Nordic Council
of Ministers

Ecosystem based management of sandeels, demersal fish and seabirds in Boreal ecosystems in Northeast Atlantic

Contents

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Extended abstract

Ecosystem based management has been a hot topic for decades and the current project aims to explore the potential of this approach on the marine shelves at Iceland, Faroe Islands and Norway, here termed boreal ecosystems in Northeast Atlantic. Ecosystem based management implies that the ecosystem function is adressed with all its variables and complex relationships. In order to reduce complexity the project focused on sandeels, demersal fish and seabirds, thus putting emphasis on the food chain from phytoplankton, zooplankton, sandeels to demersal fish and seabirds. In the work of the project it soon became clear that there were other food chains available, for example that seabirds could prey on krill, which is seen for the particular puffin to the left in the cover picture. It was noted that the relationships between oceanography/zooplankton and seabirds were as strong as relationships between forage fish and seabirds and one main reason being that seabirds could switch their preference between forage fish or even to switch to crustaceans (krill) and this issue was dealt with by broadening the focus to include fish larvae of different fish species. In the project it was noted that the strongest declines in seabird numbers were found in the shelf area from south Iceland, Faroe Islands to the Norwegian shelf up to Lofoten. This is the area where sandeels comprise an important forage fish and where other forage fish like capelin are less frequent. This area was thus chosen as the study area in the project. It was also noted that oceanographich features like the size of the subpolar gyre or the strength of the East Icelandic Current (EIC) were of great importance to demersal fish and seabirds. However, to link the ecosystem function to fisheries it was necessary to find an ecosystem component that was susceptible to fishing and the choice fell on fish larval survival. Fish larvae represent a fragile ecosystem component that is highly vulnerable to predation and that has direct links to the size of the demersal fish stocks as well as the amount of food for seabirds. The predators on fish larvae were found to be pelagic fish such as herring and mackerel, but also Norway pout was considered, although it was noted that there are other predators on fish larvae that could not be taken into account. A main finding, which probably is novel, was that the abundance of demersal fish could hamper the predatory effect of pelagic fish on fish larvae, for example by scaring pelagic fish away from the shelves or areas where the fish larvae are found. The effect of demersal fish on the survival of fish larvae seemed to be less than the effect of oceanographic variables or primary production, but, nevertheless, seemed to hold a

potential that should be further studied in the future. The report is structured as separate sections: bottom-up introduction, seabird productivity in the eastern Norwegian Sea, puffin productivity in South Iceland, seabird productivity on the Faroe Islands, and finally fish larvae dynamics and predation by pelagic fish.

Chapter 1.

Bottom-up introduction

Hjálmar Hátún

The stock size of several demersal fish stocks (e.g. Atlantic cod, *Gadus morhua*) and the size of several seabird species (e.g. kittiwakes, *Rissa tridactyla*) in the subpolar North Atlantic (SPNA) have been declining during the last 2–3 decades. A critical question is whether this is due to anthropogenic influence, natural environmental cycles or maybe (and more likely) a combination of these. The fisheries do, naturally, directly impact commercial fish stocks, but direct exploitation cannot explain e.g. the decline of kittiwakes, which are not being harvested by humans. A decline in common food resources for both fish and birds is a plausible candidate, where the ecologically important copepod *Calanus finmarchicus* and forage fish like sandeel, *Ammodytes marinus*, Norway pout, *Trisopterus esmarkii* are primary candidates. While acknowledging the importance of top-down impacts, the following introduction is limiting on bottom-up (food driven) processes. This bottom-up perspective focuses on the most plausible physical drivers underlying ecosystem changes on the south Iceland, Faroe and Norwegian shelves – especially through the trophic pathway from large zooplankton (copepods) via forage fish (e.g. sandeel and Norway pout) to commercial fish stocks and seabirds. Historical temporal changes in the SPNA are here categorized into: *i*) recurrent pulses every 5–8 years, *ii*) major longer-lasting shifts and *iii*) long-term trends.

The strong and highly variable atmospheric jet stream impacts all three shelf environments both through direct air-sea interaction, and indirectly through changes in large-scale ocean circulation, that subsequently impacts the shelves laterally by ocean-shelf interaction. In our simplified perspective, we discuss how the size and circulation strength of the subpolar gyre (SPG) regulates the hydrography (temperature and salinity) (Hátún et al., 2005) and the biogeochemical and biological content (Hátún et al., 2016; Hátún, et al., 2017) in the relatively warm and saline Atlantic Water (AW). This *Atlantic inflow* flows westwards south of Iceland, crosses the Iceland-Faroe ridge and flows poleward through the Faroe-Shetland Channel. The AW properties thus impact the south Iceland (Hátún et al., 2016) and Faroes (Hátún, Larsen, et al., 2021; Jacobsen et al., 2019) shelves directly and are likely to influence the Norwegian shelf as well. Immediately north of the Iceland-Faroe ridge, the AW meets southeastward flow of cold and low-saline waters from the East Icelandic Current (EIC), which carries large amounts of nutrients and zooplankton into the southern Norwegian Sea (Kristiansen et al., 2019). Interplay between the AW and the (modified) East Icelandic Water from the EIC determine the physical oceanography and planktonic food abundance in the southern Norwegian, which has potential to influence the Faroe (Kristiansen et al., 2021) and Norwegian shelves (Skagseth et al., 2021). Like the SPG regulates the distribution of, and mixing between, source water masses west of the British Isles, the Norwegian Sea gyre regulates waters mass distribution and mixing in the southern Norwegian Sea (Hátún et al., 2021).

i. Pulses

Periods with an intensified atmospheric jet stream, often proxied by a high North Atlantic Oscillation (NAO) index (Hurrell, 1995), increases heat losses from the SPNA oceans and this induces deep winter convection, which is especially strong in the Labrador and Irminger Seas (Yashayaev, 2007). Strong convection increases the volume/size of the SPG and invigorates nutrient upwelling and thus primary production. Increased SPG volume, as well as the action of winds (through the so-called wind stress curl) brings the nutrient and zooplankton rich SPG water closer to the south Iceland and Faroes shelves, and can in this way "blow life" to these shelf ecosystems (Hátún et al., 2016). Such pulses have been documented to *a*) increase the nutrient contents all the way from the Labrador Sea, across the Irminger Sea and the Iceland Basin and into the southern Norwegian Sea (Hátún, et al., 2017), b) increase the abundance of the subarctic zooplankton species *C. finmarchicus* in the central Irminger Sea, the south Iceland shelf (Hátún et al., 2016) and in the subartic water masses in the Norwegian Sea (Kristiansen et al., 2021), *c*) increase the breeding success of the seabird black-legged kittiwake (Hátún, et al., 2017) and the total abundance of juvenile fish on the Faroe shelf (Jacobsen et al., 2019). During the last half century, such pulses occurred during the following years: 1976, 1984–1985, 1987, 1993–1995, 2000–2001, 2009, and 2017.

ii. Major shifts

Associated with the same atmospheric drivers, but with additional profound shifts in gyre circulation and major ocean currents, we have also witnessed longer lasting shifts in the northeastern Atlantic. After a period with generally high NAO index values during the late 1980s and early 1990s, an abrupt weakening in the atmospheric forcing during winter 1995–1996 led to much weakened winter convection, which again initialized a major decline of the SPG size and circulation (Hátún et al., 2005; Häkkinen & Rhines, 2004). Less subarctic water reached the mixing region west of the British Isles, and the AW therefore became both warmer and more saline, but poorer in nutrients and the nutritious *C. finmarchicus* (Hátún, et al., 2009). Likely as a result, seabird populations like the large puffin colony in the Westman Islands started to decline (Lilliendahl et al., 2013). The strong subarctic pulse in 2000-2001 gave calanus-dependent species on the south Iceland and the Faroe shelf a much-needed injection, but after this pulse had passed these shelf ecosystems went into a serious recession (Hátún et al., 2022) . This event also had detrimental impacts along the European margin, were e.g. the sandeel abundance (ICES, 2019) and the prosperity of several seabird species strongly decline (Coulson, 2011). The mid-1990s change had, however, positive impact on the large pelagic blue whiting stock (Hátún et al., 2009), which is less sensitive to food availability early in the season (before May), and which benefits from a warmer and more stratified ocean. Many new marine species with warmer water affinity entered Faroese and Icelandic waters during this event (Valdimarsson et al., 2012), and it is therefore justifiable to refer to this as the mid-1990s regime shift (Hátún et al., 2009a).

Since the above discussed pulses and longer-lasting shifts are related to similar physical processes, it is not trivial to determine whether a present or recently observed change represents a pulse, or if it marks a shift to a new state. Although the pulses around 2000–2001 and 2008–2009 were evident in hydrographic records around the northeastern Atlantic (clearest in salinity) and in biological production on the Faroe shelf (Jacobsen et al., 2019), they were not strong enough to flip the SPNA back into a subarctic state – like in the early 1990s. A major pulse initiated by increased convection during the winters 2014–2016 (Yashayaev & Loder, 2016) managed, however, to re-invigorate the SPG. This was observed as a drop in sea surface heights south of Iceland (Hátún & Chafik, 2018) and in the most rapid salinity drop in historical records in the same region (Holliday et al., 2020). Observations during the following years have demonstrated that the system shifted back to a state resembling the early 1990s. It is therefore timely to review possible ecological changes in the northeastern Atlantic for the years after 2015. And for those species exhibiting a change, to distinguish if this was a post-2015 pulse or maybe a more lasting shift back to a subarctic/more productive state.

Discussions on the Norwegian Sea must include the additional influence by the variable EIC. The properties and transport in the EIC are, as mentioned, related to the SPG story due to similar atmospheric forcing, and since the AW properties in the clockwise circulation constitutes one of the sources for the EIC (Valdimarsson et al., 2012). The SPG and EIC signals are, however, not the same. The EIC influx was strong during the 1990s, and this brought large amounts of large and lipid rich copepods (*Calanus hyperboreus* and large stages of *C. finmarchicus*) into the Norwegian Sea. This influx declined sharply in 2003–2005, and with it decline the abundance of the nutritious zooplankton (Kristiansen et al., 2019). This relatively warm and saline Atlantic period prevailed until around 2016, when the EIC influx increased yet again, which immediately brought more of the subarctic copepods to the waters north of the Faroes, and even east to the Norwegian slope (Kristiansen et al., 2021; Skagseth et al., 2021). Possible implications of these shifts in the Norwegian Sea have already been discussed for zooplankton and the fish species, herring (*Clupea harengus*) (Kristiansen et al., 2021; Eliasen et al., 2022), mackerel (*Scomber scombrus*) (Homrum et al., 2022) and salmon (*Salmo salar*) (Utne et al., 2022)). Updates on the further development of these processes and their potential impacts on adjacent shelves and seabirds is warranted.

iii. Long-term trends

Evidence for longer-term physical and ecological trends must also be discussed, especially now anthropogenic climate change is projected to fundamentally alter the functioning of marine ecosystem during the next 50–100 years (Pörtner et al., 2019). Only few hydrographical and biological records are longer than 50 years, and since the North Atlantic Ocean is characterized by a natural cycle of 50–60 years (the Atlantic Multidecadal Oscillation, AMO, Goldenberg et al., 2001), it is not trivial to distinguish between uni-directional trends and natural variability. Although we regularly read about warming trends and biota migrating polewards, fact is that increasing temperature trends are difficult to establish from hydrographic records in the northeastern Atlantic (González-Pola et al., 2023). The first order signal in these hydrographic records is a mid-1990s warming, followed by about twenty years with anomalously high temperatures and a subsequent temperature decrease down to the early 1990s level, i.e. the above mentioned shift. The pre-bloom (winter) silicate levels throughout the entire SPNA have, on the other hand, been declining since the 1980s in a more linear fashion than what can be ascribed to SPG-related natural variability alone (Hátún et al., 2017). Silicate is the limiting nutrient in the SPNA, so if this trend persists through the coming decades, the working of North Atlantic subarctic marine ecosystems is bound to change – fundamentally. It is conceivable that the mentioned bio-physical linkages, established during a period with higher nutrient concentrations already are altered.

Based on a review of recent ecosystem changes on the Iceland, Faroe and Norwegian shelves, we should be able to test and maybe adjust/improve previously proposed hypotheses on bio-physical linkages.

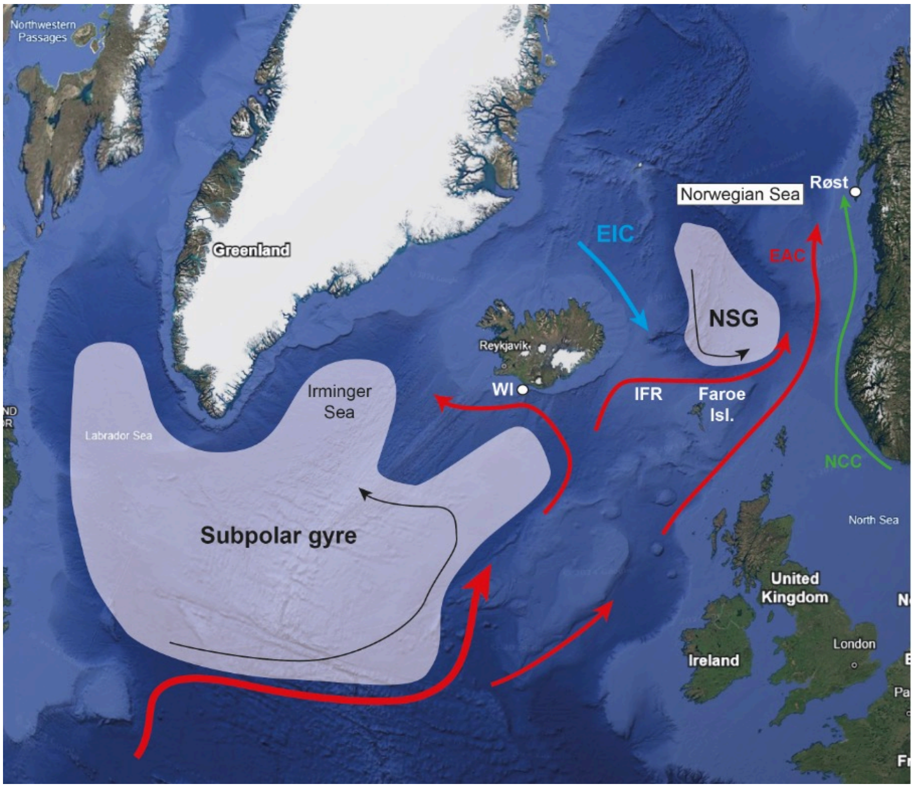

Figure 1.1 Google map showing the location of the subpolar gyre, Norwegian Sea Gyre (NSG) as well as the East Atlantic Current (EAC), the East Icelandic Current (EIC) and the Norwegian Coastal Current (NCC). The location of the Iceland Faroe Ridge (IFR) is shown as well as the seabird colonies in Vestmannaeyjar (WI) and Røst.

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Chapter 2.

Seabird productivity in the eastern Norwegian Sea

Tycho Anker-Nilssen

Key study area and colonies

The central coast of Norway between Stad (62°11′N) and Andfjorden (69°N) in Vesterålen forms the eastern limit of the Norwegian Sea. This area is not only characterised by a rugged landscape with deep fjords sheltered by thousands of islands on the outer coast but also has a large shelf continental that on the widest extends more than 200 km offshore.

As discussed in other parts of this report, the Norwegian Coastal Current (NCC) runs along the entire Norwegian coast, from the Skagerrak and the eastern North Sea in the south to the southern parts of the Barents Sea in the northeast. It transports a wide range of zooplankton and spawning products of fish that forms an important food base for a variety of marine life, including many species of seabirds. A branch of the East Atlantic Current (EAC) runs offshore of and parallel to the NCC, and the interaction between these currents, the bottom topography and wind-induced turbulence are likely to affect both the advection of nutrients and zooplankton onto the shelf, and the growth and retention time of fish larvae and forage fish (e.g. Sætre et al. 2022a).

Immediately upstream of the widest shelf area, the extremely offshore archipelago Røst is located 100 km west of the mainland coast (Bodø), 50 km SW of the Lofoten Islands and about 100 km east of the shelf edge (Eggakanten). This strategic position makes it an excellent breeding place for pelagic seabirds. The long distance to the mainland coast, where local fjord systems may provide alternative sources of food when the food availability offshore is poor, also makes Røst the ideal place to study how physical and lower trophic level processes affect the performance of long-ranging pelagic seabird populations. In the southwestern part of Røst, five steep bird cliffs surrounded by many lower islands used to hold the world's largest breeding population of Atlantic puffins *Fratercula arctica* (hereafter puffin), substantial numbers of black-legged kittiwakes *Rissa tridactyla* (hereafter kittiwake), common guillemots *Uria aalge* and razorbills *Alca torda*, as well as a wide range of more coastal seabirds.

Key study species

In the context of this project, we chose to focus on breeding puffins and kittiwakes, which in Røst are documented by GPS tracking to feed far offshore in their search for prey to sustain their offspring (Anker-Nilssen & Lorentsen 1990; Anker-Nilssen & Aarvak 2009; Fayet et al. 2021; Fayet et al. in prep.). Whereas the puffin is a medium-sized auk that dives for prey down to > 50 m depth (e.g. Piatt & Nettleship 1985), the kittiwake is a small surface-feeding gull that only can plunge-dive down to < 1 m depth and thus depends on finding prey in the top surface layer. The puffin usually feed their chick bill-loads of small fish, whereas the food the kittiwakes regurgitate to their chicks at times also contains a significant proportion of zooplankton, most often krill (Euphausiidae). In contrast to puffins, the kittiwakes sometimes also search food in near-shore waters, especially when local abundance of age 0 saithe there is high (T. Anker-Nilssen, pers. obs.). These two seabird species thus reflect two different foraging niches in the pelagic ecosystem offshore, and the foraging ranges of both species in the breeding season cover the entire extent of the shelf area around Røst.

Key data series

Productivity has proven to be the most important demographic factor determining the population growth rate for puffins in Røst (e.g. Layton-Matthews et al. 2023). Although both puffins and kittiwakes are highly philopatric, they have delayed maturity and don’t start breeding until age 3–5 (kittiwakes) or 5–7 years (puffins). Changes in breeding numbers therefore reflect mainly lagged effects of immature survival and recruitment and are consequently not a very precise indicator of the conditions the birds experience in the breeding areas. This is further substantiated by both species travelling far away to spend the non-breeding season in very different parts of the North Atlantic (Frederiksen et al. 2012; Fayet et al. 2017). From the same line of arguments, survival rates are even less accurate indicators of breeding conditions. Seabird mortality usually peaks in winter, and populations which breed far apart but overlap in wintering areas, exhibit temporal synchrony in survival rates (Reiertsen et al. 2021). Although carry-over effects from environmental conditions experienced on the wintering grounds to some extent may also affect the birds breeding performance (Bogdanova et al. 2017; Keogan et al. 2022; Charrier et al. 2024), productivity is still by far the best parameter linking seabird demography with trophic interactions in the breeding area.

The productivity of puffins and kittiwakes in Røst has been monitored annually since 1964 and 1979, respectively (Fig. 2.1), and are as such among the longest data series for seabird performance in the world (Cury et al. 2011; Sydeman et al. 2021).

Besides long-term reproductive problems driven by poor food supply, the breeding success of kittiwakes in the largest natural cliff (25,000 pairs in 1979) has more recently also been severely affected by disturbance and predation from an increasing number of immature white-tailed eagles *Haliaeetus albicilla* (Anker-Nilssen et al. 2023) that spend the summer in Røst, and the colony went extinct in 2020. The resurrection of the white-tailed eagle population in Norway is the result of targeted management actions on land and not directly related to changes in the marine ecosystem. To avoid this source of bias, we therefore chose to use the almost equally long data set from a colony breeding on buildings in the Røst harbour area, where human presence has kept the eagles on a distance and breeding success is unaffected by eagle numbers (Anker-Nilssen et al. 2023). For puffins, the eagles are not a huge problem as they breed sheltered in earth burrows and rock crevices that eagles are unable to enter. The data series used is the proportion of puffin chicks that survived the nestling period (fledging success) in each year, as registered for a selection of breeding burrows on the island of Hernyken. This island holds 8.5% of the total population of puffins in Røst, which counted approximately 1.4 million breeding pairs in 1979 (Anker-Nilssen & Øyan 1995). Based on the census and monitoring method developed by Anker-Nilssen & Røstad (1993), the population size of puffins in Røst 2023 was estimated at 208,500 pairs (SE=10,988), corresponding to only 15% of the initial population estimate (T. Anker-Nilssen, unpubl. data).

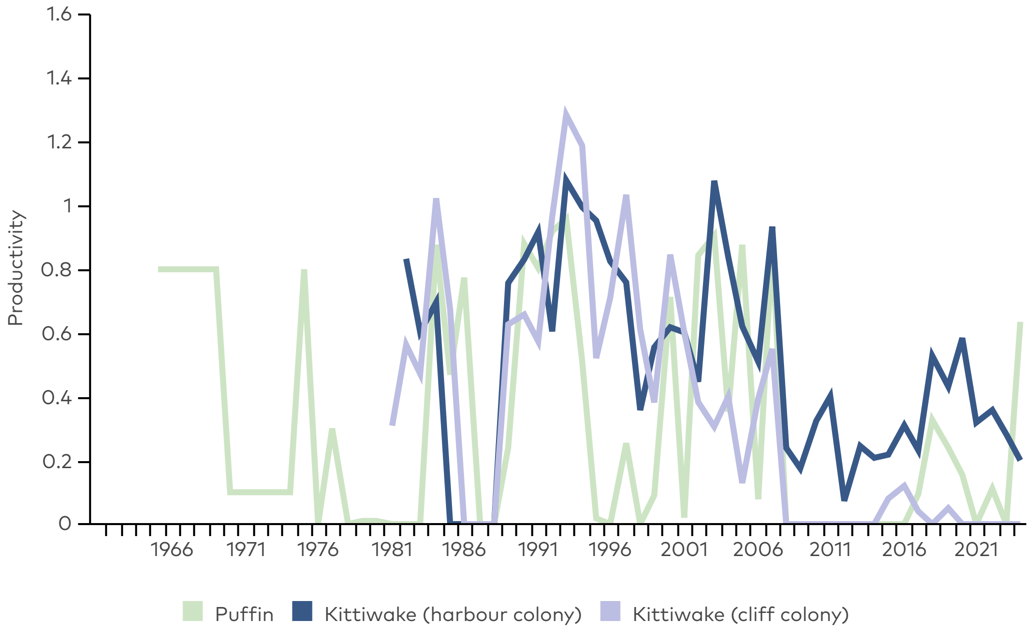

Figure 2.1 Productivity of Atlantic puffins (chick fledging success) and black-legged kittiwakes (chicks fledged per pair) in Røst, northern Norway 1964–2023. Estimates for years before 1980 are based on semi-quantitative assessments published by Lid (1980).

Effects of lower trophic levels

The trophic link between the availability of age 0 herring produced by the Norwegian spring-spawning (NSS) stock and the productivity of puffins in Røst, is a classic example of the high importance of forage fish as food for breeding seabirds (e.g. Anker-Nilssen 1992; Durant et al. 2003; Durant et al. 2005). Both the breeding success of the Røst puffins and the size of herring in their chick diet, have proven good indicators of the year-class strength of NSS herring (Sætre et al. 2002b, Durant et al. 2003), the longer-term validity of which is currently being re-examined (Walnum et al. in prep.). The threshold of this relationship also fits a global pattern, showing that breeding success of seabirds is severely reduced when the abundance of their key prey drops below a third of its historical maximum (Cury et al. 2011). As seabirds only consume a small fraction of their prey population (Saraux et al. 2021), this threshold most likely reflects the abundance needed for the birds to find enough prey to sufficiently sustain their offspring without spending too much time and energy that could jeopardize their own survival. This life-history balance is typical of long-lived seabirds, and likely depends not only on the abundance of prey but also on the abundance of seabirds competing for the same prey (Fayet et al. 2021).

The northward drift of herring and cod larvae with the NCC explains the distribution of the largest bird cliffs along the Norwegian coast, with most colonies found where these larvae appear most abundant and predictable between years in the breeding season for seabirds (Sandvik et al. 2016). This illustrates the importance of these fish as food for seabirds, as well as the value of the retention areas for young herring on the vast shelf areas surrounding Røst. Further north, age 0 cod is shown to be an important diet component of adult common guillemots breeding in the southwestern Barents Sea. It also affects the breeding success of this species there, even if the adults only carry one fish at a time and therefore need to raise the chick on larger fish prey of other species, such as sandeel and capelin (Myksvoll et al. 2013).

Compared to interactions with forage fish, the direct or indirect value of crustacean zooplankton for seabirds is less well studied on the Nordic shelves. As for the puffins, the productivity of the kittiwakes in Røst is linked to the quality of herring larvae (Anker-Nilssen et al. 2023), yet diet samples for this population are fewer and still being worked up for further analyses. However, in periods when schooling-size age 0 herring (> c. 45 mm long) are plentiful, this is also clearly the most abundant prey for the kittiwakes, even if they load small prey more easily than puffins and therefore can keep their offspring alive for longer periods by feeding them krill when fish prey is scarce. This is easily detected in the colony because the half-digested crustaceans stain the birds' plumage orange when the adults regurgitate the food to their chicks. In line with this, the breeding success of kittiwakes is highly and positively correlated ($r^2=0.66$) with the ICES/PGNAPES abundance indices for zooplankton in the Norwegian Sea basin in May, while there is no such relationship for the puffins ($r^2=0.06$). Kittiwake breeding success also correlates to some extent with the SPG index in the previous year ($r^2=0.22$) and in the last winter ($r^2=0.24$), but similar relationships are not evident for the puffin (both $r^2<0.01$).

The pooh of adult puffins is sometimes reddish in colour, indicating they may sometimes feed themselves on crustaceans that are too small to carry efficiently in the bill to support the chick. This is most often seen at the start of breeding and during incubation. Interestingly, puffin breeding success correlates better with zooplankton indices measured NE of Iceland ($r^2=0.18$) than with those in the other areas of the Norwegian Sea ($r^2<0.09$).

There are also occasional events on lower trophic level that can affect seabird productivity. Good examples are the occurrences of unusual prey species that turn up in the seabirds' chick diet. In the early 2000s, poor quality snake pipefish *Entelurus aequoreus* constituted a significant part of the diet for pelagic seabirds in many NE Atlantic colonies (Harris et al. 2007; Harris et al. 2008), including also puffins and kittiwakes in Røst (Anker-Nilssen & Aarvak 2006). In 2023, age 0 mackerel was the most frequent prey fed to puffin chicks in Røst in late summer, an event that had not been seen since 1974. Although this contributed to explain a moderate breeding success, ongoing analyses indicate that the size of age 0 herring in the diet of puffin chicks in Røst is negatively correlated ($r^2=0.53$) with the proportion of age 0 mackerel within the Norwegian Exclusive Economic Zone (EEZ NO) in the North Sea in the previous winter (range 5.8–17.4%, ICES/IBTS data 1998–2020). This could suggest that this part of the mackerel year classes follows the NCC northwards where they prey upon herring larvae (and their crustacean prey), and/or that parts of the spawning stock also can follow this route and add to that top-down effect. A significant amount of age 0 mackerel was also found in the diet of puffins breeding on Runde, immediately north of the North Sea border in western Norway (Noever et al. unpubl. data). Still, diet studies of mackerel in the eastern Norwegian Sea in spring and summer are scarce. One study made along a large part of the Norwegian coast in July 2018 showed low proportions of Teleostei prey in both immature and adult mackerel at most stations sampled (Bjørdal et al. 2022). The proportion of age 0 mackerel in the EEZ NO in the preceding winter (9.9%) was however rather low, suggesting mackerel was less abundant on the Norwegian shelf that year.

Physical drivers of change

Although the above correlations are interesting and warrants further research, it is still not known in much detail how the breeding performance of puffins and kittiwakes in Røst is linked to the large-scale oceanographic mechanisms in the Northeast Atlantic. Local physical properties of the seascape off central Norway may also act to mask the larger-scale processes. This vast shelf area has a varied bottom topography with trenches and shallow bank areas that affect the northward flow of NCC water, creating rings, eddies and jets that increase the retention time of fish larvae and other planktonic organisms (Sætre et al. 2002a). In concert with the parallel EAC and onshore/offshore winds, this is also likely to affect local advection and upwelling of zooplankton and mesopelagic fish onto the shelf. How these physical mechanisms act to affect food availability for breeding seabirds is poorly understood. Their importance is however substantiated by the fact that sea temperature and salinity within the NCC off the Lofoten Islands in March, i.e. two months prior to egg laying, explained more of the variation in puffin breeding success on Røst than the abundance or quality (size) of their main prey, age 0 herring (Durant et al. 2003; Durant et al. 2005; Durant et al. 2006; Walnum et al. in prep.).

Important challenges for further research

Effects of large- and mesoscale oceanographic processes on the Norwegian shelf ecosystem. As detailed in other chapters of this report, large-scale oceanographic variability is an important driver of the productivity of Nordic shelf ecosystems. This includes evident effect of the Subpolar Gyre (SPG) on seabird productivity in the Faroes (Hátún et al. 2017; Olsen et al. in prep.). Both the SPG and Modified East Icelandic Water (MEIW) transported by the East Icelandic Current (EIC) bring nutrient-rich water into the Northeast Atlantic. The effects of these physical processes on the productivity of keystone species of plankton, fish and top predators on the Norwegian shelf are however less well understood and warrants further research.

Top-down effects of mackerel as a predator on seabird prey and lower trophic levels need to be studied in more detail. The northward expansion of Northeast Atlantic (NEA) mackerel in summer has apparently had several effects on seabirds. The occurrence of age 0 mackerel in the diet of puffins is one effect. The establishment of the world's northernmost colony of northern gannets Sula *bassanus* on Bjørnøya is probably another. Gannets plunge-dive to several meters depth and are among the few seabirds that can feed efficiently on older mackerel than age 0.

Spatial and temporal dynamics of seabird foraging habitat use. Along the Norwegian coast, twenty large marine areas have recently been identified as especially attractive for establishing offshore wind power development, provided impacts on the environment are assessed to be acceptable (https://www.miljodirektoratet.no/aktuelt/nyheter/2023/april-2023/20-mulige-havvind-omrader-langs-hele-kysten/). The largest of them, Nordvest A, is a 11,300 km² area situated in the middle of the eastern Norwegian Sea shelf, approximately 40 km off the mainland coast and 100 km southwest of Røst. On this background alone, it is imperative to understand how different pelagic seabird species (including kittiwakes, puffins, and several other species) utilise different types of foraging habitats on this shelf in relation to variation in food availability, as reflected by what they bring to their chicks. For instance, it may seem that kittiwakes breeding in Røst travel far offshore (off the shelf edge) when their diet is dominated by krill, whereas they spread over large parts of the shelf when feeding on herring larvae or feed in near-shore waters (within Røst or along nearby Lofoten Islands) when the availability of age 0 saithe is high. Some of these patterns are currently being explored by the SEAPOP programme (www.seaopp.no/en), including the foraging behaviour of chick-feeding kittiwakes tracked with GPS from Røst each summer since 2017 (Fayet et al. in prep.).

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Chapter 3.

Puffin productivity in South Iceland

Erpur Snær Hansen

Key study area and colonies

Vestmannaeyjar archipelago is located (63°26´N, 20°17´W) on Selvogsbanki 8–46 km off the southwest coast of Iceland. Apart from western (Reykjanesskagi) and eastern (Vestrahorn) extremities Iceland´s south coastline is characterized by glacial riverbeds of black lava sand. Vestmannaeyjar are volcanically active and composed of both lava and tuff. They are the only sizable islands along the whole south coast, characterized by steep grassy slopes and high cliffs. Vestmannaeyjar are more specifically located on the eastern fringe of the shallow (80 m) Selvogsbanki (10,700 km^2 within the 200 m isodepth) the continental shelf located approximately 20 km to the east. The south coast receives the output of most of Iceland´s the largest rivers, high in silicate (200 micro mol/L) (Stefánsson & Ólafsson 1991). The costal current flows through Selvogsbanki westwards on its clockwise route around Iceland. The Irminger current approaches Iceland in the southeast, and turns southwards along the Reykjanes ridge, with Selvogsbanki in the middle. Selvogsbanki is highly productive and also receives influx of phyto- and especially zooplankton by advection (Gislason et al. 2000). Selvogsbanki is Iceland ´s key spawning area of cod, haddock, capelin, sandeel and other important fish species. Sandeel is the neritic ecosystem “wasp-waist” species, being the most abundant 1. level predator and forming the basis for all higher tropic levels ranging from predatory fish to seabirds and cetaceans. Vestmannaeyjar are surrounded to the west by vast areas of sandy bottom, an ideal sandeel burrowing habitat, and only about 20 km from the continental shelf to the east. Vestmannaeyjar are ideally located for foraging on both sandeels, and Euphusiids (mainly *Meganyctiphanes norvegicus*) in the east, and harbours now the largest puffin colony in the World, some 830,000 breeding pairs, along with kittiwakes (104,000 pairs), fulmars (47,000 pairs), of common guillemots (45,000 pairs), Northern gannets (30,000 pairs), Iceland´s only Leach´s storm-petrel colony (20,000 pairs) and virtually all Icelandic European storm-petrel population (10,000 pairs), and between 7–8000 pairs of razorbills and Manx´s shearwaters (Iceland´s only breeding colony), and other less common seabird species.

Key study species

For this project the Atlantic Puffin was chosen on the basis of availability if long term data. Puffin is the most abundant breeding bird species in Iceland, and also the most harvested one.

Key data series

Puffin productivity has been measured in Vestmannaeyjar from 2007, but puffin pole-net harvest numbers have been compiled for the whole pole-netting record 1878–2008 (Hansen et al. MS). To make the harvest numbers more biologically interpretable, a virtual production index P(H.) was calculated based on average age composition of harvest of birds ringed as chicks. Harvest is 75% composed of immature birds 2–4 years old. The P(H.) calculation sums up each cohort relative size, accounting for survival to age using estimated 87% annual survival in Vestmannaeyjar (Helgason 2012). This index reflects cohort sizes relative to a reference year of maximum cohort size (1882) and is the longest time series on seabirds in existence. It is important to keep in mind that this production index is essentially a product of breeding success (fledglings/pair) and breeding population size in a given year. However, by using fixed age composition, biases small cohorts upwards, and large cohorts downwards in numbers, thus reduces cohort real size variation. To gauge this filtering, another production index P(town) was created based on number of fledglings, either ringed (1971–2002) or rescued by the public annually in the town of Vestmannaeyjar (2003–2023). Each series is standardized by dividing by their respective maximum values (figure 3.1). The number fledglings in town and direct production estimates are highly correlated.

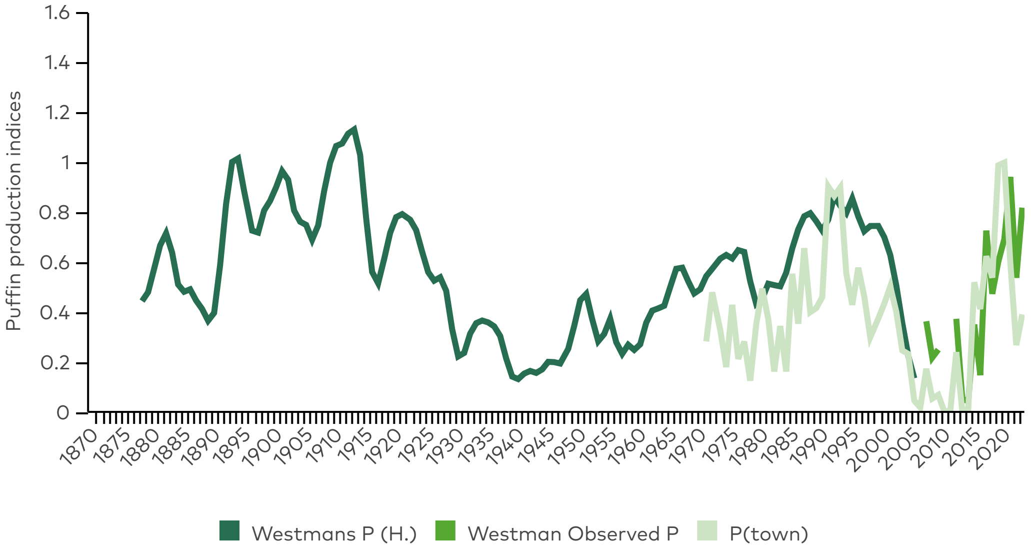

Figure 3.1 Production indices of Atlantic puffins in Vestmannaeyjar, Southern Iceland 1878–2023.

Effects of lower trophic levels

A number of environmental factors have shown substantial changes in Icelandic waters in the last two decades. Most notable are 25% decline in winter Silicate levels since 2001 and simultaneous delay of phytoplankton bloom maximum by a month (Ólafsdóttir 2021; Pétursdóttir et al. 2021). Annual Chlorophyl production has increased substantially since 2010. Migration of mackerel into Icelandic waters increased dramatically since 2005, but the proportion migrating into south Icelandic waters has steeply declined since 2018 and moved to Norwegian waters.

Physical drivers of change

Strong relationship was found between Puffin production index and SST in Vestmannaeyjar from 1878 until 2005. The effect of temperature can affect puffin production via effects on sandeel egg development time (thus hatching time), winter survival, summer growth, and fertility by direct effect on basal metabolism (van Deurs et al. 2011; Wright et al. 2017; Régnier et al. 2018, 2019). After 2000, sandeels have been observed to be smaller for a given age, with lesser energy content (unpublished data), and 60% of 0-group below a minimum length threshold for winter survival. Warming of the Atlantic in 1995 coincided with a 50% reduction the abundance of northern krill in Icelandic puffins wintering area over the Atlantic ridge (Fayet et al. 2017; Edwards et al. 2021). Northern krill is likely key puffin prey in spring and might affect survival of puffin and many other seabird species wintering in the hotspot (Davies et al. 2021). The relative contributions of summer production or winter survival to the population trajectory are currently not clear.

In 2005 puffin production declined substantially faster than in the beginning of the last warm phase of the Atlantic Multidecadal Oscillation (1930–1965) despite similar SST increase as the current warm phase starting in 1995, suggesting another causative factor/s than SST alone. Furthermore, a large (1.5x SD, or 18 days) delay in Westman puffin breeding phenology (mean fledging time) was observed during this period (after 2005) in comparison to mean (mean fledgling time 1937–2023. This phenological delay is of great interest as it seems indicative of general trophic mismatch in Selvogsbanki, affecting not only production of puffin and their sandeel prey, but also many important commercial fisheries as demonstrated by (Brander *et al.* 2001).

Important challenges for further research

Maximum cross correlations on the Puffin virtual production P(H.) from Iceland and Faroes together with Röst breeding success are significant, but with different lags, Faroes first, Iceland second and Norway last in the chronology (Table 3.1.).

Table 3.1 Maximum cross correlations (upper panel) and corresponding lags (lower panel) between puffin production in Faroes (Viðoy), Iceland (Westmans) and Norway (Røst). All three correlations are significant.

Colony	Røst	Viðoy	Westmans
Røst	0	0.64	0.35
Viðoy	7	0	1.0
Westmans	4	-4	0

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Chapter 4.

Seabird productivity on the Faroe Islands

Jóhannis Danielsen

Key study area and colonies

The Faroe Islands (61N and 7W) consists of 18 small islands located approx. 300km North-West of Shetland and approx. 500km South-East of Iceland on the Iceland-Scotland ridge and are surrounded by highly productive seas supporting large colonies of seabirds (Gaard et al., 2002).

Black-legged kittiwakes breeding success data is from “Høvdin” on the island Skúvoy (61.78N and 6.85W) which is the main long term study area for this species on the Faroe Islands. Atlantic puffin breeding success data is from the largest puffin colonies on the Faroe Islands “Lamba” and “Dalurin” on the island Mykines (62.10N and 7.65W). Tern reproductive success data and Common guillemot, Arctic tern *Sterna paradisaea* (hereafter tern) and kittiwake population trend data are from nationwide surveys.

Key study species

In the context of this project focus will be on Black-legged kittiwake, Atlantic puffin and Arctic tern breeding success as well as population trends for Common guillemot, Black-legged kittiwake and Arctic tern.

Key data series

The productivity of a subsample of kittiwake nests (1,050 nests on average) at the study site Høvdin was monitored from 1982 to 2001. After 2001 all the area has been monitored annually counting total number of adults, nests and chicks late in the breeding season (Hátún et al., 2017) (Fig. 4.1). Population size and productivity of terns has been monitored annually nationwide with the aid of a citizen science scheme since 2003 (Olsen & Sørensen 2022) (Fig. 4.1 and 4.3) and puffin reproductive success has been monitored annually since 2011 at study sites Lamba and Dalurin on the island Mykines as part of a RAMSAR monitoring scheme (Fig. 4.1). Nationwide surveys of guillemots and kittiwakes were done in 1972, 1987, 1997–1999 and 2007–2014 (kittiwake surveys started in 1987) (Fig. 4.2).

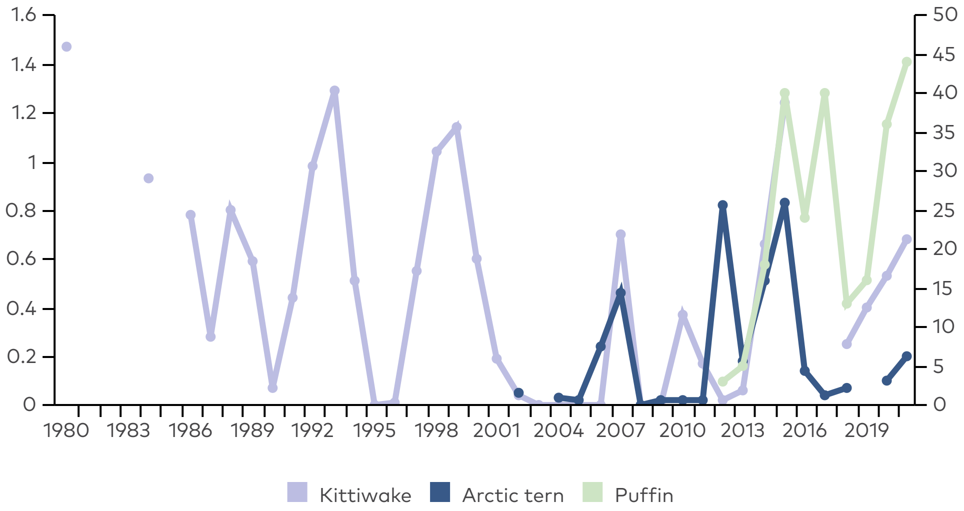

Figure 4.1 Reproductive success of Black-legged kittiwake at Høvdin, Atlantic puffin on Mykines and Arctic tern nationwide on the Faroe Islands.

Kittiwake and tern reproductive success was measured as chicks per nestnest (kittiwake) at the study site Høvdin and average chicks perpair peryear (tern) throughout the whole country while that of the puffin reflects the proportion (%) of burrows that contained a chick each year at Lamba and Dalurin study sites on Mykines.

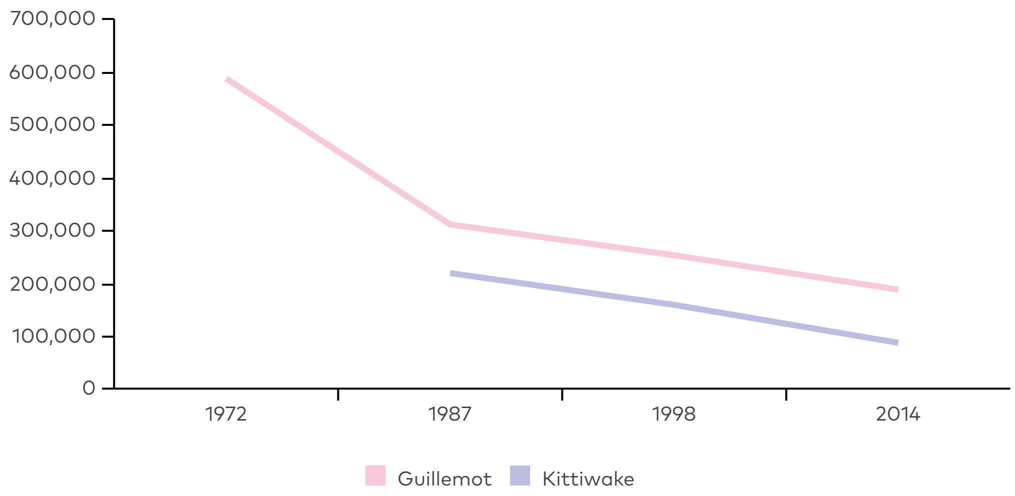

Figure 4.2 Guillemot and kittiwake population trends on the Faroe Islands.

The guillemot population declined by 68% from 1972 to 2014 while the kittiwake population declined by 60% from 1987 to 2014. Interestingly a ban on hunting guillemots during summer came into effect in 1980. Prior to this, guillemots were primarily hunted during summer. The law was adjusted in 1987, 1988 and 1989 in order to shorten the hunting period and has not been changed since. The current hunting period is from 1 October to 20 January. Interestingly there was a steep population decline until the 1980s after which even though the decline continues it is at a much lower rate. The kittiwake population has also declined massively and follows quite well the guillemot decline since the 1980s. Kittiwakes were hunted in the past but never to the same extent as guillemots. Since there are no requirements for hunting statistics for any species on the Faroe Islands there is no publicly available hunting statistics which makes it very difficult to say what effect hunting has had on these species.

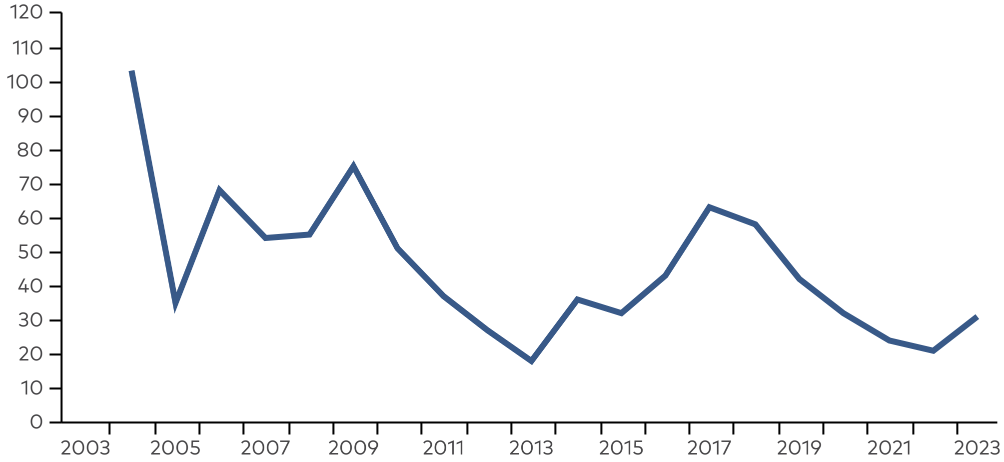

Figure 4.3 Mean number of terns on the Faroe Islands from 2004 to 2023.

Although the number of terns observed on the Faroe Islands can vary quite a lot from year to year and despite that there have been some years with a relatively large number of terns there is an overall declining trend since 2004 when monitoring started.

Effects of lower trophic levels

By combining the so-called 0-group from the main fish species cod, haddock, Norway pout and sandeel, representing more than 90% of all juvenile fish on the shelf during late June surveys, Jacobsen *et al.* (2019) developed a 0-group index which, with the exception of a few years, offered a convincing explanation for the variation in kittiwake reproductive success at the monitoring site, Høvdin. The 2009 and 2017 peak in tern reproductive success as well as mean number of terns throughout the country closely follows the kittiwake reproductive success these years and it is therefore also likely that these peaks can be explained at least partly by the 0-group index. The same is true for puffin reproductive success except in 2019 where puffins breeding success was as good as in the peak year 2017 which means that the puffins were still able to find plenty of prey even though both kittiwakes and terns were having a bad year. When comparing the abundance of 0-group fish larvae from sandeel (*Ammodytes marinus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and Norway pout (*Trisopterus esmarkii*) with the reproductive success of Atlantic puffins on Mykines, it is clear that the 0-group abundance of all four fish species was very low in 2019.

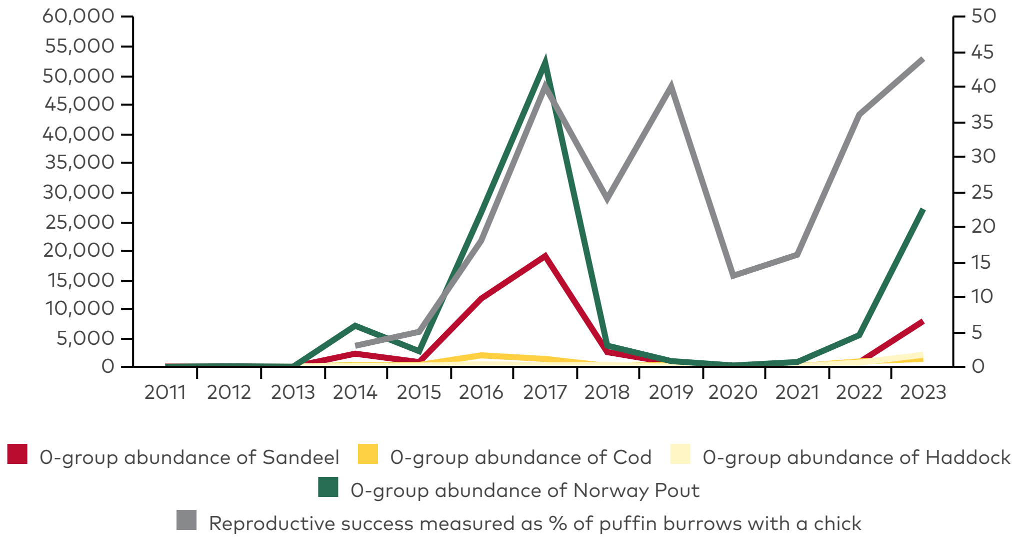

Figure 4.4 0-group abundance of sandeel, cod, haddock and Norway pout (left axis) and Atlantic puffin (AP) reproductive success on Mykines, Faroe islands (grey line, right axis).

Physical drivers of change

As previously mentioned elsewhere in this report large-scale oceanographic variability is an important driver of the productivity of Nordic shelf ecosystems. The Subpolar Gyre (SPG) and Modified East Icelandic Water (MEIW) bring nutrient-rich water into the Northeast Atlantic which affect the productivity of keystone species of plankton and fish and in turn also seabirds on the Faroe Islands (Hátún et al. 2017; Jacobsen et al. 2019; Olsen et al. in prep). To what extent this effect continues on to e.g. the Norwegian shelf is unknown but interestingly there is a strong correlation between Atlantic puffin reproductive success on Mykines and the mass of zooplankton in the Norwegian sea in May (g/m^2) from 2011 to 2020 ($r^2 = 0.74$) (Fig 5) maybe indicating that there is a common underlying driver capable of causing production peaks on both the Faroe and Norwegian shelves.

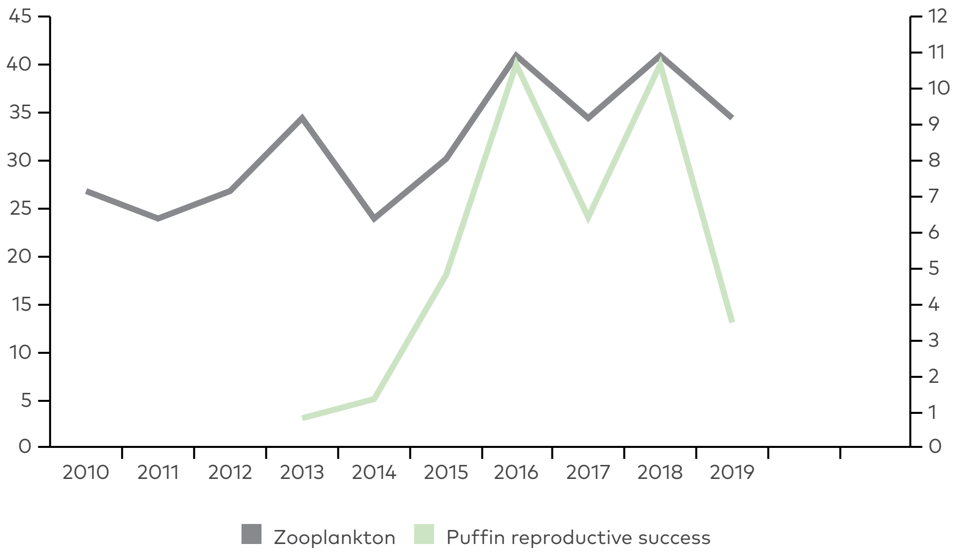

Figure 4.5 Atlantic puffin reproductive success (red line, left axis) and mass of zooplankton (blue line, right axis) in the Norwegian sea in May (g/m^2) from 2011 to 2020.

Important challenges for further research

Even though the focus in this project is on reproductive success we chose to include population trends for the species where nationwide data was available. This is to shed light on the fact that even though there seem to be relatively large peaks in reproductive success some years for all the seabird species monitored these peaks are clearly not enough to sustain the populations which have decreased since monitoring began, sometimes as much as 70% the last 50 years.

Among the biggest knowledge gaps and thereby uncertainties regarding drivers of reproductive success and population trends are the lack of data on what adults are feeding on, both during and outside the breeding season. For many species and most populations, very little is known about where the main feeding areas are, not least during the breeding season. It is however clear that the most important prey for adult survival and a successful breeding season for the various species can vary considerably between species and even for the same species in different areas.

It is also crucial that further research focuses on the effect of human activities, not least on e.g. the effect non-sustainable fisheries has on the availability of suitable prey, both during the breeding and non-breeding season.

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Chapter 5.

Fish larvae dynamics and predation by pelagic fish

Petur Steingrund

Fish larvae dynamics

The introduction pointed to the importance of hydrographich features like the subpolar gyre and the East Icelandic Current on the productivity of shelf ecosystems. In the current section we focus on the ecosystem level of forage fish, more specifically on fish larvae and which factors may control their abundances. The motivation for this focus is the notion that both seabirds and demersal fish feed on forage fish, such as sandeels, that represent a crucial trophic link in the transfer of energy through the food chain from zooplankton to demersal fish and further up to top predators (Eliasen et al., 2011). There has been some focus on the negative relationship between temperature and sandeels (Deurs et al., 2011; Régnier et al., 2019), but during the project it was realised that sandeels are not the only important forage fish species and that a broader approach is needed to explain the variations in seabird numbers.

The impression of abundant seabirds (guillemots/puffins) in the past centuries (Nørrevang, 1977) may serve as an inspiration as to which factors govern seabird numbers and productivity. The factors could be grouped into natural factors such as the general productivity (primary or secondary production) of the ecosystems or antropogenic factors, such as exploitation of fish stocks and seabirds. There have probably not been major changes in ecosystem productivity over decades or centuries while it is apparent that exploitation of e.g. fish stocks has undergone dramatic changes over the last century where many fish stocks, e.g. Faroe Plateau cod have been reduced to low levels. Here, we present a novel approach to explain annual variations of demersal fish larvae in the pelagic phase on the Nordic shelves: Icelandic shelf, Faroe Plateau, Faroe Bank, Norwegian Shelf, that takes into account:

1. ecosystem productivity,
2. predation on fish larvae by pelagic fish and
3. mitigation of the predation effect by demersal fish species.

In our modelling of the abundance of fish larvae it was not possible to use all three explanatory variables simultaneously in the same analysis, either due to lack of data or statistical power (too short time series). The stock assessment data are taken from the ICES website (www.ices.dk) under the relevant working groups NWWG (Iceland cod, Faroe haddock, Faroe saithe: ICES, 2023a and Faroe Plateau cod: local assessment), WGDEEP (Faroe ling: ICES, 2024a), AFWG (Norwegian coastal cod: ICES, 2024b) and WGWIDE (mackerel: ICES, 2023b). Other data are kindly provided by project members.

Faroe Plateau

Faroe Plateau is a good place to start since there has been conducted an 0-group survey since 1983 that can be compared with ecosystem productivity (primary production, zooplankton) since 1990 as well as fish stock assessments since 1960s and further back in time. The annual variations in the abundance and growth of larvae of different fish species has been been remarkably similar and is positively correlated with an index of primary production on Faroe Shelf (Eliasen et al., 2011; Jacobsen et al., 2019).

Although it has been recognised that predation on fish larvae is an important factor that governs their survival (Bailey and Houde, 1989) this has not been incorporated so far for Faroe Plateau. Many candidates for predatory fish on fish eggs and larvae can be proposed, including adult sandeels (Ammodytidae, Christensen, 2010), Norway pout (*Trisopterus esmarkii*, Albert, 1994), herring (*Clupea harengus*, Frederiksen et al., 2007) and mackerel (*Scomber scombrus*, Kvaavik et al., 2019). There is little data on stomach content of adult sandeels and Norway pout in Faroese waters and mackerel has been proposed to be of minor importance for cod larvae on Faroe Plateau, mainly because the spatiotemporal overlap is low, i.e. the cod larvae have settled to the bottom before mackerel enter the plateau in significant numbers during summer (project: "Makrelur á Landgrunninum", MáL, Faroe Marine Research Institute).

Nevertheless, there are normally between 0 and 20 out of 100 stations where herring and/or mackerel are caught during the spring groundfish survey that is conducted annually in March on Faroe Plateau (Figure 5.1). Even though this seems like a low number, it is not unthinkable that they may excert a predation pressure on fish larvae because the catchabilty of pelagic fish, such as herring and mackerel, in the bottom survey gear may be very low. The annual variation in mackerel is only weakly correlated with the total stock of mackerel in NE Atlantic (Figure 5.2) and for herring there is no correlation with the size of the stock of the Norwegian spring spawning herring or herring in the North Sea (not shown).

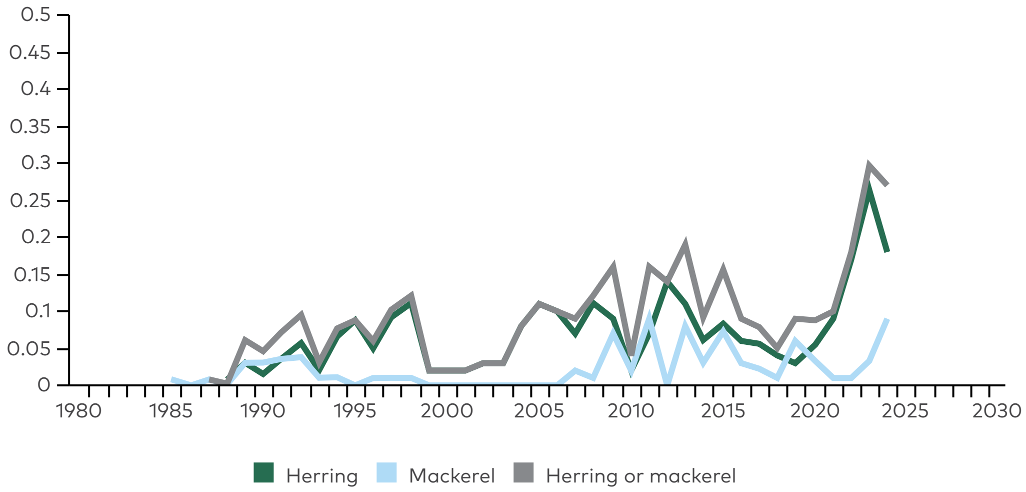


Figure 5.1 The abundance of mackerel and herring in the spring groundfish survey that occupies 100 trawl stations each year. Proportion of stations where either mackerel or herring are caught is also shown.

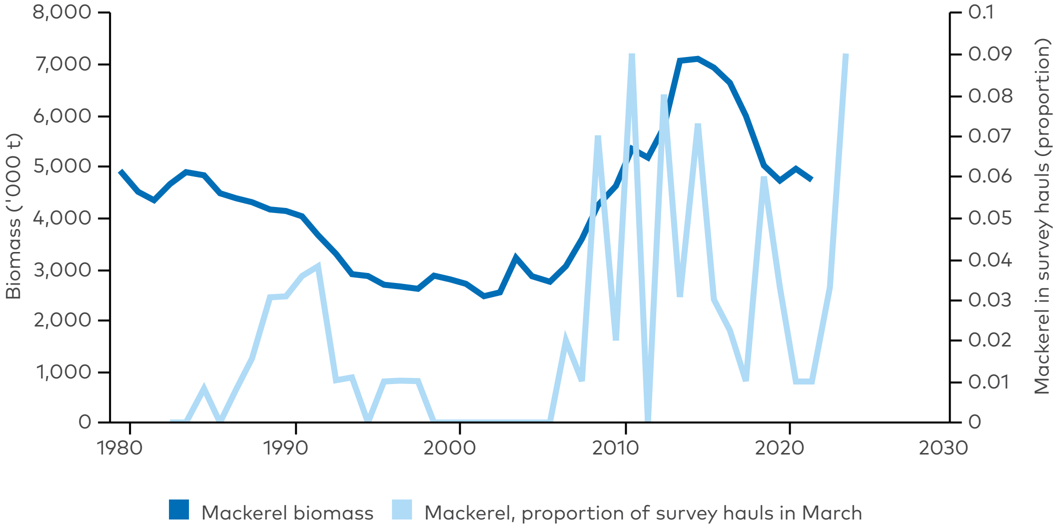


Figure 5.2 Total age 1+ biomass of the mackerel stock in the NE Atlantic ocean compared with the abundance of mackerel in the Faroese groundfish survey in March.

Stomach content analyses of cod, haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) and Greenland halibut (*Reinhardtius hippoglossoides*) on Faroe Plateau have shown that cod of age 3+, saithe of age 3+ and Greenland halibut prey on both mackerel and herring. It is, therefore, likely that these pelagic fish may reduce their own predation risk by staying away when abundances of demersal fish is high and *vice versa*. Since there is no stock assessment of Greenland halibut in Faroese waters this species was not included in the analyses, but other fish species, such as age 3+ haddock and age 3+ ling (*Molva molva*) were included in order to represent the total potential predation risk of pelagic fish on Faroe Plateau. Saithe biomass may be up to an order of magnitude larger than the other species and in order to avoid this dominance and to divide the predation threat for pelagic fish equally between truly benthic fish species (cod, haddock, ling) and benthopelagic fish (saithe), the geometric mean of the stock sizes of cod+haddock+ling and saithe was taken. This measure is negatively correlated with the abundance of pelagic fish on Faroe Plateau (Figure 5.3).

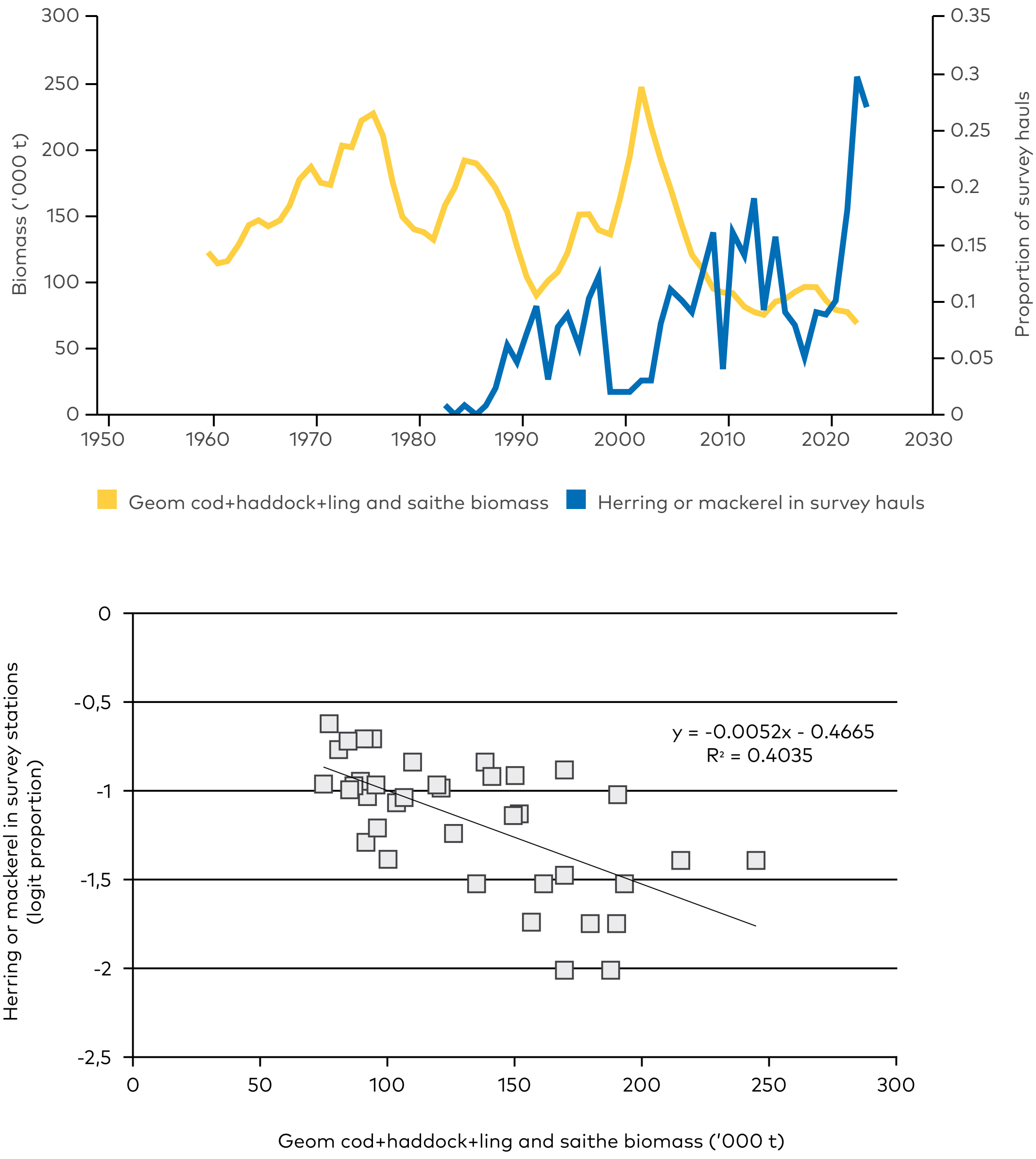


Figure 5.3 Abundance of mackerel and herring in the spring groundfish survey on Faroe Plateau in March compared with the biomass of demersal fish as observed in stock assessments. The logit transformation is used = log((x+0.01)/(1-x+0.01). In the scatterplot the years from 2021–23 are omitted due to higher uncertainties associated with the last years of stock assessments. The biomass of demersal fish is calculated as the geometric mean of cod+haddock+ling and saithe that are at least three years old.

When modelling the abundance of fish larvae on Faroe Shelf we took a geometric mean of cod, haddock, Norway pout and sandeels in order to avoid that the most abundant species (Norway pout) dominated the measure. Other attempts to combine larvae of different species has also been used by Eliasen et al. (2011) and Jacobsen et al. (2019). Since the annual variation in larval abundance was several orders of magnitude we log-transformed the values. As the first explanatory variable we used a measure of ecosystem productivity, i.e., an index of primary production (e.g. Steingrund and Gaard, 2005). The second explanatory variable was the aforementioned biomass of demersal fish. The model (multiple linear regression) was run from 1990 to 2020 when all the variables were available and the biomass estimates of demersal fish were considered accurate. The model explained 41% of the variance and both explanatory variables were significant (p-value < 0.05). Importantly, both explanatory variables showed positive signs (+) meaning that increasing the value of the variables increased the value of the dependent variable. Hence, both primary production and biomass of demersal fish had a beneficial effect on the abundance of fish larvae. To illustrate the influence of the explanatory variables on the dependent variable, we have compiled a sensitivity analysis (Table 5.2). Varying the primary production from lowest to highest values increases fish larvae abundance by a factor of 26 while doing the same with fish biomass increases fish larvae abundance by a factor of 13. According to this model there is a great potential to increase the survival of fish larvae by managing the demersal fish stocks in such a way that their biomasses are high.

Table 5.1 Model output from multiple regression statistics performed in Microsoft Excel.

Regression Statistics						
Multiple R	0,6709					
R Square	0,4502					
Adjusted R Square	0,4109					
Standard Error	0,5666					
Observations	31					
ANOVA						
	df	SS	MS	F	Significante F	
Regression	2	7,3609	3,6804	11,4624	0,00023	
Residual	28	8,9905	0,3211			
Total	30	16,3514				
	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	0,9742	0,3926	2,48	0,019371	0,16990	1,77847
Primary production index	0,1209	0,0296	4,08	0,000339	0,06020	0,18157
Geomean cod+haddock+ling and saithe biomasses ('000 t)	0,0054	0,0024	2,3	0,029359	0,00058	0,01025

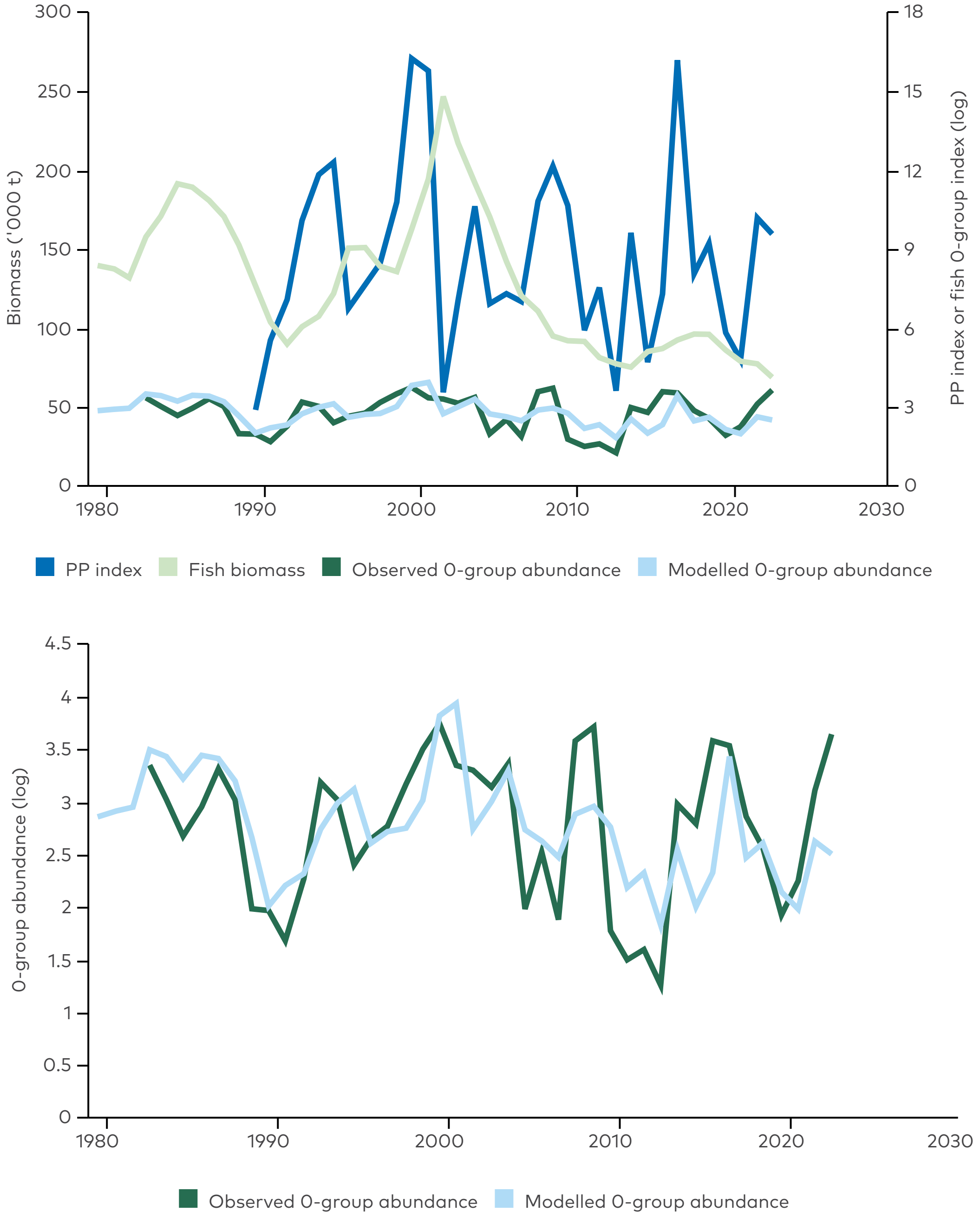


Figure 5.4 Modelling fish 0-group abundance on Faroe shelf by a primary production index and demersal fish (cod, haddock, ling, saithe) biomass. The panel to the left shows all variables while the right panel shows observed and modelled 0-group abundances.

Table 5.2 Sensitivity analysis of the output of the multiple regression model. The effect on the dependent variable (log of 0-group abundance) of varying the primary production and biomass values from the lowest to highest observed values and the ratio between them. Also, the ratio of the highest and lowest value in the table is shown in bottom right part of the table. The upper panel shows log-values and the lower panel back-transformed (antilog) values.

		Biomass ('000 t)					
	Primary prod.	**50**	**100**	**150**	**200**	**250**	**Max-min**
Log-values	3	1,42	1,91	2,19	2,39	2,55	1,13
	6	1,78	2,26	2,55	2,75	2,91	1,13
	9	2,13	2,62	2,90	3,1	3,26	1,13
	12	2,49	2,97	3,26	3,46	3,62	1,13
	15	2,84	3,33	3,61	3,82	3,97	1,13
	Max-min	1,42	1,42	1,42	1,42	1,42	2,55
		50	**100**	**150**	**200**	**250**	**Max/min**
Antilog	3	26	81	156	248	355	13
	6	60	184	353	561	805	13
	9	136	416	800	1273	1825	13
	12	308	944	1815	2887	4138	13
	15	699	2140	4116	6548	9385	13
	Max/min	26	26	26	26	26	355

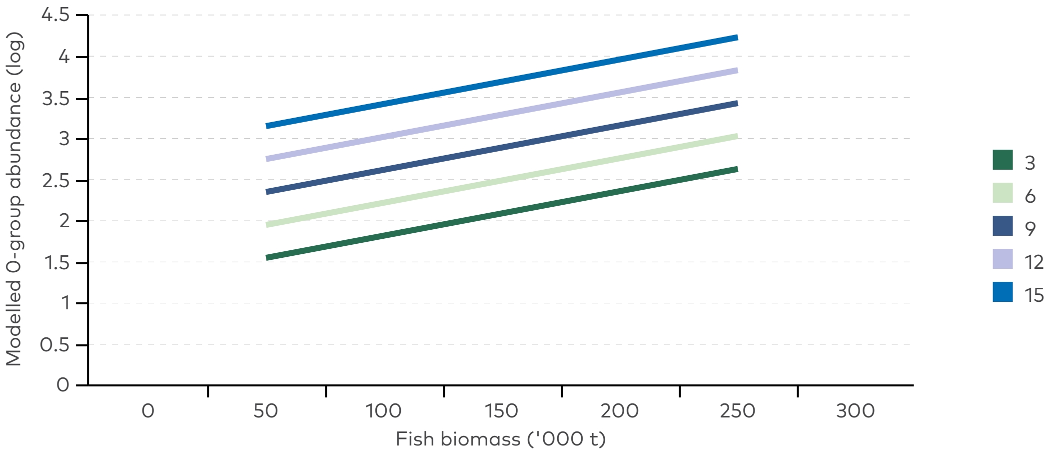


Figure 5.5 Sensitivity analysis of the multiple regression model, see Table 5.2. The lines represent primary production indices of 3 to 15.

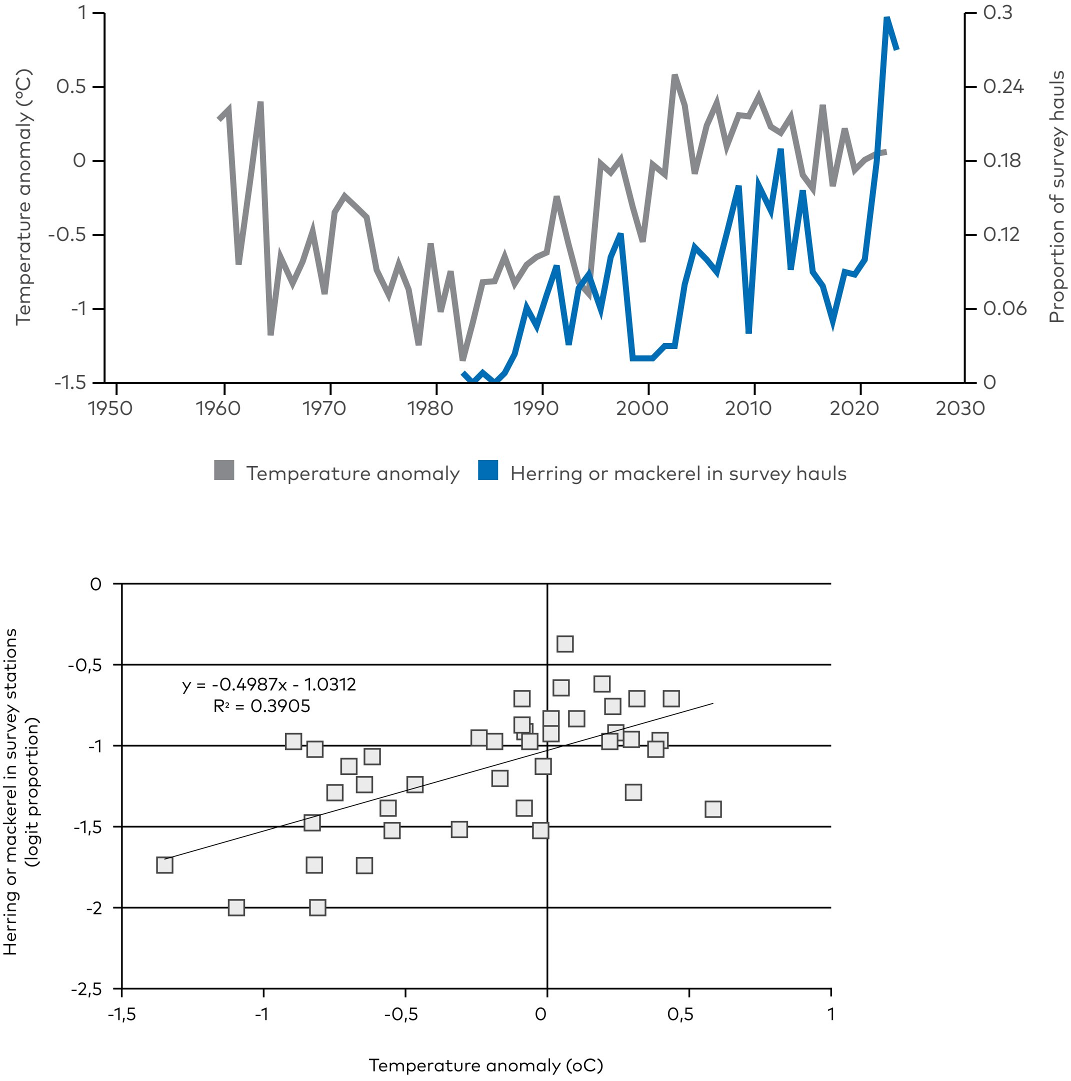


Figure 5.6 Abundance of mackerel and herring on Faroe Plateau in March and corresponding sea surface temperature in January-May (anomaly based on the 1992–2023 period).

Our model states that it is the productivity of the ecosystem and fishing mortality that drive the biomass of dermersal fish that in turn scare away pelagic fish or otherwise hamper the predation on fish larvae. This may represent a feedback loop where low biomasses of demersal fish are reinforced by high mortality on fish larvae. There are competing mechanisms, e.g. that temperature drives the abundance of pelagic fish on Faroe Plateu (Figure 5.6) or that temperature in combination with demersal fish determine the amount of pelagic fish and hence the predation on fish larvae. Even if our model is correct it is still possible that very high biomasses of demersal fish would reduce the abundance of fish larvae, e.g. by predation on sandeel larvae or other larvae.

Faroe Bank

Since no productivity index is available for Faroe Bank an index from Faroe Plateau is used that is based on the growth rate of the phytoplankton eating longlived shell *A. Islandica*, actually the difference between 'shelf' shells and 'coastal' shells (Matras et al., 2022). There is no stock assessment for demersal fish on Faroe Bank so a catch-per-unit effort measure is used instead. The model covered the years from 1996 to 2013, omitting years with missing data. The model explained 63% of the variance where the productivity index had a significant positive effect ($p < 0.05$) while the demersal fish index had a marginal positive effect ($p = 0.17$). The results therefore tend to support our hypothesis and also predicts that the sandeel abundances since 2017 should be high.

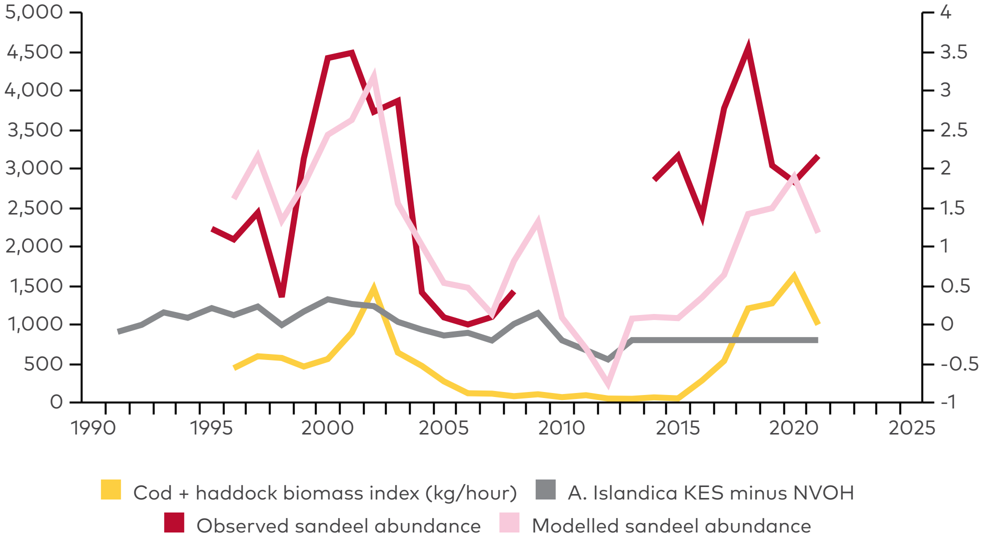


Figure 5.7 Modelling sandeel 0-group abundance on Faroe Bank by a productivity index (growth of *A. islandica* on Faroe Plateau) and a demersal fish index (cod+haddock catch per unit effort in the September groundfish survey).

Norwegian Shelf

Since there is no 0-group survey available along the Norwegian coast or time series of sandeels abundances, the breeding success of black-legged kittiwakes *Rissa tridactyla* was used as a proxy. The only available stock assessments of demersal fish in the area around Røst is the coastal cod stock (62–67 N) (providing a ratio between spawning stock biomass and sustainable biomass) and the coastal cod stock north of 67 N, where the spawning stock biomass in tons is available. Since Røst is situated just on the boundary of these two cod stocks we used a geometric average. The predation pressure on 0-group larvae was expressed as the biomass of age 1+ mackerel in the NE Atlantic, since no local time series of mackerel were available. The model was run for the years where data were available (1981–2020) even though a constant value for coastal cod was used prior to 1995. The model explained 49% of the variance and there was a significant positive effect of coastal cod biomass and a significant negative effect of mackerel biomass. Hence the model tends to support our hypothesis that demersal fish hamper pelagic fish in their predation of fish larvae.

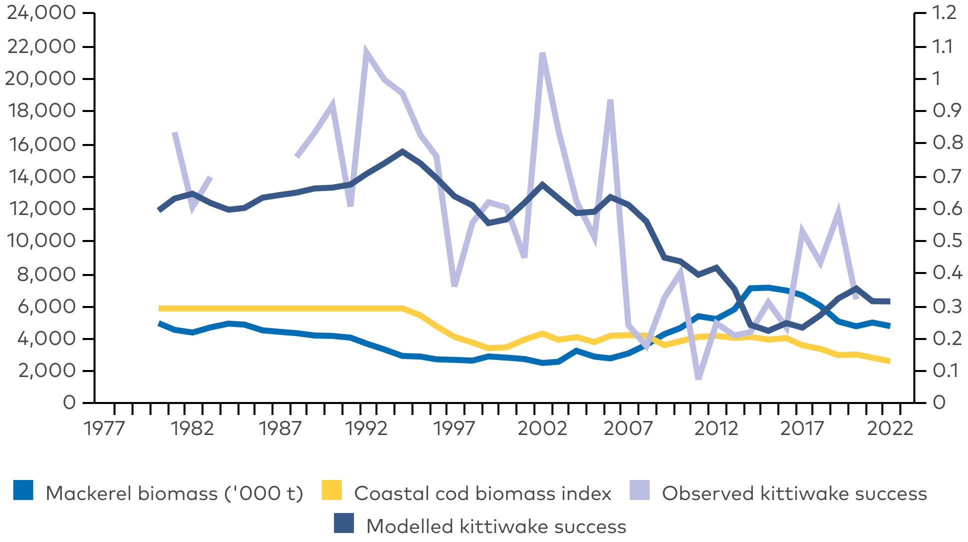


Figure 5.8 Modelling kittiwake breeding success on the Norwegian shelf at Røst (62°11'N) as a function of coastal cod biomass and mackerel biomass in NE Atlantic. Coastal cod biomass was taken as the geometric mean of the biomass estimates of the two adjacend coastal cod stocks, i.e., southern stock (62°–67° N) and northern stock (north of 67° N).

Iceland shelf

Since the cod stock at Iceland dominates the biomass of demersal fish we only used cod as a measure of demersal fish on the Iceland shelf. We used the age 1+ biomass of mackerel in the NE Atlantic as a proxy for the predation on fish larvae by pelagic fish. The model covered the 1996–2023 period and explained 30% of the variance where cod had a significant positive effect on sandeels and mackerel a significant negative effect on sandeels (Figure 5.9). Hence, these results support our hypothesis that demersal fish hamper pelagic fish in their predation of fish larvae. However, the model expects high abundances of sandeels back in the 1950–60s, which contrasts the harvest of puffins in Vestmannaeyjar that was low during this period. Either puffins rely much on other food types than sandeels (krill) or a top-down effect of cod on sandeels has occurred at high cod stock sizes or that our model is wrong. Hence, our hypothesis is not so well established for the Iceland shelf.

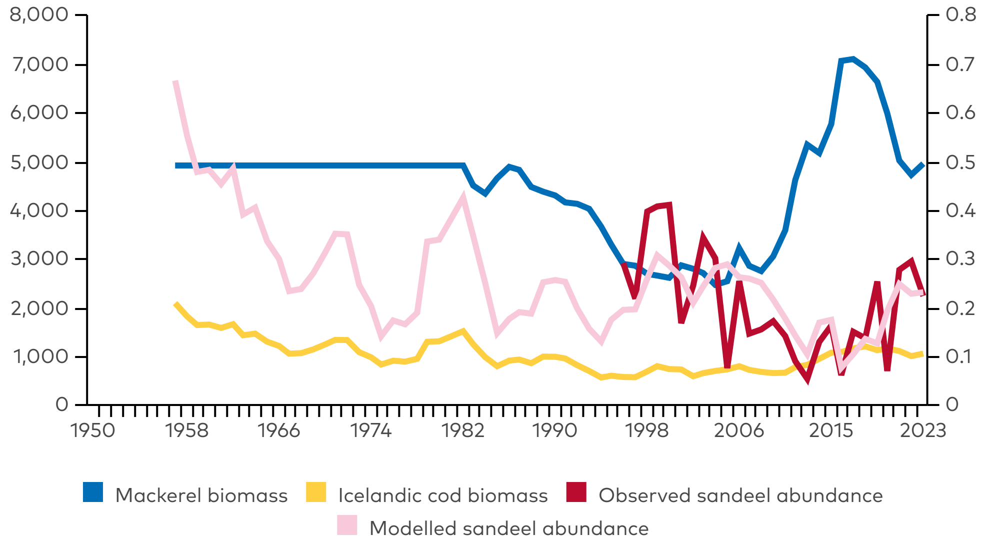


Figure 5.9 Modelling sandeel abundance on the Icelandic shelf (at age ca. 2 years as observed in cod stomachs) as a function of cod age 3+ biomass (two years before to reflect age 0 sandeels) and 1+ mackerel biomass in NE Atlantic (two years before).

Investigating Norway pout as a potential predator on fish larvae

The models explored above were based on the assumption that pelagic fish, such as herring and mackerel are important predators on fish larvae. In order to use a broader approach, we also briefly explore the potential of Norway pout to be a predator on fish larvae on Faroe Plateau. As already noted, Norway pout prey on both fish eggs and fish larvae (Albert, 1994) and this is also observed by the current author on Faroe Plateau (Figure 5.10). There is probably a feedback loop between cod, Norway pout and sandeel larvae, that again affect cod recruitment (Figure 5.11):

1. cod prey on Norway pout and hamper their abundance (Figure 5.12)
2. large Norway pout (modelled as Norway pout biomass index two years later) hamper the year-class strength of sandeel larvae (Figure 5.13).
3. Sandeel abundance has a positive effect on juvenile cod survival and recruitment to the cod stock, which affects the biomass of cod positively (Figure 5.14), although the cod age 3+ biomass (Steingrund et al., 2010) and the amount of Modified East Icelandic Water (MEIW) north of Faroe Islands also have a positive effect.

Sandeel larval abundance is also affected by the level of the primary production (Figure 5.15). Sandeel larval abundance can be modelled by primary production and Norway pout biomass two years before (Figure 5.16).

A preliminary modelling exercise was performed where the fishing mortality on cod was varied. Fishing mortality on cod reduces the age 3+ biomass of cod and hence cod recruitment that again reduces the predation rate on Norway pout that again increase the predation rate on larval sandeels that again decrease the recruitment of cod. The observed primary production as well as MEIW values 1990s to 2020 were projected into the future, i.e., to year 2149, while the cod and Norway pout biomasses and sandeel larval abundance were modelled. The average values from year 2050 to year 2149 were used as output.

The results (Figure 5.17) showed, as expected, that cod biomass decreased with increasing fishing mortality as well as cod recruitment (here shown as number of 2 year old cod, N2). Importantly, the catch was highest at F=0.2, i.e., at a much lower fishing mortality than experienced during the last decade where F has been around 0.6. If the values of Norway pout and sandeel larvae are standardized to the current F of 0.62, i.e. set to 1 at this fishing mortality, it is seen that the abundance of sandeel larvae is expected to increase by a factor of 2.3 if the fishing mortality is reduced to 0.2 while the biomass of Norway pout is expected to be orders of magnitude less compared with the F of 0.62. The amount of Norway pout is expected to increase by a factor of 2 if the fishing mortality is increased to 0.8. If it is assumed that seabirds would benefit from a diet of sandeels rather than Norway pout the modelling exercise shows that the optimization of cod catch and seabird food go hand in hand and that there is probably much to gain. More work should be done to validate that Norway pout actually are so important predators on sandeel larvae. More model settings could be explored, for example that cod actually are the causal agent of Norway pout biomass.

Future studies should explore in more details to which degree pelagic fish, such as herring and mackerel, affect fish larval survival and, if so, whether the effect of demersal fish biomass really decreases the predation by pelagic fish on fish larvae. Going one level down in the food chain, to zooplankton, and broadening the perspective much more, it should be investigated whether there are top-down effects of pelagic fish (herring and blue whiting) on the zooplanktonvorous amphipod *Themisto* in the Norwegian Sea, which is an important predator on *Calanus finmarchicus* (Skjoldal et al., 2004), and, if so, whether the effect is strong enough to increase the biomass of *Calanus finmarchicus* in the Norwegian Sea. If this holds true, it could affect the whole Norwegian Sea ecosystem a be an excellent case of ecosystem based management.

Figure 5.10 Gut content of Norway pout that was captured in the Faroese 0-group trawl survey in June 2022. In the upper part of the gut content, sandeel larvae can be observed.

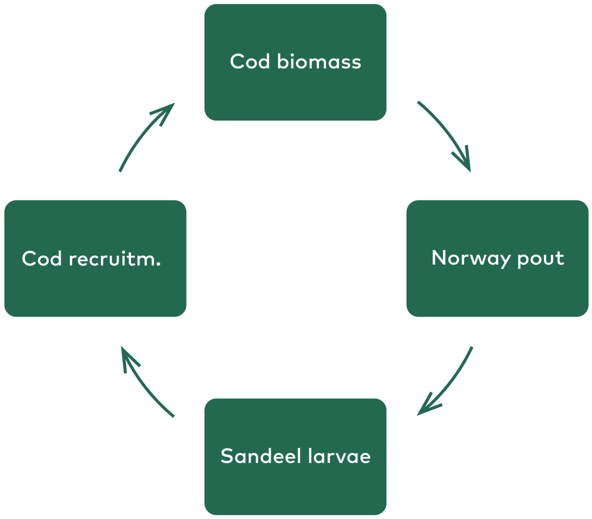


Figure 5.11 Feeback loop between cod, Norway pout and sandeel larvae. Cod have a negative effect on Norway pout abundance, that prey on sandeel larvae, that have a positive effect on cod juveniles (recruitment) that in turn has a positive effect on cod biomass.

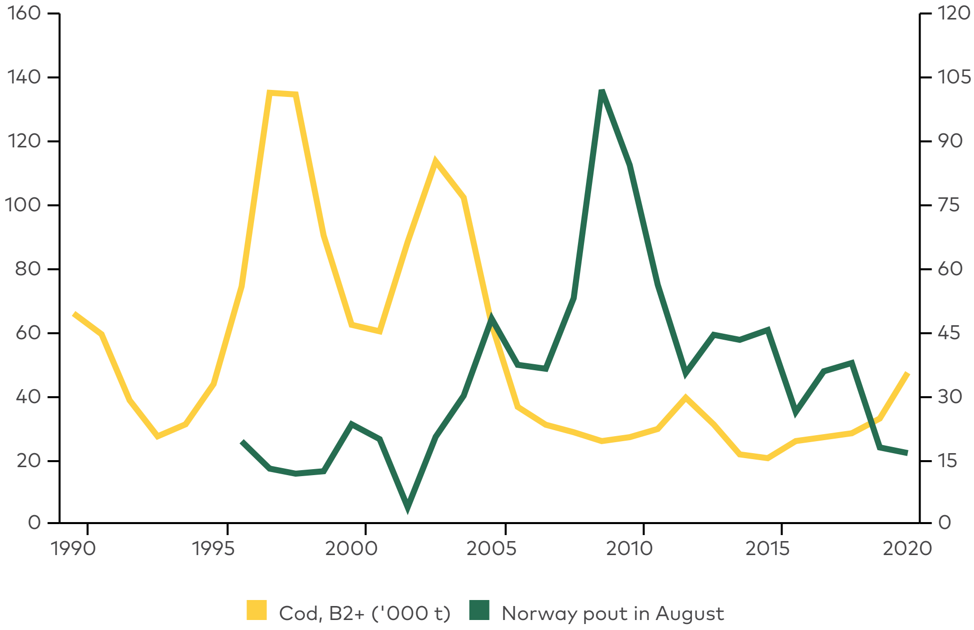


Figure 5.12 Biomass index for Norway pout on Faroe Plateau in the August groundfish survey compared with cod biomass two years before (y-2) as obtained from the stock assessment.

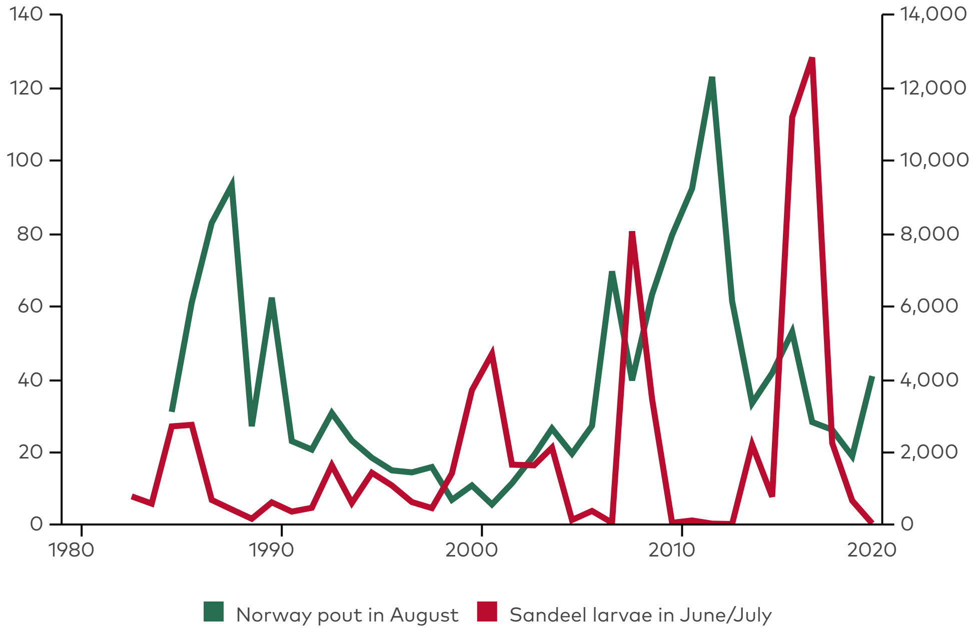


Figure 5.13 Biomass index of Norway pout, two years before (y-2), and abundance index of sandeel larvae.

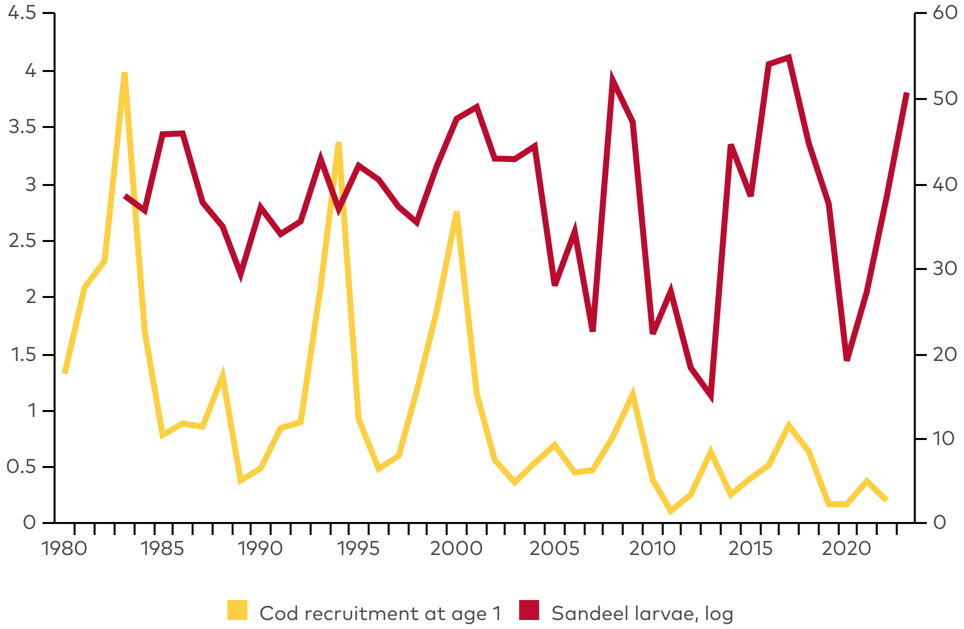


Figure 5.14 Sandeel larvae and cod recruitment at age 1.

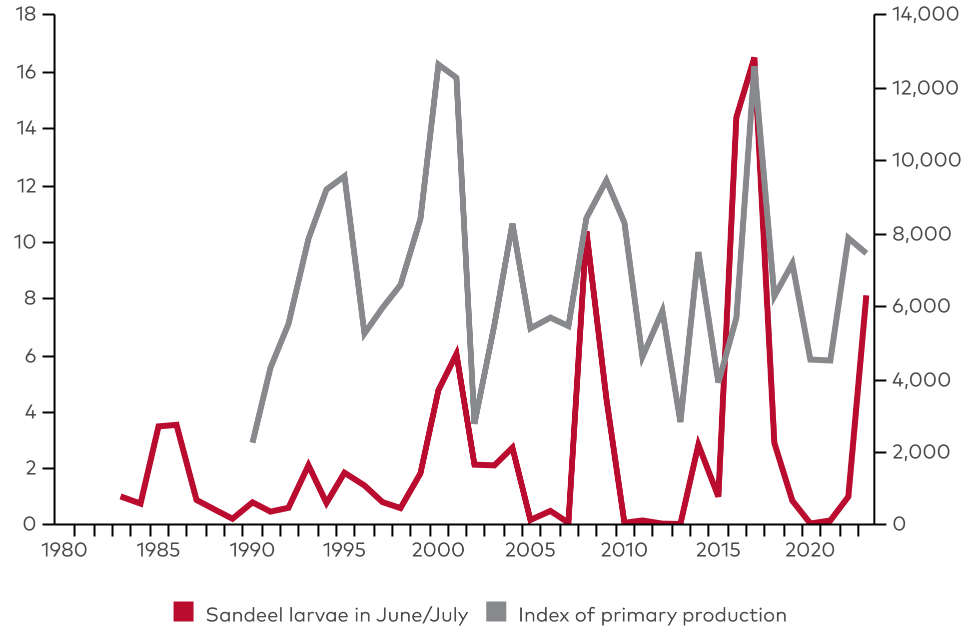


Figure 5.15 Sandeel larvae and primary production on Faroe Plateau.

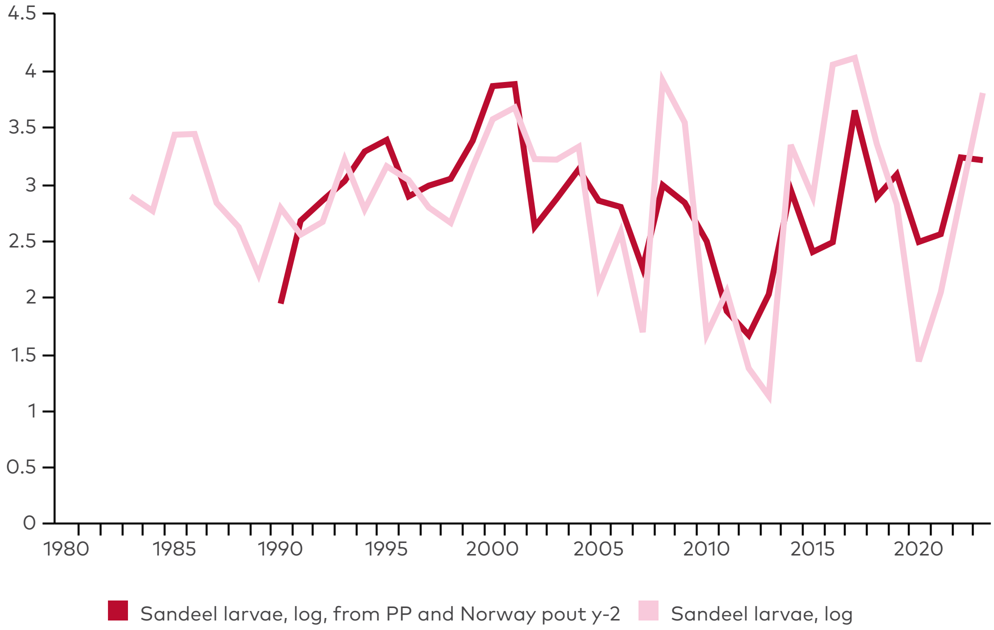
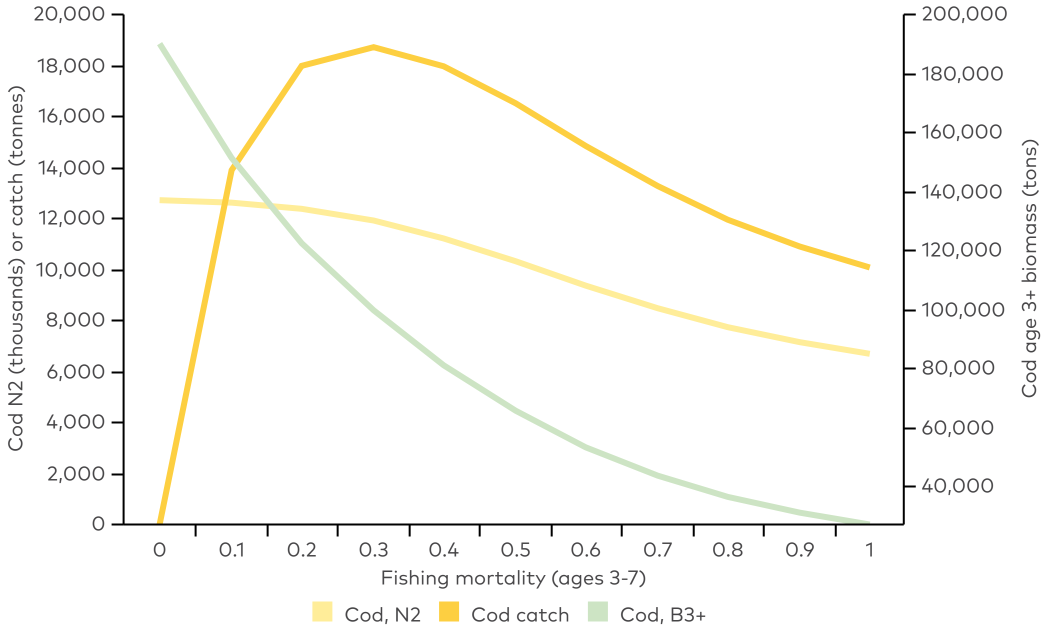


Figure 5.16 Abundance of sandeel larvae modeled by primary production and Norway pout two years before (y-2).



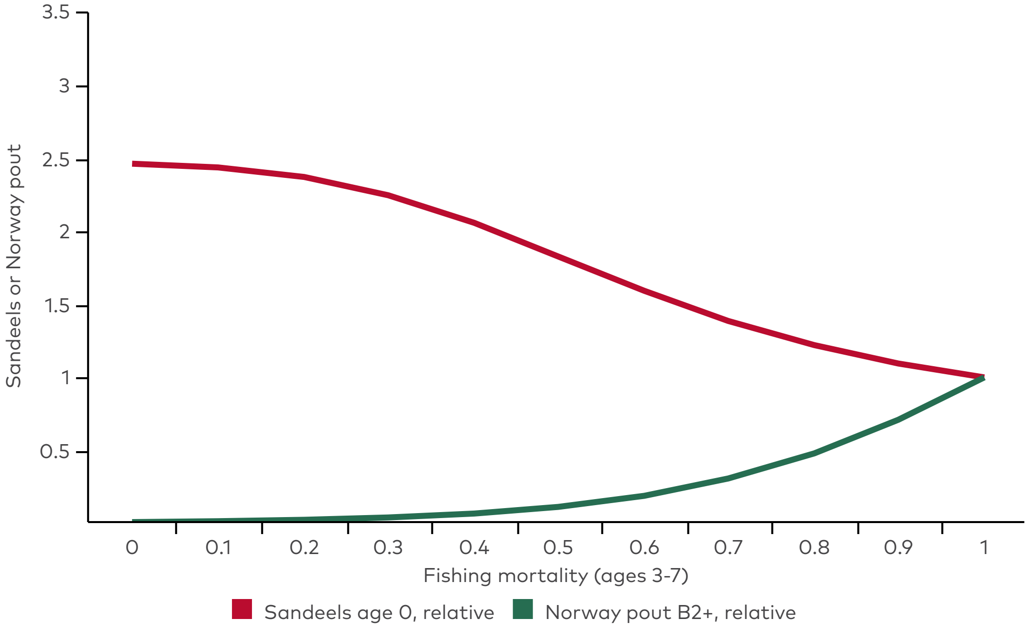


Figure 5.17 Upper: Simulations of cod recruitment, biomass and catch as a function of fishing mortality. Lower: Relative amounts of sandeels and Norway pout. The simulations are shown for medium amounts of MEIW. Results reflect the average values of the 2050–2149 period. N2: number of 2 year old cod. B2+: biomass of 2 year old fish and older. B3+: biomass of 3 year old fish and older.

Concluding remarks and future studies

Our hypothesis is that the abundance of fish larvae is regulated by ecosystem productivity, predation by pelagic fish (and probably Norway pout) and mitigation of the predatory effect by demersal fish. Our hypothesis seems to have some support in all four Nordic shelves although there were potential caveats in all four cases. To our knowledge our hypothesis is novel and should be substantiated with future studies. The hypothesis indicates the existence of a feedback loop between demersal fish, survival of fish larvae due to predation by pelagic fish that is mitigated by demersal fish and this closes the circle back to demersal fish. It is implied that once the demersal fish have reached a low biomass they might stay there for long periods and *vice versa*. If the hypothesis turns out to be correct it may be a means to restore not only demersal fish stocks but also seabirds in the NE Atlantic. An important finding might be that restoring demersal fish populations goes well along with restoring seabird populations. However, since juveniles of pelagic fish, such as herring, mackerel and blue whiting might be closely associated with the Nordic shelves during their first year of life it should be investigated whether it results in higher mortality from large restored demersal fish populations and whether it leads to smaller pelagic fish stocks. The case provided in this section of the report could provide a good basis of ecosystem based management.

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Chapter 6.

Summary of the report

Petur Steingrund, Tycho Anker-Nilssen, Høskuldur Bjørnsson, Valur Bogason, Jóhannis Danielsen, Erpur Snær Hansen, Espen Johnsen, Hannipoula Olsen and Hjálmar Hátún.

Hydrography (Chapter 1)

Chapter 1 focuses on large-scale oceanographic processes in the North Atlantic Ocean. It is noted that the stock size of several demersal fish stocks and several seabird species have been declining during the last 2–3 decades. A critical question is whether this is due to anthropogenic influence, natural environmental cycles or maybe (and more likely) a combination of these. A bottom-up perspective focuses on the most plausible physical drivers underlying ecosystem changes on the south Iceland, Faroe and Norwegian shelves – especially through the trophic pathway from large zooplankton (copepods) via forage fish (e.g. sandeel and Norway pout) to commercial fish stocks and seabirds. Historical temporal changes in the SPNA are here categorized into:

i. recurrent pulses every 5–8 years. These include the effects from the subpolar gyre, a large body of less saline water south of Iceland, on the atlantic inflow (AW) into the areas south of Iceland, over the Iceland-Faroe ridge, and through the Faroe-Shetland Channel – the larger the SGP the more nutrients/zooplankton is contained in the AW. The strength of the East Icelandic Current (EIC) has a similar effect on the Icelandic, Faroese, and Norwegian shelves.
ii. major longer-lasting shifts. These include long term dynamics of the subpolar gyre that is affected by wind circulation patterns like NAO. A weaking of the SPG after 1996 likely affected seabird populations negatively, although there was a subarctic pulse in 2000–2001.
iii. long-term trends. These include long term changes in the scale of 50–100 years that may be related to either natural cycles, e.g. the Atlantic Multidecadal Oscillation, AMO) of 50–60 years but also antropgenic climate change. It may be difficult to distinguish these effects from each other due to the lack of long time series, but at least it is known that there has been a

> decline in the nutrient silicate throughout the entire SPNA since the 1980. If this trend continues it will change North Atlantic subarctic marine ecosystems fundamentally.

Future studies could focus on a review of recent ecosystem changes on the Iceland, Faroe and Norwegian shelves, that could be used to test and maybe adjust/improve previously proposed hypotheses on bio-physical linkages.

Seabird productivity (Chapters 2–4)

Seabirds associated with the Norwegian Shelf (Chapter 2) are in many respects good indicators of marine ecosystem dynamics, especially with regards to advection of nutrients and zooplankton onto the shelves and the growth and retention time of fish larvae and forage fish. Seabirds, like kittiwakes and puffins feed far offshore in their search for prey to sustain their offspring, although kittiwakes may also search for food in near-shore waters. These two seabird species thus reflect two different foraging niches in the pelagic ecosystem offshore, and the foraging ranges of both species in the breeding season cover the entire extent of the shelf area around Røst in Northern Norway. Productivity, e.g., chick fledging success for puffins or chicks per pair for kittiwakes, is the far best parameter linking seabird demography with trophic interactions in the breeding area. The productivity of Atlantic puffins in Røst, Norhern Norway has been monitored since 1964 and for kittiwakes in Røst since 1979. The results show the existence of high and low productive periods. Low productive periods have been observed during the 1970s and in the period from 2007 to 2015. This can be attributed to the availability of age 0 herring produced by the Norwegian spring-spawning stock. Further north, age 0 cod is shown to be an important diet component of adult common guillemots in the southwestern Barents Sea, which also affects the breeding success there. Crustaceans, such as krill, may also be important food for seabirds when forage fish are lacking. Physical drivers, although not well understood, may be of importance to seabird production since sea temperature and salinity within the NCC off the Lofoten Islands in March, i.e. two months prior to egg laying, explained more of the variation in puffin breeding success on Røst than the abundance or quality (size) of their main prey, age 0 herring.

Seabirds, i.e. puffins, in Vestmannaeyjar, Iceland, are also good marine ecosystem indicators (Chapter 3). A virtual production index, P(H.) is based on average age composition of harvest of birds ringed as chicks. Harvest is 75% composed of immature birds 2–4 years old. The P(H.) calculation sums up each cohort relative size, accounting for survival to age using estimated 87% annual survival in Vestmannaeyjar (Helgason 2012). This index reflects cohort sizes relative to a reference year of maximum cohort size (1882) and is the longest time series on seabirds in existence. It is important to keep in mind that this production index is essentially a product of breeding success (fledglings/pair) and breeding population size in a given year. However, by using fixed age composition, biases small cohorts upwards, and large cohorts downwards in numbers, thus reduces cohort real size variation. To gauge this filtering, another production index P(town) was created based on number of fledglings, either ringed (1971–2002) or rescued by the public annually in the town of Vestmannaeyjar (2003–2023). Each series is standardized by dividing by their respective maximum values (Figure 3.1). The number fledglings in town and direct production estimates are highly correlated. The length of the data series is impressive, as it covers the 1878–2023 period. Results show that there was a low-productive period from 1930 to 1962 and also from 2004 to 2015 while a low-productive period probably also was observed in the 1970s. These fluctuations are strongly correlated negatively with sea surface temperature in Vestmannaeyjar (1878–2005), likely via effects on sandeel egg developmental time (thus hatching time), winter survival, summer growth, and fertility by direct effect on basal metabolism. Also, warming of the Atlantic in 1995 coincided with a 50% reduction the abundance of northern krill in Icelandic puffins wintering area over the Atlantic ridge. Northern krill is likely key puffin prey in spring and might affect survival of puffin and many other seabird species wintering in the hotspot. In 2005 puffin production declined substantially faster than in the beginning of the last warm phase of the Atlantic Multidecadal Oscillation (1930–1965) despite similar SST increase as the current warm phase starting in 1995, suggesting another causative factor/s than SST alone. Furthermore, a large (1.5x SD, or 18 days) delay in Westman puffin breeding phenology (mean fledging time) was observed during this period (after 2005) in comparison to mean (mean fledgling time 1937–2023. This phenological delay is of great interest as it seems indicative of general trophic mismatch in Selvogsbanki, affecting not only production of puffin and their sandeel prey, but also many important commercial fisheries.

Seabirds at the Faroes confirm the above described patterns (Chapter 4). There is a strong positive correlation between Atlantic puffin reproductive success on Mykines and the mass of zooplankton in the Norwegian sea in May (g/m^2) from 2011 to 2020 ($r^2 = 0.74$) maybe indicating that there is a common underlying driver capable of causing production peaks on both the Faroe and Norwegian shelves. A low-production periods is observed from 2004 to 2013. Local effects are also important since the 2009 and 2017 peak in tern reproductive success as well as mean number of terns throughout the country closely follows the kittiwake reproductive success these years and it is therefore also likely that these peaks can be explained at least partly by the local 0-group fish larvae index that is mainly driven by the local primary production. In addition to the abovementioned factors, seabird hunting may have contributed to the overall decline in seabirds (68% for guillemots 1972–2014, 60% for kittiwakes 1987–2014) at the Faroes.

Future research should focus on 1) the effects of large- and mesoscale oceanographic processes on the Norwegian shelf ecosystem, 2) *top-down effects of mackerel as a predator on seabird prey and lower trophic levels, and 3) spatial and temporal dynamics of seabird foraging habitat use. Also, 4)* time lags in productivity of seabirds among the Nordic shelves should be investigated as well as 5) getting more data on what adult seabird feed on and where the feeding area are located.

Fish larvae dynamics and predation by pelagic fish (Chapter 5)

The sections above have shown that large-scale hydrographic conditions, e.g. the dynamics of the Subpolar gyre or the amount of zooplankton in the Norwegian Sea, have a large effect on the productivity of seabirds via the effects on zooplankton and/or forage fish. Importantly, some low-productive periods were identified, such as the last one from around 2003 to around 2014 that seemed to affect both the Icelandic shelf, Faroe shelf and the Norwegian shelf.

The great question is whether something can be done to mitigate the effects of the low-productive periods on the shelf ecosystems. The short answer is yes. A novel approach is used to explain annual variations of demersal fish larvae in the pelagic phase that takes into account 1) ecosystem productivity (as shown above), 2) predation on fish larvae by pelagic fish (herring and mackerel) and 3) mitigation of the predation effect by demersal fish species (cod, haddock, ling, saithe).

The motivation for this approach is that pelagic fish larvae of demersal fish, e.g. sandeels, seem to be the crucial link between lower and higher trophic levels and that predation mortality is of paramount importance to the functioning of the shelf ecosystems. Although fish larvae may have many predators, it was focused on herring and mackerel that are present at the same time (March–April) and place as the fish larvae. It was, however, noted that the amount of herring/mackerel were negatively correlated with the amount of adult demersal fish, such as cod, haddock, ling and saithe where the mechanism was interpreted as predation avoidance since these demersal fish are observed to prey on herring and mackerel in Faroese waters.

A modelling approach on the Faroe Plateau showed that the survival of fish larvae was a factor of 13 higher in demersal large-stock years compared with low-stock years. Environmental factors were also of great importance since the survival of fish larvae varied by a factor of 26 between years with the highest primary production compared with the lowest. Simpler modelling approaches for the Icelandic shelf, Faroe Bank and the Norwegian shelf seemed to confirm these results, i.e., that there was a positive relationship between the survival of fish larvae and the amount of demersal fish. This means that reducing the fishing mortality on demersal fish can mitigate the mortality on fish larvae that is caused by pelagic fish, although the extent of the effect was not evaluated.

A modelling approach was also performed for the Faroe Plateau where adult Norway pout were regarded as predators on fish larvae and were cod preyed on, and suppressed the biomass of, Norway pout. Results indicated that a low fishing mortality on cod was able to increase the amount of sandeels as well as giving higher yield per recruit for cod.

Future research should focus on the extent that pelagic fish (herring, mackerel, Norway pout) eat fish larvae. It should also be investigated whether the negative relationship between the amount of pelagic fish and demersal fish is real and, if so, whether demersal fish just scare pelagic fish away or they actually eat sufficient numbers of them to create the observed pattern.

It is worth noting that during this report a quite simple approach is used. Although we have used some models to evaluate the effect of e.g. primary production and the amount of demersal fish, via a scaring effect on predatory pelagic fish, on the survival of demersal fish larvae, such models only give a hint on whether the proposed mechanisms are valid or not. In order to do this work properly we, at least, need more information about the distribution of pelagic fish during the year and how much fish larvae they consume and whether adult demersal fish really have a scaring or predatory effect on pelagic fish. As such, we have only scratched the surface of a much bigger research topic. Also, when evaluating low- and high-productive periods of seabirds in relation to oceanographic forcing this is actually only to scratch the surface of a much bigger field of research. What is needed in the future is a much greater research effort that combines environmental factors as well as biological factors over a large area (NE Atlantic) that also needs to incorporate human effects, e.g. fishing on pelagic fish as well as demersal fish. This could certainly contribute to improved ecosystem-based management of marine sources in the NE Atlantic and probably elsewhere.

Appendix 1. Project activity

Kick-off meeting in Tórshavn, Faroe Islands, 7. –9. January 2020. Due to Corona no other physical meetings were held.

Status report, June 2020.

Teams meeting 15 February 2021.

Status report, June 2021.

Teams meeting 1 December 2021.

Status report, December 2021.

Zoom meeting 16 February 2022.

Zoom meeting 28 March 2022.

Zoom meeting 20 April 2022.

Zoom meeting 18 May 2022.

Status report, June 2022.

Zoom meeting 23 November 2022.

Appendix 2. Information about the project

On the web site of Faroe Marine Research Institute (https://www.hav.fo/verkaetlanir/).

Presented the project in the NovasArc meeting at the Faroes in May 2022.

Some results from the project were used in an online presentation by Eydna í Homrum in The 3rd International conference on the Ecosystem Approach to Management in Arctic Large Marine Ecosystems. Ecosystem Based Management in a Rapidly Warming Arctic, Tromsø, Norway 15–18 April 2024.

Appendix 3. Participants in the project

Table: Project organisation

	Role	Name and (if appropriate) title	Organisation	Country
Decision level	Project owner	Petur Steingrund	Faroe Marine Research Institute	Faroe Islands
	Project manager	Erling í Liða	Faroe Marine Research Institute	Faroe Islands
Implementation level	Participants	Jóhannis Danielsen	Faroe Marine Research Institute	Faroe Islands
		Hannipoula Olsen	Faroe Marine Research Institute	Faroe Islands
		Hjálmar Hátún	Faroe Marine Research Institute	Faroe Islands
		Høskuldur Bjørnsson	Marine and Freshwater Institute	Iceland
		Erpur Snær Hansen	South Iceland Nature Research Centre	Iceland
		Espen Johnsen	Institute of Marine Research	Norway
		Tycho Anker-Nielssen	Norwegian Institute for Nature Research (NINA)	Norway

Appendix 4. Table of abbreviations

Abbreviation	Explanation	Remarks
SST	Sea surface temperature	
SPG	Subpolar gyre	
NAC	North Atlantic Current	
NSG	Norwegian Sea Gyre	
EAC	East Atlantic Current	
EIC	East Icelandic Current	
NCC	Norwegian Coastal Current	
AW	Atlantic water	
Røst	The islands of Røst, Norway	Holding big seabird colonies
Westmans (WI)	The islands of Vestmannaeyjar, Iceland	Holding big seabird colonies
IFR	Iceland Faroe Ridge	

About this publication

Ecosystem based management of sandeels, demersal fish and seabirds in Boreal ecosystems in Northeast Atlantic

Petur Steingrund, Tycho Anker-Nilssen, Høskuldur Bjørnsson, Valur Bogason, Jóhannis Danielsen, Erpur Snær Hansen, Espen Johnsen, Hannipoula Olsen and Hjálmar Hátún

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Cover photo: Picture taken by Polar Films. The picture shows puffins in Mykines, Faroe Islands, in August 2019. Note that the puffin to the left carries krill while the puffin to the right carries fish of different species.
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