Nordic Council
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Advection of zooplankton onto the Nordic shelves and effects on forage fish, demersal fish and seabirds

Contents

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The abundance of zooplankton in the Norwegian Sea is of great importance to the ecosystem in the Norwegian Sea and has gained considerable interest in recent years. The East Icelandic Current (EIC) flows southeast towards the Faroes from an area that contains the highest amounts of zooplankton in the Norwegian Sea. The zooplankton biomass in the Norwegian Sea in May has been monitored annually since 1995 in connection with an internationally coordinated ecosystem survey (ICES/PGNAPES). It is noteworthy that the zooplankton biomass has decreased over time with a relatively strong negative shift around year 2005 and a small increase in the last five years. Not surprisingly, the distribution and diet of Norwegian Spring Spawning Herring in May seems to be closely linked to the zooplankton biomass in the southwestern Norwegian Sea.

In connection with the NHK project "Ecosystem based management of sandeels, demersal fish and seabirds in boreal ecosystems in the North-east Atlantic" (project number 200004, 2020-2022), that synthesized data on forage fish, demersal fish and seabirds in NE Atlantic, it was noticed that the abundance of zooplankton in the Norwegian Sea is of great importance to the productivity of the shelf ecosystems in Nordic waters (Iceland, Faroes, Norway). This hypothesis is not new, but when comparing the various national data it was clear that many of the available time series support this concept. Zooplankton (and probably also nutrients) in the south-western Norwegian Sea is advected with the East Icelandic Current southwards towards the Faroe Plateau and remnants of this water mass, termed Modified East Atlantic Water (MEIW), is observed north of the Faroes and even along the Norwegian Shelf.

Hence, the goal of the project was to evaluate the hypothesis that oceanographic features, i.e. the subpolar gyre (SPG) and the East Icelandic Current (EIC), cause an advection of nutrients and/or zooplanton onto the Icelandic, Faroe and Norwegian shelves that stimulate the abundance of forage fish, demersal fish recruitment and production of seabirds. In short, we found good support for this hypothesis, which is outlined in two parts of the project.

→ Part 1. The broad perspective: ocean currents in NE Atlantic and its influence on the marine ecology on the Nordic shelves

→ Part 2. A case study for the Faroe Shelf: East Icelandic waters fuel the Faroe shelf ecosystem

PART 1.

The broad perspective: Ocean currents in NE Atlantic and its influence on the marine ecology on the Nordic shelves

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Abstract

The goal of this article is to evaluate the hypothesis that oceanographic features, i.e. the subpolar gyre (SPG) and the East Icelandic Current (EIC), cause an advection of nutrients and/or zooplanton onto the Icelandic, Faroe and Norwegian shelves that stimulate the abundance of forage fish, demersal fish recruitment and production of seabirds. We compared indices of SPG and EIC with zooplankton, forage fish (capelin *Mallotus villosus*, sandeels *Ammodytes spp.*, herring *Clupea harengus*), recruitment of demersal fish (cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*) and production of seabirds (Atlantic puffin *Fratercula arctica*, black-legged kittiwake *Rissa tridactyla*) on the three Nordic shelves where we concentrate on the 1970–2023 period with most data and focus on the area from Iceland, Faroe Islands and along the Norwegian shelf up to Lofoten Islands in Northern Norway. We found good support for our advection hypothesis, e.g., that a large SPG and/or strong EIC seemed to cause elevated levels of zooplankton, forage fish, demersal fish recruitment and seabird productivity on the three Nordic shelves. Importantly there was a prominent low-production period from 2003 to 2014 that could clearly been seen in most of the data series. Confounding factors, such as direct metabolic effects of temperature on zooplankton and forage fish or grazing of zooplankton by pelagic fish were not directly adressed, but could have played a role. Our study is of importance for ecosystem based management of marine fish and seabirds on the Nordic shelves. Future studies are suggested to fill in important knowledge gaps and quantify mechanistic links in trophic interactions.

PART 1.

1.1 Introduction

1.1.1 Long term variability of marine ecosystems

There has been a long history of research on common drivers of environmental change in NE Atlantic and fluctuations in atmosperic pressure and sea temperature have received a lot of attention (e.g., Stenseth et al. 2004). One of the most notable observations was that there were long periods of herring fishery along the Norwegian coast and Iceland when temperatures were higher than normal and the conspicuous absence of herring in colder periods and curiously enough, there was an opposite pattern in the herring fishery along the Swedish west coast, i.e., a rich fishery when temperatures were low and no fishery when temperatures were high (Alheit and Hagen 2003). Although it was first proposed that this was caused by large-scale variations in migration pattern of a common herring stock in the NE Atlantic, it was later discovered that there were two stocks of herring in the areas that responded differently to temperature (Höglund 1978). Another example was the observation that the abundance of cod in the Barents Sea and in Greenland tended to show the opposite pattern (see Sundby 2000). Such large-scale differences in development of fish stocks targeted by commercial fisheries have later been attributed to variations in climate, more specifically the wind pattern and the NAO index (Drinkwater 2013). There was a large focus on the connection between NAO and fish stocks in the 1990s (Stenseth et al. 2004), but these relationships tended to break down in the 2000s. With a focus on coastal shelf ecosystems in Nordic waters, our project attempts to unravel some of the important mechanisms through which climate change drives the bottom-up productivity of marine food chains, from zooplankton to fish and seabirds.

1.1.2 Oceanography and how it affects the shelves

In our search for drivers of productivity and biogeographical changes in the NE Atlantic an obvious choice is the dynamics of the subpolar gyre (Hátún et al. 2009) . During years with strong winds and heat losses in the Labrador and Irminger Seas, intensified winter convection brings large amounts of nutrients from the deep water masses and up to the surface (Hátún et al. 2017a). This fuels a large production of phytoplankton and zooplankton within the subpolar gyre (Hátún et al., 2016; Tesdal et al., 2022) and expands the subpolar gyre eastward (Hátún et al. 2005), and fuels shelf ecosystems along boundaring the northeastern Atlantic (Hátún et al. 2022a, 2017b).

Another candidate for a driver of productivity is the strength of the East Icelandic Current (EIC). The area NE of Iceland is rich in zooplankton (ICES 2021) and advection of the zooplankton with the EIC is crucial to the production in the southern and eastern part of the Norwegian Sea. There have been marked interannual variations in the strength of the EIC where especially the years from 2004 to 2016 were characterised by low amounts Modified East Icelandic Water (MEIW) north of Faroe Islands and along the Norwegian Shelf (Hátún et al. 2022b; Kristiansen et al. 2019; Skagseth et al. 2022). A marked increase in this subarctic intermediate water mass happened subsequently in 2017 to 2021 (see Part 2).

1.1.3 Zooplankton

The copepod *Calanus finmarchicus* is a key secondary producer in the North Atlantic (Melle et al. 2014), and dominates the meso-zooplankton biomass in Icelandic, Faroese and Norwegian waters (Gaard and Hansen 2000; Melle et al. 2004). One of the key life history traits for this copepod species is dormancy, a strategy acquired in order to persist through seasonally adverse conditions (winter). As such, in late summer in the Northeast Atlantic, pre-adult *C. finmarchicus* copepodites descend to deep waters to overwinter in a resting state known as diapause (Heath et al. 2000), and the Norwegian Sea gyre and the Atlantic Subpolar Gyre are regarded central overwintering areas (Melle et al. 2014). Shortly prior to the spring bloom the animals ascend from diapause at depth to surface waters, molt into adults and begin reproduction. The egg production is to a large degree dependent on the concurrent food concentration (Stenevik et al. 2007; Head et al. 2013; Melle et al. 2014), but lipid reserves may also fuel the initial production (e.g. Madsen et al. 2008). Once in the upper layers, *C. finmarchicus* is advected onto adjacent shelves, where it is an important prey for larva and juvenile fish of several benthic fish species e.g. cod (Sundby 2000; Heath & Lough 2007). Furthermore, *C. finmarchicus* is considered a main prey for pelagic fish stocks such as herring, blue whiting and mackerel (Prokopchuk et al. 2006; Langøy et al. 2012).

The amount of zooplankton has shown similar long-term trends for large oceanic areas in the Nordic Seas. For the period 1995 to mid-2000s the plankton abundance in spring was relatively high, with fluctuations between years. Since around mid-2000s the zooplankton biomass decreased and has since been at lower levels (ICES 2024d). The period with lower zooplankton biomass coincides with higher-than-average heat content in the Norwegian Sea and reduced inflow of Arctic water into the southwestern Norwegian Sea. The arctic indicator species *Calanus hyperboreus* showed the same pattern, with higher abundance in the

Norwegian Sea in periods with increased inflow of Arctic water (Skagseth et al., 2022). The zooplankton biomass to the south of Iceland has been shown to vary according to the strength of the SPG (Hátún et al. 2017a), and the zooplankton biomass as well as the abundance of *C. finmarchicus* in the southern Norwegian Sea has been linked to the EIC (Kristiansen et al., 2016; Skagseth et al. 2022). In addition, the phenology (i.e. the timing) of *C. finmarchicus* in the southern Norwegian Sea changes dependent on the influx of MEIW (Kristiansen et al. 2016; Kristiansen et al. 2019), which may also affect higher trophic level species. In the North Sea, the variability in abundance of *C. finmarchicus* has been linked to the recruitment of cod (Beaugrand et al. 2002), and for the Faroe shelf, it has recently been shown that interannual variability in advection of *C. finmarchicus* on to the Faroe shelf in spring affects the variability in abundance of pelagic juvenile Faroe Plateau cod (Jacobsen et al., submitted).

The zooplankton biomass and the abundance of *C. finmarchicus* at the south-western Norwegian shelf show a similar long-term trend as the oceanic Norwegian Sea, with lower abundance after 2010, but the signals are weaker (Dupont et al. 2017; C. Broms, not published). This may indicate that the shelf is affected by the amount of zooplankon advected from surrounding oceanic areas. However, several local factors may also play a role, as predation, and the Norwegian Coastal Current flowing along the coast in a south-north direction. For the Norwegian shelf it has been shown that the density of zooplankton in the drift route of the herring larvae dropped significantly after 2004, and their centre of gravity shifted northwards, concluding that presence of food and overlap with high food concentrations are likely important regulators of survival in herring larvae (Toresen et al. 2019).

1.1.4 Forage fish

Forage fish play a vital role in the linkage between lower and higher trophic levels of marine foodwebs (Pikitch et al. 2012; van der Kooij et al. 2008); there amongst are sandeels (*Ammodytes spp.*), a lipid rich schooling fish, of great dietary importance for several demersal fish stocks as well as seabirds (Eliasen 2013; Greenstreet et al. 2006; MacDonald et al. 2019).

There has been much focus on the relationship between sea temperature and the life history and ecology of sandeels in the North Sea (Réginer et al. 2018). Year class strength is estabished during early larval development and depends on the degree of temporal synchrony between hatching time and *Calanus helgolandicus* egg producion (Régnier et al. 2017). Rising temperatures might negatively affect the growth rate, body size and fat reserves of sandeels and, consequently, reduce both the first-winter survival of the age 0 year class (van Deurs et al. 2011) and the reproductive investment of older sandeels (Wright et al. 2017). Elevated sea temperatures also increase the metabolism of sandeels during winter when sandeels do not feed and lead to increased mortality, not only in the North Sea but also in the Faroes (Eliasen 2013) and in Selvogsbanki in South Iceland (E.S. Hansen & V. Bogason, unpublished data).

Several studies indicate that the lesser sandeel *Ammodytes marinus* will be vulnerable to climate change in the North Sea due to two factors. Firstly, warmer water will affect the composition of zooplankton. An increase in warm-water species and a decline in the occurrence of Calanus finmarchicus (Beaugrand et al. 2002) is expected, leading to a reduced amount of suitable zooplankton for the lesser sandeel (van Deurs et al. 2009). This could affect larval survival, growth rate, and spawning biomass of the lesser sandeel. Secondly, buried lesser sandeel will have a higher metabolism in warmer water, resulting in a reduced likelihood of winter survival and lower energy reserves for spawning (van Deurs et al. 2009; van Deurs et al. 2011; Eliasez 2013; Henriksen et al. 2021). Additionally, Johnsen et al. (2017) show that higher densities of lesser sandeel increase school formation and predator avoidance, so a general decline in the amount of sandeel will reduce school structures and natural predator avoidance. The lesser sandeel's dependence on a suitable habitat in relatively shallow water with a substrate of oxygen-rich gravel and coarse sand limits its ability to move to new areas. Therefore, it is particularly vulnerable to significant environmental changes.

In the North Sea, repeated stock assessments of the sandeel stocks have provided time series of recruitment, biomass and fishing mortality, but such data are not available for sandeels on the Nordic shelves. Although it has been acknowledged that *Calanus* copepods are very important prey for sandeels (Eliasen 2013) there are few studies that link sandeel abundance with oceanographic features and zooplankton advection onto the Nordic shelves (e.g., Henriksen et al. 2018). Research in the North Sea indicates that trophic mismatch of Calanus spp. and hatching time of sandeel larvae can affect recruitment of sandeels (Arnott et al. 2002; van Deurs et al. 2011; Régnier et al. 2017). Both spawning and hatching time of sandeel larvae in the North Sea have also shown correlations with bottom sea temperature (MacDonald et al. 2019).

1.1.5 Demersal fish recruitment

Fish stock assessments are routinely done for many demersal fish stocks on the Nordic shelves, e.g., cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*). They provide time series of recruitment, spawning stock biomass and fishing mortality. Curiously enough, all stocks seem to be special in the sense that they exhibit their own variation over time that normally is not matched by any other fish stock in the same or other areas. Reasons for this might be that the fishery itself affects the size of the spawning stock and, if the spawning stock is low, also the recruitment. The fishery might be subjected to certain management plans that affect the fishing mortality and therefore the size of the spawning stock and, probably, the recruitment. It is rare to encounter clear environmental effects on e.g. recruitment, but an obvious exception is the link between primary production and cod production on the Faroe Shelf (Steingrund & Gaard 2005) that also is seen for haddock (ICES 2023).

1.1.6 Production of seabirds

Seabirds are an ecologically diverse group of species, most of which are totally dependent on marine food sources (e.g., Croxall 1987). Their feeding ecology reflects species-specific adaptations to different foraging habitats (e.g., coastal vs. pelagic waters) and types of prey to feed their young (e.g., many small vs. few large). Parallel differences in foraging range (short vs. long trips) and foraging behaviour (e.g., surface-feeding vs. diving) also contribute to reduce inter- and intraspecific competition among individuals breeding in large colonies. The most typical seabirds are long-lived (adult survival rate of 85–95% p.a.) and reproduce slowly (clutch size of 1–3 eggs, dependig on species). This life history is favourable in environments where conditions for raising young vary markedly between years but also make the populations more sensitive to increased mortality of adults (e.g., due to disease, periods of food shortage, extreme weather events or longer-lasting effects of (other) antropogenic pressures). The current status and trends of seabirds in the NE Atlantic is of great concern (e.g., OSPAR 2024) and parallels a drastic global decrease in their population sizes for more than half a century (Paleczny et al. 2015).

The energetic requirements of seabirds peak in the chick period in mid summer (June–July) in the Nordic countries). Raising young is thus totally dependent on the availability of food within reach of the breeding site. A global study shows that the breeding success of seabirds is negatively affected when the biomass/abundance of their staple prey drops below a third of its historical maximum (Cury et al. 2011). Many seabirds feed on small fish, such as sandeels, capelin and young stages of herring and gadids, some also on large zooplankton, such as krill (e.g., Croxall 1997). The availability of these food sources is highly variable in time and space and the diet of seabirds varies accordingly, even between colonies of the same species. Sandeels are a nutrient-rich forage fish for breeding seabirds in Nordic waters. As they lie buried in the bottom sediments during winter (September to February), sandeels prefer sandy habitats, which are patchily distributed and not available in all areas. Larval and juvenile fish of other species are more important than sandeels in many areas. They are especially abundant in spring, but reach a more proftable size for seabirds in summer if their growth match in time and space with the availability of their key copepod prey, such as *Calanus finmarchicus*. Seabirds colonies function as important information centres where the movements of birds returning with prey guide their conspecifics towards the prey-rich areas. This reduces the time needed to locate good food patches and enables the birds to travel longer distances in their search for food, thereby reducing the risk of over-exploiting the prey sources closest to the colony (Ashmole 1963). Larger foraging areas also enable them to feed on a wider variety of prey. This may help explain cases where breeding success is better correlated with the productivity on lower trophic levels than with the abundance of their staple fish prey, or even with physical parameters such as sea temperature and salinity (e.g., Durant et al. 2003, 2006). A spatio-temporal match in trophic interactions between keystone species in the food chain is a prerequisite for high productivity of coastal ecosystems (Cushing 1990) and therefore also paramount for the success of top predators such as seabirds and demersal fish (e.g., Durant et al. 2005).

1.1.7 Research aims – the advection hypothesis

In the management of fish stocks as well as in conservation of seabirds in NE Atlantic it is imperative to understand and identify the main drivers of productivity in the shelf ecosystems. Broadly defined, the drivers can be divided into two main groups, firstly the local phytoplankton production that may regulate the production at higher trophic levels (e.g. Steingrund & Gaard 2005) and secondly, the production that originates from other places, for example by inputs of nutrients or zooplankton that are advected onto the shelves by ocean currents. In this report we will focus on the latter, not only because it may be the simpler option, but also because an analysis of oceanography, plankton, forage fish, demersal fish and seabirds apparently has not been done previously for the shelf ecosystems in NE Atlantic. In our analysis, we will study the area from South Iceland to Faroe Islands and along the Norwegian Shelf up to Lofoten Islands, i.e., we will omit coldwater ecosystems like the Barents Sea, since they might be governed by other processes. We will however consider elements of relevant processes in the North Sea, when similar data from the study area is lacking.

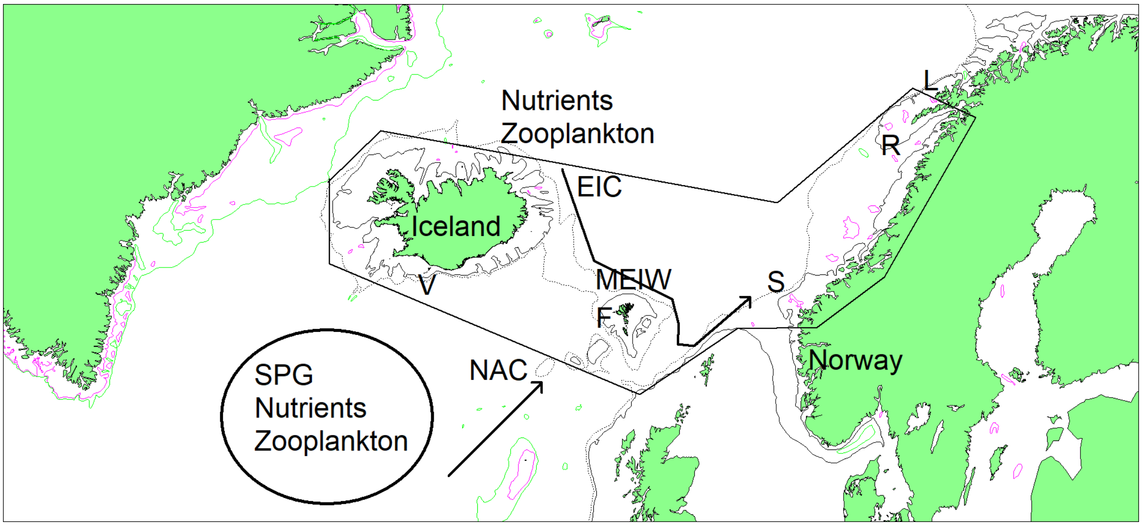


Figure 1.1 The study area (thin polygon) comprising the sea areas around Iceland, Faroe Islands (F) and along the Central Norwegian shelf up to the Lofoten Islands (L). The subpolar gyre (SPG), holding large concentrations of nutrients and zooplankton, is indicated as well as the North Atlantic Current (NAC) that flows towards the north-east. Large concentrations of nutrients and zooplankton are also found north-east of Iceland. The East Icelandic Current (EIC) transports these water masses (Modified East Icelandic Water, MEIW) towards the Faroe Plateau and onto the Norwegian Shelf, but note that not all currents are shown in this map. S denotes the location of the Svinøy hydrographical section. Large concentrations of nutrients and zooplankton are indicated. Important colonies of seabirds are found in Vestmannaeyjar (V) and Røst (R), as well as in the Faroes. For a more detailed figure, see Figure 2.1 in Part 2 of this report.

1.1.8 Materials and methods

Data on sea temperature were kindly provided by group members or from ices.dk. Data series included Faroe Mykines/Oyrargjógv annual temperature (Steingrund et al. 2024), Svinøy section temperature (ICES 2024a) and temperatures north of Iceland.

The subpolar gyre dynamics has been represented by a gyre index, based on sea surface height obtained from simulations (Hátún et al. 2005) and satellite altimetry ((Hátún & Chafik 2018; Chafik et al. 2020). These gyre indices are merged to give a continuous time series from 1960 to 2023. The recentmost data are calculated by winter (Jan)- centered annual mean altimetry values, with the mean 1994–2023 trend in the sea surface height data removed prior to the analysis.

Data on the strength of the East Icelandic Current were kindly provided by group members. This strength was quantified as the amount of MEIW north of Faroe Islands, measured as a cross-sectional area of seawater with specific temperature and salinity characteristics (1–3 °C, < 34.85) (Kristiansen et al. 2019) along standard hydrographic section N, crossing the north Faroe slope.

Data on zooplankton abundance/biomass were kindly provided by group members. They included data on zooplankton in May south of Iceland (Eyðsteinsson et al. 2021), zooplankton biomass data (large and small) on the Svinøy section (W/Norway) as well as *Calanus finmarchicus* and *Calanus hyperboreus* data north of Faroe Islands. In order to omit the shallow zooplankton data on the Norwegian Shelf, only deep stations (bottom depth larger than 250 m) were used. In order to make a common zooplankton signal for the south Iceland and southern Norwegian Sea the following series were normalised and the average taken: Icelandic zooplankton in May, Faroe *Calanus finmarchicus*, Faroe *Calanus hyperboreus*, Svinøy small zooplankton and Svinøy large zooplankton. This combined zooplankton series was compared with the zooplankton biomass index for the South Norwegian Sea that was obtained in the joint ICES coordinated ecosystem May cruise 1995–2023 (ICES 2024b).

Data on forage fish abundance/biomass were kindly provided by group members. They included sandeels in cod stomachs (frequency of occurrence) in Iceland in October and on Faroe Plateau in March and October combined.

Long-term time series of annual data on seabird performance were kindly provided by the group members and their affiliated institutions and monitoring activities. This included the longest time series data on the harvest of Atlantic puffins (*Fratercula arctica*, hereafter 'puffin') in South Iceland Vestmannaeyjar (since 1880, Hansen et al. 2021), and in Faroe islands Viðoy (since 1978) and Streymoy (since 1981). When the harvest mainly targets immature birds, these data reflect the variability in chick production of the species lagged by a few years (Hansen et al. 2021). A relative production index based on the number of chicks found in the town of Vestmannaeyjar since 1971 was also provided. In addition, there were data series on the factual breeding success for puffins in Røst, Northern Norway (since 1964), Vestmannaeyjar (since 2007) and Faroe island Mykines (since 2011), as well as for black-legged kittiwakes (*Rissa tridactyla*, hereafter 'kittwake') in Røst (since 1979) and on Skúvoy in the Faroes (since 1992). Breeding success was monitored following methods described by Walsh et al. (1995), which are an established international standard for such work. For puffins, this is based on regularly checking the contents of a selection of occupied nest burrows from the incubation period until the fate of the single offsprings (fledged/died) can be determined. The long-term metrics used were chicks fledged per egg laid (Vestmannaeyar), percentage of burrows containing a chick (Mykines) or chicks fledged per egg hatched (Røst). For kittiwakes, breeding success was determined within designated study plots based on counting the number of large, ready-to-fledge chicks per nest shown to be occupied in the incubation period. Further, site-specific descriptions of methods and materials are found in e.g., Anker-Nilssen & Aarvak (2006), Hátún et al. (2017b) and Olsen et al. (in review). By normalising the data series presented in this report, we also reduce the chance that any more subtle differences in methods (such as in techniques used to determine nests contents) or effort affect the comparison of time series across species and shelf areas.

Data on demersal fish production were obtained by ICES (ices.dk) where recruitment at age 1 was used as a measure of production. Although available we did not use stock biomass data since they may be affected by fisheries activity. We selected cod and haddock recruitment indices in Iceland (ICES 2023), Faroe Islands (Faroe Plateau) (ICES 2023) and along the Norwegian coast (Norwegian coastal cod north of 67°N) (ICES 2024c). The recruitment was set to the year of age 1 due to the indications from Faroese waters that recruitment is determined at age 1.

All of the abovementioned variables were normalised by subtracting the mean from the individual values and then dividing by the standard deviation. Averages productivity for the three shelves separately, and combined, was taken when at least two series were available. For exploratory purposes the sum of the normalised SPG and MEIW values were added together to see how a combination of the two indices compared with the average production of the trophic levels on the three Nordic shelves.

No statistics was performed although Pearson correlation coefficients were calculated to facilitate the interpretation of the results.

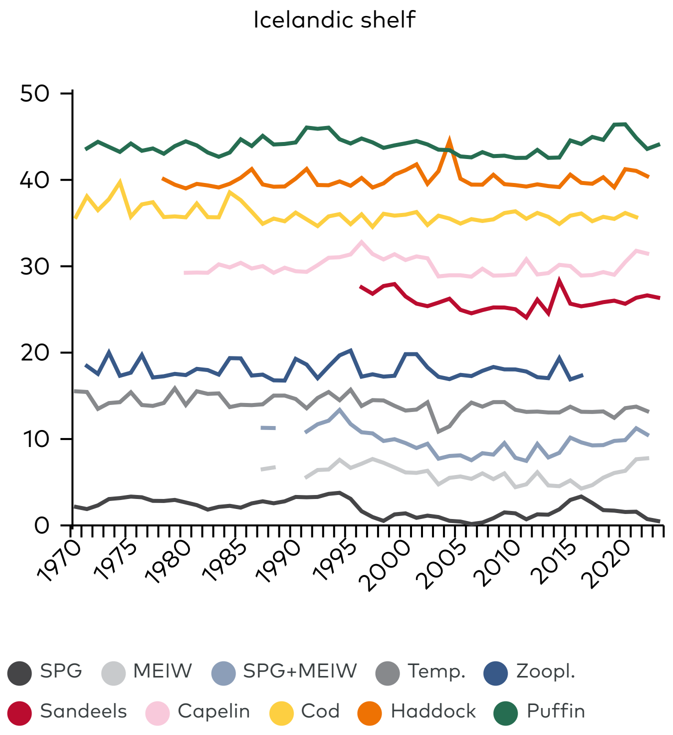
1.2 Results

1.2.1 Oceanographic features

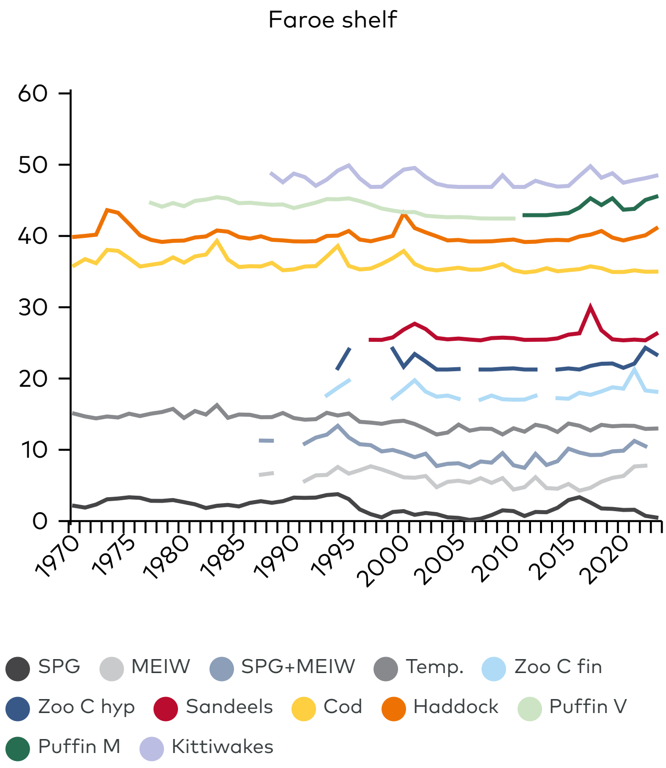
The study area comprises the NE Atlantic from (mainly South) Iceland, via Faroe Islands towards the Norwegian Shelf up to around the Lofoten Islands (Figure 1.1). The subpolar gyre is a large body of water that holds large concentrations of nutrients and zooplankton that are transported northwards with the North Atlantic Current. The East Icelandic current flows from East Iceland towards Faroe Shelf and further onto the Norwegian shelf and therefore affects all three shelves. The results will first be presented by the three shelves, then by trophic level and finally a combined analysis is presented. In every case a comparison with the subpolar gyre and the East Icelandic Current (EIC, or MEIW) is made. The subpolar gyre was largest in the mid 1990s but was small from 1997 to 2013. A peak occurred around 2017, but has decreased afterwards. The East Icelandic Current was strong in the 1990s but was weak from 2003 to 2018 (Figure 1.2). Figure 1.2 is the basis for the results if not stated otherwise.

1.2.2 Icelandic shelf

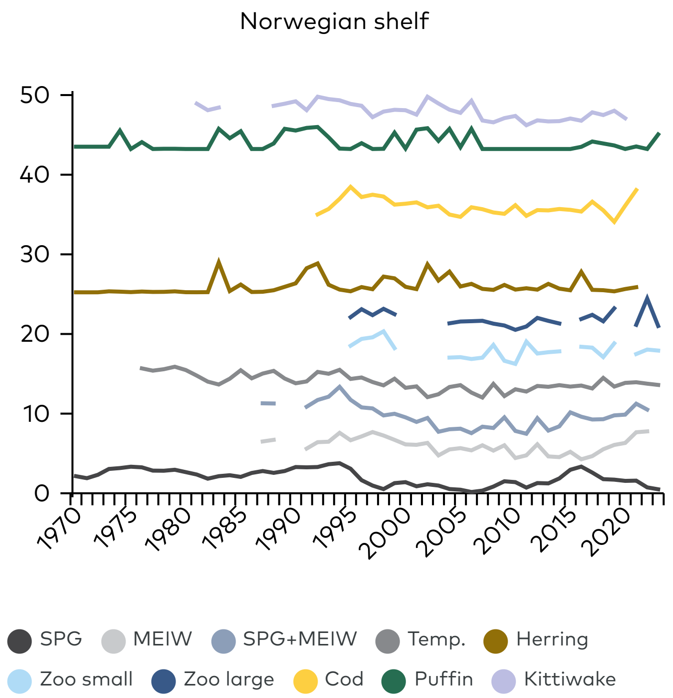
On the Icelandic shelf, sea surface temperatures have been increasing since the mid-1990s and an increase in the recruitment of haddock was observed (note that temperature is inverted in Figure 1.2). Zooplankton south of Iceland demonstrates peaks 5–10 years apart up to 2002, but past 2002 only one peak has been observed (in 2014). Sandeels were abundant in the 1990s, but began to decline in 2000 with poor period from 2004 to the peak in 2014. The peak in 2014 was mostly sandeels off the Westfjords. In the last four years there has been notable increase mostly due to sandeels off the south and west coast. Capelin recruitment was weak in the period from 2003 to 2019, but has since improved – much the same as the development in EIC (MEIW). Puffin productivity showed periodic changes, with the 2005–2013 period being particularly poor. Cod recruitment was higher prior to 1986, but has remained lower since then.



Icelandic shelf



Faroe shelf



Norwegian shelf

Figure 1.2 Normalised variables (values minus average and then divided by standard deviation) associated with the three Nordic shelves. SPG: Subpolar gyre with large values showing a large gyre, MEIW: Modified East Icelandic Water, SPG+MEIW: the sum of them, SST: Sea surface temperature (low values indicating high temperatures). Zooplankton: measured at Selvogsbanki in May. Icelandic Sandeels: percentage of cod that were eating sandeels in October from Ingólfshöfði to Hornbjarg in the Westfjords (clockwise). Icelandic Capelin: recruitment of 1–2 year old capelin. Icelandic puffin: production of puffins in town in Vestmannaeyjar. Icelandic cod: recruitment at age 3 shifted to y-2. Icelandic haddock: recruitment at age 2 shifted to y-1. Faroe zooplankton: Calanus finmarchicus and Calanus hyperboreus north of Faroe Islands, Faroe sandeels: percentage in cod that were eating sandeels in March and October, Faroe cod and haddock: recruitment at age 1. Faroe puffin: production in Viðoy or in Mykines, Faroe kittiwakes: breeding success, Norwegian zooplankton: small and large zooplankton at the Svinøy section, Herring recruitment at age 2 shifted to y-2. Norwegian coastal cod north of 67°N: recruitment at age 3 shifted to y-2. Norwegian puffin: breeding success, Norwegian kittiwakes: breeding success. Each time series is offset to different intervals on the y-axis for better comparison.

1.2.3 Faroe Shelf

On the Faroe shelf, sea surface temperatures have also increased in recent decades (inverted values Figure 1.3). Zooplankton abundances north of the Faroes in the southern Norwegian Sea were low from 2003 to 2018, thus mirroring the development in the MEIW. Puffin production seemed to follow a pattern that was influenced by both the SPG and MEIW. Sandeels were abundant in 2001–2003 and in 2017–2018 but were else infrequent. Puffin production seemed to follow a pattern that was influenced by both the SPG and MEIW. Cod and haddock recruitment fluctuated normally in the same way with peaks prior to 2002 and a poor period from 2003 to 2016.

1.2.4 Norwegian Shelf

On the Norwegian shelf, sea surface temperatures were highest between 2003 and 2017, but have decreased afterwards. Zooplankton biomass was high in the 1990s, followed by low values from 2004 to 2015, and somewhat higher afterwards. Cod recruitment was strong in the 1990s followed by low values from 2003 to 2019, after which an increase has been apparent. Puffin production has shown prominent on-off periods that match the year class strength of Norwegian spring-spawning herring).

1.2.5 Zooplankton

Zooplankton abundance values north of Faroe Islands and on the deep stations in the Svinøy section showed the same time development with high values in the 1990s and a poor period from 2003 to 2014 after which there was an increase. This development is similar to the SPG and MEIW. The zooplankton on the shallow Selvogsbanki in Iceland showed a different pattern, but some of the peaks overlapped.

1.2.6 Forage fish

Forage fish seemed to be linked to the oceanographic features, i.e., the SPG and MEIW, especially MEIW and capelin at Iceland. There was probably a signal that first occurred for capelin at Iceland, then in sandeels at Iceland, then sandeels at Faroes and lastly for the Norwegian spring spawning herring recruitment indicating a delayed timing of the effects of the environmental features moving eastwards (Appendix: Figure A1.1).

1.2.7 Demersal fish recruitment

Demersal fish recruitment was somewhat different for the three shelves. While there was a low period from 2003 to 2014 for the Faroe and Norwegian shelves, the pattern was different for the Icelandic shelf that partly showed a more constant level, although with occasional peaks, after 1993.

1.2.8 Seabird production

Puffin production was quite similar for the Icelandic and Faroese populations with a prominent poor period from 2004 to 2013 that matched the development in SPG and MEIW. The Norwegian population showed a somewhat different pattern that, as already seen, matched the year class strength of Norwegian spring spawning herring (Figure 1.2). The poor period on the Norwegian shelf started a few years later than in Iceland and the Faroes but also lasted a few years longer, with clear signs of improvement only in the last two years.

1.2.9 Assemblage of all trophic levels and common patterns among the Nordic shelves

All the trophic levels are assembled in a single figure in order to facilitate comparisons between the trophic levels as well as between the shelves (Appendix: Figure A1.1). A cyclical pattern is apparent for most of the data series with probably exceptions of zooplankton at Iceland, cod and haddock recruitment at Iceland and puffin productivity at Røst, Northern Norway (Figure 1.3).

A syncronous cyclical pattern was observed for most of the data series where the period from 2003 to 2014 was particularly poor, although an increase was observed afterwards. Comparing the variables with SPG or MEIW showed positive correlations, especially when SPG and MEIW were combined into a single index (Figure 1.3), indicating that nutrient- or zooplankton-rich water may come from both these sources and stimulate the productivity on the three shelves. Interestingly, the recent increase in the MEIW may nearly be counterbalanced by the decrease in SPG. Comparing with SPG and MEIW 1–3 years before indicated that a lag of 1–3 years gave higher correlations (Table 1.1). Combining the three Nordic shelves by taking the average of the productivity in the three shelves gave the strongest correlations (Table 1.1).

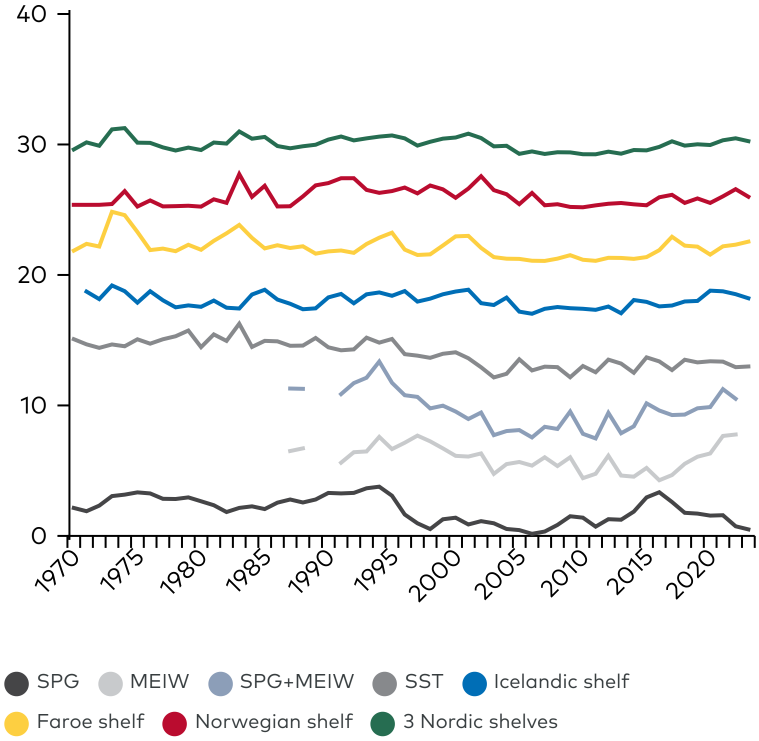


Figure 1.3 Average productivity for the Nordic shelves compared with oceanographic features. SPG: Subpolar gyre with large values showing a large gyre, MEIW: Modified East Icelandic Water, SPG+MEIW: the sum of them, SST: Sea surface temperature at the Faroes (low values indicating high temperatures). Each time series is offset to different intervals on the y-axis for better comparison.

Table 1.1 Aid to interpret Figure 1.3: Correlation coefficients when comparing the Subpolar gyre index (SPG), Modified East Icelandic Water (MEIW) and SPG and MEIW combined (SPG+MEIW) with the average productivity for the Icelandic, Faroese, Norwegian shelves and an average of the three shelves (Nordic). Time lags up to 3 years are shown.

Variable	Lag	Shelves			
		Icelandic	Faroese	Norwegian	Nordic
SPG	No lag	0.24	0.43	0.04	0.34
MEIW		0.56	0.40	0.39	0.55
SPG+MEIW		0.56	0.61	0.40	0.64
SPG	1 year	0.27	0.44	0.11	0.39
MEIW		0.41	0.40	0.48	0.54
SPG+MEIW		0.47	0.65	0.55	0.70
SPG	2 years	0.24	0.36	0.18	0.37
MEIW		0.55	0.34	0.56	0.59
SPG+MEIW		0.64	0.57	0.64	0.75
SPG	3 years	0.26	0.30	0.20	0.35
MEIW		0.43	0.26	0.48	0.48
SPG+MEIW		0.60	0.42	0.61	0.66

PART 1.

1.3 Discussion

1.3.1 Summary of results

The results show an overall picture that there are positive associations between oceanographic features (SPG and MEIW), via amount of zooplankton and forage fish to seabirds and recruitment of demersal fish. A large subpolar gyre and/or a strong East Icelandic Current has been, therefore, beneficial through out the foodweb up to higher trophic levels. Interestingly, a combination of SPG and MEIW seemed to show a closer association with the higher trophic levels than each of them (SPG or MEIW) separately. There is probably a lag of one to three years between SPG/MEIW and higher trophic levels.

1.3.2 Oceanography in relation to nutrients and zooplankton

Our results show that the occurrence of a large subpolar gyre, i.e., cool water south of Iceland and a strong East Icelandic Current (EIC) coincided with lower temperatures in NE Atlantic. The fact that a combined index of SPG and EIC seemed to be more closely associated with higher trophic levels indicates that SPG as well as EIC might act as two separate sources of nutrients/zooplankton to the three shelves. It should be stressed that this only is meant as an inspiration for future investigations. A lag of at least one year is expected if water particles originating in the SPG are physically transplanted to the three shelves (Koul et al. 2022; Orvik 2003). A similar lag of one year is expected for a water particle to move from the core area north-east of Iceland with high concentrations of zooplankton (Kristiansen et al. 2019) to the Faroese and Norwegian shelves (Skagseth et al. 2022). A lag of two to three years between SPG/EIC and higher trophic levels, which probably is best supported by the data (Table 1.1), indicates that nutrients are main causative agents, i.e., there is lag of at least one year for the nutrients to reach the shelves, then a lag of one year before they are expressed in the spring blooms on the shelves (Hátún et al. 2022a).

As with nutrients it seems straightforeward to interpret the increased amounts of zooplankton adjacent to the Faroese or Norwegian shelves as a result of an advection of zooplankton-rich water from the area north of Iceland. However, there appears to be a strong correlation between the total amount of zooplankton in the

Norwegian basin (ICES 2024d) and the amount found close to the Faroese and Norwegian shelves. The fact that the combined index of SPG and MEIW showed closer associations with higher trophic levels indicates that zooplankton might be transferred from the SPG, in addition to EIC, to the three shelves.

By being present outside the three shelves does not guarantee that the zooplankton or nutrients will become available to the shelf ecosystems, but this apparently happens in such a degree that there are clear associations between zooplankton and forage fish or demersal fish recruitment (Table 1.1). An indication of advection of zooplankton and/or nutrients onto the shelves may come from the growth of the long-lived clam *Arctica islandica* that feeds on phytoplankton that enters the bottom, although the local primary production might also affect the growth (Matras et al. 2022). In this case we have used the difference between deep and shallow shells as the measure of benthic productivity (thus cancelling potential temperature effects or other unknown effects that may be associated with the location rather than advection). The actual advection process of nutrients and zooplankton onto the shelves is a field of its own and far outside the scope of this paper.

1.3.3 Forage fish

The advection of nutrients or zooplankton onto the shelves may be spread to different kinds of forage fish such as fish larvae/juveniles (Jacobsen et al. 2019), sandeels (Greenstreet et al. 2006), Norway pout *Trisopterus esmarkii* and age 0 herring (Anker-Nilssen 1992). These fish species might however react differently to SPG, EIC or temperature. For example, biomasses of adult Norway pout on Faroe Shelf tend to be negatively correlated with sandeel abundance (FaMRI, unpublished material). Also, herring recruitment is positively correlated with temperature (Toresen and Østvedt, 2000), i.e., the opposite of sandeels. Hence, 0-group of forage fish (capelin, sandeels, herring) might be somewhat heterogenious but apparently show as strong association with SPG/MEIW as do zooplankton or seabird production. We are not able to tell whether the apparent time lag of one to three years between the Icelandic and Faroe/Norwegian shelves with regards to forage fish is real or just an artifact (i.e. only based upon peaks that may be caused by unknown random processes) but this could be substantiated by other evidence.

Of particular importance is the timing of events and top-down effects. On the Faroe shelf the abundance of fish larvae is crucial to the zooplankton. A large number of fish larvae in May, as a consequence of high primary production, may excert such a grazing pressure on zooplankton that their abundance is low during summer (June–July) and vice versa: a low amount of fish larvae causes a high abundance of zooplankton during summer (Jacobsen et al. 2019). This apparently leads to a "compensatory" food chain that is based on zooplankton during summer and associated forage fish, which in this case is adult Norway pout. In our project we have not included such “compensatory” food chains, but this is expected to affect both demersal fish and seabirds since they prey on Norway pout (Steingrund et al. 2024).

1.3.4 Demersal fish recruitment

As was the case with forage fish the assemblage of demersal fish might also be somewhat heterogenious. In our case we selected cod and haddock recruitment on the Icelandic and Faroese shelves and Norwegian coastal cod as our production indices. As described above Icelandic and Faroese cod and will most likely not have the same reaction to SPG/MEIW. In addition, recruitment of Icelandic haddock increases with increased temperature (Figure 1.2). This might be attributed to large areas north of Iceland becoming habitable by haddock when temperature increases. This does not apply for the Faroese or Norwegian shelves. Icelandic cod is probably less affected by this mechanism, but its main nursery areas are in all years north of Iceland. Norwegian coastal cod (north of 67°N) might be composed by different local populations that may make this production index heterogenious and influenced by local conditions. It is also important to note that there is a local phytoplankton production that, in addition to advected nutrients/zooplankton, forms the basis for the upper trophic levels (Steingrund & Gaard 2005). Hence, it is not so surprising that the associations between SPG/MEIW and demersal fish recruitment were weaker than for the lower trophic levels.

1.3.5 Seabird production

Although not synchronous at a year-to-year level, the large-scale pattern of trends in productivity of seabirds breeding at the three Nordic shelves was relatively similar. An extraordinary long period of poor productivity started in the early 2000s and lasted for a decade before showing signs of improvementafter 2015. Before this, multi-year peaks in productivity were observed in all areas, especially in the 1990s (Figure 1.2).

Compared with forage fish or demersal fish production, seabird (puffin) production showed the strongest association with SPG/MEIW, especially with the combined SPG+MEIW index (Table 1.1). To some extent, this might be because the flight abilities enable seabirds to exploit a wider range of prey resources over larger areas than the less mobile forage fish and demersal fish. The zooplankton or nutrients that are either produced locally or advected onto the shelves may benefit different forage fish, depending on location. Hence, one should not always expect strong linkages between seabird productivity or diets and local forage fish species although several such relationsships have been documented, including the Røst puffins’ strong dependency on age 0 herring to breed successfully (e.g., Anker-Nilssen 1992; Sætre et al. 2002; Durant et al. 2003; Walnum 2024) and the importance of young saithe *Pollachius virens* for the breeding performance and diet of European shags *Gulosus aristotelis* (Bustnes et al. 2013; Lorentsen et al. 2018).

In Southwest Iceland, Hansen et al. (2021) showed that the annual average sea temperature explained as much as 74% of the variation in the polenetting harvest of immature puffins in Vestmannaeyar over a 130 year period since 1880. This is one of very few studies documenting the importance of climate-induced effects on the producticity of a marine top predator over such a long term. The cyclic nature of this relationship follows the Atlantic Multidecadal Oscillation (AMO) pattern and is furthermore strongly influenced by the SPG control of the inflow of warmer, less nutrient-rich Atlantic Water of tropical origin (Hátún et al. 2005). As the hunters always have avoided capturing birds carrying food loads, and immature higher air attendance than breeders in the colonies, make the harvest highly age-selective, with 75% of the birds taken belonging to three cohorts of immature birds (age 2–4) that often visit the colonies in summer. This allowed the calculation of a relative cohort stength index lagged by -3 years. As immature birds are known to move widely between regions within Iceland (and to the Faroes, Hammer et al. 2014), the index likely reflects the larger-scale production of puffins in Iceland.

For a better representation of the Selvogsbanki shelf, the local production index based on the number of puffin chicks reported in the town of Vestmannaeyjar in 2007–2024 was proven to be highly correlated (r=0.75) with the parallel measurements of breeding success in the colony on the same island, demonstrating its value as a productivity signal. The temporal pattern in this data series since 1971 can be split into four dissimilar periods: (1) 1971–1986 had a highly variable success, but the low production years (especially 1978, 1982–1984) were considerably larger in absolute magnitude than the best years, (2) 1987–1996 was characterised by many good years, peaking in 1991–1993, (3) 1997–2014 showed a decline in productivity, followed by a decade of poor production in 2005–2014 with total breeding failure or very low breeding success in most years (parallelled by an estimated 56% drop in breeding numbers (E.S. Hansen, unpublished)), and (4) 2015–2024 when production rised to a high level, peaking in 2021 and 2024. Period (3) was concurrent with a rapid warming of the Icelandic shelf and also accompanied by a delay in puffin breeding of an unpresidented scale (18 days, or 1.5 SD higher than the long-term average in 1937–2024 (E.S. Hansen, unpublised)). This pattern strongly suggests a temporal mismatch in the food chain, and is also corroborated by a significant delay in phytoplankton bloom timing (Pétursdóttir et al. 2021), and virtual disappearance of zooplankton peaks (save 2014).

In the Faroes, kittiwake success was especially high in 1982, 1995, 2001 and 2017, whereas the success of puffins on Mykines improved after a total breeding failure in 2011–2013 and was relatively high in four of seven years from 2017. It should be noted that all harvest data from the Faroes were provided by local communities. Interpretations of such data can be a bit challenging since data quality can be affected by e.g. local decisions. The low values from 1989 to 1993 at Stakkurin on

Streymoy are also affected by a hunting ban during those years and thus not only reflecting bad environmental conditions. At the other end of the scale, harvest numbers at Seyðtorvu on Viðoy from 2006 onwards are inflated since, from that year, the harvest reports also include numbers from an additinal area, which means the results overestimate the true conditions. Nevertheless, there seems to be a clear general pattern, especially during the period between 2005 and 2013 with relatively low harvest mumbers and poor breeding success of both species. This matches quite well with the development in the SPG and MEIW, as also demonstrated by Hátún et al. (2017b).

In Norway, above average success was observed for both study species in Røst in 1983–1985, in 1989-1992 and in most years between 1999–2006, but for neither species this was sufficient to maintain their populations. In 16 consequtive years (2007–2015) the Puffins experienced virtually total breeding failures at the population level (mean 0.1 chicks/pair), which succeeded a long-lasting history of reproductive problems for this population (e.g., Anker-Nilssen & Røstad 1993; Anker-Nilssen & Aarvak 2006; Cury et al. 2011) with an average yearly breeding success of only 0.3 chicks/pair from 1964 to date. This is far below the annual rate needed to sustain the population with sufficient self-recruitment (about 0.5 chicks/pair; Anker-Nilssen & Aarvak 2006). As a direct consequence of failed recruitment, the breeding population has dropped by 86% from more than 1.4 million pairs in 1979 to less than 0.2 million pairs at present (Anker-Nilssen & Aarvak 2006; T. Anker-Nilssen, unpublished data). The same is the case for the Røst kittiwakes. Their average success after 2006 has been less than a third of the level needed for self-sustained level for that species (> 1 chick/pair, Frederiksen et al. 2024). Over the last four decades they have only surpassed that level twice (in 1992 and 2002) and the average productivity of the kittiwakes breeding in Røst harbour has been approximately half of what's required to maintain the population (Figure 1.2). The largest colony on natural cliffs (Vedøy) was also harassed by white-tailed eagles *Haliaeetus albicilla*, which reduced the kittiwakes' productivity further, and the colony went extinct in 2020 (Anker-Nilssen et al. 2024). As a total consquence of failed recruitment, breeding numbers of kittiwakes in Røst dropped by 97% from 25,000 pairs in 1980 to only 692 pairs remaining in 2024 (T. Anker-Nilssen, unpublished data).

Common considerations across all areas. The effects of white-taile eagles on kittiwake breeding success (Anker-Nilssen et al. 2023) exemplifies how top-down effects act to reduce the statistical relationship between marine species and their key prey. Given the high nest fidelity of most seabirds between years, insufficient recruitment rates will tend to reduce the breeding density within the colony. This will in turn lower the adults' collective defence against predators with negative consequences for both breeding success and survival rate. Furthermore, as also shown for puffins (Fayet et al. 2021), the time spent away from the colony in search of food increases with decreasing prey availability, reducing the adults' ability to defend their offspring even further. For open-nesting species such as kittiwakes, this helps explain why populations breeding in/near human settlements (and even on offshore oil rigs), where such predation pressure is much lower, have higher productivity and better population trends than nearby colonies on natural cliffs (e.g., Christensen-Dalsgaard et al. 2019; Anker-Nilssen et al. 2023).

In addition to such density-dependent effects of predation, the relationship between breeding success and prey availability is rarely linear but more often shows a threshold-shaped response because the life-history strategy of seabirds favours a dynamic trade-off between the individuals' investment in reproduction vs. own survival. When food availability drops below the threshold, conditions quickly get inadequate for raising offspring. Given the long life expectancy of adults, it is then more profitable for them to abandon the breeding to maximise their own survival until the next season. When surpassing the threshold, conditions are often sufficient to secure breeding success for most individuals. Consequently, the effect of changes in prey abundance is strongest around the threshold and weak at other levels of prey abundance. Also, the extreme population declines registered for some of these seabird populations would lead to less intra- and interspecific competition for food and thereby also reduce the statistical relationships with the abundance of staple fish prey and zooplankton species. Top-down effects of seabird consumption on their key prey stocks seem to be important only when prey abundance is very low and has not yet been shown to correlate with prey dynamics (Saraux et al. 2021). When prey is plentiful, the spatial correlation between the distribution of prey patches and seabirds is also shown to be reduced (e.g., Axelsen et al. 2001; Fauchald et al. 2011).

The life-history balance between these vital rates may also vary between populations of the same species, with some showing higher survival rates and lower productivity rates than others (e.g., Frederiksen et al. 2005). Data series on survival rates are not available for puffins and kittiwakes in Iceland and the Faroes, making it difficult to calculate more exactly the short- and long-term effects of the observed variability in lower trophic levels and oceanography. Nevertheless, Harris et al. (2005) found no differences in survival rates of puffins across five colonies in the Northeast Atlantic, suggesting the levels of breeding success needed to sustain the populations based on natal recruitment alone are relatively similar for populations breeding in the Nordic countries. Even if the contribution of breeding success to the observed population trends varies between colonies (Layton-Matthews et al. 2023), the larger-scale decrease in breeding numbers of these species over the last decades were mainly caused by poor breeding success, indicating also that recruitment from other breeding areas cannot be expected to buffer the negative trends.

1.3.6 Temperature and pelagic fish as confounding factors

Temperature responses in fish and zooplankton may vary by life phases (Beaugrand et al. 2002; Barbeaux & Hollowed 2018; Kjesbu et al. 2022), and the same species can react differently across life stages due to ecological differences, leading to conflicting predictions for stock development under increasing temperatures. Thus, temperature might be a confounding factor since high temperatures might cause higher basic metabolim in zooplankton and forage fish (MacDonald et al. 2018). On the other hand, in our study low temperatures might also signal ecosystem productivity by showing how much water from the subpolar gyre or EIC is present in the vicinity of the three Nordic shelves. We have not attemped to separate these factors.

Pelagic fish graze on zooplankton (Bachiller 2018) and this could potentially confound our results. We compiled a 'zooplankton grazing biomass of pelagic fish' by adding the Norwegian spring spawning herring biomass of age 3+ together with the mackerel biomass of age 0+ and the biomass of age 1 blue whiting. We noted that the correlation between pelagic fish and temperature was positive and tended to be negative with forage fish and demersal fish recruitment. However, the zooplanktonvorous amphipod *Themisto* in the Norwegian Sea seems to be a more important predator on Calanus finmarchicus than pelagic fish (Skjoldal et al. 2004). This indicates that grazing by pelagic fish might not determine the fate of zooplankton that enters the three shelves, but may, neverthless, play a role.

1.3.7 Knowledge gaps and future research

Our approach has been quite simple by constructing common time series of zooplankton and forage fish that were regarded as representative for the Nordic shelves. We also compared demersal fish recruitment and seabird productivity among the Nordic shelves. To keep the approach as simple as possible, we avoided to analyse in any detail the time lags involved in the mechanistic links between different variables, even though such lags are apparent between some of the variables (Table 1.1, Figure A1.1). For example, many of the ecological effects associated with SPG/MEIW seem to be lagged by 1–3 years, depending on the trophic levels and shelf areas involved. In general, there is an urgent need to explore in more detail the spatial and temporal differences in the functioning of the Nordic shelf ecosystems to better understand (and be able to account for) the mechanisms that drives the productivity of these important hotpots of marine life and human exploiation of natural resources. Since the sum of normalised SPG and MEIW indices was more closely associated with productivity of the trophic levels than each index alone, this indicates that both of them may act as sources of nutrients/zooplankton to the Nordic shelves, but the oceanographic foundation for this needs to be investigated.

In this study we did not include any calculations of fluxes of zooplankton or nutrients onto the shelves. Neither did we include any estimate of the consumption of zooplankton by forage fish or the consumption by demersal fish or seabirds of forage fish as this would be far outside the scope of this project. When such trophic models hopefully are further developed in the future, the results from our project will, nevertheless, be of value by indicating some of the main ecological pathways.

Our results do not adress local effects on the Nordic shelves, such as the importance of the local, on-shelf primary production. This is basically because we first and foremost wanted to explore the larger-scale dynamics of the productivity in Nordic waters, which we expected to be reflected best by offshore features. Still, we do know that an inclusion of parameters of on-shelf productivity would be needed to reflect a wider range of mechanisms, for example the high amount of sandeels at the Faroes in 2017 due to a high primary production there in that year that was not seen on the Icelandic shelf.

PART 1.

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PART 1.

Appendix

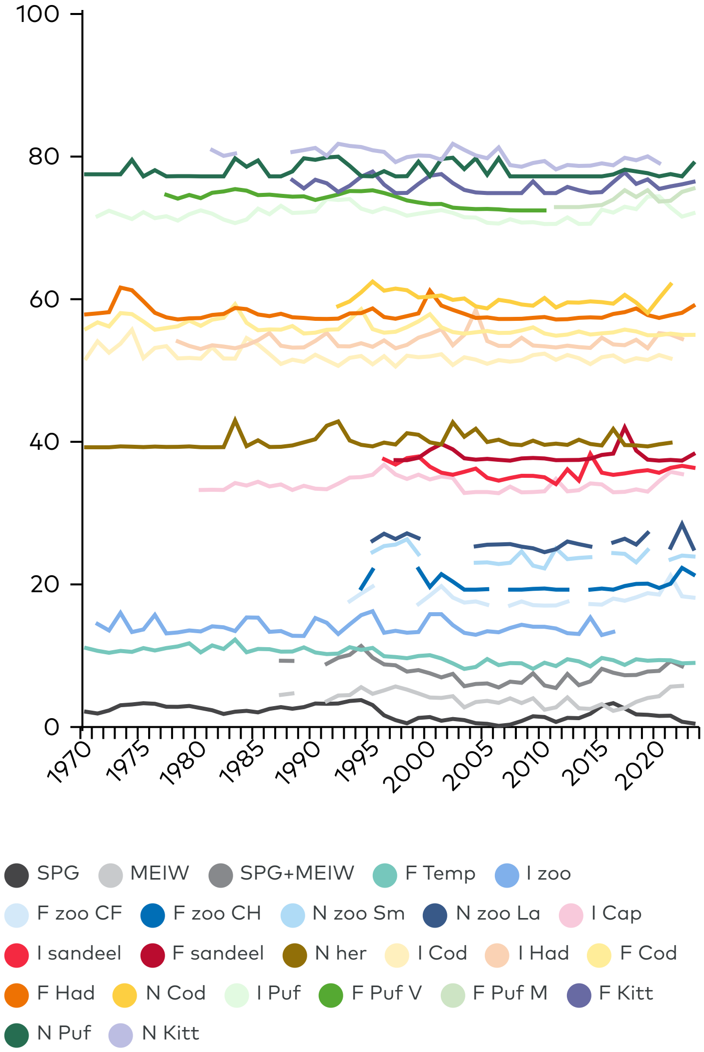


Figure A1.1 Normalised variables (values minus average and then divided by standard deviation) of all variables of zooplankton, forage fish (capelin, sandeels, herring), demersal fish recruitment (cod, haddock) and puffin or kittiwake productivity associated with the Icelandic shelf (I), Faroe shelf (F) and Norwegian shelf (N). SPG: Subpolar gyre with large values showing a large gyre, MEIW: Modified East Icelandic Water, SPG+MEIW: normalised variables added together. Sea surface temperature is shown for the Faroe shelf and high values on the graph indicate low temperatures. Each time series is offset to different intervals on the y-axis for better comparison.

PART 2.

A case study for the Faroe Shelf: East Icelandic waters fuel the Faroe shelf ecosystem

Hátún, H., Jacobsen, S., Vang, H.B.M, Kristiansen, I., Gaard, E., Steingrund, P., Skagseth, Ø., Broms, C.

Abstract

Demersal fish stocks and seabird populations on the Faroe shelf have declined profoundly over the past half-century, and the relative role of exploitation and climate remains a key question. We propose that reduced transport of nutrient- and zooplankton-rich subarctic waters from the Iceland-Jan Mayen region is a contributing causal mechanism. The volume of subarctic waters and the abundance of calanoid copepods around the Faroe Shelf determine whether peaks in on-shelf primary production, juvenile fish and recently fledged seabirds contribute to the populations of adult fish and seabird.

PART 2.

2.1 Introduction

Following the development of accurate oceanographic instruments (the Nansen bottle) in the late 1800s, a cold tongue of subarctic waters (SAW) from northeast of Iceland extending into the southern Norwegian Sea was among the first thoroughly studied oceanographic features in marine science. In their seminal book, 'The Norwegian Sea', Helland-Hansen and Nansen (1909) hypothesized that increased eastward extensions of this dynamic 'Icelandic tongue' stimulated ecosystems along the Norwegian slope and shelf. This hypothesis received little attention until recent studies by Kristiansen et al. (2016, 2019) demonstrated that the variable extent of this tongue into the waters north of the Faroe Islands regulates zooplankton communities there: a large tongue results in large biomasses of fatty and nutritious large stages of *Calanus finmarchicus* and *Calanus hyperboreus*, which can reach the Norwegian slope as well (Skagseth et al., 2022). *C. finmarchicus* is the critical prey item, transferring energy from primary production to higher trophic levels in the Norwegian Sea (Melle et al., 2014), and on adjacent shelves (Sundby, 2000). *C. hyperboreus* plays a similar role north and northeast of Iceland during spring (Gislason and Silva, 2012). The fact that these subarctic copepods vanish from the southern Norwegian Sea when the Icelandic tongue retracts westwards (Kristiansen et al., 2019), likely has significant ecological implications.

SAW circulates clockwise around the Faroe plateau, creating a complex oceanographic system that establishes the hydrographic foundation for Atlantic inflows, that pass this shelf on their journey towards higher latitudes. Confluence of lower trophic level biomass along the interface between the SAW and the overlying Atlantic water – the permanent thermo/pycnocline, feeds a large biomass of krill, mesopelagic fish and their larger predators (e.g. blue whiting, mackerel, Greenland halibut and several other fish species. This "Wall of mouths" (Hamner et al., 1988) is clearly identifiable as a Deep Scattering Layer (DSL) in acoustic data from these waters (Cisewski et al., 2021). Ascended zooplankton and other near-surface, passive, food items can potentially also be advected from the Iceland tongue towards the Faroe shelf break in a low-saline surface layer, which builds during the summer and fall (Perkins et al., 1998). A thorough discussion on the ocean-to-shelf advection is, however, beyond the scope of the present work.

Biological production on the Faroe shelf is characterized by marked peaks every 6–10 years, i.e.: 1974, 1983 (weak), 1994, 2000, 2009, 2017, and a recent weak peak in 2023–2024 (Jacobsen et al., 2019).

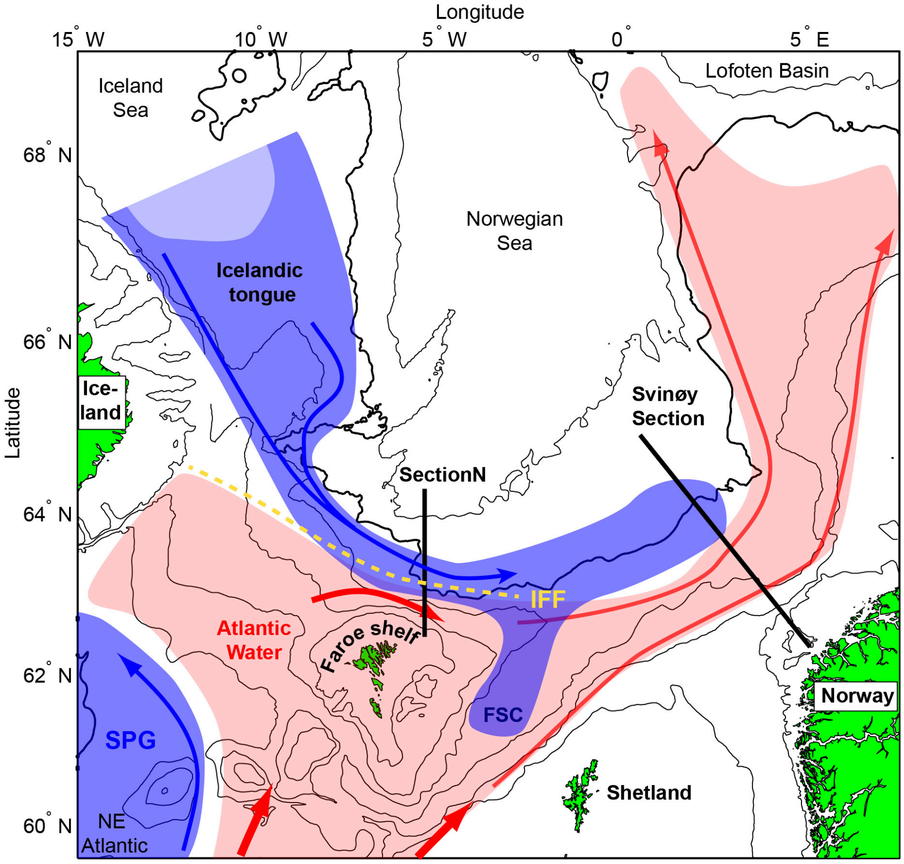


Figure 2.1 Overview over the study region. Subarctic currents and water masses are shown with blue arrows and shading, while the warmer Atlantic counterpart is shown in red colours. FSC: Faroe-Shetland Channel, IFF: Iceland-Faroe Front and SPG: Subpolar gyre.

These peaks are reflected in a so-called primary production index (PPI) (Gaard et al., 1998), and 0-group length index (Jacobsen et al., 2019) breeding success of seabirds (Olsen et al., submitted), and recruitment to commercial fish stocks (ICES, 2023). While these synchronizations are tight, the magnitude of peaks in the PPI and 0-group length index are not always reflected in recruitment. Particularly, production peaks after 2003 have not benefitted the adult cod (*Gadus morhua*) stock as they did before. While the Faroese fish stocks and seabird populations (biomass) exhibit rounded peaks following productive periods, they also show clear longer-term shifts and trends (ICES, 2023) (Olsen et al., submitted), which cannot be explained by the PPI or the 0-group length index.

This calls for consideration of other environmental indicators, likely with a larger-scale 'footprint' than just the Faroe Shelf itself. Acknowledging previously suggested links between ecological shifts in the NE Atlantic and indices like the subpolar gyre index, the North Atlantic Oscillation (NAO) index, and the Atlantic Multi-decadal Oscillation (AMO) (Hátún et al., 2009), we specifically discuss potential links to changes in SAW from the Icelandic tongue.

Guillemots (*Uria aalge,* hereafter guillemot) have historically constituted the largest and most exploited seabird population in the Faroe Islands (Nørrevang, 1977). A major decline in this species during the 1960s elicited concern (Olsen, 1990; Reinert, 1976) and initiated structured seabird counts in the Faroe Islands. The and the here discussed guillemot record is the longest if its kind from this shelf (Olsen et al., submitted). Cod has always been the main demersal commercial fish species, sustaining a considerable portion of the Faroese economy. This stock has therefore been closely monitored, providing extensive data material and long robust time series (ICES, 2023). Cod and guillemots share similar prey species (e.g. sandeel), and the piscivorous guillemots also prey directly on juvenile cod (Myksvoll et al., 2013), which makes the breeding performance of this seabird a useful indicator of the status and recruitment of the cod stock. Motivated by this expected ecological coupling, the economic and cultural significance, and large data availability, the total attendance of guillemots and the total cod biomass are employed as indicator records for upper trophic levels on the Faroe Shelf. With these records, we want to test the following hypothesis: *the biomass of upper trophic levels on the Faroe shelf is driven by both on-shelf production and off-self food abundance*.

The data material is described in Section 2.2, spatial and temporal changes in the subarctic waters are illustrated in Section 2.3.1 and updated oceanic zooplankton records are provided in Section 2.3.2. Recruitment and biomass of cod is presented in 2.3.3, and guillemot attendance is in 2.3.4. A comparison with the Faroe Bank cod is provided in 2.3.5 and the results are discussed in 2.4.

2.2 Material and Methods

2.2.1 Volume of subarctic water

Spatial view To describe the annual 3-D hydrographic variability from 1995 to present, we combined data sets from ICES (International Council for the Exploration of the Sea), PINRO (Polar Research

Institute of Marine Fisheries and Oceanography, Russia), and the Argo Global Data Assembly Centre in France (Argo, 2000) (Mork et al., 2019). These data are processed as described in Skagseth et al. (2022). Spatial maps showing SAW thickness defined as 1 °C < T < 4 °C and S < 34.9 (Fig. 2.2).

Section N Hydrographic observations were made 3–4 times a year along a standard section (Section N), crossing the Faroe slope along the 6°W meridian (Fig. 2.1). These numerous measurements at Section N enable us to construct a proxy record for the SAW volume back to 1992. A cross-sectional area of SAW (actually Modified East Icelandic Water, MEIW) – our estimate of the influence from the cold Icelandic Tongue – is calculated for each measurement of Section N by integrating the areal representation of observations in the T-S range (1–3 °C, < 34.85) (Kristiansen et al., 2019).

Svinøy Section A SAW proxy series is also estimated as the area along the Norwegian Svinøy section (0–500 m depths), which extends north-westward from the Norwegian slope (Fig. 2.1). The cross-section area is here represented by water fresher than 34.9 in July–August.

2.2.2 Calanoid copepods

Section N Monitoring of zooplankton abundance and composition (WP-2 net) was initiated at Section N in 1994 with data being collected in mid-to late May, refined our analysis to the overwintering generations. No data are available for 1996, 1998 and 2006. The overwintered stages of *C. finmarchicus* (CIV to CVI) (Kristiansen et al., 2016) and all the developmental stages of *C. hyperboreus* from the truly subarctic (north of the Iceland-Faroe Front, Fig. 2.1) were used in our analysis, which follows Kristiansen et al. (2019).

Svinøy Section The zooplankton time-series from the Svinøy section started in 1995, and only the three westernmost stations from 17 April to 17 May are used here (following the example of Skagseth et al., 2022). *C. hyperboreus* has been identified to copepodite stages and only the copepodite stage IV, V, and adult females and males were used in the present analysis. Younger stages were omitted because they exhibit great fluctuations in abundance during the growth season (Gislason, 2018). The older stages will in addition represent the overwintering stages (Gislason, 2018). The data are presented as abundance per m^3.

2.2.3 Demersal fish and guillemots

Faroese waters host two distinct cod stocks: the Faroe Plateau Cod and the Faroe Bank Cod. The International Council for the Exploration of the Sea (ICES) regularly assesses both stocks to guide sustainable fishing practices. The Faroe Plateau Cod stock is a data-rich (ICES category 1), allowing for comprehensive stock assessments that provides estimates of recruitment, spawning stock biomass, total stock biomass, and fishing pressure from 1959 to 2024 (ICES, 2023). Conversely, the Faroe Bank Cod is classified as data-limited (ICES category 3), and the assessments for this stock rely primarily on survey biomass indices, and estimates of recruitment or spawning stock biomass are not currently available. The primary biomass index used in assessments is a CPUE (Catch Per Unit Effort) series derived from groundfish surveys conducted in September from 1996 to 2024 (ICES, 2023). Additionally, a secondary CPUE series from groundfish March surveys (1994–2024), is available, with gaps in 1996, 2004, and 2005.

2.2.4 Guillemots

We use counts of the total number of guillemots attending a long-term study colony for these species in the Faroe Islands (the Høvdin breeding cliff on the islands Skúvoy) since 1972 (see Olsen et al., submitted).

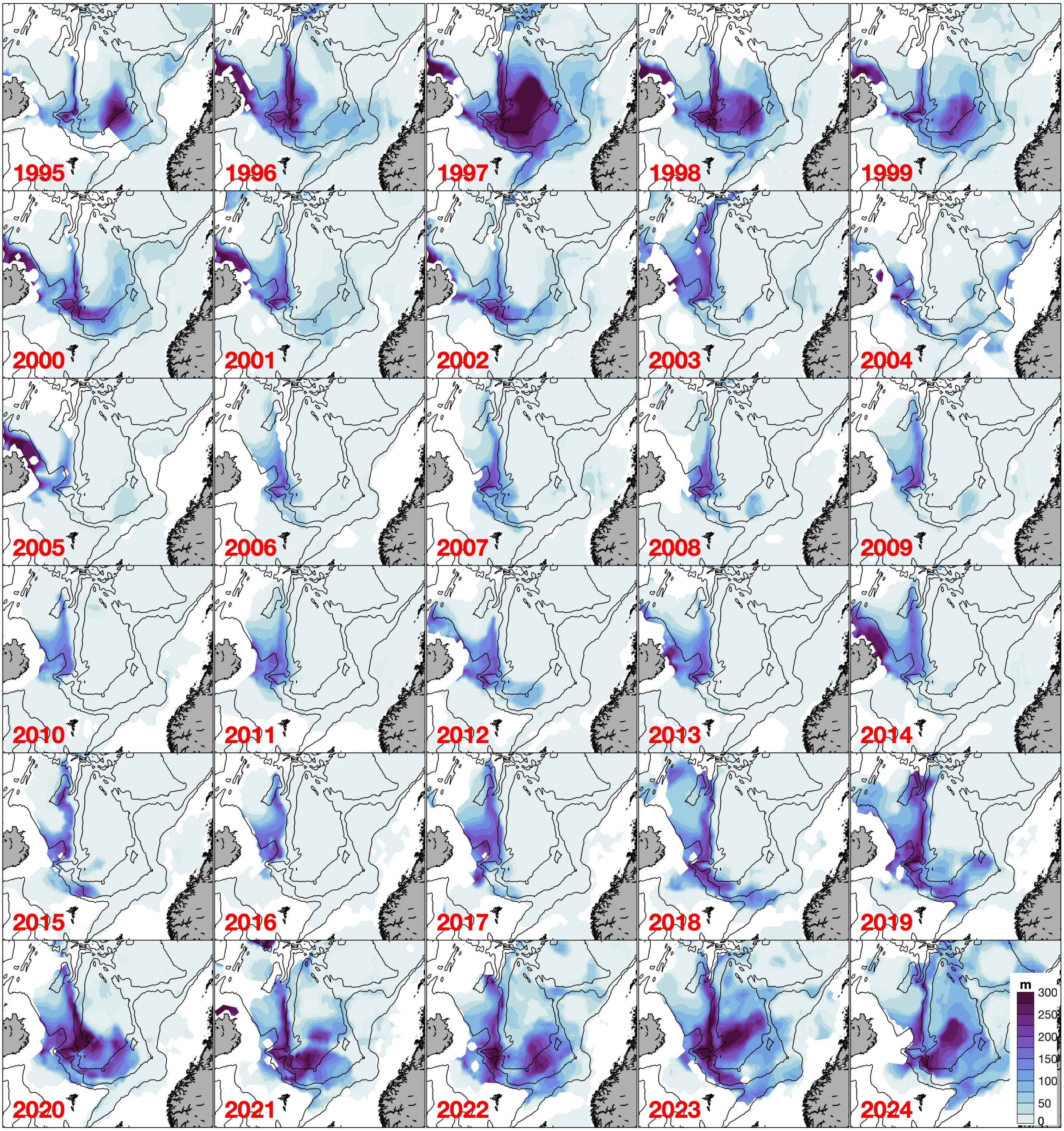


Figure 2.2 Spatio-temporal changes in SAW thickness (see blue color scale) in the greater Norwegian Sea (including eastern parts of the Iceland Sea and the Faroe-Shetland Channel).

2.3 Results

2.3.1 Shifting volumes of subarctic waters

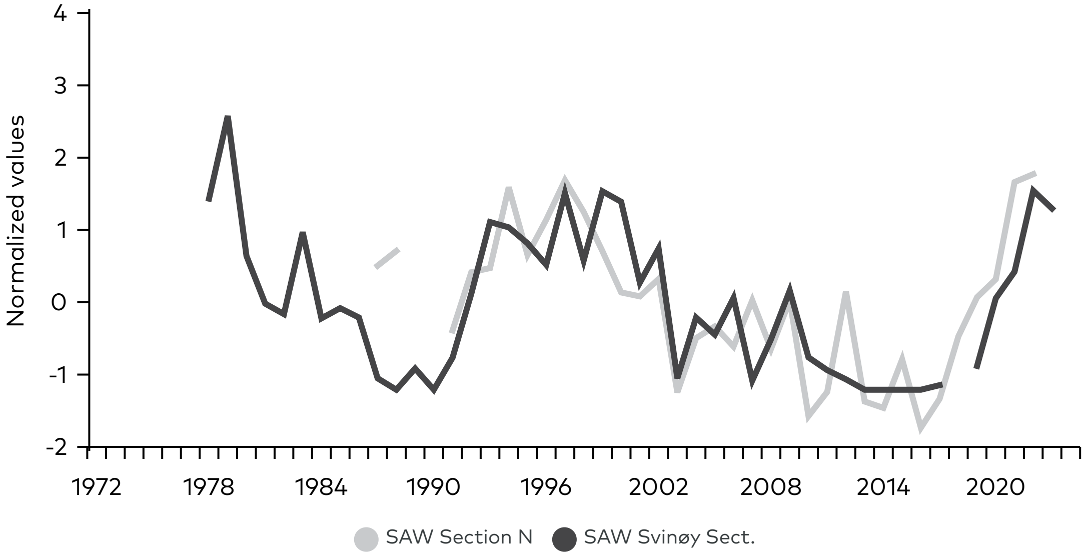
Spatial view

The SAW layer remains thick along a U-shaped region between the NE Icelandic shelf and the Jan-Mayen ridge (Fig. 2.2). The thickest layer is generally observed near the deep and steep trough where the Jan-Mayen Ridge intersects the Iceland-Faroe Ridge. The SAW layer thickness varies substantially between years, both within this U-shaped region and particularly in the southeastward 'leakage' into the Norwegian Sea and into the Faroe-Shetland Channel. Volumes of SAW were large from 1995 to 2002, but the leakage region thinned abruptly in 2003. Apart from smaller pulses (e.g. in 2012), the apparent eastward flow remained weak until 2018, after which a much thicker SAW layer was again observed north of the Faroe slope and along the Norwegian slope.

Sectional view

The SAW proxy record from the north Faroe slope (Section N, updated from Kristiansen et al., 2019) confirms that the eastward flow of SAW increased after 2017 (Fig. 2.3a). This increase was steep, and the SAW volume in the 2020s reached values matching the highest levels of the 1990s. The SAW proxy record from the Norwegian slope (Svinøy Section) closely follows the development at Section N (Fig. 2.3). The post-2017 increase was also dramatic in this more eastern location, and appears to have lagged behind Section N by about a year. The longer record available from the Svinøy section shows that the SAW volume in the southern Norwegian Sea was likely highest in the late 1970s, declined to very low values in 1987–1990, increased rapidly in the early 1990s, and remained high until 2002. It dropped, as evident in the spatial view (Fig. 2.2) in 2003 and remained low until the aforementioned rapid post-2017 increase.

a) SAW Volume only



b) SAW Volume and zooplankton

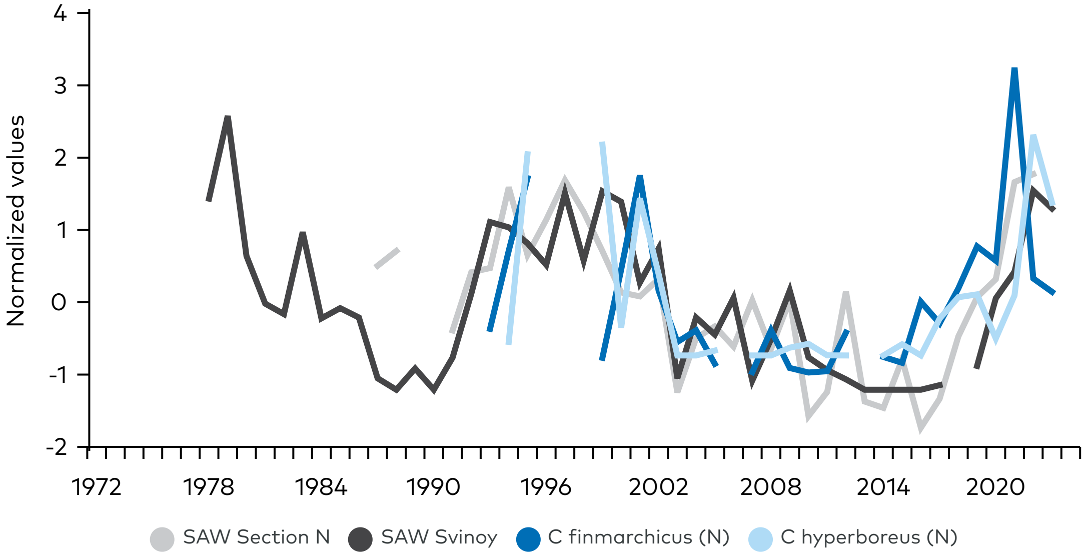


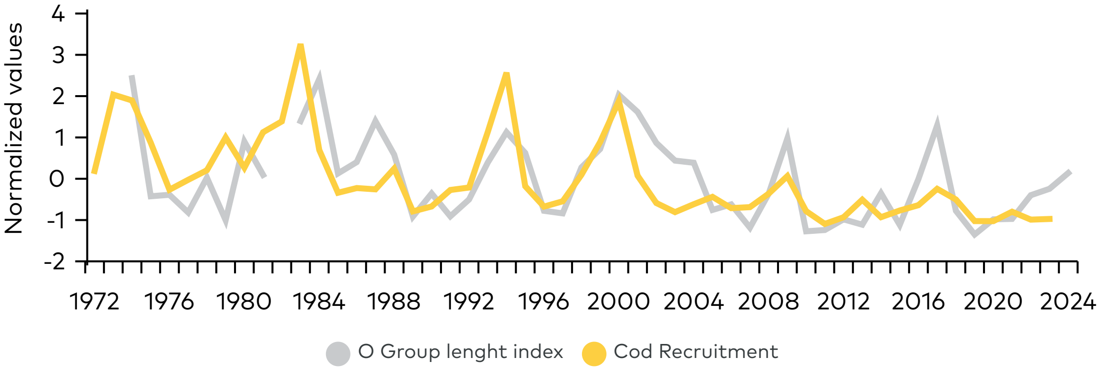
Figure 2.3 SAW volume in the southern Norwegian Sea and oceanic zooplankton. a) Indicators of SAW volume at Section N at the north Faroe slope and the Svinøy Section (Norwegian slope, see Fig. 2.1). These are actually estimates of the area of SAW at each respective section; b) As in panel (a), complemented with the abundance of the subarctic calanoid copepods *Calanus finmarchicus* and *Calanus hyperboreus* at the subarctic (northern) flank of Section N, in May.

2.3.2 Calanoid copepods abundances

The post-2017 SAW increase, and especially the very large SAW volumes in 2021–2022, coincided with marked peaks in overwintering *C. finmarchicus* (in 2021) and *C. hyperboreus* (in 2022) at Section N, both exceeding the levels of the 1990s (Fig. 2.3b).

As proposed by Kristiansen et al. (2019), large volumes of SAW lead to increased biomasses of subarctic zooplankton in May, thus supporting this hypothesis. To recapitulate the findings from Kristiansen et al. (2019, 2022) and Skagseth et al. (2022), the high SAW volumes during the 1990s and early 2000s (a subarctic period) were associated with high abundances of these subarctic copepods, the Atlantic period (2004–2014) with low SAW volumes was characterized by low abundances. This was followed by the above-mentioned increase, which commenced in 2016 (before the SAW increase) and amplified in the early 2020s.

a) Cod recruitment



b) Cod biomass

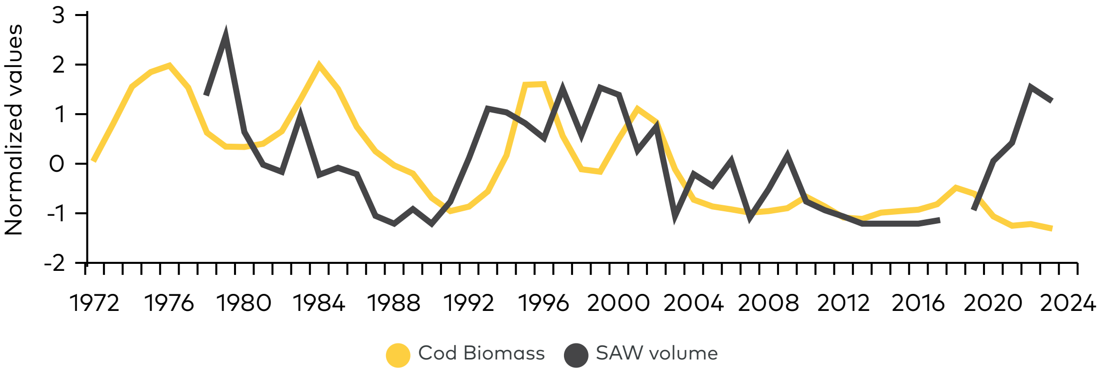


Figure 2.4 The Faroe cod stock and environmental drivers. a) Cod recruitment, the 0-group length index and the SAW volume, divided into subarctic periods (blue shades) and Atlantic period (red shades), based on a selected threshold. B) Cod biomass and the SAW volume. The timing of cod recruitment peaks is emphasized with vertical dashed lines, in both panels. The question mark in the 2020s refers to the discussed uncertainty.

2.3.3 Cod on the Faroe shelf

Recruitment

Peaks in cod recruitment occurring at 6–10 years are clearly linked to peaks in the 0-group length index, which represent the biological production of the Faroe shelf. The recruitment peaks in 1973–1974, 1994, 2000, 2009, and 2017 align precisely, while the recruitment peak in 1982 precedes the 0-group peak by a year, and the small recruitment peak in 1988 follows the 0-group peak by a year (Fig. 2.4a). However, recruitment peaks magnitude varies much more than the peaks in the 0-group length index.

The high recruitment peak in 1982 coincided with large volumes of SAW, and the high peaks in 1994 and 2000 were preceded by peaks in SAW volume in the previous years (1993 and 1999, respectively). The three low peaks in 1988, 2009, and 2017 correspond with low SAW volumes (Table 1). Years with large SAW volumes and low 0-group length indices generally do not result in good recruitment, although the very high SAW peak in 1979 did actually coincide with a low recruitment peak. These findings support our hypothesis, except for the 2020s increase in SAW volume and recently elevated 0-group length index (2023–2024), which has not led to increased cod recruitment – yet.

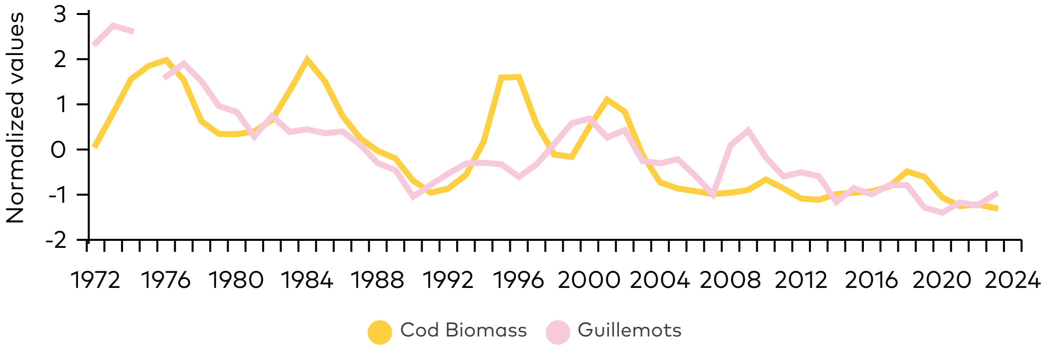
Biomass

Strong recruitment peaks lead to more rounded peaks in total cod biomass after a lag of 1–3 years (Fig. 2.4b). The biomass declines rapidly after these peaks, and the low recruitment peaks in 1988, 2009, and 2017 result in strong declines in cod biomass in the late 1980s/early 1990s and after 2004. Although direct correlations between cod biomass and SAW volume are not high, high SAW volumes (subarctic periods) are associated with large biomasses, while low SAW volumes (Atlantic periods) correspond to reduced biomasses. The only exception occurs in the 2020s, when the SAW volume has been very high, while the cod stock has remained very small.

Table 2.1 Assessment of the proposed hypothesis, that high recruitment requires both strong on-shelf production and a large SAW volume (proxy for off-shelf food abundance).

Production Peak year	SAW Volume	Recruitment peak	Validated
1974	-	High	-
1984	High (1983)	High (1983)	Yes
1987	Low	Low (1988)	Yes
1994	High	High	Yes
2000	High	High	Yes
2009	Low	Low	Yes
2017	Low	Low	Yes
2024	High	Low	No

a) Guillemots and cod



b) Guillemots and SAW

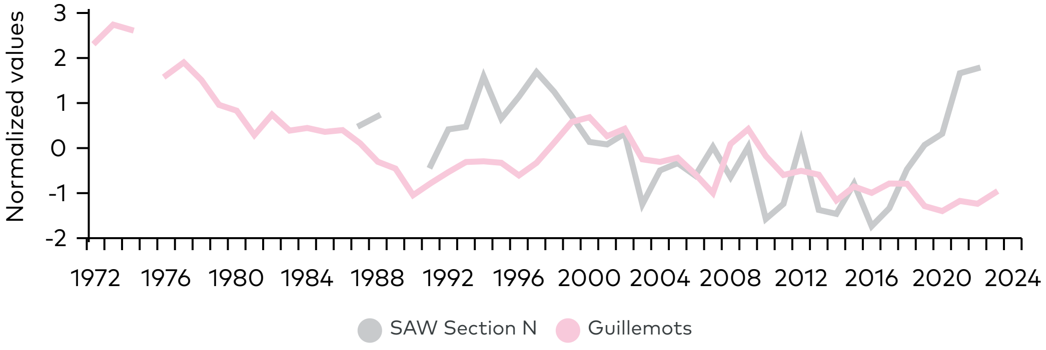


Figure 2.5 Attendance of guillemots in the Faroe Islands against: a) the Faroe cod biomass and b) the SAW volume.

2.3.4 Guillemots

The biomass of the Faroe cod stock and the attendance of guillemots have correlated during the last half century (Fig. 2.4a). A clear negative trend exists in both records, primarily caused by the marked cod decline during the late 1980s and early 2000s and a corresponding guillemot decline during these periods (Olsen et al., submitted). Rounded peaks in guillemot attendance roughly coincide with cod recruitment peaks, which lead the cod stock size by 1–3 years. The guillemot attendance closely follows the volume of SAW from the late 1970s to immediately before the post-2017 increase (Fig. 2.5b). The 1970s to 1990 and early 2000s declines, and the 1990s increase are evident in both records, and even shorter-term variability aligns; e.g. a 'plateau' during the early 1980s and peaks around 1993-1995, 1999–2000, and 2008-2009. However, there exists a strong contrast during the 2020s, when guillemot counts remained very low despite the SAW increase.

2.3.5 Cod on the Faroe Bank

The cod stock on the Faroe Bank, located immediately west of the Faroe Plateau, is included to provide a broader spatial perspective. The cod stock size, here proxied by the CPUE of cod in both March and September show increases in the 2020s (Fig. 2.6). The March records shot up in 2020, while the September record soared in 2021 and 2023. The apparent link to the SAW volume record has also persisted back in time, with low and declining CPUE during the late 1980s, high CPUEs in the late 1990s and early 2000s, and a rapid drop after 2003.

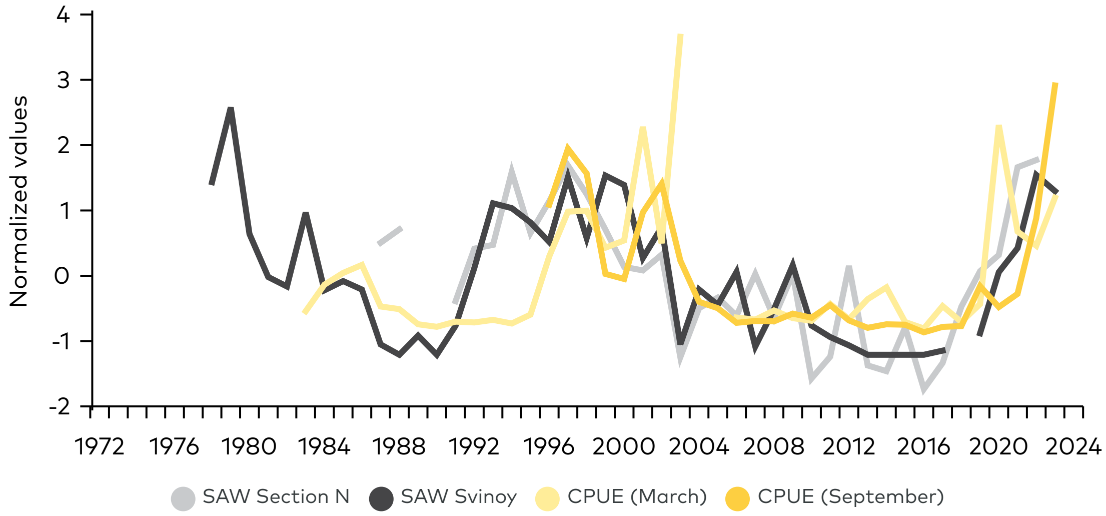


Figure 2.6 The cod stock size on the Faroe Bank, proxied by the Catch Per Unit Effort (CPUE) in March and September, respectively, and both indicators of SAW volume.

2.4. Discussion

Our results support the hypothesis, that biomass of upper trophic levels on the Faroe shelf is driven by both on-shelf production and off-shelf food abundance. Using a simplistic straightforward approach, that considers the volume of SAW as the sole off-shelf driver and the 0-group length index as the on-shelf production indicator, we can explain three phenomena since the late 1970s: Faroese cod stock recruitment, cod stock biomass development and guillemot attendance at the Faroese seabird cliffs.

The previous proposed linkage between eastward transports from the Icelandic tongue and the volume of SAW at both the northern Faroe slope (Section N) and along the Norwegian slope (Svinøy Section) (Hátún et al., 2022b; Kristiansen et al., 2019; Skagseth et al., 2022) is supported. Our SAW volume indicator therefore likely represents a fundamental aspect of the marine environment in the entire southern Norwegian Sea. Our findings demonstrate a marked shift to subarctic conditions in the 2020s, similar to a shift that took place during the early 1990s (Fig. 2.3). The marine environment was also highly subarctic during the late 1970s, before shifting to an Atlantic state in the late 1980s, with a similar abrupt shift to an Atlantic state in 2003. The rapid 'subarctification' in the 2020s resulted in a dramatic increase in subarctic zooplankton abundance north of the Faroes in May, which strongly supports the previous hypothesis (Kristiansen et al., 2019; Skagseth et al., 2022) that a variable influx from the Icelandic tongue regulates the zooplankton community in the southern Norwegian Sea. This large zooplankton increase is, however, not reflected in broad-scale zooplankton biomass estimates in the Norwegian Sea (ICES, 2024). The discrepancy between localized abundance and regional biomass measurements highlights the complexity of marine ecological assessment. Determining the ecological importance of species-specific zooplankton indicator records compared to coarse biomass indicators warrants a more in-depth discussion.

Our new hypothesis can explain why seemingly favorable conditions - some peaks with strong on-shelf primary production, and numerous and large juvenile fish in the summer, do not translate to high adult cod stock numbers. The weaker than expected cod recruitment peaks (1987–1988, 2008–2009 and 2016–2017) coincide with Atlantic conditions, characterized by small SAW volume and, by inference, limited ocean-to-shelf food supply throughout the year. While abundant food supply shortly after hatching is certainly a prerequisite for a good year-class, young fish need continuous food supply throughout the year, and for several years, which the relatively short spring/summer bloom cannot sustain. Ocean-to-shelf food transport can benefit many marine species (e.g. greater sandeel – *Hyperoplus lanceolatus*) providing larger cod with a richer and more persistent diet. Guillemots are known for their ability to dive deep (up to 150–200 meters) to catch prey, making them efficient marine hunters, but their prey size is generally limited to smaller fish species (Piatt & Nettleship, 1985). This seabird species feed both on and off the Faroe shelf (Olsen et al., submitted), and thus also over region directly influences by the SAW. However, elaborating of this bottom-up trophic cascade is beyond the scope of the present work.

Strong recruitment peaks consistently lead to a marked increase in adult cod stock biomass within 1–3 years. The low SAW volumes and low recruitment peaks quickly resulted in major declines in the cod stock biomass in the late 1980s and in the 2000s. Although the SAW volume indicator and cod biomass are not strongly correlated, they share important characteristics. Excluding the 2020s peaks in the SAW volume, both series clearly show a negative trend. It is evident that subarctic periods have led to higher biomasses, while Atlantic periods result in reduced biomasses. Excessive fishing pressure has certainly contributed to these declines, but, the explanation power of our new hypothesis suggests that consideration of both on-shelf production and off-shelf marine climate and food abundance could complement management of this stock.

The cod stock has, however, not reacted to the 2020s increase in SAW volume and increased abundance of oceanic subarctic copepods, as our hypothesis would predict. Given the cod recruitment estimate is uncertain for the recent 2–3 years (Beverton & Holt, 1993), it is possible that the Faroe cod recruitment and biomass are somewhat higher than indicated by the presented assessment records.

A strong correlation between cod biomass and guillemot attendance in the Faroes enables using the guillemot record as an assessment-independent indicator for the cod stock. The low guillemot numbers in recent years further support evidence of a very low cod biomass, validating the cod assessment. Guillemot attendance numbers have declined dramatically since the 1970s, with significant decreases in the late 1980s and early 2000s (Olsen et al., submitted). Rounded guillemot peaks, which precede the cod biomass peaks by 1–3 years, concur with peaks in cod recruitment.

The major decline in Faroe guillemot populations initiated in the 1960s, and continuing until present remains a puzzle to seabird scientists and hunters alike. This negative trend was linked by Olsen et al. (submitted) to changes in the marine environment, but the here demonstrated close link to SAW volume provides a new perspective. Hunting has, as with the cod, certainly put additional pressure on the guillemot population, but this cannot account for the population growth during the 1990s and the peak in 2008–2009. And, like with cod, there is a stark contrast between the 2020s SAW increase and the low guillemot attendance counts.

However, the 2020s discrepancy may not invalidate our hypothesis. The cod stock on the adjacent Faroe Bank started to rise in the late 2010s, and increased sharply in 2022, exceeding the previous high levels of the 1990s and early 2000s. Relationships between the 0-group length index, haddock recruitment, and SAW volume are similar to the presented cod linkages, and haddock recruitment and biomass increased during the 2020s (Fig. A2.1), supporting our hypothesis. Furthermore, some seabird species have experienced improved conditions in recent years (e.g. Faroe puffins and kittiwakes, Olsen et al., submitted).

Given the recent high SAW volume, large abundance of subarctic oceanic zooplankton, a moderate lower-level on-shelf production peak in 2023–2024 (Olsen et al, submitted) and the above-mentioned improvement for other species, the persistently low cod/guillemot populations appear counterintuitive. This may be because intense fishery has reduced the cod stock to levels too low for recovery, consequently impacting the guillemot population more severely than other seabird species (puffins and kittiwakes). Additionally other environmental drivers beyond SAW volume, such as the long-term decline in pre-bloom silicate concentrations in the Atlantic water passing the Faroe plateau (Hátún et al., 2022a, 2017) may have impacted the cod-guillemot trophic pathway more severely than other trophic paths. Although marine scientists often associate environmental drivers with seawater temperature (Edwards et al., 2021), we do not consider this the sole driver of the discussed trends. While the unproductive Atlantic period (2004–2014) was associated with high temperatures, the highly productive period of the late 1950s to the early 1960s experienced equally high temperatures (www.hav.fo). Correlations between the presented biological time series and temperature are, furthermore, not significant.

A third possibility is that according to our hypothesis, an anticipated cod-guillemot increase has indeed taken place around 2023–2024, but remains not evident in data on the populations sizes of adults – yet. Under this scenario, we should expect a marked increase in cod biomass and guillemot attendance during the coming year(s). Similar conditions potentially occurred in the early 1990s; SAW volume reached a high level in 1993, followed by high on-shelf production (proxied by the 0-group length index) in 1994. Cod recruitment increased dramatically in 1994, and cod biomass rose from 1991 levels, which were comparable to current very low estimates, to very high values in 1995 and 1996 (Fig. 2.4b). Notably, due to poor fishery in the late 1980s to the early 1990s, the Faroe Islands went bankrupt and the fishing fleet was largely dismantled in the early 1990s, resulting in very low fishing pressure (ICES, 2023).

Our assessment of the future development of a cod stock and a guillemot population should not be regarded as a proper forecast, but rather as a simple hypothesis upon which well-founded forecasts could be developed. Our hypothesis cannot, for example, explain the increase in haddock on both the Faroe Plateau and the Faroe Bank, and the improved conditions for puffins and kittiwakes already after 2015 (Olsen et al., submitted); these changes likely require consideration of the rapid intensification of the subpolar gyre around that time (Hátún & Chafik, 2018).

2.5 Conclusions

Ecological changes on the Faroe shelf have previously been discussed in relation to primary production on this shelf. While these earlier studies provided foundational insights into the ecosystem's dynamics, their explanation model primarily explains the marked production peaks, which recur in this system every 6–10 years. Inclusion of oceanic food abundance, represented by the volume of subarctic water masses around the Faroe plateau, in this ecological assessment enables us to explain longer-term trends, which also characterize this ecosystem. This expanded approach offers a more comprehensive understanding of the ecosystem's complex temporal dynamics.

PART 2.

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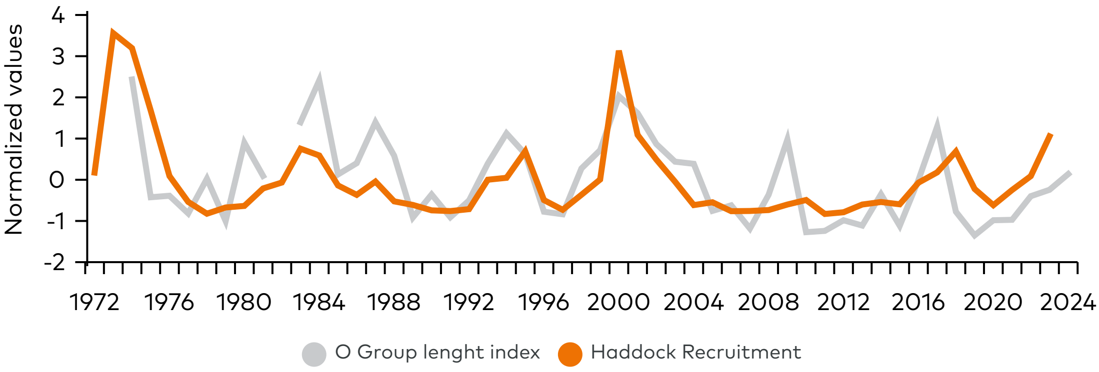
PART 2.

Appendix

Haddock

The haddock stock in Faroese waters is assessed annually. This assessment is data-rich (ICES category 1) and provides comprehensive information on the haddock population, including estimates of recruitment, spawning stock biomass, total stock biomass, and fishing pressure from 1957 to 2024 (ICES, 2023).


a) Haddock recruitement

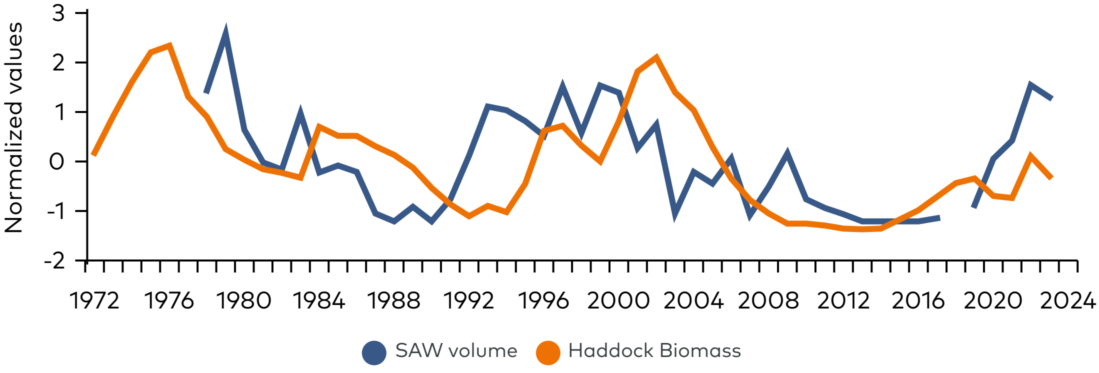

b) Haddock biomass

Figure A2.1 The Faroe haddock stock and environmental drivers. a) Haddock recruitment, the 0-group length index and the SAW volume, divided into subarctic periods (blue shades) and Atlantic period (red shades), based on a selected threshold. B) Haddock biomass and the SAW volume. The timing of haddock recruitment peaks is emphasized with vertical dashed lines, in both panels.

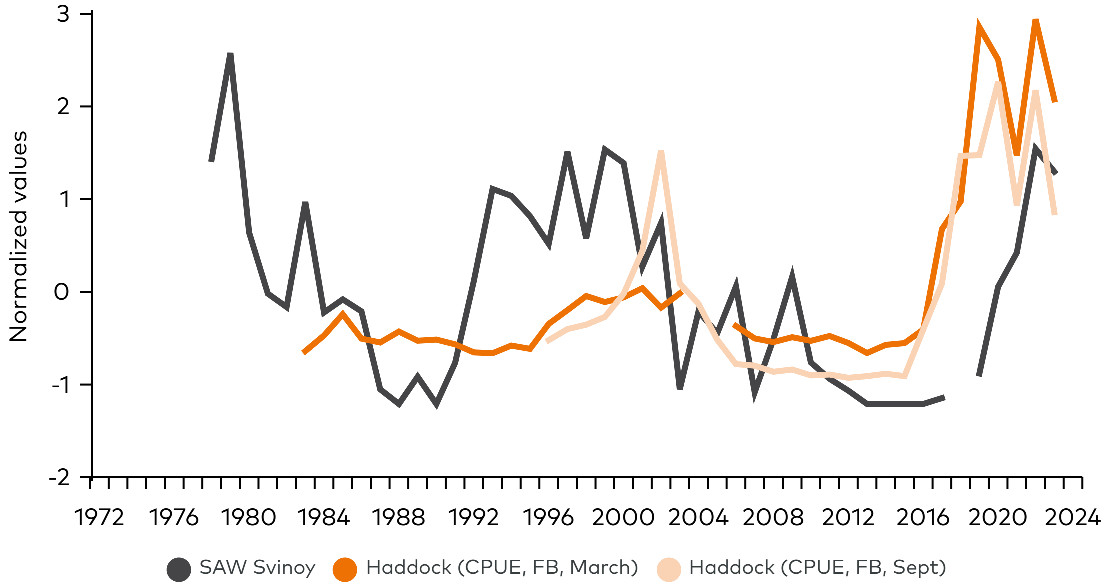


Figure A2.2 The haddock stock size on the Faroe Banks, proxied by the Catch Per Unit Effort (CPUE) in March and September, respectively, and the Svinøy Section indicator of SAW volume.

About this publication

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Cover photo: The picture shows a puffin carrying sandeels to the colony in Røst, Northern Norway. Picture taken by Tycho Anker-Nilssen.
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