individual is 6.8 g/day. This difference would result in substantial overestimation of consumption when scaled up to population level.

The consumption estimate used in the capelin stock assessment is based on individual cod stomachs (Tjelmeland 2005), but cod cannibalism and the consumption of other prey species are estimated from pooled (averaged) stomachs (Bogstad and Mehl 1997). A correction factor is applied to account for the bias introduced by averaging

(Bogstad and Mehl 1997). The correction factor is based on experiments by dos Santos and Jobling (1995), who showed that cod consumption based on pooled stomachs was always higher and had lower variance than consumption based on individual stomachs. Considering its importance for consumption estimates, the validity of the current correction factor for different years, seasons, cod sizes, and prey types should be explored in future work.

3.5.4 Seasonal dynamics of the cod-capelin interaction

During the winter migration period, mature cod and capelin spatial distributions are highly dynamic in both time and space. In contrast, distributions are relatively stationary during the late summer feeding period. The late summer interaction is anchored by bathymetric features; cod aggregate on banks where the vertical range of the pelagic habitat is smaller, and capelin descend closer to the seafloor (**P3**). In winter, capelin vertical distribution appears to change considerably over large spatial and temporal scales, suggesting that important variation in the interaction occurs over a larger range of scales in winter compared to autumn (**P2**). This may be further analysed using data on individual cod feeding from winter. The influence of seasonal changes in light level on cod feeding also warrants further investigation. For small cod juveniles, the midnight sun offers an opportunity to feed continuously, which increases growth rate compared to juveniles in more southern populations (Helle 2000). But as discussed above, cod feed heavily on capelin during winter when there is very little light, and the results from **P3** suggest that cod may feed on capelin at night. At the same time, light influences the vertical distribution of pelagic prey, and a combination of high prey availability and favourable light levels appear to drive capelin close to the seafloor on Barents Sea banks during the light season. Zooplankton and polar cod perform diel vertical migrations during the polar night, but the migrations are less pronounced compared to seasons with stronger light cycles (Berge et al. 2009, Benoit et al. 2010). If the same is true for capelin in the Barents Sea, this may be an additional source of seasonal variation in the cod-capelin dynamics.

4. Combining empirical and theoretical models in ecology

In this thesis, I have used a combination of theoretical modelling and empirical analyses to study the cod-capelin interaction. It is my sincere belief that this cross-disciplinary approach has contributed to deeper ecological insight. One of the pioneers of foraging theory, Merritt Emlen, wrote in 1966,

“A model is useful only inasmuch as it either has predictive value or can be used to explain hitherto inexplicable phenomena. The latter use must be approached with especial caution since theoretical formulations are rarely exact replicas of the natural state, and empirical models have no intrinsic meaning at all.”

This encapsulates the fundamental difference between theoretical and empirical approaches in ecology; theoretical models conceptualise observed patterns by making qualified guesses on the most important mechanisms that drive them, while empirical models explain observed patterns by relating them to measurable variables that may or may not be directly related to the underlying mechanisms.

Research on commercial fish is primarily an empirical discipline; successful management of fish populations requires extensive *in situ* monitoring (Caddy and Cochrane 2001). However, data on commercial fish are often gathered and analysed without prior theoretical expectations about the small-scale individual ecological processes that give rise to larger-scale patterns (Persson et al. 2014). At the same time, a management system often needs to anticipate consequences of ecological situations where no data exist, and the quality of the advice then rely on our intuition and quantitative representations of the system. For example, analyses of stomach contents tell us about the recent meal of an individual but not the sequence of mechanisms leading to the ingestion. It is thus difficult to predict the diet composition under other prey mixtures or environmental circumstances than those sampled.

To meet this challenge, it is necessary to combine empirical data and analyses on species distributions, overlap, consumption and environmental variation with theoretical models that conceptualise mechanistic drivers of the system. Ideally, theoretical and empirical models work in an iterative framework, where model predictions are compared with data and the results used to refine assumptions in the model to improve its predictive capacity ('pattern-oriented modelling', Grimm and Railsback 2012). The results from this thesis is a starting point for developing such a framework for cod-prey dynamics in the Barents Sea.

5. Conclusions and outlook

This thesis has explored the cod-capelin interaction from three perspectives using theoretical and statistical modelling. The work has contributed new information about the interaction in late summer and winter, with implications for population dynamics, the fisheries management of capelin, and the general study of predator-prey interactions.

First, a theoretical optimal foraging model was used to study individual-level mechanisms of cod prey selection, finding that capelin is the most profitable prey, that gut processing may limit cod's feeding rate at high prey density, and that cod feed less on capelin than predicted from a model that assumes homogeneous prey distributions, active search for prey, and maximisation of energy intake. We propose that gut processing may be an important constraint on consumption in omnivorous predatory fishes, such as the gadoids, that rarely go long periods without food, and that this mechanism may reduce the strength of spatial predator-prey associations.

Secondly, survey data was analysed with statistical models to study species distributions and overlap, evaluating relationships between species distributions, population sizes and environmental variables, and identifying the main overlap areas in late summer and winter. Cod had a stronger association with bank areas than capelin, and the spatial matching of cod and capelin densities was weak. The late summer distributions and overlap shifted toward the northeast during the 2004-2015 study period, concurrent with increases in population sizes and temperature. The winter overlap reflected the dynamic species distributions during the cod and capelin spawning migrations. The relatively high overlap between immature cod and capelin in the north, and between mature cod and capelin in the south gave support to the previously proposed revisions of the cod consumption estimate used in the capelin stock assessment. The analysis also gave further insight into the methodological challenges of estimating the capelin stock in winter. This is the first time that the spatial overlap between Barents Sea cod and capelin has been explicitly estimated.

Finally, cod stomach data collected in the overlap area was analysed with statistical models to study biological and physical drivers of variation in cod's feeding on capelin. Half of the consumed biomass was capelin, but just over a third of the individuals had fed on this prey. In this synthesis, I show that this individual variation may bias estimates of consumption based on averaging. Capelin consumption was highest at intermediate depths corresponding to the bank areas, especially during the day when capelin was distributed closer to the sea floor. Capelin density was a less important predictor of variation in cod feeding, and the empirical functional response rapidly reached saturation. The study highlights the role of bathymetric features in facilitating species interactions in aquatic environments and suggest a role for less conventional measures of prey availability when studying interactions between species that are partly separated in time and space.

Cod and capelin are probably the most studied species in the Barents Sea, yet I have been able to outline several potential directions of future research in this synthesis. In summary, the mechanisms behind the broad diet of the cod population may be further disentangled by isolating environmental effects on diet from true individual variation using historical stomach data. Individual diet composition may also be better understood with a broader perspective on prey nutrient composition, which can be explored with theoretical models. Theoretical modelling may also be applied to the dynamics and trade-offs involved in the cod-capelin-zooplankton interaction on the banks to explore the importance of the light cycle, prey patchiness and vertical migrations on trophic interactions. The model can be confronted with and calibrated against data on species distributions and consumption from different environmental conditions, ideally collected in fine-scale surveys with diel stations at multiple depths. Further, individual variation in cod's feeding on capelin in winter should be examined in a similar way as I have done here for late summer, to the extent that this is possible with the data at hand. This is important since individual variation may bias estimates of interaction strength, which should be considered in addition to the assumptions on immature versus mature cod feeding in future developments of the capelin stock assessment. Finally, analyses of small and large-scale variation in

capelin vertical distribution in winter is needed to understand variation in the availability of capelin to cod, and to develop methods for estimating the capelin spawning stock in winter.

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Fig. 1: Gjertsen, K. E., and Ingvaldsen, R. 2018. *Map of currents in the Barents Sea*. Havforskningsinstituttet.

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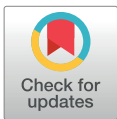
RESEARCH ARTICLE

Seasonal dynamics of spatial distributions and overlap between Northeast Arctic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) in the Barents Sea

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Abstract

The trophic link between cod (*Gadus* sp.) and capelin (*Mallotus* sp.) is important in many panarctic ecosystems. Since the early 2000s, the Northeast Arctic cod stock (*G. morhua*) in the Barents Sea has increased greatly, and the sea has been exceptionally warm. Such changes have potentially large effects on species distributions and overlap, which in turn could affect the strength of species interactions. Due to its high latitude location, the Barents Sea has strong seasonal variation in physical conditions and interactions. To study drivers of variation in cod-capelin overlap, we use data from two annual surveys run in winter and in autumn of 2004–2015. We first model winter and autumn spatial distributions of mature and immature cod and capelin. We then calculate overlap from model predictions on a grid with similar spatial resolution as the survey data. Our approach allowed us to interpret changes in overlap as species-specific effects of stock size and temperature, while accounting for sampling variation due to sampling time and depth. We found that during winter both species expanded their distribution in response to increased stock sizes, but how strongly and where the expansion occurred varied. The effect of temperature on distributions varied in space, and differed for cod and capelin and for different components of the two species. The results for autumn were clearer and more consistent. Both species expanded their distribution areas as their stock sizes increased. A positive effect of temperature was found in the north-eastern Barents Sea, where temperatures were lowest at the start of the study. Overlap increased and shifted north-eastwards during the study period and remained high despite a decline in the capelin stock. The increased overlap during autumn could mainly be attributed to the shift in cod distribution with increased cod stock biomass.

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Data Availability Statement: The data in this article was collected during the joint Norwegian-Russian Barents Sea Ecosystem Survey and the Barents Sea Winter Survey conducted by the Institute of Marine Research (IMR, Norway) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia). The surveys are funded by the Norwegian and Russian governments, and the data sets are interchanged between the two parties and integrated immediately after the cruise. The full data set is not Open Access due to Russian Law permitting

Introduction

Spatial association or *overlap* between predator and prey is a prerequisite for predation to take place. Understanding the drivers of overlap is thus underlying any assessment of predation

publication of data collected on Russian territory. Data collected by Norwegian ships are deposited at the Dryad Repository (<https://doi.org/10.5061/dryad.pv3rc1m>). These data represent 53% of autumn data and 80% of winter data. In the article, we present results from analyses on the full data set (Norwegian + Russian). Analyses on the Open Access Norwegian data give similar results on the drivers of species distributions and overlap in winter. For autumn, we get somewhat different species density-temperature relationships when the cold areas sampled by Russian vessels are excluded. Access to the entire data set can be granted through contracted collaboration in joint projects including IMR and PINRO. Inquiries about the Russian data and research collaboration can be sent to the acting Research Director of PINRO, Evgeny Shamray (shamray@pinro.ru).

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rate and natural mortality of a prey. In a fishery context, overlap has potentially important implications for management because of its influence on stock dynamics [1]. A strong overlap giving a positive linear relationship between predator and prey densities across space is expected if a predator perfectly tracks its prey [2–4]. However, both predators and prey are influenced by other factors that vary in space, such as interaction with other species and physical properties of the environment. These factors may impose constraints on behaviour and distributions, creating non-linear and spatially varying relationships between predators and prey. Spatially explicit analyses, where species distributions are evaluated for given geographic locations in a heterogeneous landscape [5], are therefore more appropriate than aggregating across space for understanding factors underlying changes in predator-prey overlap over time [6, 7].

In several shelf ecosystems in the panarctic region, cod (*Gadus* sp.) and capelin (*Mallotus* sp.) are abundant species forming an important predator-prey interaction [8]. In the Barents Sea, too, the trophic link between the commercially important stocks of Northeast Arctic cod (*Gadus morhua*; hereafter cod) and Barents Sea capelin (*Mallotus villosus*; hereafter capelin) is key for the ecosystem dynamics. Cod is the main predator on post-larval capelin [9–11], and although cod is a generalist, it has an apparent preference for capelin [10, 12, 13]. The spatial distributions and life cycles of both species are adapted to the strong seasonality in this high latitude ecosystem. The northern Barents Sea is seasonally ice-covered, and here the spring bloom after ice melt supports a rich zooplankton production [14]. Capelin migrate northwards to feed on the zooplankton, followed by cod [13]. The main feeding season lasts throughout the summer into early autumn, after which cod and capelin shift further south. Both species spawn in early spring; capelin spawns along the northern coast of Norway and Russia, while cod's main spawning ground is further south along the Norwegian coast in the Lofoten area [13]. As a consequence, the overlap and interaction between the species vary seasonally; from diet data, it appears that cod's preference for capelin is stronger during winter than in summer [15].

During the past ten years, the cod stock has increased to similar levels as in the late 1940s, when abundance had increased in the absence of fishing during World War II [16]. Concurrent with the increase in stock size, cod has expanded northwards both in winter and in the late summer/early autumn feeding season [16–18], potentially affecting the cod-capelin overlap. The Barents Sea capelin stock is known for strong fluctuations in abundance, resulting in a pattern of stock collapses and recoveries [19]. Currently, the stock is recovering from a collapse [20]. While the fishery is closed during stock collapses, mature capelin is subject to commercial harvesting in periods of high abundance. The stock assessment of capelin was among the first to extend beyond single-stock evaluation by explicitly modelling effects of the cod stock on capelin mortality in the stock projection simulation [21–23]. The stock assessment model relies on several assumptions related to the seasonal interaction between cod and capelin [24], but recent changes in seasonal cod distribution and feeding have not been incorporated [15, 16, 19]. For a long time, it has also been an unachieved objective to include spatially explicit information about the cod-capelin interaction in the model [24].

Based on cod stomach data and a large body of work describing seasonal distributions and migration patterns of cod and capelin ([9, 25], and references therein), the overlap between the species has been inferred, but not studied directly. Furthermore, overlap metrics and robust statistical methods for predicting overlap have not been established.

Here, we study seasonal and spatial aspects of cod-capelin overlap from 2004–2015, covering a period with exceptionally high water temperatures [26], two capelin collapses and a more than doubling of cod biomass (Fig 1). We address the need for new knowledge and improved methods for appraising cod-capelin spatial overlap through 1. Examining how cod and capelin distributions in late summer and winter relate to temperature and stock biomass using

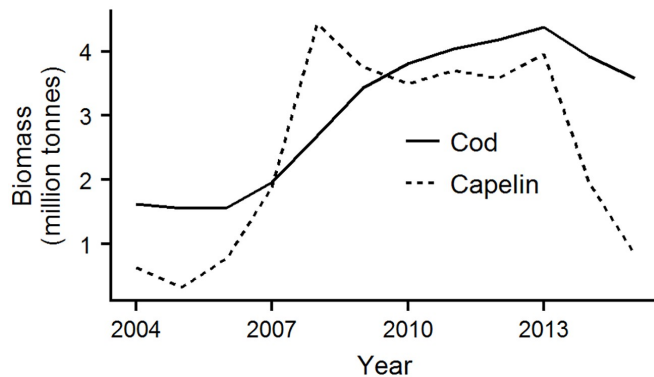


Fig 1. Cod and capelin stock biomass. Biomass of cod (age 3+, estimated in winter) and capelin (age 1+, estimated in autumn) in the study years 2004–2015. The capelin biomass is from the assessment based on the acoustic estimate from the ecosystem survey, and the cod biomass is the most recent published stock assessment (cod 3+, capelin 1+, Tables 3.18 and 9.4 in [27]).

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spatially explicit modelling tools, 2. Developing an index of spatial overlap, and assessing cod-capelin overlap in each season during the study period, and 3. Discussing how variation in the overlap across the study period relates to the factors identified in 1.

Methods

Study area and data collection

The Barents Sea is a high latitude shelf sea bordering the polar basin to the north and the coasts of Russia and Norway to the south (Fig 2). Two Norwegian-Russian surveys with comprehensive coverage are conducted annually in the Barents Sea: the *winter survey* (1981–) covering the south-central Barents Sea in the pre-spawning season of cod and capelin when both species undertake their spawning migration (Fig 2A), and the *ecosystem survey* (2004–) covering the whole shelf in the main feeding season (Fig 2B). To be able to compare the two seasons, only data collected in the period 2004–2015 were used here. Data from the Norwegian surveys are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pv3rc1m>.

Both surveys use a Campelen demersal shrimp trawl at fixed stations for near-bottom sampling as a basis for swept area abundance estimation. The interstation distance has ranged between 15 and 35 nautical miles (nmi) (28–65 km, Fig 2). All vessels have been equipped with Simrad EK60 echo sounders (on some vessels Simrad EK500 during the first years) for recording and integrating fish echoes along the survey tracks. The acoustic backscatter is allocated to target groups based on species-specific acoustic properties and the catch composition in pelagic and bottom trawls, and then integrated over a horizontal distance of 5 nmi (9.3 km, 2004–2007) or 1 nmi (1.9 km, 2008–2015). The most important biological data support for the pelagic acoustic data interpretation comes from “Harstad trawl” samples [28], which provide data both from fixed stations and from sampling of specific acoustic recordings for validation. CTD casts for temperature measurements are made in conjunction with trawl tows, and depth at the start of the tow is recorded by Scanmar trawl sensors (for more details about the two surveys, see [29] and [30]).

Cod densities (number of individuals/nmi²) were estimated using standard methods for cod swept area calculation in the Barents Sea, that is, number caught at each trawl station

a) Winter survey (first quarter)

b) Ecosystem survey (third quarter)

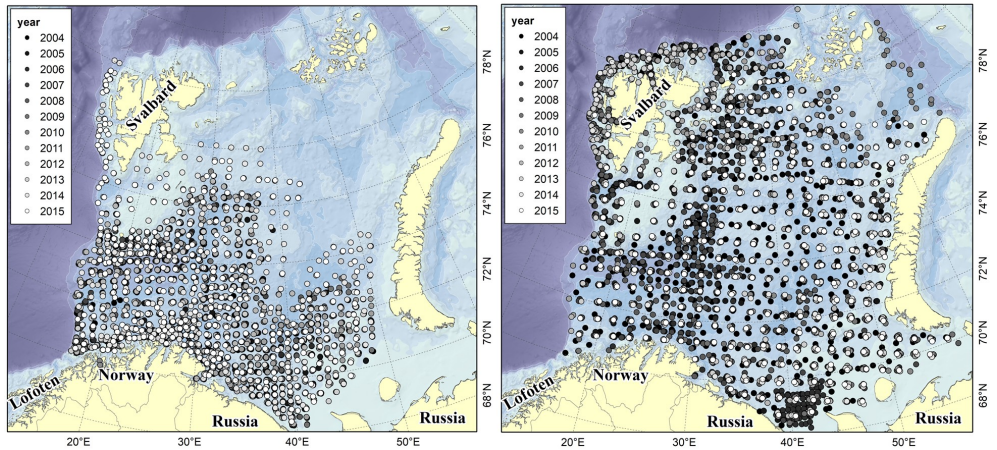


Fig 2. Study area and sampling stations. Demersal trawl stations used in the present study from A) the winter survey and B) the ecosystem survey in 2004–2015. The shade of the points indicates if the station was sampled early (dark) or late (light) in the study period. The background highlights the main bathymetric features of the Barents Sea. The winter survey runs in January–March each year with the purpose of obtaining abundance indices for stock assessment of cod and haddock (*Melanogrammus aeglefinus*). The winter survey has a stratified regular design with higher station density in strata with historically higher abundance of cod to minimize the overall sampling variance in the cod estimates. The ecosystem survey covers most of the Barents Sea shelf in August to early October. The aim of the survey is firstly to provide an acoustic estimate of the capelin stock for assessment and quota advice, and secondly to assess the ecosystem state by monitoring the most important ecosystem components. The ecosystem survey has a regular sampling grid, but higher station density around Svalbard due to strong depth gradients in this area, in the Hopen trench (2004–2007) due to higher densities of *Pandalus borealis*, and east of Svalbard due to higher density of capelin. In 2014, unusual ice conditions restricted the coverage of the northern Barents Sea in the ecosystem survey.

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divided by trawled area, assuming that the effective fishing width along the trawled transect is dependent on cod length [30]. The standard trawled distance was 1.5 nmi (2.8 km) for the winter survey in 2004–2010, and 0.75 nmi (1.4 km) for the entire autumn survey and the winter survey after 2010. Since immature and mature cod have different distributions, particularly in winter [31], we divided the swept area density estimates into one immature and one mature cod component, using the average age at 50% maturity for the study years and length at age data from the surveys (winter: mature cod ≥ 70 cm, autumn: mature cod ≥ 75 cm, [27]).

Autumn capelin acoustic densities (in units of Nautical Area Scattering Coefficient; NASC; m^2/nmi^2) were based on data collected during the ecosystem survey, the same data which is used to provide an absolute abundance estimate for the capelin stock assessment each year [27]. The acoustic data from winter is based on the same methodology, but is of lower quality as this survey mainly targets demersal fish and has few pelagic trawl hauls for acoustic target verification (on average 6 hauls versus 38 for the ecosystem survey). The winter survey also coincides with the period when the mature part of the capelin stock is undertaking its spawning migration, and capelin seems to be less available to acoustic detection during spawning migration than at other times [32, 33]. We therefore chose to supplement the winter acoustic data with density estimates of capelin from the demersal trawl (number of individuals/nmi towed), and hereafter refer to capelin from the different sampling methods as “acoustic capelin” and “trawl capelin”, respectively.

Data preparation and analysis

We first developed single species distribution models for cod and capelin for autumn and winter using Generalised additive models (GAM, [34]) (*Single species distribution models* below), and then calculated overlap from model predictions of local species densities (*Quantifying overlap* below). We chose to do this rather than calculate overlap directly from the raw data, since we wished to relate changes in overlap to *species-specific* responses to the environment. In addition, our model predictions included variables controlling for sampling variation that could have biased indices calculated on raw data [35].

Single-species distribution models. As density-independent predictors in the species distribution models, we used water temperature (bottom temperature for cod, and mean pelagic temperature from 50–200 m depth for capelin), bottom depth, sun height, survey day, and year. The temperature variables were allocated to each trawl station from the nearest CTD measurement from the same survey. The bottom depth was that measured at the beginning of trawling. Sun height was included to account for sampling variation associated with diurnal vertical migrations, and was calculated from the day of the year, geographical position, and sampling time. Survey day was expressed relative to the earliest day of the season (autumn, winter) across the study period when sampling took place, and was included to account for the quasi-synoptic coverage and inter-annual differences in timing of sampling in relation to the migrations of cod and capelin. The geographical coordinates x,y were projected stereographically with centre in the middle of our study area at 75° N and 35° E, and expressed in deviation from this centre in nautical miles. Finally, we included the annual total stock biomasses [27] of each species as covariates to test for potential density-dependent effects on species distributions. As the capelin stock assessment is done on data from the autumn survey, we used the capelin stock biomass from the previous year in the winter models of capelin distribution.

All data points containing missing values in any covariate were removed. To avoid large outliers in the covariates, we also limited the data to include bottom temperatures in the range -2 to +7.5°C, and depths of 50–500 m, which contained the bulk of observations in both seasons, leaving 3994 observations for analysis in winter, and 4644 observations in autumn. Calculation of variance inflation factors indicated that the correlations between covariates were not a cause for concern (values < 3, [36]), except for the correlation between year and stock biomasses. We therefore used stock biomass only.

Since the Barents Sea contains many islands and complex coastlines, we applied the soap film smoother in the GAMs (for details, see [S1 Appendix](#)). All analyses were done in R version 3.4.1 for Windows [37], using the packages *mgcv* [38, 39] for GAM fitting, and *ggplot2* [40], *cowplot* [41] and *itsadug* [42] for visualisation.

The response variables in the models were local cod and capelin densities. Due to the large amount of acoustic data and the application of the soap film smoother, convergence of the capelin models was problematic. We therefore chose to include only acoustic registrations adjacent to the bottom trawl stations, using distance weighted interpolation of the area backscatter (NASC) within a 15 nmi (28 km) radius with weights of the form $w_i = (1 + d_i)^{-1}$, where d_i is the Euclidian distance between the acoustic sampling points and the station [43]. This did not lead to any loss of information relevant to our objectives, as initial runs using the finer resolution data gave similar response-covariate relationships.

For each season and *component* (immature cod, mature cod, acoustic capelin, trawl capelin), we fitted separate distribution models with the untransformed species density $D_{(x,y),t}$ in position x,y in year t as the response, conditional on other environmental covariates, using a GAM with Tweedie distribution and the default log-link. The variance of the Tweedie

distribution is related to the mean by a power function (Eq 1):

$$var(Y) = \mu^p \tag{1}$$

While a p of 0, 1 or 2 corresponds to the familiar Gaussian, Poisson and Gamma distributions, respectively, for $1 < p < 2$, the Tweedie distribution is a compound Poisson–gamma distribution with mass at zero, appropriate for our data. This is also the range where automatic estimation of the power parameter during fitting is implemented in *mgcv* [44]. Firstly, we fit models with basic smooth term predictors to establish baselines for comparison with more complex formulations, and to evaluate the overall (across-space) relationships between covariates and response (*habitat model Eq 2*):

$$D_{(x,y),t} = \alpha + s_1(x, y) + s_2(bio_t) + s_3(depth_{x,y}) + s_4(sun_{(x,y),t}) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + \epsilon_{(x,y),t} \tag{2}$$

Here s_{1-6} are smooth functions of geographical position, stock biomass, depth, sun height, temperature, and survey day, respectively, α is the global intercept and $\epsilon_{(x,y),t}$ is the error term whose variance is related to the mean according to Eq 1 under the Tweedie distribution. To avoid overfitting the smooth functions, we constrained their level of wiggleness by limiting the maximum number of basis dimensions (“knots”) to 5 on the univariate smooths and 20 on the two-dimensional smooth of geographical position. Thereafter, we systematically increased model complexity, ending up with seven *candidate models* describing the distribution of each component. These models included different combinations of the covariates in Eq 2 and spatially variant terms of stock biomass, temperature, and survey day. Spatially variant terms test for linear effects of a variable, but the effect is also allowed to vary smoothly in space so that there may be a positive effect in one part of the study area, and a negative effect in another [45]. The most complex candidate models were on the form:

$$D_{(x,y),t} = \alpha + s_1(x, y) + s_2(depth_{x,y}) + s_3(sun_{(x,y),t}) + s_4(x, y) \times temp_{(x,y),t} + s_5(x, y) \times s.day_{(x,y),t} + s_6(x, y) \times bio_t + \epsilon_{(x,y),t} \tag{3}$$

Where each product of geographical position and a covariate represents a spatially variant term. The models contained either a regular smooth or a spatially variant term of the same covariate.

From the candidate models, one model for each component was selected for overlap calculations based on minimisation of the Akaike Information Criterion (AIC) and maximisation of deviance explained after backwards elimination of non-significant predictors. The relationships between response and covariates were assessed by examining their robustness across model formulations, i.e., if the relationships were stable or varied, where the latter could indicate that the predictor captured residual variation in the model rather than a meaningful pattern. The models were visually inspected for residual correlation using the R-functions *pacf* (temporal correlation) and *variog* (spatial correlation, library *geoR*, [46]). None of the model residuals showed temporal autocorrelation, but the residuals of the capelin models using acoustic data were spatially autocorrelated. Since this may cause an underestimation of confidence intervals, we performed a wild bootstrap [47] on the capelin habitat models. The wild bootstrap followed the same steps implemented by Llope et al. [48] to model phytoplankton distribution in the North Sea. Specifically, year was treated as a sample unit, and all scaled residuals within a year were randomly switched in sign. The new residuals were added to the model predictions to fit a new GAM. The operation was repeated 1000 times to estimate mean and confidence intervals for each covariate response. However, the bootstrapped mean effects

and confidence intervals were similar to those observed in the models (S2 Appendix). We therefore concluded that accounting for the residual autocorrelation would not alter our conclusions, and kept the original model formulations.

For cod, we also fit separate habitat models that included local capelin density as predictor (*extended habitat models*). These models were used for inference only, not for calculation of overlap.

Quantifying overlap. To calculate overlap, the best candidate distribution model for each component was used to predict species density on a 35 x 35 nmi (65 x 65 km) regular grid of the study area with covariate values corresponding to the nearest observation from the central point of the grid cell in year t . The grid resolution was the same as the standard inter-station distance of the survey with the coarsest station grid (the ecosystem survey). By using a standard grid, the seasons and years could be compared, despite variation in survey design and execution. Grid cells containing fewer than 5 (autumn) or 8 (winter) observations across the study period, as well as cells falling outside the sampled area in year t , were eliminated from the grid. In this way, we only predicted on locations where the models had been given a reasonable amount of data. The overlap $O_{(x,y),t}$ in position (grid cell) x,y in year t was then calculated for each combination of components, using the formula:

$$O_{(x,y),t} = \frac{\widehat{Cap}_{(x,y),t}}{\max \widehat{Cap}_t} * \frac{\widehat{Cod}_{(x,y),t}}{\max \widehat{Cod}_t} \tag{4}$$

Where $\widehat{Cap}_{(x,y),t}$ and $\widehat{Cod}_{(x,y),t}$ are the predicted capelin and cod densities in the grid cell, and $\max \widehat{Cap}_t$ and $\max \widehat{Cod}_t$ are the maximum predicted densities in the same year and season. With this formulation, the overlap can range from 0 to 1, where 0 means that one or both species are absent from the grid cell, and 1 means that both species are present in their maximum predicted densities in that year and season. Note that the index is symmetric with respect to species. Thus, our overlap index gave spatially explicit information about how well cod and capelin densities matched in a given year and season. The correlation (Kendall's rank correlation tau) between the predicted cod and capelin densities across the grid was also calculated for comparison with the spatially explicit overlap formulation. The overlap between all capelin and cod component combinations (autumn: 2, winter :4) were mapped for each year and season.

Finally, the mean overlap across the grid and the extent of the overlap (n grid cells with overlap > 0.001 divided by the total number of grid cells) were calculated for each year, season and cod-capelin component combination to get an overview of the temporal dimension of the overlap, i.e., the between-year variation in how well cod and capelin densities matched.

Results

Species distribution models

For all models, the estimated Tweedie power parameters fell within the range 1.4–1.8, indicating that the compound Poisson-gamma distribution was a good fit for our data. The covariates generally contributed significantly to explaining species distributions, except for sun height in the capelin autumn models, and depth in the candidate models of both acoustic and trawl capelin in winter (Table 1). The deviance explained by the best candidate models ranged from 39.6% for capelin trawl data in winter to 74.5% for capelin acoustic data in autumn (Table 1). The relationships between species densities and sun height and survey day are shown in S3 Appendix.

Table 1. GAM statistics for all models by season and component (immature cod, mature cod, acoustic capelin, trawl capelin).

Season	Species	Component	Model type	Model terms	Tw-p	ΔAIC	Dev %	
Autumn	Capelin	Acoustics	Habitat	$Base^a + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.452		62.6	
			Candidate	$Base^a + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.434	-443.2	69.0	
			Candidate	$Base^a + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.45	-206.5	65.3	
			Candidate	$Base^a + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.432	-470.4	68.8	
			Candidate	$Base^b + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.43	-459.4	69.7	
			Candidate	$Base^a + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.41	-723.5	72.9	
			Candidate	$Base^a + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.411	-633.5	71.1	
			Candidate	$Base^b + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.399	-806.2	74.5	
		Cod	Immature	Habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.62		51.3
				Extended habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + s_7(\log_{10}(capA_{(x,y),t} + 1))$	1.616	-150.8	52.7
				Candidate	$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.605	-837.9	59.5
				Candidate	$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.616	-81.5	52.7
				Candidate	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.612	-278.3	54.8
				Candidate	$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.603	-890.5	60.3
	Candidate			$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.597	-969.3	61.4	
	Candidate			$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.607	-410.6	56.6	
	Candidate			$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.595	-1052.0	62.5	
	Mature			Habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.418		47.1
			Extended habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + s_7(\log_{10}(capA_{(x,y),t} + 1))$	1.424	-64.2	48.1	
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.389	-615.9	55.7	
			Candidate	$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.406	-151.8	50.2	
			Candidate	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.407	-160.1	50.2	
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})^{d1}$	1.379	-694.4	57.3	
	Winter		Capelin	Acoustics	Habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.58	
		Candidate			$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.576	-79.7	61.6
		Candidate			$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.555	-212.0	64.3
		Candidate			$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.571	-76.8	61.2
		Candidate			$Base^c + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})^{d1}$	1.557	-249.5	65.6
		Candidate			$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.576	-101.1	62.5
		Candidate			$Base^c + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.559	-172.8	64.3
Candidate		$Base^c + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$			1.55	-295.2	67.3	
Trawl		Habitat		$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.793		31.0	
		Candidate		$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})^{d1}$	1.786	-205.0	35.4	
		Candidate		$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.79	-78.6	33.0	
		Candidate		$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.786	-236.4	35.7	
		Candidate		$Base^c + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})^{d1}$	1.784	-250.7	36.5	
		Candidate		$Base^c + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t})^{d1} + s_6(x, y) \times s.day_{(x,y),t}$	1.782	-311.2	37.5	
		Candidate	$Base^c + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.784	-248.8	36.3		
		Candidate	$Base^c + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.779	-400.6	39.6		

(Continued)

Table 1. (Continued)

Season	Species	Component	Model type	Model terms	Tw-p	ΔAIC	Dev %
	Cod	Immature	Habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.658		50.4
			Extended habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + s_7(\log_{10}(capA_{(x,y),t} + 1))$	1.657	+10.0	50.6
			Extended habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + s_7(\log_{10}(capT_{(x,y),t} + 1))$	1.655	-48.7	51.2
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})^d$	1.661	-204.1	53.5
			Candidate	$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.65	-165.6	53.0
			Candidate	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.654	-54.6	51.9
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})^d$	1.661	-201.1	54.0
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.664	-81.6	52.8
			Candidate	$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times (s.day_{(x,y),t})$	1.657	-26.1	52.1
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.657	-284.5	55.5
		Mature	Habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.533		54.2
			Extended habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + s_7(\log_{10}(capA_{(x,y),t} + 1))$	1.537	+99.3	53.1
			Extended habitat	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t}) + s_7(\log_{10}(capT_{(x,y),t} + 1))$	1.537	+102.8	53.0
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(s.day_{(x,y),t})$	1.541	-114.0	55.3
			Candidate	$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.535	+46.2	54.0
			Candidate	$Base + s_4(bio_t) + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.534	+50.7	54.1
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(temp_{(x,y),t}) + s_6(x, y) \times s.day_{(x,y),t}$	1.539	-78.8	55.6
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(s.day_{(x,y),t})$	1.538	-101.0	55.7
			Candidate	$Base + s_4(bio_t) + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.538	+145.3	53.0
			Candidate	$Base + s_4(x, y) \times bio_t + s_5(x, y) \times temp_{(x,y),t} + s_6(x, y) \times s.day_{(x,y),t}$	1.533	-195.8	57.4

The terms for spatial position, $s_1(x, y)$, sun height, $s_2(sun_{(x,y),t})$, and depth, $s_3(depth_{(x,y)})$, were included in all models and are denoted “Base” in the table. Tw-p is the estimated Tweedie power parameter. Deviance explained (Dev %) is presented for the final model after removal of non-significant (n.s., $p > 0.05$) terms, and ΔAIC is the change in AIC relative to the habitat model for each component. The extended habitat models included local capelin density as predictor; here capA represents capelin sampled with acoustics and capT represents capelin caught in the bottom trawl. The chosen candidate model for each component is indicated in bold font.

^aSunheight n.s.

^bSunheight and depth n.s.

^cDepth n.s.

^dn.s. term

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Factors affecting species distributions in autumn. The estimated relationships between local densities and depth and temperature from the habitat models in autumn (Table 1) are shown in Fig 3. Capelin did not associate strongly with bottom depth, but occurred in lower than average densities in the deepest areas (Fig 3A). The relationship between temperature and capelin density was bimodal: higher capelin densities were found in sub-zero waters, and in temperatures of around 5°C (Fig 3B). However, the confidence intervals for depth and temperature were relatively wide, and the bootstrapped confidence intervals resulted in non-significant p-values (S2 Appendix).

Capelin was mainly restricted to the central-northern parts of the Barents Sea, with a core distribution area east of Svalbard (Fig 4A). For capelin, an increase in stock biomass led to an expansion of the core distribution area towards the north and south, as well as density increases in the core area and farther east (Fig 4A and 4B). This effect was significant across all models. Including a spatially variant effect of temperature further improved model fit, as increased temperature in the north-eastern area was associated with higher local capelin densities (Fig 5A). The final model for capelin in autumn explained 74.5% of the deviance and included, in addition to the effects described above, a locally linear effect of survey day (Table 1, S3 Appendix).

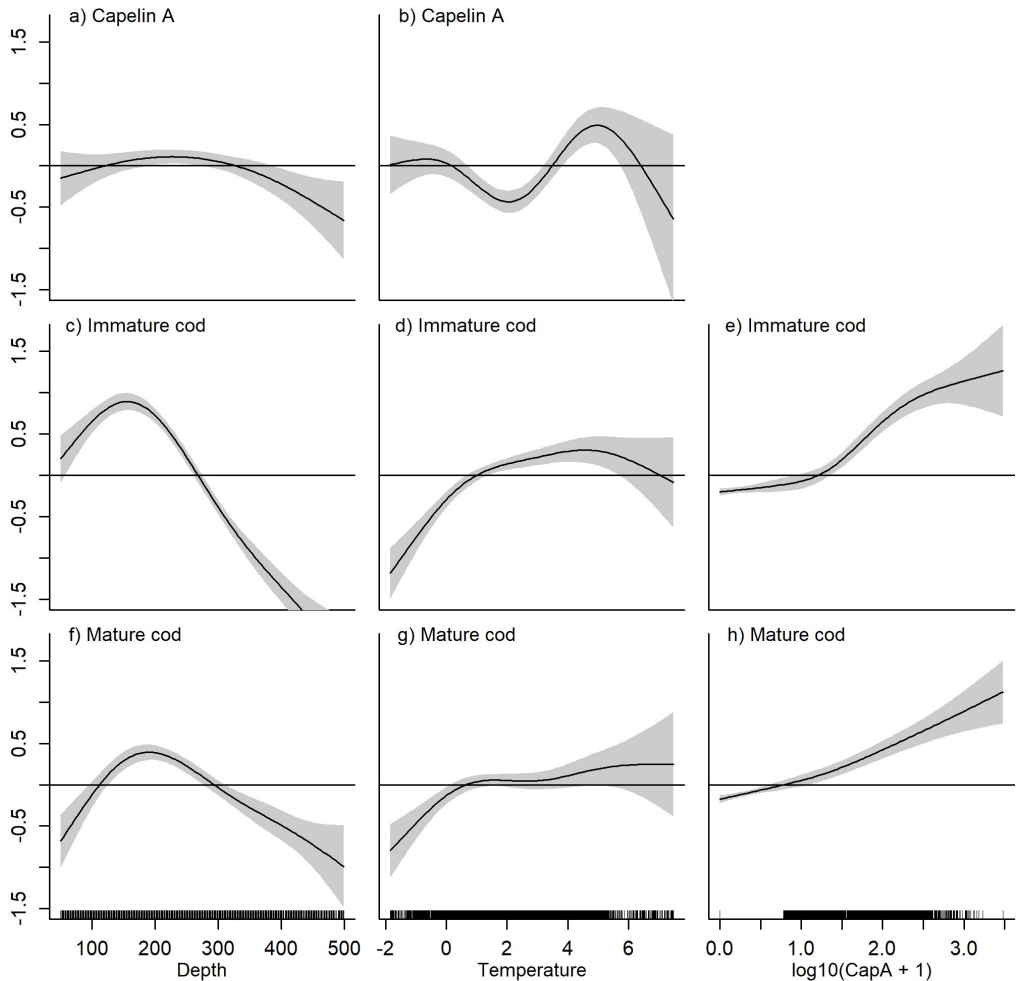


Fig 3. Autumn GAM smooth functions from the habitat models. Non-linear regression between local densities of A-B capelin, C-D immature cod, and F-G) mature cod and the density-independent covariates depth (m) and temperature ($^{\circ}\text{C}$). The effect of local capelin density ($\log_{10}[\text{NASC}+1]$) from the extended habitat models on E) immature cod density and H) mature cod density is also shown. The plot shows the (centered) \log local species density as a function of each covariate when accounting for the other covariate effects. The horizontal line at $y = 0$ represents a neutral contribution of the covariate to the response. The grey bands represent ± 2 standard errors around the smooth estimate.

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Immature cod occurred in areas with slightly shallower bottom depths compared to mature cod (Fig 3C and 3F). Peak densities of both components fell within the range 150–200 m. Less than average cod densities were found in temperatures below 1°C , but above that any effect of temperature on mature cod was generally weak and variable (Fig 3G), while immature cod associated more strongly with water masses of intermediate temperature (2– 5°C , Fig 3D). Including local capelin density as a predictor of local cod density, we found a positive

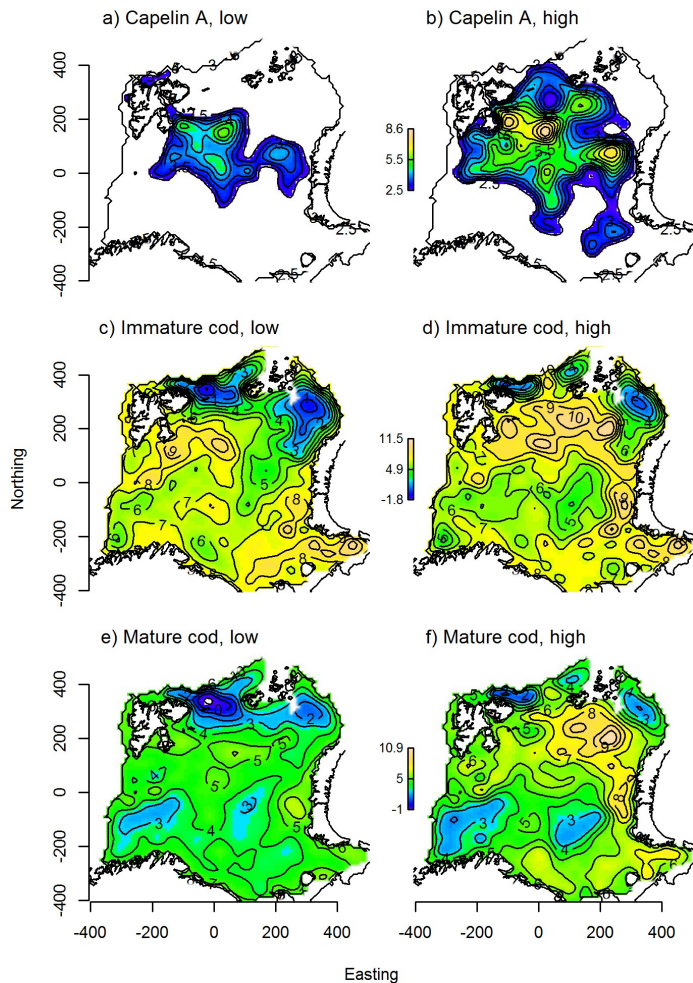


Fig 4. Predicted autumn distributions. Autumn distributions of A-B) capelin, C-D) immature cod, and E-F) mature cod, as predicted from the best candidate model for each component (Table 1). The different columns show the partial effects of stock biomass when the other model predictors were set to their across-year mean values at each location; the left column shows species distributions at low stock biomass (capelin: 0.628, cod: 1.63 million tonnes, measured in 2004), and the right at high stock biomass (capelin: 3.96, cod: 4.38 million tonnes, measured in 2013). The contour lines indicate local species density on the log-link scale, and the colours range from blue at low density to yellow at high density.

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association, though the effect was more variable for immature than mature cod at high capelin densities (Fig 3E and 3H). Including capelin gave a modest improvement in model fit compared to the basic habitat models (1–2% increase in deviance explained, Table 1). Both immature and mature cod were found throughout the study area, with density maxima both in central-northern and south-eastern Barents Sea (Fig 4C and 4E). The distributions of mature

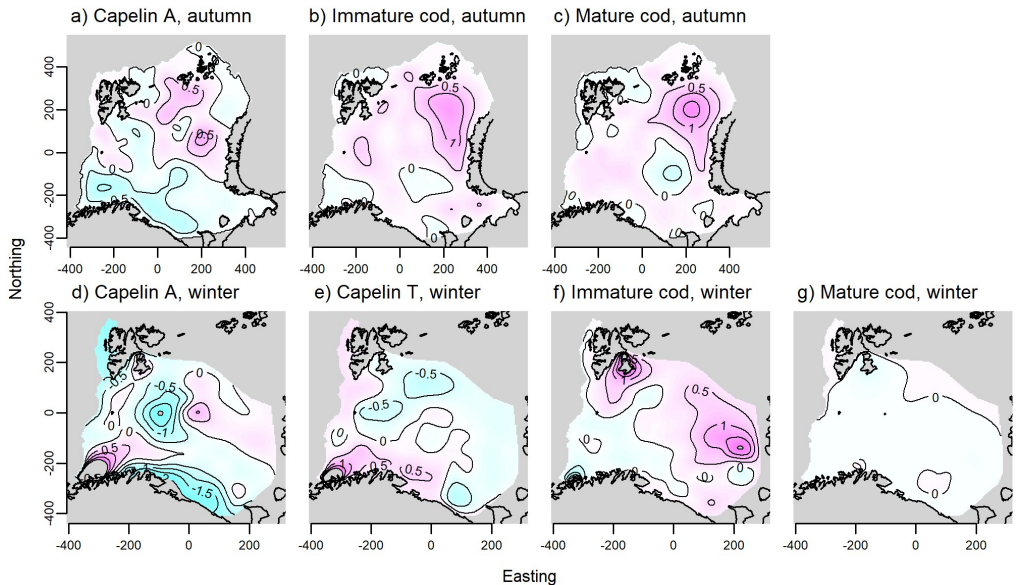


Fig 5. Spatially variant effect of temperature on local cod and capelin densities. The contour lines show how the slope of the linear regression between local species density and mean pelagic temperature (capelin) or bottom temperature (cod) from the best candidate models vary in space for A) acoustically estimated capelin in autumn, B) immature cod in autumn, C) mature cod in autumn, D) acoustically estimated capelin in winter, E) trawl-caught capelin in winter, F) immature cod in winter, and G) mature cod in winter. Blue colours indicate negative slopes, and pink colours indicate positive slopes.

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and immature cod were similar, but the highest mature cod densities occurred slightly east of the immature cod density maximum in the north. The spatially variant effect of cod stock biomass on cod density was significant across model formulations for both immature and mature cod. As stock biomass increased, the main density increases for both components occurred in the north/north-eastern part of the study area (Fig 4C–4F). Including a spatially variant effect of bottom temperature further improved model fit (Table 1). Here, an increase in density of both components coincided with increasing bottom temperatures in the north-easternmost corner of the study area (Fig 5B and 5C). Finally, spatially variant effects of survey day were also retained in the final models for cod in autumn, which explained 62.5% and 58.6% of the deviance for immature and mature cod, respectively (Table 1, S3 Appendix).

For all autumn models, the effect size of stock biomass was larger than that of temperature as judged by the difference in AIC between the habitat models and the candidate models with the respective spatially variant term (Table 1).

Factors affecting species distributions in winter. The estimated relationships between local species densities and depth and temperature from the habitat models in winter (Table 1) are shown in Fig 6. Higher than average densities of acoustic capelin were found in shallow areas and in the deepest areas, though variability in the response was high at large depths (Fig 6A, see also S2 Appendix; depth was non-significant after the wild bootstrap). Trawl capelin occupied the shallow part of the depth range (Fig 6C), but note that in the best candidate models, depth was non-significant for both capelin components (Table 1). The acoustic capelin was strongly and positively associated with the coldest waters ($< 2^{\circ}\text{C}$, Fig 6B), reflecting the

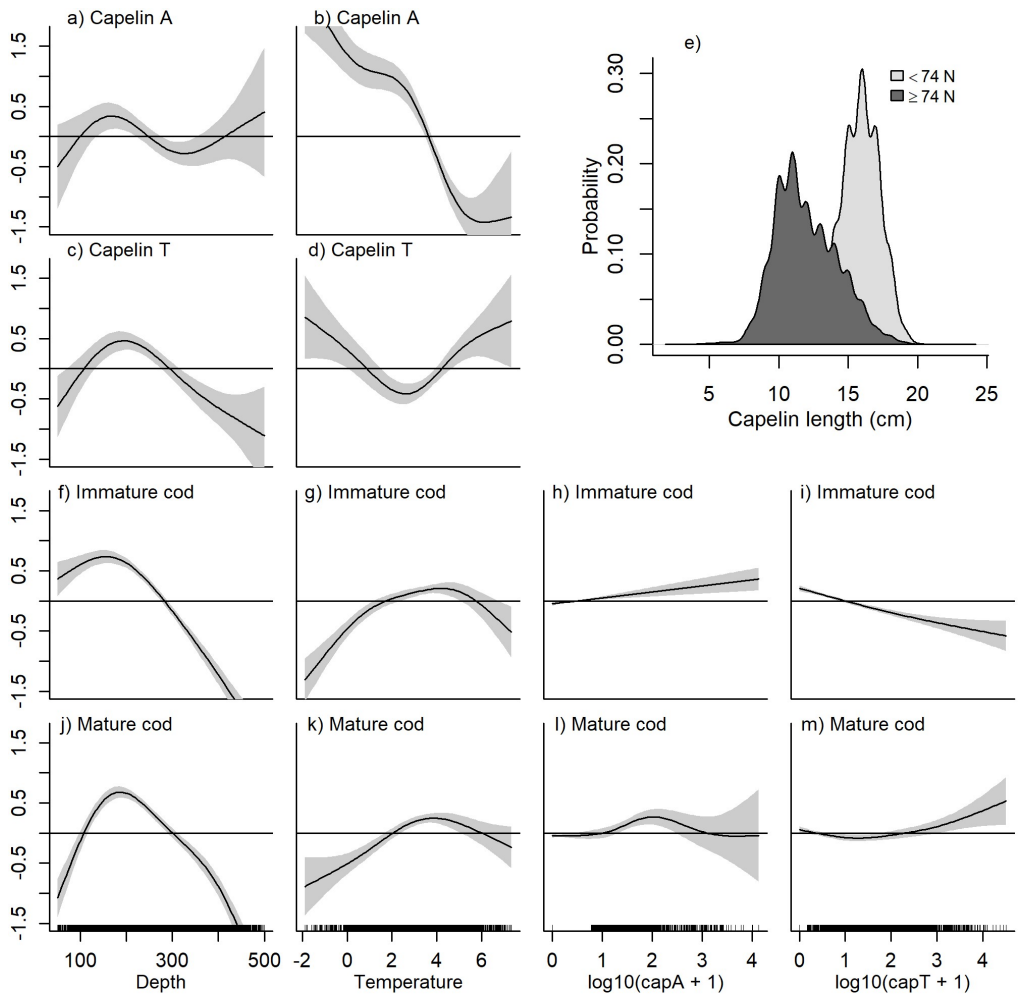


Fig 6. Winter GAM smooth functions from the habitat models. Non-linear regression between local densities of A-B) capelin sampled acoustically, C-D) capelin sampled with demersal trawl, F-G) immature cod, J-K) mature cod, and depth (m) and temperature (°C). The effect of local acoustic ($\log_{10}[\text{NASC}+1]$) and trawl capelin ($\log_{10}[\text{ind} \times \text{nm}^{-2}+1]$) densities from the extended habitat models are shown for H-I) immature cod and L-M) mature cod. The plot shows the (centered) log local species density as a function of the covariate when accounting for the other covariate effects. The horizontal line at 0 corresponds to a neutral contribution of the covariate to the response. The grey bands illustrate ± 2 standard errors around the smooth estimate. Panel E) shows probability density distributions of capelin length in demersal trawl hauls south and north of 74°. The distributions were calculated from the catch numbers of capelin in each 1 cm-length group using R base function “density” with default settings. Capelin matures at approximately 14 cm [23].

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northern distribution, while the highest trawl catches of capelin coincided with the lowest and highest temperatures, but not those in between (Fig 6D). However, the number of observations at these temperature extremes were relatively few, and there was high variability in the response.

Partly different geographic distributions were evident from the two sampling methods; the main concentrations of capelin sampled acoustically were found in the central Barents Sea (Fig 7A and 7B), while high densities were caught in the demersal trawl around Svalbard, but also in an area extending across the central areas down to the Norwegian/Russian coasts (Fig 7C and 7D). Smaller individuals dominated the demersal trawl catch in the north, while larger individuals dominated in hauls from the south (Fig 6E). Comparatively lower densities of capelin were measured acoustically along the coast (Fig 7A).

The best models for capelin (both acoustics and trawl) in winter included spatially variant effects of temperature (Table 1). For acoustic capelin, there were negative effects of temperature in the central Barents Sea and along the eastern Norwegian/Russian coasts (Fig 5D), while for trawl capelin, local density decreased with temperature in the north, and increased with temperature in the south (Fig 5E). The effect size of temperature was larger than that of biomass for acoustic capelin, while the biomass effect was larger for trawl capelin (Table 1). The final models explained 67.3% and 39.6% of the deviance for acoustic and trawl capelin, respectively, and also included spatially variant effects of survey day (S3 Appendix) and capelin biomass (Fig 7A–7D).

In winter, immature and mature cod were associated with similar depths as in autumn, that is between 150–200 m (Fig 6F and 6J), while they occupied a narrower and warmer range of temperatures in winter (approx. 2–6°C Fig 6G and 6K). The overall association between acoustic capelin and both immature and mature cod was weak in winter (Fig 6H and 6L). Immature cod had a negative association with trawl capelin (Fig 6I), while mature cod was positively associated with the highest trawl capelin densities (Fig 6M). However, including capelin (either trawl or acoustics) as a predictor contributed little to improving model fits, or even reduced the explained deviance (Table 1).

Cod was found throughout the study area, with density peaks of immature cod in the western- and easternmost areas (Fig 7E) while mature cod occurred in higher densities closer to the Norwegian coast (Fig 7G). Stock biomass was important for explaining variation in the local density of both cod components; the areas of high immature cod density in the east expanded as stock biomass increased (Fig 7E and 7F), while mature cod density increased with stock biomass throughout most of the surveyed area (Fig 7G and 7H). Increased local temperature was associated with an increase in immature cod density in the north and east, and a weak decrease in density in the south-west (Fig 5F). Temperature had a small positive effect on mature cod density in the north (Fig 5G). The effect size of stock biomass was larger than that of temperature for both components (Table 1). The final models for immature and mature cod in winter also included spatially variant effects of survey day (S3 Appendix), and explained 55.5% and 57.4% of the deviance, respectively (Table 1).

Cod-capelin overlap

Maps of overlap by year and season for all cod-capelin component combinations can be found in S4 Appendix. Maps of overlap in years with contrasting capelin and cod stock biomasses are shown in Fig 8 for autumn and winter, respectively. The mean annual overlap and overlap extent are shown in Fig 9.

Cod-capelin overlap in autumn. Capelin was distributed in a comparatively smaller area than cod, mainly restricted to the central-northern parts of the Barents Sea (Fig 4). The main overlap area between cod and capelin coincided with the main distribution area of capelin in all years (Fig 8A, S3 Appendix). The mean overlap was higher between mature cod and capelin compared to the immature cod and capelin overlap in the beginning of the time series, but became similar towards the end as the overlap between immature cod and capelin increased

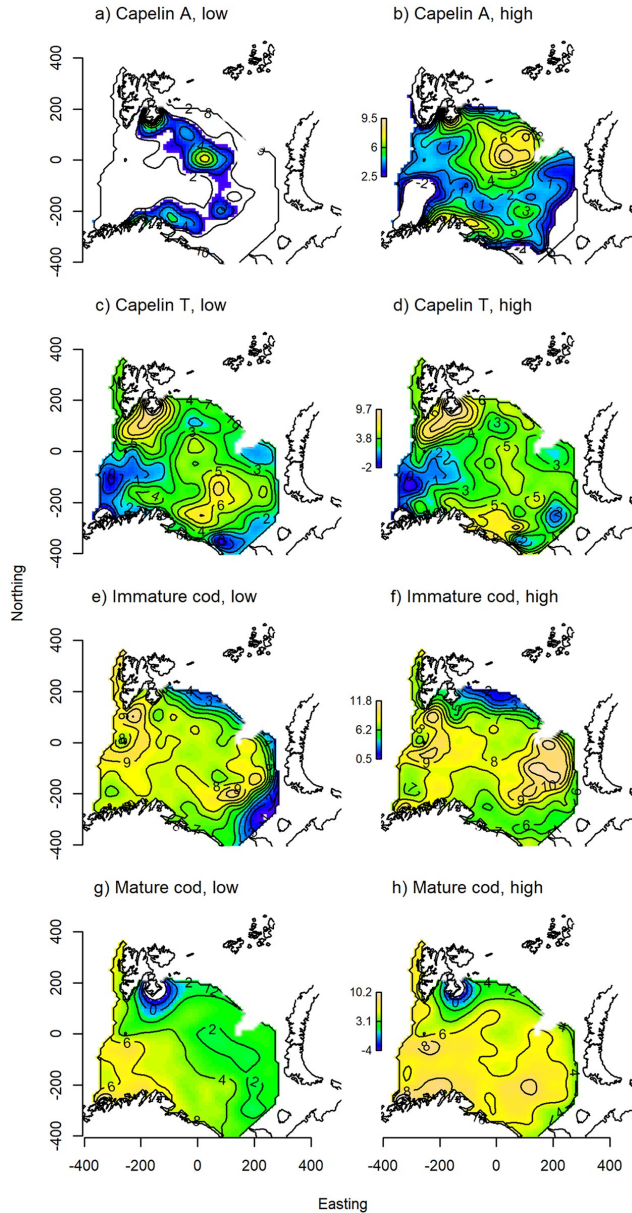


Fig 7. Predicted winter distributions. Winter distributions of A-B) acoustically estimated capelin, C-D) trawl-caught capelin, E-F) immature cod, and G-H) mature cod from the best candidate model for each component (Table 1). The different columns show the partial effects of stock biomass when the other model predictors were set to their across-year mean values in each location; the left column shows species distributions at low stock biomass (capelin: 0.628, cod: 1.63 million tonnes, measured in 2004), and the right at high stock biomass (capelin: 3.96, cod: 4.38 million tonnes, measured in 2013). The contour lines indicate local species density on the log-link scale, and the colours range from blue at low density to yellow at high density.

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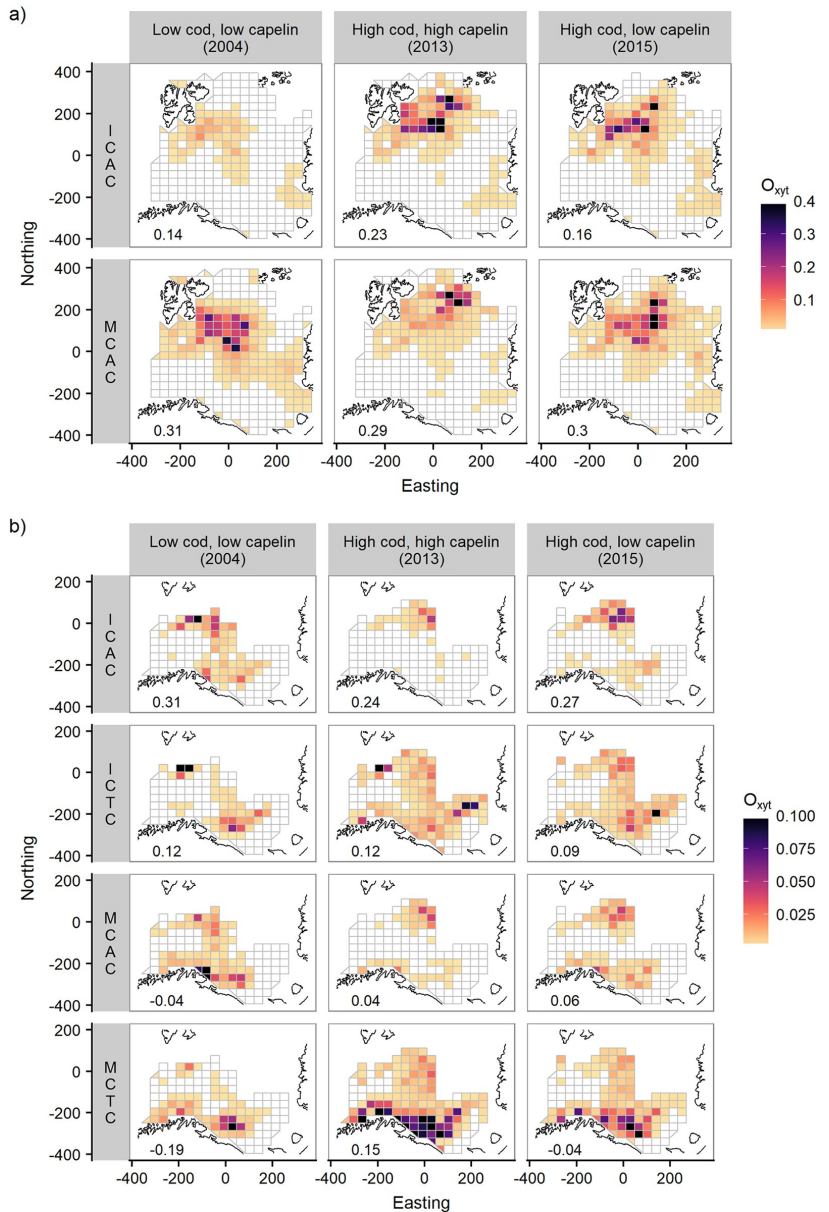


Fig 8. Cod-capelin overlap by season. Overlap ($O_{(x,y,t)}$) by component at contrasting cod and capelin biomass for A) autumn and B) winter, calculated on model predictions from the best candidate models. ICAC = immature cod and acoustic capelin, ICTC = immature cod and trawl capelin, MCAC = mature cod and acoustic capelin, MCTC = mature cod and trawl capelin. Overlap values > 0.4 ($n = 11$) in autumn and > 0.1 ($n = 20$) in winter were set to black colour to enable good visualisation of the variation in the main overlap range. Note the different ranges of the colour scales in the two seasons. The values in the bottom left corners of each panel is the correlation coefficient (Kendall's tau) between the predicted cod and capelin densities across the grid.

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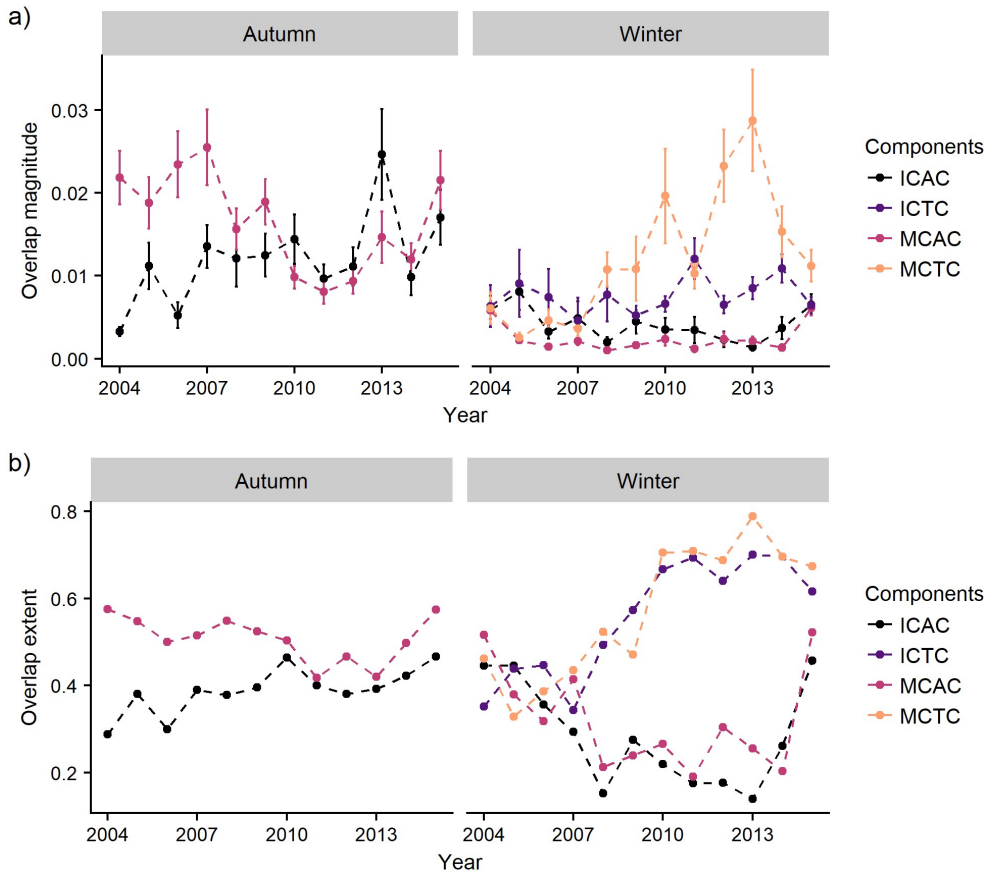


Fig 9. Temporal trends in the overlap. Mean overlap across the grid (magnitude, upper panels) and overlap extent (number of grid cells with overlap > 0.001 divided by the total number of grid cells, lower panels), by year, season, and component pair. ICAC = immature cod and acoustic capelin, ICTC = immature cod and trawl capelin, MCAC = mature cod and acoustic capelin, MCTC = mature cod and trawl capelin. The error bars show 95% confidence intervals of the mean. The sharp dip in the autumn ICAC overlap in 2014 is likely due to incomplete coverage of the immature cod component [27].

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(Fig 9, upper left panel). The overlap between immature cod and capelin was low when both stocks were at a relatively low level (2004), high when both stocks were at a high level (2013) and remained high as the cod stock remained at a high level and the capelin stock had collapsed (2015, Fig 8A, upper panel). There were less clear temporal trends in the overlap between mature cod and capelin (Fig 8A, lower panel). The overlap extent (number of grid cells with overlap > 0.001) between immature cod and capelin showed a positive trend across the study period, while the extent was more variable for the mature cod-capelin overlap (Fig 9, lower left panel).

Cod-capelin overlap in winter. Cod had a wider distribution than capelin also in winter (Fig 7). Immature cod overlapped with acoustic capelin mainly near the northern limit of the

area covered by the winter survey, except in the first years when they also overlapped farther south (Fig 8B, upper panels, S3 Appendix). There was also a region of overlap between immature cod and trawl capelin in the central-eastern part of the surveyed area and along the coast of Norway and Russia (Fig 8B, second row panels). Mature cod had a more southerly distribution than immature cod and this was reflected in the overlap with capelin. The highest overlap was along the Russian and Norwegian coasts; this was particularly pronounced for overlap with trawl capelin (Fig 8B, lower panels). There was also some overlap with acoustic capelin in the south and north (Fig 8B, third row panels). The highest mean overlap in winter was between mature cod and trawl capelin, and this overlap increased over time (Fig 9, upper right panel). The overlap extent was highly variable in winter for all component pairs, but increased over time for both the immature and mature cod-trawl capelin components (Fig 9, lower right panel).

Discussion

This is the first study to explicitly estimate overlap between cod and capelin in the Barents Sea. While overlap does not on its own imply consumption, the spatial pattern of overlap tells us where cod and capelin are more likely to interact as predator and prey. We found that overlap varied with season; the main overlap areas were east of Svalbard in autumn, and south of Svalbard and along the Norwegian/Russian coasts in winter. In autumn, the overlap area shifted towards the north-east during the study period. This could be attributed to increased cod stock biomass, and to a lesser extent, increased capelin stock biomass and increased temperature in this area. The autumn overlap remained high after the capelin stock collapse at the end of our study period. The spatial pattern of overlap in winter reflected the disjoint distribution of capelin when matures migrate towards the southern coasts of the Barents Sea to spawn and immatures remain closer to the autumn distribution area (discussed below).

Methodological considerations

The autumn survey has been designed to collect synoptic data on several trophic levels [29], while the winter survey has demersal fish as primary target. Therefore, factors related to winter survey methodology may influence the capelin part of the spatial analysis. In winter, mature capelin may migrate in the acoustic blind zones close to the bottom or close to the surface [9]. We therefore complemented the acoustic data with demersal trawl data, which include individuals in the acoustic blind zone at the bottom but not at the surface. The two data sources could not be combined; target trawl hauls for capelin are too few to reliably convert acoustic backscatter to biomass of immature and mature capelin at the resolution we used to study overlap. However, on a broad scale, the length distribution in demersal trawl samples is consistent with the generally acknowledged distribution of capelin in winter, and we used this to aid interpretation of the winter results (see below). The limitations of the winter survey data on capelin should be kept in mind when interpreting the results (but see [49, 50]).

In the present study, a main aim was to investigate spatial match between cod and capelin densities. For this purpose, the overlap index was defined such that high values of overlap at any given location resulted from high density of both species. Moreover, in order to express seasonal and inter-annual variation in overlap at a comparable scale, we considered overlap relative to densities within—not across—each year and season (see also [51] for a similar scaling approach). Having an index with the above-mentioned characteristics allowed us to assess spatial changes over time. Various indices of cod-capelin overlap have been applied in previous studies in other areas, with characteristics reflecting the objectives of the investigations. Cianelli and Bailey [43] applied the product of species densities at a given location. Rose and

O'Driscoll [52] applied the number of capelin available to cod within a specific radius. For future studies, it could be valuable to complement our index with, e.g., the potential contact index [53] to examine the number of capelin available to cod within a radius relevant to cod foraging. We may then be able to determine how the magnitude of our overlap index relates to the strength of potential predator-prey interaction.

Seasonal and temporal trends in the overlap

We found seasonal differences both in where and how strongly cod and capelin overlapped. The generally lower overlap in winter could partly be due to under-sampling of capelin in winter, particularly with acoustics (see above). However, differences in overlap between seasons are expected due to the seasonal variation in behaviour of both species. In autumn, feeding has high priority for cod and capelin, and both species remain in the feeding areas throughout the survey. We found that the autumn overlap was concentrated to the east of Svalbard for both immature and mature cod, and the overlap area moved towards the northeast during the study. The capelin stock was in a state of collapse during the last year of our study period, but the estimated consumption of capelin by cod remained high [27]. This is consistent with our result on autumn overlap which remained high in the year of collapse.

In contrast, in winter, immature and mature individuals of both species differ in their spatial preferences. Immature capelin overwinter in the northernmost ice-free areas of the Barents Sea, whereas mature capelin separate from the rest of the stock to start their spawning migration to the southern coasts [9]. Immature cod following migrating mature capelin to the coast of northern Norway have sustained a traditional spring fishery on cod for centuries [54]. Mature cod spawn along the northwest coast of Norway somewhat later than capelin, but they start migrating towards the spawning grounds around the time of the winter survey [25]. Mature cod feed when they are still inside the Barents Sea, while feeding is reduced on the spawning grounds [55]. We found that the overlap area with acoustic capelin was disjunct, with one overlap area southeast of Svalbard and one along the coast. Based on the length distribution in trawl samples (Fig 6E), we interpret the first overlap area as immature capelin (<14 cm, [23]) overlapping with cod. The cod here were immatures that had not followed mature capelin to their spawning sites, and mature cod that either had not started spawning migration or skipped spawning [56]. The second overlap area along the coast was between both immature and mature cod and mature capelin. For trawl capelin (and acoustic capelin in the first year, Fig 8B), the two areas were connected through the central parts of the surveyed area, and it is likely that the overlap here was with migrating capelin individuals (c.f. Fig 8 in [9]). Therefore, while capelin appears to be relatively more important as prey during winter (comprising 30–60% of the diet in winter, and 15–30% in autumn, study years 2004–2013, [15]), the overlap was more spatially and temporally variable than in autumn.

Constraints on the overlap

Prey availability to predators may be constrained by physiological adaptations to factors such as depth and/or temperature that differ from those of the prey (e.g., [57]). The prey can benefit from these constraints and find refuges, resulting in reduced predator-prey overlap (e.g., [3]). In the present study, we tested if the occupied habitat differed between cod and capelin by including temperature and depth in the distribution models. Differences in habitat could imply spatial refuges for capelin from cod. In autumn, no indication of refugia with respect to temperature for capelin was found, as cod and capelin occupied similar temperature ranges (Fig 3). The result contrasts with findings from other cod-capelin systems. In the Bering Sea, with co-occurrence of the Pacific cod (*Gadus macrocephalus*) and capelin, the cod-capelin link

is much weaker than in the Atlantic ecosystems. This weak link is the result of a cold pool that in some years keeps cod confined to the warmer waters on the southern shelf while capelin finds a refuge in the north [43]. In the Newfoundland-Labrador ecosystem, cod were spatially constrained to intermediate temperatures while capelin had a refuge in both the coldest and warmest waters [3]. Off Iceland, observed reduction in cod-capelin overlap during autumn in the early 2000s was related to increased inflow of warm Atlantic water triggering capelin to migrate farther off the shelf into deeper waters where cod did not follow [58, 59]. We found depth-related constraints for cod, but not so for capelin. A refugium in deep waters for capelin is thus possible, potentially due to costs of maintaining neutral buoyancy for cod in the deep ([60], and references therein).

Our results from the winter regarding overlapping habitats and spatial refuges were less clear than the results from autumn. The across-space correlations between cod and capelin densities were weak or negative in some years, reflecting the complex spatial distribution of the capelin stock (Figs 6I and 8, and S4 Appendix, values in bottom left corner of each panel). Parts of the capelin stock occurred in the coldest waters while cod appeared to avoid these water masses, providing capelin with a refugium (Fig 6). The density of trawl capelin increased along the coast in the south when local temperature increased, while the distribution of immature cod shifted north (Fig 5E and 5F). These reverse patterns suggest that increased temperature reduced the overlap in the north. The higher capelin densities in the south with higher water temperatures might be caused by earlier spawning migration in warm years [61].

Generally, the match between cod and capelin densities was low; the overlap never reached maximum value (across all years, two grid cells in autumn had overlap > 0.75 , but the majority of overlap values were ≤ 0.4 in autumn and ≤ 0.1 in winter). Possibly, the spatial match is stronger at a different scale. A process should be observed at the smallest scale where a driving variable affects the outcome of the process (the process scale, [62]). For the cod-capelin interaction, the process scale corresponds to the scale where cod or capelin can detect and respond to a change in the other's density, which is likely at a much smaller scale than we could study with the data at hand. However, the behavioural response race between predator and prey would most likely result in negative predator-prey associations and a weaker spatial match at a finer scale [2, 53].

Distribution of alternative prey could also influence the spatial distribution of cod, but was outside the scope of this paper. Johannesen et al. [63] studied cod-prey interaction in autumn (2004–2009), including capelin, amphipods (*Themisto* sp.), herring (*Clupea harengus*), shrimp (*Pandalus borealis*) and polar cod (*Boreogadus saida*) as alternative prey. The only consistently positive relationship between both cod diet and cod distribution and prey density was found for capelin. The strongest candidate as important alternative prey during autumn is polar cod, which is found in the cold waters of the northern Barents Sea.

A possible explanation for the weak spatial match is that it is not necessary for cod to track the highest densities of capelin. Considering that it takes several days for a cod to digest a stomach full of capelin in the cold waters of the Barents Sea [64], the time and energy required to track the highest capelin densities is perhaps better spent digesting while remaining in an area of intermediate capelin density. In the Newfoundland cod-capelin system, no evidence of aggregative response of cod to capelin was found at scales up to 10 km or 100 km [53, 65] (but see also [3]). Using bioenergetic calculations, Horne and Schneider [65] argued that cod did not need to actively track capelin since the prey encounter rate was higher than the digestive rate at the observed capelin density. Constraints on cod digestion, in turn influenced by temperature, may therefore reduce predation when capelin is above a certain density threshold and cod is satiated. Finally, we considered horizontal overlap only, but diurnal vertical migration by capelin [66] may affect cod's ability to efficiently track capelin.

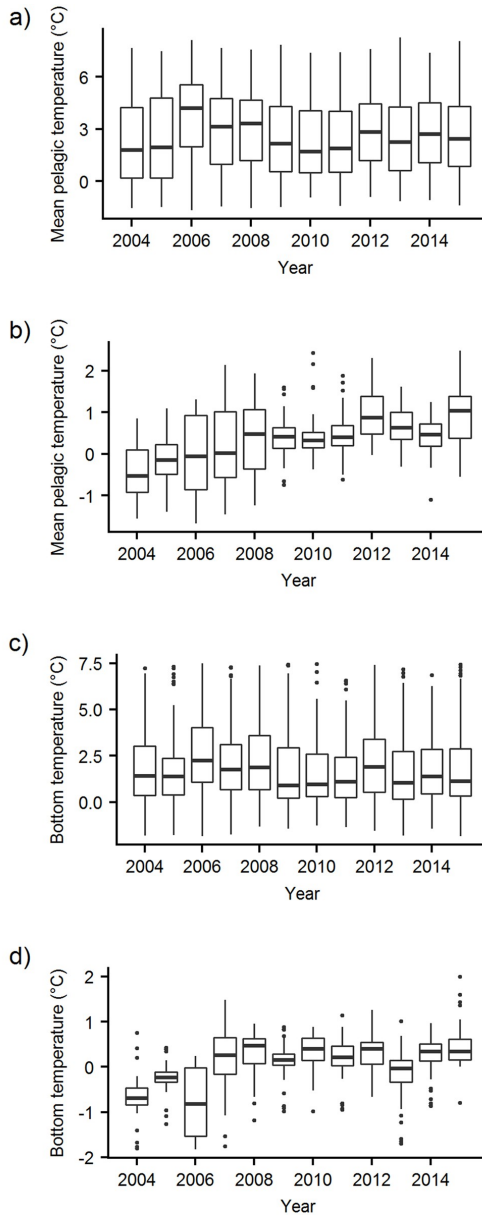


Fig 10. Autumn temperatures. Ecosystem survey measurements of A) mean pelagic temperature (50–200 m) in the entire study area, B) mean pelagic temperature in the north-eastern area (east of 40 E, north of 75 N), C) bottom temperature in the entire study area, D) bottom temperature in the north-eastern area, throughout the study period.

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The relative role of temperature and abundance on spatial distributions and overlap

Effects of the physical environment and of species abundance on distributions have been difficult to disentangle in other cod-capelin systems (e.g., [8]), and the Barents Sea is no exception. The large-scale distributions of both cod and capelin have been related to ocean temperature, as well as stock size [13, 16, 17, 63, 67–71]. Here we attempted to separate the two by accounting for both stock biomass and temperature in our models. We found strong effects of stock biomass on both cod and capelin distributions in autumn, which in particular affected the strength and spatial pattern of overlap between immature cod and capelin (Fig 8 a, upper panels), but more moderate effects of temperature. Similarly, in the Baltic cod population, stock size had a stronger effect on local cod density than hydrography [72]. While our study period was characterised by high and relatively stable temperatures [26], the stock sizes of cod and capelin varied greatly (Fig 1). Our results are thus consistent with the lack of inter-annual contrast in the temperature data. However, there was one exception to the stable autumn temperatures observed throughout the study period. In the north-eastern area, local temperature increased with almost 1 °C early in the study period (Fig 10), and we saw strong positive local effects of temperature on both cod and capelin densities in the same area (Fig 5A–5C). Together with the local effects of stock biomass, this explained the north-eastward shift in the overlap area between both cod components and capelin (Fig 8A and S4 Appendix).

In winter, influence of both temperature and stock biomass on the overlap was more variable than in autumn, since these factors either did not have strong effects on local species densities, had opposite effects on cod and capelin densities, or did not affect species densities in the main overlap areas. It is likely that the diverging behavioural motivation between immature and mature capelin, and the lack of a strong quantitative index of capelin density contribute to masking any clear signals in the winter data.

Implications for stock assessment and future work

Due to the difficulty of monitoring and estimating the capelin stock in winter immediately prior to the fishing season, the capelin stock prediction model used in the assessment simulates the stock six months into the future from the time of monitoring in autumn to terminated spawning. Predation by immature cod on mature capelin is explicitly modelled for the first three months of the year, while interactions between other cod-capelin components are ignored [22, 23]. Our results on winter overlap (Fig 8B) demonstrate that interactions between other cod-capelin components may be important (see also [23, 24, 55]), emphasising that assumptions in stock prediction models that rely on an understanding of predator-prey interactions in highly dynamic systems should be tested regularly. The analytic framework applied here can be used to analyse and assess predator-prey overlap as part of regular monitoring.

Supporting information

S1 Appendix. Soap film smoother construction.
(PDF)

S2 Appendix. Wild bootstrap code and results.
(HTML)

S3 Appendix. Smooth functions of sun height and survey day.
(PDF)

S4 Appendix. Predicted overlap by year. (PDF)

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Construction of a border and internal knots for the soap film smoother

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Consider a marine species distributed in a region that contains a physical boundary, such as an island. Species density is naturally zero on land, and we can conceive of a situation where the density on one side of the island is very different from that on the other side. When using conventional smoothing splines, such as the default thin-plate regression splines in GAM (Wood 2003), the smooth functions are fitted over the entire x-y-space defined by the range of our sampling locations. Since the model does not know that this space contains an island, there is a risk of it fitting a non-zero density on the land area, and the model is also likely to fit very similar densities on all sides of the island since smooth functions must change gradually with the Euclidian distance (Miller and Wood 2014). These issues can lead to prediction errors. One way to account for geographical boundaries in the GAM is to use the soap film smoother (Wood et al. 2008, see also Miller and Wood 2014 for an alternative approach). The idea is to restrict the smooth function by fitting it within a certain boundary, much like the shape of a soap bubble is determined by the bubble wand. In our case, we used the coastline of Norway and Russia, as well as the contours of the main island groups within the Barents Sea (Svalbard, Franz Josef Land, and Novaya Zemlya) as our boundary.

Two things need to be specified in order to construct a soap film smoother:

1. The boundary within which to fit the smooth function, which can include holes for islands.

2. A number of knots with grid spacing delta, inside this boundary area. These knots are not the same as the ones specified with the 'k' argument in the GAM; those knots determine the number of basis functions that will be solved when fitting a smooth term, while the interior knots determine the accuracy of those functions.

To check that 1. and 2. have been set up correctly, this function is helpful [Miller 2015, https://github.com/dill/soap_checker].

The following code is based on the one proposed by Simpson (2016 [<http://www.fromthebottomoftheheap.net/2016/03/27/soap-film-smoothers/#fn9>]), see also Augustin et al. 2013), extended to include the construction of a complex border from a shapefile of the Barents Sea. Libraries required are: *raster*, *rgdal*, *sp*, *rgeos*, *rmapshaper*, *broom*, *dplyr*, and *mgcv*.

First, we construct the boundary, or the soap bubble wand:

```
#This is a shapefile that contains the coastline and islands of interest
#The readOGR function converts the shapefile into a SpatialPolygonsDataFrame
polygons <- readOGR(dsn = 'C:/JF Library/WP2/WP2 analyses/Shapefiles BS/50m',
                    layer = 'land_BS')

## OGR data source with driver: ESRI Shapefile
## Source: "C:\JF Library\WP2\WP2 analyses\Shapefiles BS\50m", layer: "land_BS"
## with 51 features
## It has 2 fields

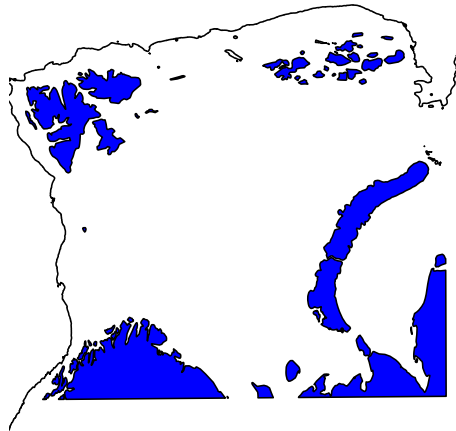
#This shapefile describes the 500 m isobath. This will be a part of the
#outer border as a way of restricting the
#study area to the Barents Sea shelf.
iso500 <- readOGR(dsn = 'C:/JF Library/WP2/WP2 analyses/Shapefiles BS',
                  layer = 'Kontur500_2')
```

```

## OGR data source with driver: ESRI Shapefile
## Source: "C:\JF Library\WP2\WP2 analyses\Shapefiles BS", layer: "Kontur500_2"
## with 423 features
## It has 1 fields

par(mar=c(0,0,0,0))
plot(polygons, col = "blue")
plot(iso500, add = T)

```



The outlines need to be simplified since they are too complicated for the soap smoother to handle, and the isobath data extends outside the study area. The level of complexity that can be used in the GAM is a matter of trial and error. Here, I settle on keeping 10 % of the original data for the islands and coast, and 1 % for the 500 m isobath, which contained a lot of data. This way a few small islands and fine contour details are lost, but we keep the most important features.

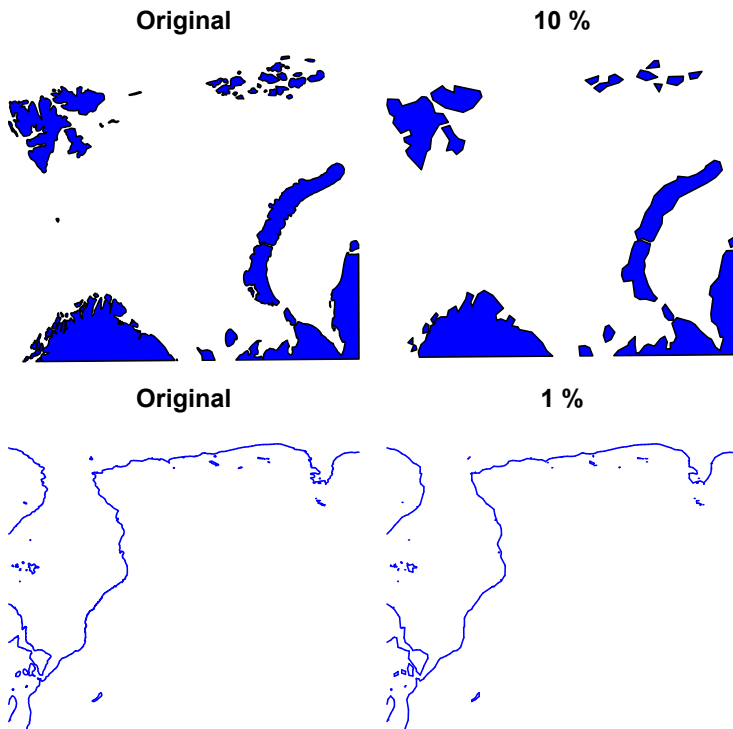
```

#Simplify the outline of the land masses
ocean.simp <- ms_simplify(polygons, keep = 0.1,
                          keep_shapes = FALSE, explode = TRUE)

```

```
iso.simp <- ms_simplify(iso500, keep = 0.01,
                        keep_shapes = FALSE, explode = TRUE)
```

```
par(mfrow = c(2,2), mar=c(0,0,1,0))
plot(polygons, col = "blue", main = "Original")
plot(ocean.simp, col = "blue", main = "10 %")
plot(iso500, col = "blue", main = "Original")
plot(iso.simp, col = "blue", main = "1 %")
```



```
## null device
##      1
```

I then convert the coordinates to stereographic projection, centered in the approximate middle

of our study area. This coordinate system accounts well for the curvature of the earth at high latitudes.

```
#Project in polar stereographic coordinate system
land <-
  spTransform(ocean.simp, "+proj=stere +lat_0=75 +lon_0=35 +datum=WGS84 +units=m")
isobath <-
  spTransform(iso.simp, "+proj=stere +lat_0=75 +lon_0=35 +datum=WGS84 +units=m")
```

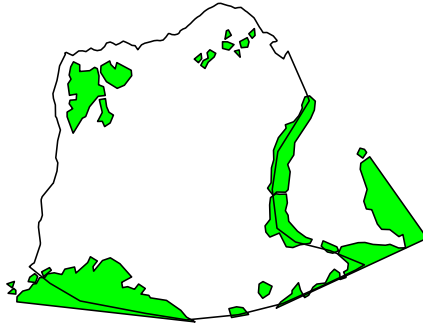
Because the isobath data that describes the 500 m depth contour is in a SpatialLines format and not polygons, some processing is needed to get everything ready for clipping out the islands from the ocean.

```
#This file contains a simple boundary encircling the isobath,
#from which we will clip out the contours of the isobath
boundary <-
  read.table("C:/JF Library/WP2/WP2 analyses/Soap smooths/boundary clipping polygon auto
            header = TRUE)
#Convert it to a polygon
p <- Polygon(boundary)
ps <- Polygons(list(p),1)
sps <- SpatialPolygons(list(ps))
proj4string(sps) <- CRS("+proj=stere +lat_0=75 +lon_0=35 +datum=WGS84 +units=m")
par(mar=c(0,0,0,0))
plot(isobath)
plot(sps, add = TRUE)
```



```
#Clip out the isobath from the boundary polygon:
# intersect the line with the polygon
lpi <- gIntersection(sps, isobath)
# create a very thin polygon buffer of the intersected line
blpi <- gBuffer(lpi, width = 0.000001)
# split using gDifference
dpi <- gDifference(sps, blpi)
# convert polygon to data frame
dpi.df <- tidy(dpi)
# select the piece of interest
dpi.df <- dpi.df[dpi.df$piece == 1, ]
#Make new polygon from the fixed border
dpi.list <- list(x = dpi.df$long, y = dpi.df$lat)
p <- Polygon(dpi.list)
ps <- Polygons(list(p),1)
sps <- SpatialPolygons(list(ps))
proj4string(sps) <- CRS("+proj=stere +lat_0=75 +lon_0=35 +datum=WGS84 +units=m")
```

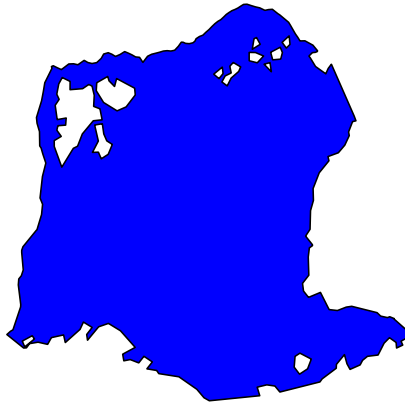
```
plot(land, col = "green")
plot(sps, add = TRUE)
```



```
#Simplify the outer border a little more
sps.simp <- ms_simplify(sps, keep = 0.30, keep_shapes = TRUE, explode = TRUE)
#Add a buffer and clip out the land masses from the ocean layer
tst <- gBuffer(sps, byid=TRUE, width=0)
tst2 <- gBuffer(land, byid=TRUE, width=0)
ocean.aut <- erase(tst, tst2)
#Check so the geometry of this new polygon is valid, and plot it
rgeos::gIsValid(ocean.aut)

## [1] TRUE

plot(ocean.aut, col = "blue")
```



```
#Convert the spatial object to a data frame
ocean.xy.aut <- tidy(ocean.aut)
#express coordinates in nautical miles instead of metres to match the data
ocean.xy.aut$long <- ocean.xy.aut$long/1852
ocean.xy.aut$lat <- ocean.xy.aut$lat/1852
ocean.xy.aut <- ocean.xy.aut %>% rename(x = long, y = lat)
```

This is our boundary polygons that contain area we want to fit the soap film smooths in.

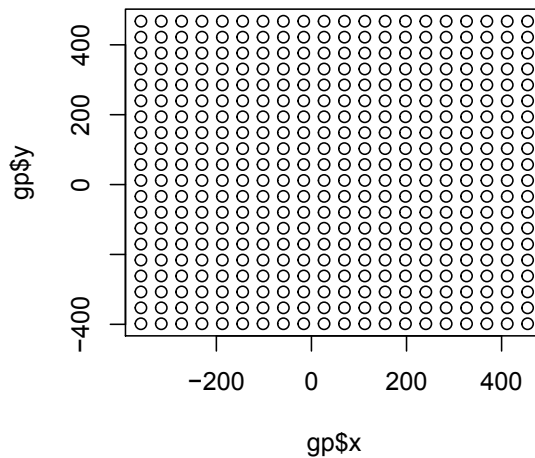
Next we define the interior knots. Following the method of Simpson (2016), I use the extent of the data to define a regular grid over the study area. According to Wood (2008), the spacing of the interior knots should generally be smaller than the distance between the observations. However, since our study area is so large this gives us a very large number of knots that slows down the gam-function considerably. Such a fine resolution also leads to the spatial term capturing previously robust patterns of the other covariates, suggesting that we are overfitting the model. Therefore, I settle on using a knot spacing of 40 nm, slightly larger than the ~35 nm interstation distance of the autumn data.

```

#Load the data
autdat <-
  read.table("C:/JF Library/WP2/WP2 analyses/Eco/eco trawl clipped for soap.txt",
            header = TRUE)

#Make knots from the geographical extent of the observations
N <- floor((abs((max(autdat$x)-min(autdat$x)))/40))
gx <- seq(min(autdat$x), max(autdat$x), length.out = N)
gy <- seq(min(autdat$y), max(autdat$y), length.out = N)
gp <- expand.grid(gx, gy)
names(gp) <- c("x","y")
plot(gp$x, gp$y)

```



```

#The GAM needs the border coordinates as a list of lists,
#where each list describes one border segment or island:
oceancoords <- ocean.xy.aut %>% dplyr::select(x,y,piece)

```



```

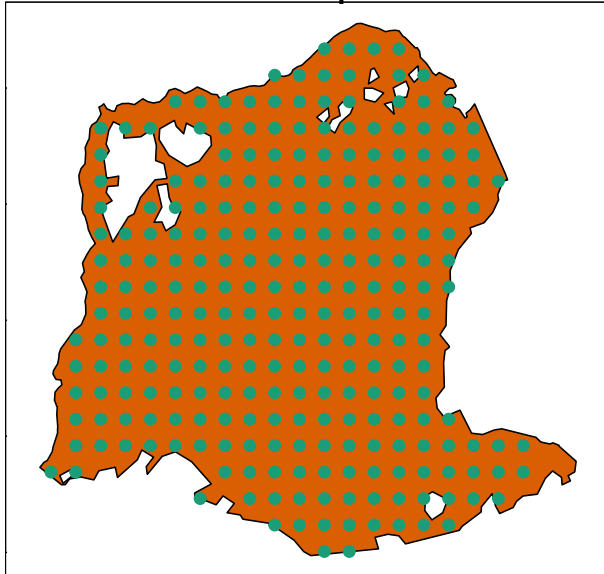
names(oceancoords) <- c("x", "y", "piece")
borderlist <- split(oceancoords, oceancoords$piece)
names(borderlist)

## [1] "1" "2" "3" "4" "5" "6" "7" "8" "9" "10" "11" "12" "13"

border.aut <- lapply(borderlist, `[,`, c(1,2))
nr <- seq(1,13)
border.aut <- lapply(nr, function(n) as.list.data.frame(border.aut[[n]]))
#We can now use the inSide function from mgcv to select knots
#that are inside the border
knots <- gp[with(gp, inSide(bnd = border.aut, x, y)), ]
names(knots) <- c("x", "y")
#And then check that the border and knots are in order with the
#soap_check function
source("C:/JF Library/WP2/WP2 analyses/Soap smooths/soap_check.R")
par(mar=c(0,0,1,0))
soap_check(bnd = border.aut, knots = knots)

```

Red indicates soap film surface



```
## [1] TRUE
```

This seems to be in order, but unfortunately the algorithm that GAM uses to check if the knots are inside the boundary is not the same as the one used by the `InSide` function. It is therefore often necessary to adjust the location of some knots manually.

```
#Load a table of adjusted knots
```

```
knots.aut <-
```

```
  read.table("C:/JF Library/WP2/WP2 analyses/Soap smooths/knots autumn 40 nm.txt",  
            header = T)
```

Finally, we must make sure that all the data we want to analyse is inside the boundary area.

```
#Make sure there is no data outside the boundary defined by the ocean polygon
```

```
#Convert data to spatial
```

```
autdat.sp <- autdat
```

```
autdat.sp$x <- autdat.sp$x*1852 #convert back from nmi to m
```

```

autdat.sp$y <- autdat.sp$y*1852
autdat.sp <-
  SpatialPointsDataFrame(autdat.sp[,c(6,5)], autdat.sp,
proj4string = CRS("+proj=stere +lat_0=75
                    +lon_0=35 +datum=WGS84 +units=m"))
#Clip the data to match the ocean polygon -
#this removes a few observations from a year when ice conditions
#allowed sampling north-east of Franz Josef Land.
data.clipped <- crop(autdat.sp, ocean.aut)
par(mar=c(0,0,1,0))
plot(data.clipped)
plot(ocean.aut,add=T)

```



```

autdat <- data.frame(data.clipped)
autdat$x <- autdat$x/1852 #convert back to nmi
autdat$y <- autdat$y/1852

```

Now we are ready to fit a GAM with soap film smooths. I will illustrate this with a model that describes the density of immature cod in autumn as a function of a spatial term fitted

with the soap basis, in addition to conventional smooth terms of bottom depth, bottom temperature, and sunheight and survey day to correct for timing of sampling. This model takes a bit longer to run than one with a conventional smoothing basis, but we can control this to some extent by reducing the number of internal knots that is supplied in the 'knots = knots.aut' argument (as constructed above). The soap basis is specified in the 'bs = "so"' argument, and the list of border coordinates in the 'xt = list(bnd = border)' argument. We also put a constraint of 20 on the basis dimension ("k") of the spatial smooth to reduce runtime and avoid overfitting the spatial field.

```
imm.aut.soap <- gam(cod.imm ~ s(bio_cod, k = 5) +
                    s(x, y, k = 20, bs = "so", xt = list(bnd = border.aut)) +
                    s(sunheight, k = 5) + s(s.day, k = 5) +
                    s(b_depth, k = 5) + s(b_temp, k = 5),
                    data = autdat, family = tw(), method = "REML", knots = knots.aut)
```

```
summary(imm.aut.soap)
```

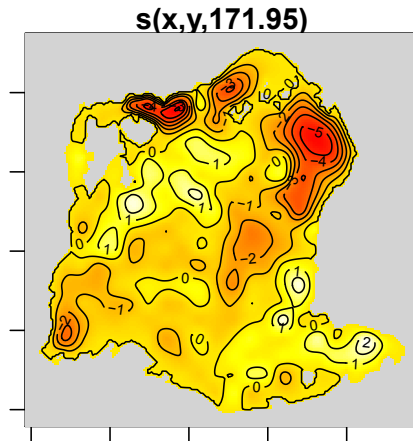
```
##
## Family: Tweedie(p=1.628)
## Link function: log
##
## Formula:
## cod.imm ~ s(bio_cod, k = 5) + s(x, y, k = 20, bs = "so", xt = list(bnd = border.aut))
##     s(sunheight, k = 5) + s(s.day, k = 5) + s(b_depth, k = 5) +
##     s(b_temp, k = 5)
##
## Parametric coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)   6.8459      0.0801   85.47  <2e-16 ***
```

```

## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##           edf Ref.df      F p-value
## s(bio_cod)   3.308   3.743 26.526 < 2e-16 ***
## s(x,y)      171.948 250.000   8.168 < 2e-16 ***
## s(sunheight) 3.132   3.618 30.101 < 2e-16 ***
## s(s.day)     3.161   3.634   4.620 0.00159 **
## s(b_depth)   3.827   3.970 113.427 < 2e-16 ***
## s(b_temp)    3.663   3.924 15.587 1.23e-12 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) = 0.144  Deviance explained = 49.2%
## -REML = 30742  Scale est. = 23.134  n = 4644

par(mar=c(1,1,1,1))
plot(imm.aut.soap, select = 2)

```



Let us compare this model with one fitted with the usual “tp” smoothing basis. Here we put no constraint on the $s(x,y)$ -term to let the gam-function find the best fit of this term, i.e., the best possible model with tp-basis.

```
imm.aut.tp <- gam(cod.imm ~ s(bio_cod, k = 5) + s(x, y) +
                  s(sunheight, k = 5) + s(s.day, k = 5) +
                  s(b_depth, k = 5) + s(b_temp, k = 5),
                  data = autdat, family = tw(), method = "REML")
```

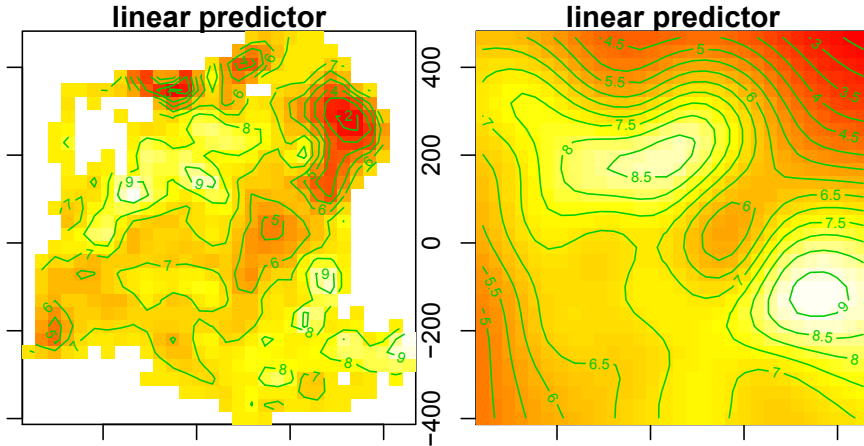
```
summary(imm.aut.tp)
```

```
##
## Family: Tweedie(p=1.653)
## Link function: log
##
## Formula:
## cod.imm ~ s(bio_cod, k = 5) + s(x, y) + s(sunheight, k = 5) +
## s(s.day, k = 5) + s(b_depth, k = 5) + s(b_temp, k = 5)
##
```

```

## Parametric coefficients:
##           Estimate Std. Error t value Pr(>|t|)
## (Intercept) 6.67663    0.02311   288.9 <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##           edf Ref.df      F p-value
## s(bio_cod)  2.667  3.188  25.620 < 2e-16 ***
## s(x,y)      27.802 28.901  37.665 < 2e-16 ***
## s(sunheight) 3.135  3.624  27.737 < 2e-16 ***
## s(s.day)    2.628  3.164   4.031 0.00586 **
## s(b_depth)  3.797  3.974 174.393 < 2e-16 ***
## s(b_temp)   3.557  3.898  38.870 < 2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) = 0.0887   Deviance explained = 38.7%
## -REML = 30944   Scale est. = 22.656    n = 4644
par(mfrow = c(1,2), mar=c(1,1,1,1))
vis.gam(imm.aut.soap, view = c("x", "y"), plot.type = "contour")
vis.gam(imm.aut.tp, view = c("x", "y"), plot.type = "contour")

```



It is immediately apparent that the tp-model predicts high densities in a land area in the south east, since we have sampled high cod densities close to the coast there. Though it is more complex, the soap model has higher explanatory power than the tp-model, and lower AIC.

```
##                df      AIC
## imm.aut.soap 195.08419 61197.12
## imm.aut.tp   48.91781 61901.69
```

Choosing the number of internal knots

As mentioned above, choosing the number and placement of internal knots can be tricky and time consuming. It is also crucial to the fit of the model, since these knots determine the spatial resolution of the smooth function(s). This sets the soap film smoother apart from other basis functions where it is often enough to specify them directly in the call to `gam` without previous preparation. It is therefore important to explore the effect of changing the number and placement of the knots in order to find a reasonable trade-off between resolution and computational time; the latter is particularly crucial for highly complex models. For this

analysis, we got a similar general pattern of distribution if we removed up to 20 % of the knots we had settled on using, but relevant finer features were lost. Thus, when using the soap film smoother, consider how fine features are relevant to the objectives of your study and how this will affect the runtime of your models.

References

Augustin, N. H., Trenkel, V. M., Wood, S. N., & Lorance, P. (2013). Space-time modelling of blue ling for fisheries stock management. *Environmetrics*, 24(2), 109-119. doi:10.1002/env.2196

Miller, D. L., and Wood, S. N. 2014. Finite area smoothing with generalized distance splines. *Environmental and Ecological Statistics*, 21: 715-731. doi:10.1007/s10651-014-0277-4

Miller, D. L. 2015, August 15. "Check whether a soap film smoother boundary and knots make sense". *Github.com*. Retrieved August 29, 2017, from https://github.com/dill/soap_checker

Simpson, G. 2016, March 27. "Soap-film smoothers & lake bathymetries". *fromthebottomoftheheap.net*. Retrieved August 29, 2017, from <http://www.fromthebottomoftheheap.net/2016/03/27/soap-film-smoothers/#fn9>

Wood, S. N., Bravington, M. V., & Hedley, S. L. (2008). Soap film smoothing. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 70(5), 931-955. doi:10.1111/j.1467-9868.2008.00665.x

See also: [<https://people.maths.bris.ac.uk/~sw15190/talks/soap-talk.pdf>]

Wild bootstrap on the capelin acoustic data

Johanna Fall and Lorenzo Ciannelli

September 21, 2018

Example code for winter acoustic data

```
##### Wild bootstrap on the capelin acoustic data
##### after Llope et al. (2009) #####

#Fit a gam to the data. Since the fitting of soap smooths is too slow
#to do 1000 iterations in a reasonable time, we fit a model with the default
#tp-basis. This model has similar residual autocorrelation as
#the corresponding model with soap basis. We will run the bootstrap
#separately for each year and therefore do not include year
#(or biomass which is correlated with year) as a covariate.
gam1 <- gam(capelin ~ s(x, y, k = 20) + #using same k as in the soap models
            s(sunheight, k = 5) + s(s.day, k = 5) + s(b_depth, k = 5) +
            s(p_temp, k = 5), data = windat, family = tw())

# summary(gam1)
# Family: Tweedie(p=1.607)
# Link function: log
#
# Formula:
# capelin ~ s(x, y, k = 20) + s(sunheight, k = 5) + s(s.day, k = 5) +
# s(b_depth, k = 5) + s(p_temp, k = 5)
#
# Parametric coefficients:
# Estimate Std. Error t value Pr(>|t|)
# (Intercept) 2.292 0.050 45.85 <2e-16 ***
# ---
# Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
#
# Approximate significance of smooth terms:
# edf Ref.df F p-value
# s(x,y) 18.322 18.948 72.838 < 2e-16 ***
# s(sunheight) 1.005 1.010 33.023 9.09e-09 ***
# s(s.day) 3.856 3.987 9.015 1.48e-06 ***
# s(b_depth) 3.083 3.595 1.892 0.0838 .
# s(p_temp) 3.902 3.994 36.259 < 2e-16 ***
# ---
# Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```

#
# R-sq.(adj) = 0.168  Deviance explained = 50.2%
# -REML = 9052.9  Scale est. = 19.718  n = 3994

#Extract the response residuals for calculating CIs.
#We use the response residuals since they
#are straightforward to add back to the predicted values,
#while still preserving the autocorrelation in the data
cap.res.response <- residuals(gam1, type = "response")

#Extract scaled pearson residuals (scaled to the variance
#of the model fit) for calculating p-values. We use the scaled residuals
#here to get more accurate p-values,
#since they reflect the true error of the model
cap.res.scaled<-residuals(gam1,type='scaled.pearson')

##P-values and CI
years<-unique(windat$year)

#Create matrices to iterate over, one for the smooth terms
#(and one for the parametric terms if any)
#Here we will store the F-statistic for each term
#one column for each smooth term in model
ps.boot<-matrix(NA,ncol=5,nrow=1000)
#if there are parametric terms in model
# pp.boot<-matrix(2000,ncol=1,nrow=1000)*NA

#Create matrices for each covariate
#where we will store the predicted values for each iteration
cs.pos<-matrix(nrow(windat)*1000,ncol=1000,nrow=nrow(windat))*NA
cs.depth<-cs.pos
cs.sunheight<-cs.pos
cs.sday <- cs.pos
cs.temp <- cs.pos

#Create new variables for the scaled residuals
#that will be randomly assigned
#a new sign for each iteration
windat$res.scaled<-NA
windat$res.response<-NA

#Number of iterations in the bootstrap
b<- 1000

```

```

#Run the bootstrap (took approximately 7 hours for this model)
for(i in 1:b){
  for(j in 1:length(years)){
    #randomly change sign of all residuals within a year:
    windat$res.scaled[windat$year==years[j]]<-
      cap.res.scaled[windat$year==years[j]]*sample(c(-1,1),1)
    windat$res.response[windat$year==years[j]]<-
      cap.res.response[windat$year==years[j]]*sample(c(-1,1),1)
    #add residuals to model fit
    windat$newy[windat$year==years[j]]<-
      gam1$fitted.values[windat$year==years[j]]+
      windat$res.response[windat$year==years[j]]
    #make sure there are no negative predictions
    #(capelin must be >=0 - the response in untransformed
    #in a model with Tweedie distribution)
    windat$newy[windat$year==years[j] & windat$newy < 0] <- 0}
    #fit a model to the scaled residuals (whose sign were randomly flipped),
    #these models will be used to calculate p-values
    boot.gam<-gam(res.scaled ~ s(x, y, k = 20) + s(sunheight, k = 5) +
      s(s.day, k = 5) + s(b_depth, k = 5) +
      s(p_temp, k = 5), data = windat)
    #add the response residuals to the data and fit a new model,
    #these models will be used to get the upper and lower CI-limits
    boot.gam.data<-gam(newy ~ s(x, y, k = 20) + s(sunheight, k = 5) +
      s(s.day, k = 5) + s(b_depth, k = 5) +
      s(p_temp, k = 5), data = windat, family = tw())
    #Store predictions for the data +/- residuals
    cs.posW[,i]<-predict(boot.gam.data,type='terms')[,1]
    cs.sunheightW[,i]<-predict(boot.gam.data,type='terms')[,2]
    cs.sdayW[,i]<-predict(boot.gam.data,type='terms')[,3]
    cs.depthW[,i]<-predict(boot.gam.data,type='terms')[,4]
    cs.tempW[,i]<-predict(boot.gam.data,type='terms')[,5]
    #Store the table of smooth term fits for residuals model
    ps.bootW[i,]<-summary(boot.gam)$s.table[,3]
  }
}

#Calculate new p-values based on the mean F statistic over the 1000 runs.
#The new p-value is the percentage (probability) of the bootstrapped
#F or t values larger or equal to observed ones (original gam)
p.vals.posW<- sum(1*(ps.bootW[,1]>=summary(gam1)$s.table[1,3]))/b
#0
p.vals.sunW<- sum(1*(ps.bootW[,2]>=summary(gam1)$s.table[2,3]))/b
#0.02
p.vals.sdayW<- sum(1*(ps.bootW[,3]>=summary(gam1)$s.table[3,3]))/b

```

```

#0.004
p.vals.depthW<- sum(1*(ps.bootW[,3]>=summary(gam1)$s.table[4,3]))/b
#0.327
p.vals.tempW<- sum(1*(ps.bootW[,3]>=summary(gam1)$s.table[5,3]))/b
#0

#Calculate CI for each smooth term

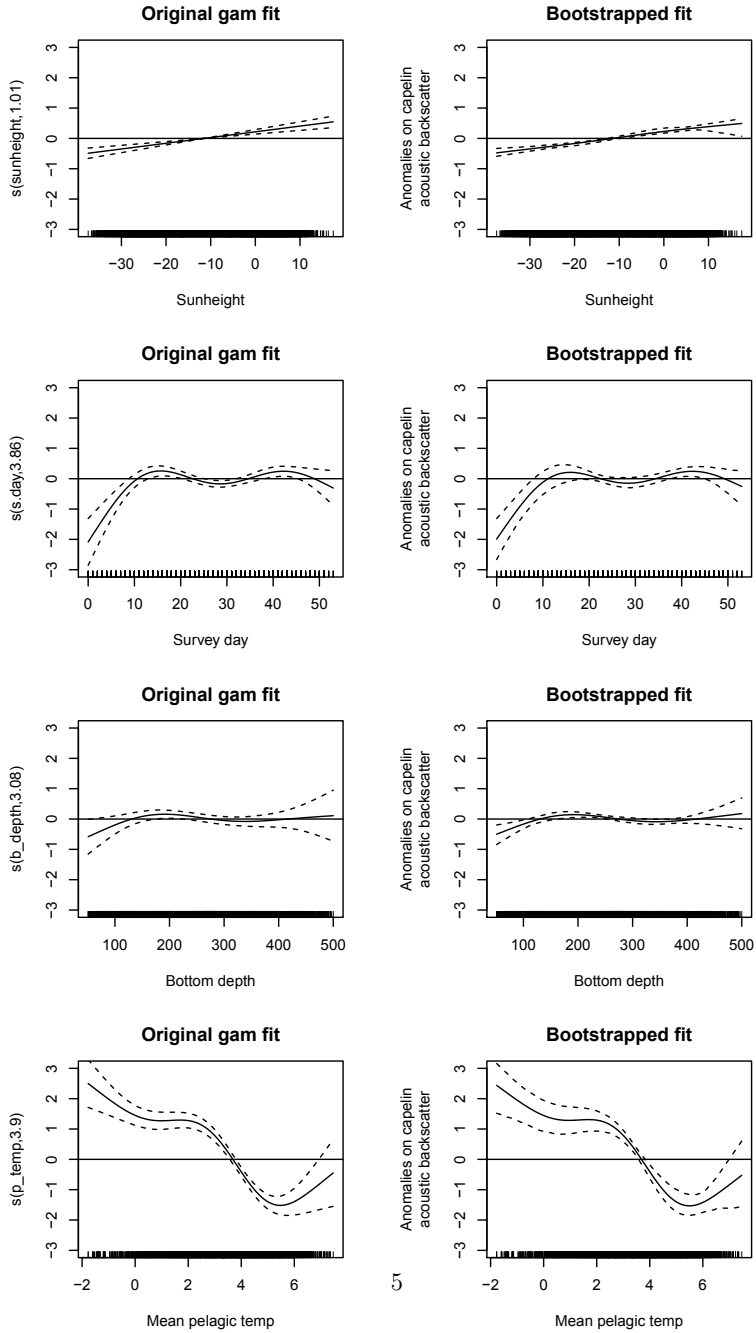
#1. calculate the mean predicted value (smooth contribution)
#for each data point across the 1000 iterations.
mean.sunW<-apply(cs.sunheightW,1,mean)
#2. and the lower bounds of the 95 % CI
low.sunW<-apply(cs.sunheightW,1,function(x)quantile(x,0.025))
#3. and the upper bounds
up.sunW<-apply(cs.sunheightW,1,function(x)quantile(x,0.975))

#Similarly, for the other covariates
mean.sdayW<-apply(cs.sdayW,1,mean)
low.sdayW<-apply(cs.sdayW,1,function(x)quantile(x,0.025))
up.sdayW<-apply(cs.sdayW,1,function(x)quantile(x,0.975))
mean.depthW<-apply(cs.depthW,1,mean)
low.depthW<-apply(cs.depthW,1,function(x)quantile(x,0.025))
up.depthW<-apply(cs.depthW,1,function(x)quantile(x,0.975))
mean.tempW<-apply(cs.tempW,1,mean)
low.tempW<-apply(cs.tempW,1,function(x)quantile(x,0.025))
up.tempW<-apply(cs.tempW,1,function(x)quantile(x,0.975))

```

Plotting the bootstrapped smooth functions

Winter

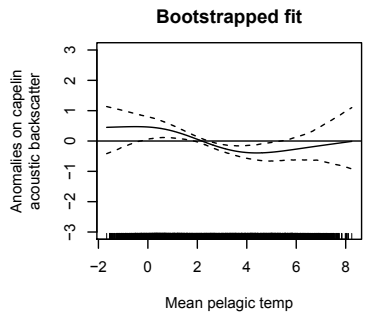
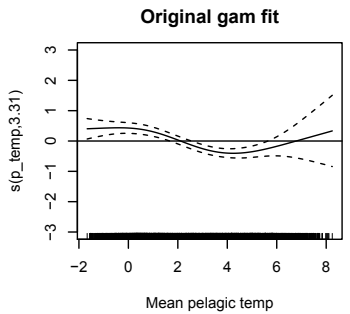
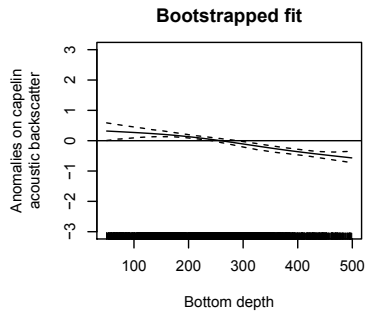
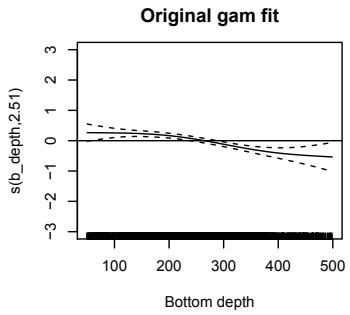
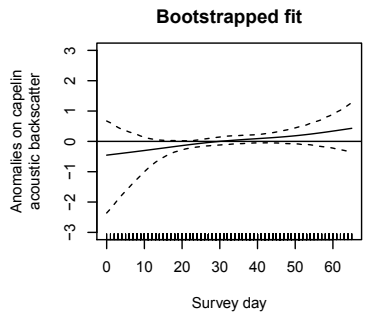
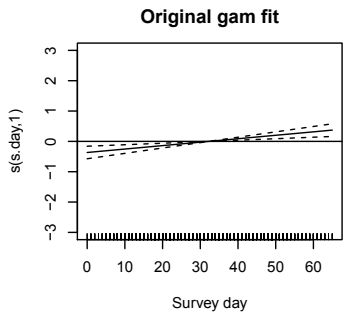
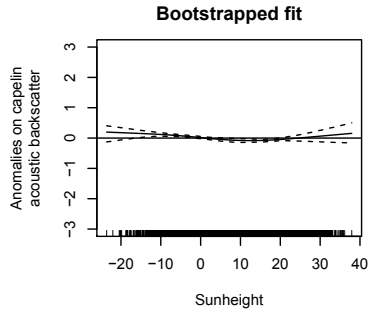
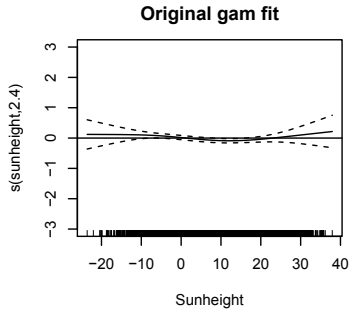


In this case, all covariates except depth remained significant ($p < 0.05$) after the bootstrap. This is in line with depth being near- or non-significant in some of our more complex candidate models (see main paper). Generally, the mean effects and confidence intervals were similar between the original model fit and the bootstrapped fit.

Autumn

For the autumn data, the bootstrapped confidence intervals for survey day, depth, and temperature resulted in non-significant p-values. While depth was non-significant in some of the more complex candidate models, survey day and temperature were clearly important contributors to model fit when added as spatially variant terms in the candidate models. It is likely that the spatially variant formulations and the soap smoother then captured more of the residual autocorrelation in the models. For the autumn data, too, the confidence intervals and mean effects effects were nevertheless similar between the original model fit and the bootstrapped fit.

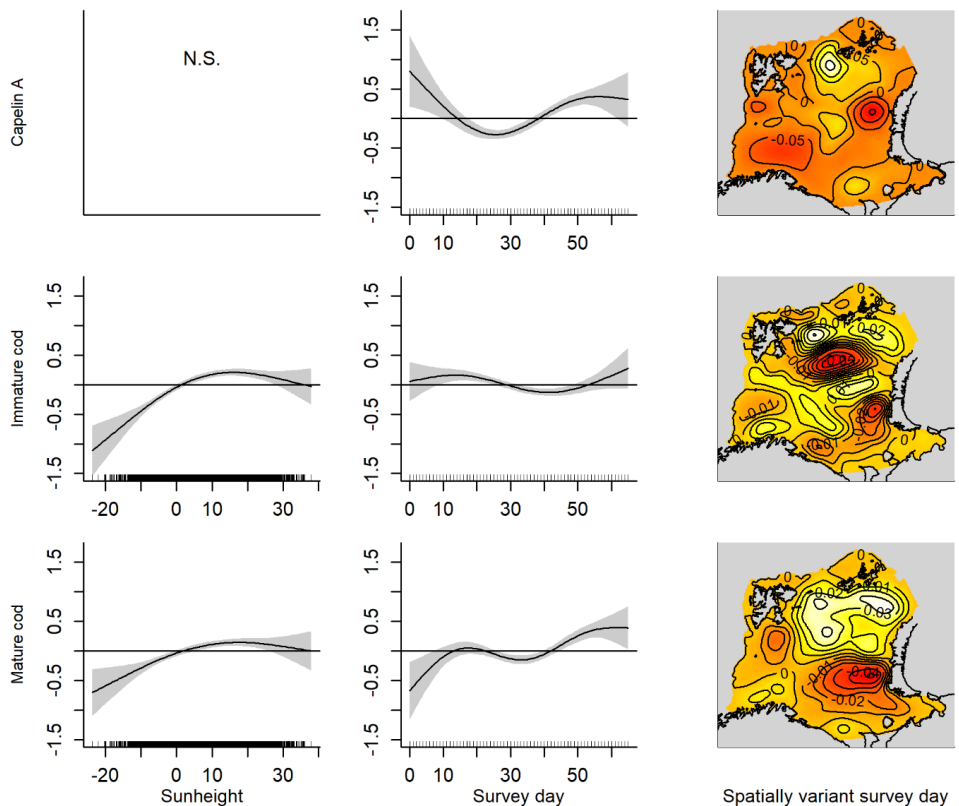
```
#Calculate new p-values based on the mean F statistic over the 1000 runs.  
#The new p-value is the percentage (probability) of the  
#bootstrapped F or t values larger or equal to observed ones (original gam)  
p.vals.pos<- sum(1*(ps.boot[,1]>=summary(gam2)$s.table[1,3]))/1000  
#0  
p.vals.sun<- sum(1*(ps.boot[,2]>=summary(gam2)$s.table[2,3]))/1000  
#0.029  
p.vals.jul<- sum(1*(ps.boot[,3]>=summary(gam2)$s.table[3,3]))/1000  
#0.081  
p.vals.depth<- sum(1*(ps.boot[,3]>=summary(gam2)$s.table[4,3]))/1000  
#0.123  
p.vals.temp<- sum(1*(ps.boot[,3]>=summary(gam2)$s.table[5,3]))/1000  
#0.118
```



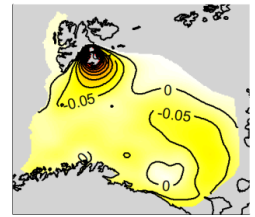
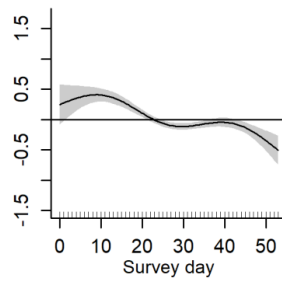
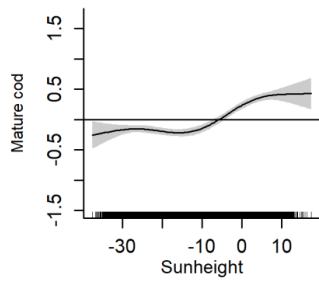
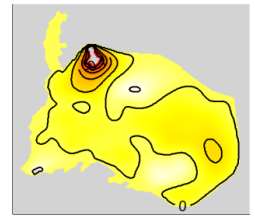
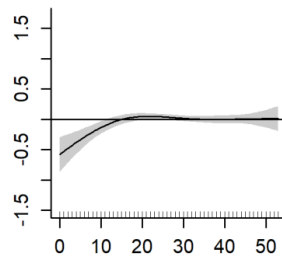
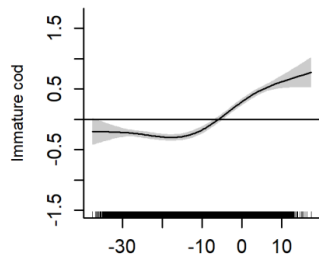
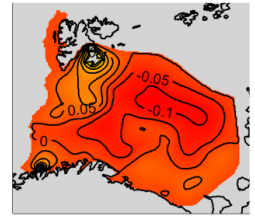
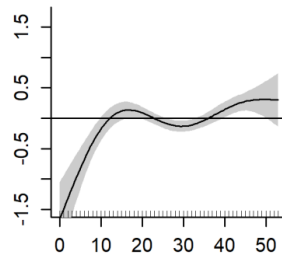
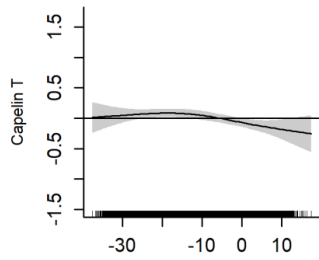
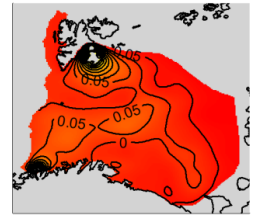
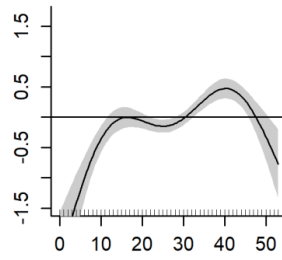
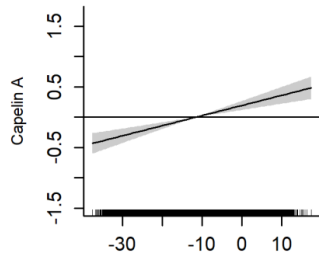
Supplement 2: Smooth functions of sun height and survey day

Here we show the one-dimensional smooth functions of sun height (degrees below or above the horizon) and survey day (sampling day relative to the first day of sampling across the study period for each season) from the *habitat models*, and spatially variant effects of survey day from the best *candidate models* for all components (immature cod, mature cod, capelin A = capelin sampled with acoustics, capelin T = capelin sampled with bottom trawl) from a) autumn and b) winter. Only effects retained in the models ($p < 0.05$) are shown, otherwise they are denoted n.s. (non-significant). For 1d-smooths, the y-axis represents the degree to which variation in the predictor can explain variation in the response, where the horizontal line at 0 represents a neutral effect. For the spatially variant effect, the contour lines show how the slope of the linear regression between species density and survey day varies in space. Yellow colours represent positive slopes and red colours negative slopes. Though there were clear spatial patterns, the changes in slopes were small.

a) Autumn



b) Winter



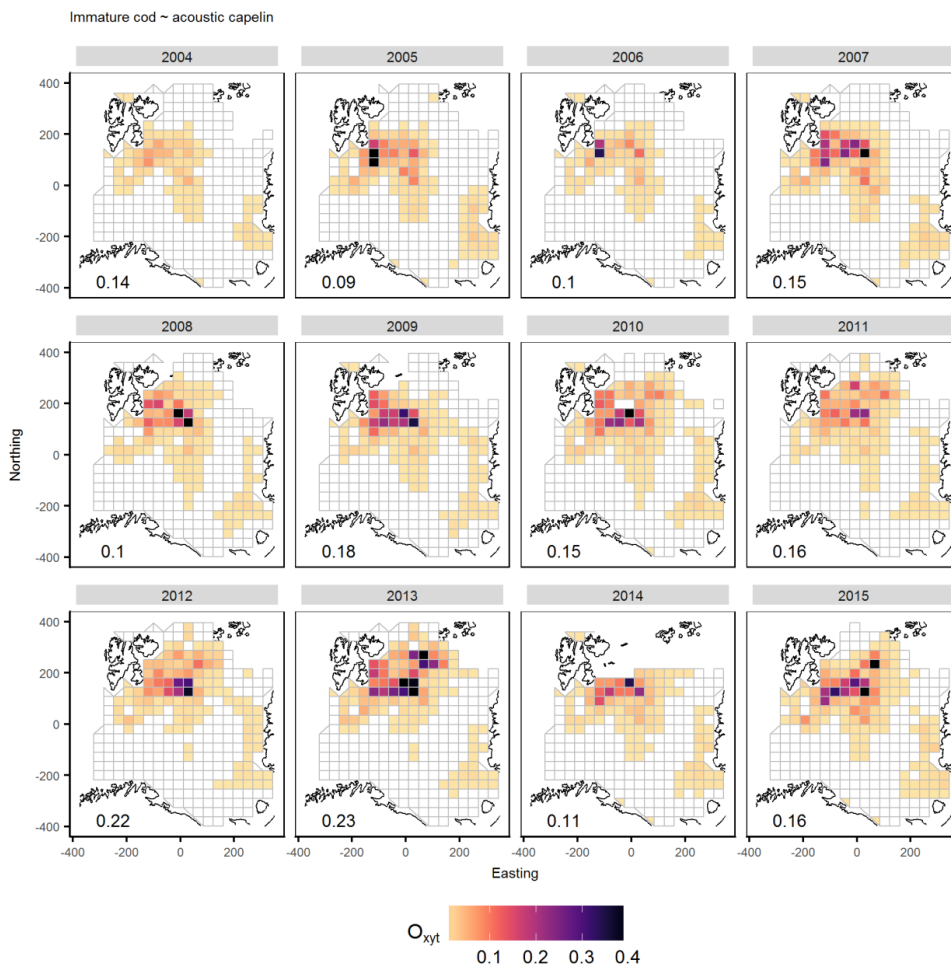
Spatially variant survey day

Supplement 3: Predicted overlap by year for each season and component pair

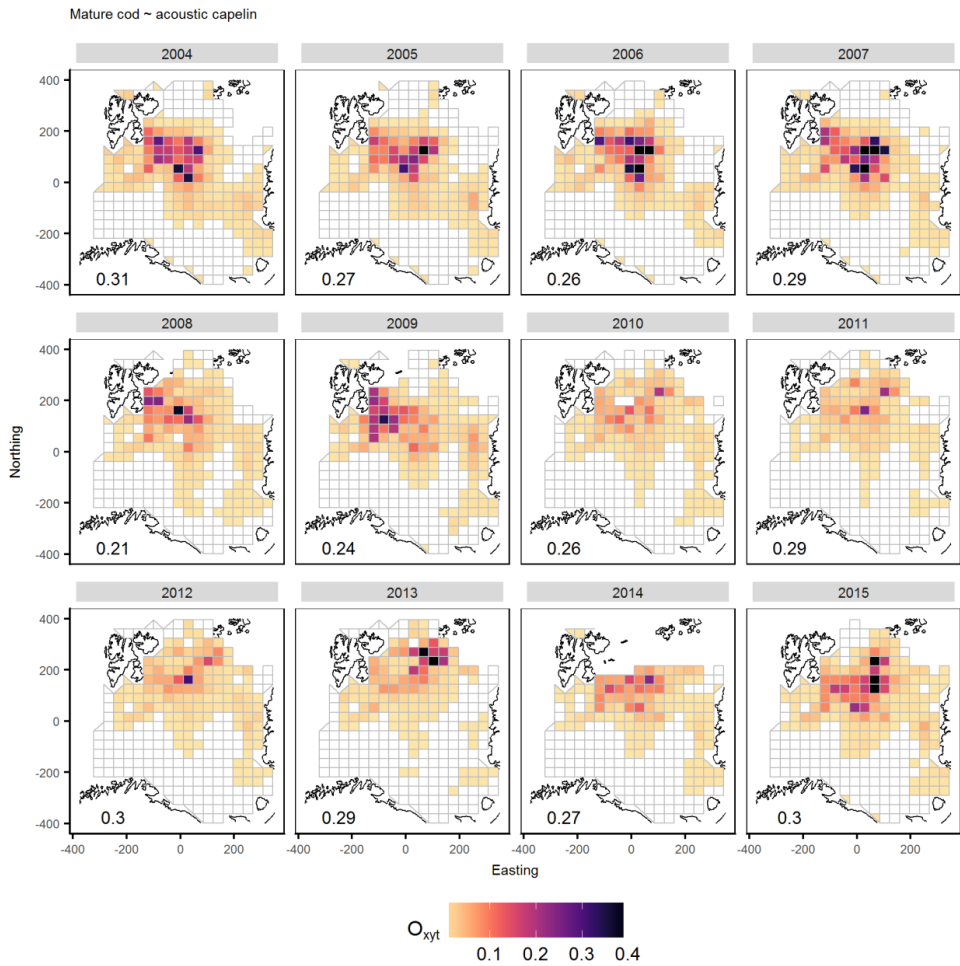
The overlap index O_{xyt} ranges from 0-1, where 1 means that the highest (year-specific) densities of cod and capelin are found in the grid cell. Because there were a few very high overlap values that made visualisation difficult, these were set to black color to enable a good representation of the variation in the main overlap range (values ≤ 0.4 in autumn and ≤ 0.1 in winter). The numbers in the bottom left corner of each panel represents the strength of correlation (kendall's tau) between the predicted densities of cod and capelin across the grid. This document contains the following figures:

- a) Autumn: immature cod and acoustic capelin
- b) Autumn: mature cod and acoustic capelin
- c) Winter: immature cod and acoustic capelin
- d) Winter: immature cod and trawl capelin
- e) Winter: mature cod and acoustic capelin
- f) Winter: mature cod and trawl capelin

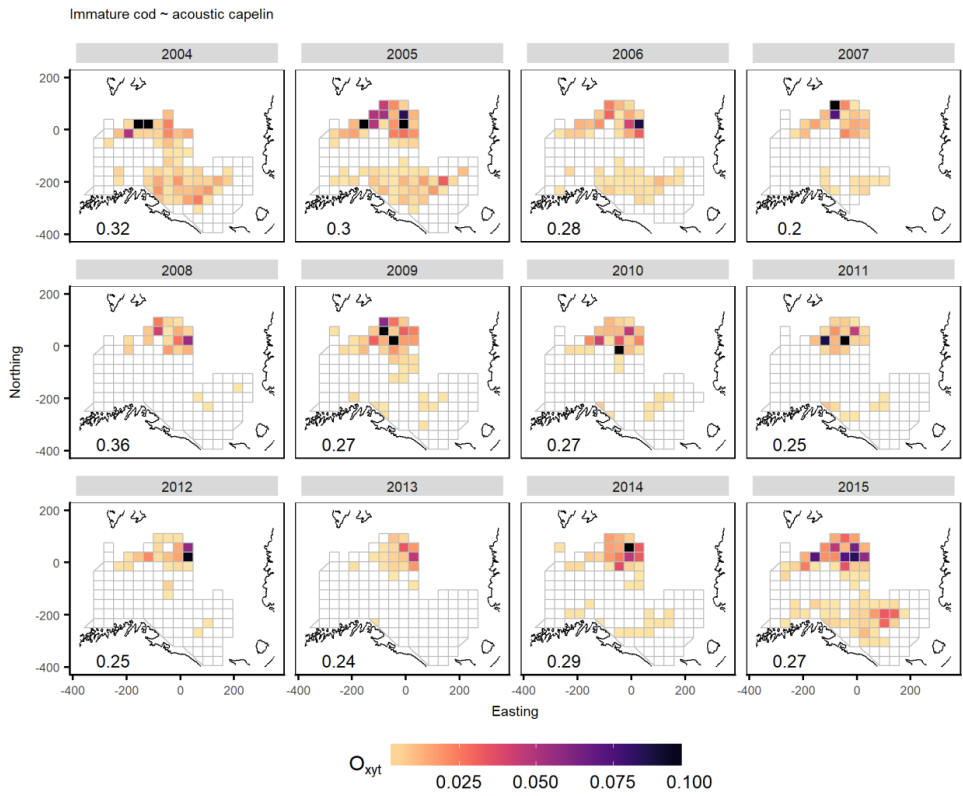
a) Autumn: immature cod and acoustic capelin



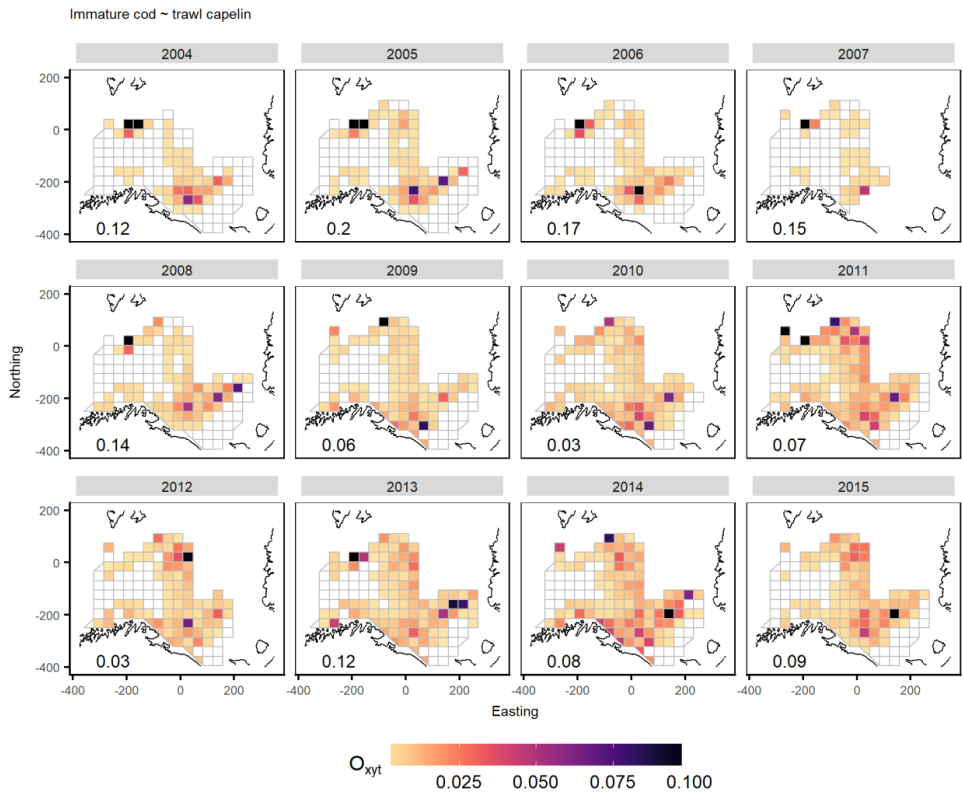
b) Autumn: mature cod and acoustic capelin



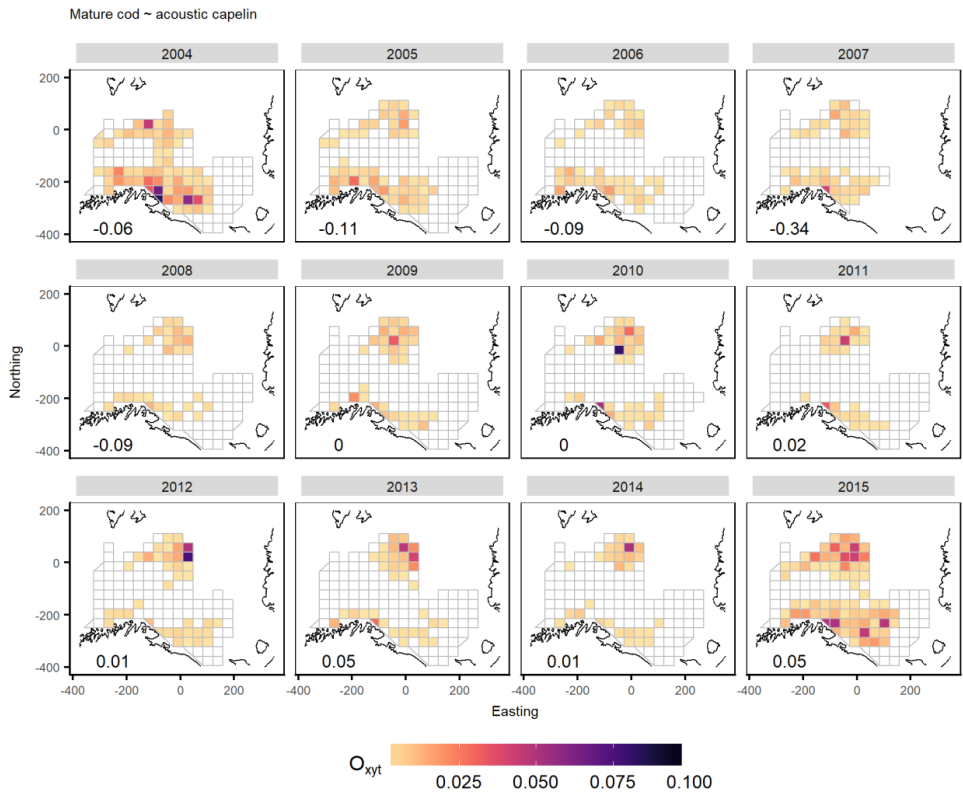
c) Winter: immature cod and acoustic capelin



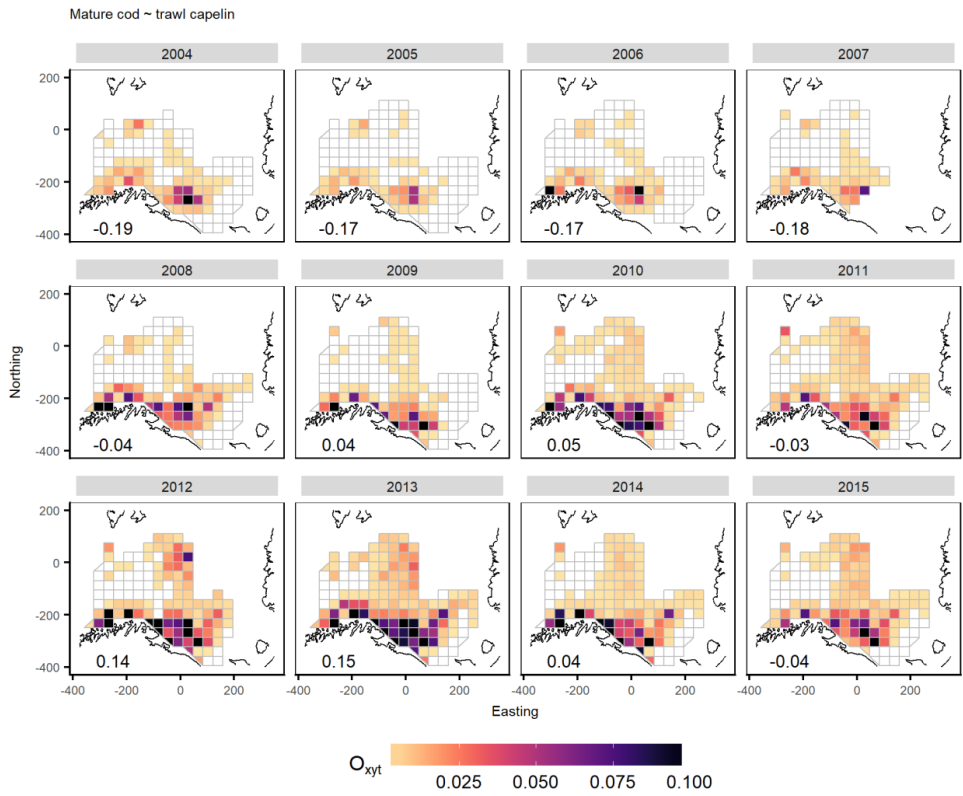
d) Winter: immature cod and trawl capelin



e) Winter: mature cod and acoustic capelin



f) Winter: mature cod and trawl capelin

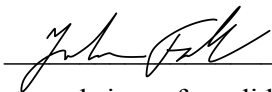


**Errata for
“Drivers of variation in the predator-prey interaction
between cod and capelin in the Barents Sea”**

Johanna Fall



Thesis for the degree philosophiae doctor (PhD)
at the University of Bergen



(date and sign. of candidate)

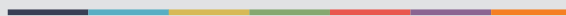
(date and sign. of faculty)

Errata

- Page 17 Error from spelling control: “Norwegian Seasouthwestuth-west” – corrected to “Norwegian Sea in the south-west”
- Page 30 Duplicate word: “Great Bank in in early autumn” – corrected to “Great Bank in early autumn”
- Page 30 Extra word: “in low light or in darkness using or other senses” – corrected to “in low light or in darkness using other senses”
- Page 31 Error from spelling control: “than cod o – banks – especially a – night –“ – corrected to “than cod on banks – especially at night – “
- Page 33 Spelling error: “such an individual differences” – corrected to “such as individual differences”
- Page 33 Missing word: “contributing factor to weak empirical functional response” – corrected to “contributing factor to the weak empirical functional response”
- Page 34 Figure 8: blue points adjusted to a lighter colour for clarity
- Page 35 Missing word in figure 9 text: “highest cod and capelin from a given year” – corrected to “highest cod and capelin densities from a given year”
- Page 35 Missing word: “overlap area northeastward” – corrected to “overlap area shifted north-eastward”
- Page 43 Missing word: “fundamental difference theoretical and empirical approaches” – corrected to “fundamental difference between theoretical and empirical approaches”
- Pages 48-57 References: added missing volume numbers and journal names.
- Synthesis and Paper 3: missing reference – added “Skaret G, Johansen GO, Johnsen E, Fall J, Fiksen Ø, Englund G, et al. A tri-trophic spatial game in an Arctic shelf ecosystem – Bottom dwelling cod ambush small pelagic fish hunting for krill. *Submitted.*”
- Paper 1 pages 26-32 References: added missing volume numbers and journal names.
- Paper 3 missing page numbers – corrected
- Paper 3 References: added missing volume numbers and journal names.
- Paper 3 two copies of Appendix 1 and missing Appendix 3: the committee requested Appendix 3 during the evaluation – replaced duplicate Appendix 1 with Appendix 3



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