



**UiT** The Arctic University of Norway

Faculty of Biosciences, Fisheries, and Economics

**Climate-driven redistribution of fish and reconfiguration of coastal food webs in Northern Norway**

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## Abstract

Rapid climate change at northern latitudes induces poleward redistributions of fish leading to reconfigurations in biodiversity and food webs. This thesis aims to broaden our understanding of the climate-driven biogeographical alterations in fish and the subsequent reorganization of food webs along the coast of Northern Norway. Documenting and understanding the ongoing, rapid ecological change in coastal waters is crucial to inform climate adaptation of conservation and ecosystem-based management. This thesis examines the climate-driven reorganization of coastal communities over the period 1995-2019, comparing three study areas in Northern Norway ( $> 67^\circ$ ), using trawling samples from the Norwegian Institute of Marine Research together with metaweb data. The objectives are to i. assess the climate-driven, temporal change in fish species diversity, prevalence, and co-occurrence frequencies; ii. investigate changes in the topological food web structure due to incoming species; and iii. characterize the changes in frequency of interactions between fish due to changes in co-occurrences over time. The implications of fish redistribution for species richness, prevalence, and co-occurrence were studied using occurrence data from the coastal trawling survey. The changes in food web topology due to incoming species in the three study areas used available metaweb data for the region, with selection and aggregation of trophospecies tailored to the scope and purpose of the study. The changes in interaction frequencies within the fish food webs were visualized using co-occurrence data, providing insights into the dynamic relationships among species in the studied areas.

The findings reveal a notable increase in species richness and prevalence across all study areas from the earlier, cooler period (1995-2000) to the later, warmer period (2014-2019). The increase is consistent with expectations that increasing ocean temperatures along the north Norwegian coast facilitate boreal species' expansions into northern latitudes, altering local biodiversity and community structures. The increased prevalence of incoming boreal species leads to higher co-occurrence frequencies among fish, suggesting a reconfiguration of northern coastal food webs. The food web implications of fish redistributions included a distinct increase in the number of links, and a decrease in connectance and clustering indicating a shift towards less densely connected but more structurally complex food webs.

*Keywords:* biogeography, coastal ecosystems, northern Norway, fish, poleward redistribution, food web metrics, co-occurrences



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## Preface

The brilliant biologist Thomas Huxley stood before the British parliament in the late 1800s and said that mankind couldn't possibly exhaust the oceans. Some seventy years later Rachel Carson's *Silent Spring* was published and ignited the environmentalist flame. That was merely sixty years ago. Our species' ability to impact nature in the magnitude that we do is both astonishing and ever-present. A changing climate is at play and future management plans and regulations must therefore follow its rules.

There is no doubt that humankind is the apex predator of every ecosystem on the planet. As we are building out and moving into the natural world and extracting more resources; other species we share the earth with must give up their habitats and resources. More extreme weather alongside food security being harder for a growing human population is a fine recipe for dystopia. And amidst all the gloomy science and political talks, and summit meetings; climate justice and equity are central topics that should demand more of our attention. The adverse consequences affect human populations and will continue to do so, no matter how defenseless the group is. Low-income countries with the least financial resources to adapt, and low capability of climate mitigation and resilience are especially at risk, as well as indigenous people, the urban poor, women in vulnerable regions, and coastal communities. Climate change knows no borders and acts neither just nor equitable. Therefore, it falls upon us to ensure that management and regulation include and protect the most vulnerable of us.

And that's just the issue within our own species. What about all the other living beings we share this planet with? Species are experiencing habitat loss, phenology mismatches, an increase in extreme weather events, increased disease, loss of genetic diversity, and extinction risk, and they need to shift towards more suitable habitats due to changes in their environment. All these changes are challenging us to rethink our strategies and way of life, and in doing so, hopefully laying the groundwork for a global movement towards a more sustainable future. Not just for us, but for the entire planet.

Good things are happening. People want to act. The momentum is here, and most of us want to ride it. Therefore, I am optimistic.

The time has come for change. The time has come to do. We know enough. Now we act.





# 1 Introduction

## 1.1 Climate change in the north

Climate change is reshaping nature around the world (IPCC, 2023). Globally, the average temperature has increased by at least 1.1 °C (NASA, 2024). The Arctic is warming nearly four times faster (Rantanen et al., 2022). The temperature increase is also observed in the oceans, with a reported average temperature of 21.1 °C in August 2023 and January 2024 compared to the average temperature in the 1982-2011 period of 20.3 °C (NOAA, 2023). For mobile species, the first response to climate change is often to move towards more suitable habitat conditions (Pecl et al., 2017; Poloczanska et al., 2013; Walther et al., 2002), and temperature has emerged as the best predictor for species distributions in the ocean (Boyce et al., 2015; Tittensor et al., 2010). The expected and observed response to the increase in ocean temperatures is the poleward redistribution of species (Chaudhary et al., 2021; Pinsky et al., 2020). The resulting changes in species composition alter biodiversity and trigger the reconfiguration of food webs, modifying marine ecosystems' state, functioning, and vulnerability (Ingvaldsen et al., 2021). The rapid, climate-driven ecological transition at high latitudes is well documented in the open sea, but not in coastal waters.

At higher latitudes, the rates of water temperature increase during the last three decades have been staggering (IPCC, 2019). The Norwegian seas exemplify such rapid, climate-driven change. The average sea surface temperatures (SST) in the Norwegian Sea have shown a warming trend of 0.04-0.07 °C per year according to Yang et al. (2023). Further north, in the Barents Sea, the rate of sea-ice loss has been unprecedented, but SST has fluctuated, with an annual mean temperature range spanning 0.2 °C to 3 °C. The fastest rise in SST in the Arctic is that of the Northeast Passage (Yang et al., 2023). The main driver for an increase in ocean temperatures in the North Atlantic is the influx of warm Atlantic waters from the south (Skagseth et al., 2011; Østerhus et al., 2005). Increased inflow of Atlantic water in recent years has changed the physical and biogeochemical properties of the north-Atlantic Ocean, leading to a transition from Arctic water to Atlantic water – a process named *atlantification* (Ingvaldsen et al., 2021). This process sees the traditionally cold, ice-influenced, and stratified Arctic waters, with low pH, becoming warmer with less ice cover and a weakened stratification, alongside an increase in pH, as seen in the Barents Sea (Gerland et al., 2023).

## 1.2 Climate-driven poleward redistribution and biodiversity

The climate-induced poleward shifts of marine species reshape biogeographic patterns and reorganize food webs (Cheung et al., 2009; Fossheim et al., 2015; He & Silliman, 2019; Kortsch et al., 2019). The introduction of new species in an area can affect the variety of species that co-occur in a particular place (alpha diversity), change the composition of communities in space and time (beta diversity), and influence the total number of species within a broader area (gamma diversity), reshaping biodiversity within a region (Whittaker, 1972). Marine species, and fish in particular, exhibit some of the most rapid and substantial ecological responses to increased sea temperatures (Fossheim et al., 2015; Hoegh-Guldberg & Bruno, 2010). The poleward distributional shifts observed in fish species span a broad latitudinal range, from tropical waters to the Arctic, where the rate of change is highest (Ingvaldsen et al., 2021; Smith et al., 2019). The main driver for the observed poleward shifts is an increase in sea temperatures, with many fish species being capable of tracking climate velocities (Pinsky et al., 2013; Sanz-Martín et al., 2024). These well-documented responses lead to changes in biodiversity and reorganization of marine ecosystems (Ingvaldsen et al., 2021; Masson-Delmotte et al., 2021).

Poleward shifts in distributions can, at least temporarily, increase fish diversity at high latitudes, as documented for shelf areas and open sea (Alabia et al., 2023; Frainer et al., 2017; Ingvaldsen et al., 2021). The boreal fish species moving into northern waters often differ from Arctic species with regard to body size, foraging behavior and life history characteristics (Frainer et al., 2017). Boreal fish species typically have larger body size, more diverse diet, later maturation, and greater fecundity (Bernardo et al., 2024; Frainer et al., 2017). The compositional changes resulting from poleward shifts of boreal fish species thus modify functional characterization and diversity of Arctic communities (Frainer et al., 2017). Further, boreal species establish new feeding links, reorganizing food webs (Ingvaldsen et al., 2021; Kortsch et al., 2015; Pecuchet et al., 2020). The introduction of generalist boreal species, such as *Gadus morhua* and *Melanogrammus aeglefinus*, into the arctic marine food web, may establish many new feeding interactions profoundly altering the food web structure (Pecuchet et al., 2020; Pedersen et al., 2008).

### 1.3 Food web reconfiguration

Boreal species are redistributing further north, potentially affecting high-latitude marine food webs and ecosystems (Polyakov et al., 2020). New species entering an ecosystem can be established as predators or prey, creating novel interactions and pathways within the food web. As the Arctic environment becomes more hospitable to boreal species due to climate warming, there is a notable advection of anomalous Sub-Arctic Atlantic water and biota into low- and sub-Arctic regions which, together with the active dispersal of boreal species, results in a *borealization* of high-latitude marine ecosystems (Polyakov et al., 2020). This shift brings new species into the Arctic marine food webs, including plankton, fish, sea mammals, and seabirds. The loss of sea ice and increased light penetration lead to higher primary production and greater visibility, thus changing pelagic interactions involving fish and other visual predators (IPCC, 2019; Langbehn & Varpe, 2017). The enhanced primary production supports the growth of boreal species like *Calanus* copepods, krill, and capelin, potentially reshaping the base of the food web and impacting higher trophic levels, including commercially important fish like *Gadus morhua* and *Melanogrammus aeglefinus* (ICES, 2021; Tarling et al., 2022; Aarflot et al., 2017). The introduction of these species alters existing food web structures and establishes new ecological interactions (Ingvaldsen et al., 2021; Kortsch et al., 2015; Pecuchet et al., 2020).

With the influx of boreal species, the number and character of feeding links in high-latitude food webs change (Kortsch et al., 2015; Pecuchet et al., 2020). These species often have broader diets, feeding on both pelagic and benthic prey, thus linking different food web compartments, as documented for *Gadus morhua* (Kortsch et al., 2015). This increased connectivity in the food web leads to a reduction in its modularity and introduces new pathways for energy and material flow (Kortsch et al., 2015). While boreal species thrive in the new conditions, Arctic species face habitat deterioration and increased competition and predation. This may lead to a decrease in Arctic species and a potential decline in biodiversity over time, despite the initial increase due to the influx of boreal species (Ingvaldsen et al., 2021). Coastal marine ecosystems at high latitudes are experiencing a similar increase in biodiversity due to rapid warming (Siwertsson et al. 2024). The climate-induced biodiversity change might reconfigure coastal food webs, an expectation in urgent need of evaluation (McLean et al., 2018).

### **1.3.1 North Norwegian coastal ecosystems**

High-latitude, Norwegian waters have become a hotspot for climate-driven redistribution of species (Ingvaldsen et al., 2021). However, much of the evidence for species redistributions and for their ecosystem implications comes from open ocean studies, whereas coastal areas remain less studied (Siwertsson et al., 2024). This knowledge gap is concerning, given the vital ecological and socio-economic roles played by marine species, and especially fish, in coastal ecosystems (Barbier et al., 2011). Coastal marine ecosystems represent some of the most diverse and productive marine areas globally, offering many ecosystem services (Barbier et al., 2011). Marine ecosystems have played a significant role in the shaping of coastal human communities, both geographically and culturally, having supported both local and indigenous populations for generations (Perdikaris, 2012; Varpe et al., 2005). Furthermore, these ecosystems provide valuable services, including provisioning for fisheries and aquaculture, water purification, and shoreline protection (Doney et al., 2012).

Coastal ecosystems, like their open ocean counterparts, are not immune to the pervasive effects of climate warming (Varela et al., 2023). Factors such as increasing sea temperatures, changes in salinity, and rise in sea level, are all expected to affect coastal ecosystems and their biodiversity (He & Silliman, 2019; IPCC, 2022). Coastal ecosystems also house more heterogeneous habitats, supporting communities with greater biological diversity (Barbier et al., 2011). Fish benefit from and contribute to biotic diversity, serving both as prey for upper trophic levels, including marine mammals and seabirds, and as consumers of benthic and pelagic prey. This significant ecological role of fish, coupled with the socio-economic importance, especially in regions with a strong reliance on marine resources, underscores the critical importance of understanding how climate-driven fish redistribution is reshaping coastal ecosystems (He & Silliman, 2019).

In this context, Northern Norway provides a prime example of high-latitude coastal ecosystems undergoing significant transformations due to climate change (IPCC, 2023). The Northern Norwegian coast houses a diverse fish fauna and extends over a bioclimatic transition zone, the sub-Arctic zone, which has been strongly affected by climate warming over the last three decades, leading to rapid ecological change.

This study aims to look at biodiversity and food web implications of climate-induced shifts in fish distributions along the Norwegian coast over the last three decades (1995-2019). The research focus is on the climate-induced temporal changes in fish diversity, prevalence, and co-

occurrences, and on how these impact food web configurations. The observational approach compares the colder period 1995-2000 with the warmer 2014-2019 across three adjacent study areas along the North Norwegian coast. The analyses rely on long-term data from the coastal fish trawling survey by the Norwegian Institute of Marine Research, and on regional food web data. The objectives of my thesis are to: i. assess the climate-driven, temporal change in fish species diversity, prevalence, and co-occurrence frequencies; ii. investigate changes in the topological food web structure due to incoming species; and iii. characterize the changes in frequency of interactions between fish due to changes in co-occurrences over time.

The hypotheses are:

- a) There will be an increase in species richness and prevalence over time in each area and this will in turn increase the frequency of fish co-occurrence.
- b) Incoming boreal species in the warmer period will increase the number of links, decrease connectance, clustering, modularity, and increase path lengths in the food web.
- c) There will be an increase in the contact frequency with boreal fish predators and prey.

## **2 Material and methods**

### **2.1 Study area**

Norway has the second longest coastline in the world after Canada, with all its small and big islands, inlets, skerries, holms, peninsulas, and fjords (Fjørtoft, 2013). The large latitudinal range covered, from 58° to 71° North, results in a substantial water temperature gradient spanning about 8 °C from south to north (Siwertsson et al., 2024). Historical records indicate variations in SST in the North Atlantic, transitioning from relatively cold conditions a century ago to warmer temperatures in the 1930s-1960s and cooler phases in the 1960s-1990s according to the AMO (Atlantic Multi-decadal Oscillation) index (Sutton & Hodson, 2005). The thermohaline circulation of the North Atlantic Ocean (the Gulf Stream) and particularly, the Norwegian Atlantic Current (NAC, a branch of the Gulf Stream) is moderating the regional climate here (Eldevik et al., 2014). The ocean along the coast of Norway is shaped by the inflow of warm and saline Atlantic water into the Nordic Sea via the NAC, as well as the properties of lower-salinity coastal water moving northwards along the coast, known as the Norwegian Coastal Current (NCC), transporting fresh and brackish water from the Baltic Sea and additionally influenced by land runoffs, fjord, and rivers (Sætre, 2007). The NAC experiences a progressive decline in temperature and salinity due to mixing with the NCC, freshwater

discharge, precipitation, and atmospheric cooling (Ingvaldsen et al., 2021). Albretsen et al. (2012) noted an increase in ocean temperatures, both in the upper and deeper layers along the Norwegian coast between 1990 and 2009. This increase was attributed to the reduction of the North Atlantic Subpolar Gyre (Hátún et al., 2005), combined with a decrease in the North Atlantic Oscillation and possibly an increase in hemispheric warming.

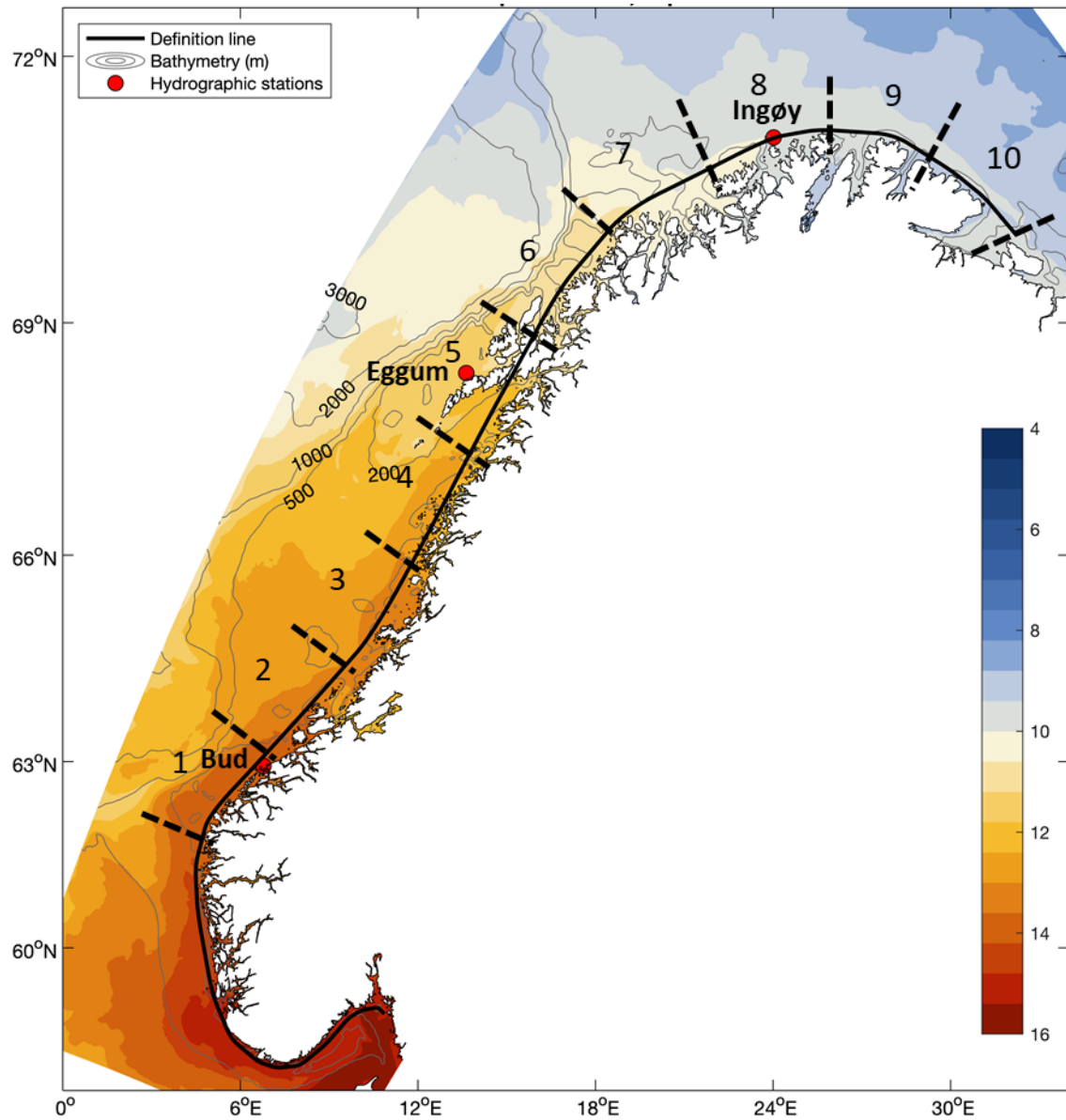


Figure 1: Map of the study area, comprising the delineated areas 5 to 10, highlighting the latitudinal gradient in water temperature in the upper 10 m (September mean °C). Areas 5 to 10 are aggregated in adjacent pairs into the larger areas 1, 2 and 3 used in this thesis. Map by Jofrid Skardhamar.

The geomorphic, oceanographic, and biogeochemical characteristics of the north Norwegian coast set the stage for diverse and spatially heterogeneous habitats. Pelagic and demersal fish

play an important ecological and socio-economic role along the coast having shaped coastal settlements over many centuries (Collie et al., 2008; Perdikaris, 2012). Coastal habitats also form the spawning and feeding grounds for several large migratory and stationary fish populations, such as the Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*), beaked redfish (*Sebastes*), long rough dab (*Hippoglossoides platessoides*), saithe (*Pollachius virens*) and herring (*Clupea harengus*) (Albert et al., 1998; Berg & Albert, 2003; IMR, 2024; Olsen et al., 2010). The northern coastal regions of Norway, north of 62° N, also support fisheries for over 70 different taxa, with an average annual value of more than 0.8 billion euros worth of landings, equivalent to more than 9 billion Norwegian kroners (Siwertsson et al., 2024)

## **2.2 Biological data**

The data used in the study consist of fish presence-absence data for the periods 1995-2000 and 2014-2019, obtained from the annual trawling survey provided by the Norwegian Institute of Marine Research (IMR), and of a metaweb for the region summarizing the feeding links among some of the most prevalent species (<https://doi:10.5061/dryad.73r6j>).

### **IMR coastal survey**

Fish occurrence data for the relevant periods were obtained from the Norwegian Coastal survey carried out by IMR. In autumn each year, the survey covers the Norwegian coast, from approx. 61° North (4° E) to 71° North (32° E). The bottom trawl samples are collected both close to shore, within fjords, and further off the coast up to approximately 65 nautical miles (120.38 km).

### **Fish sampling**

Demersal fish were sampled using shrimp trawls with a towing speed of approximately three knots. Stations where the trawling coverage was less than 0.5 nautical miles or exceeded 2.1 nautical miles were excluded from the dataset, as were stations for which fish occurrence data were unavailable. Additionally, stations situated at depths greater than 500 meters, which are rare and not representative of coastal fish communities, were also excluded. In total, 546 trawl samples were included in the analysis for the 1995-2000 period, and 755 for the 2014-2019 period (Fig 2).



The fish species were identified to the lowest taxonomic level possible, with the majority being identified to species level. Out of 129 taxa present in the dataset, we selected the 59 most widely distributed and abundant ones, ensuring consistency of taxonomic identification over the study period. These selected taxa have consistently appeared in the survey and collectively represent over 99.9% of the total catch abundance. Among these 59 taxa, some were categorized at a lower taxonomic resolution, aggregated to the genus level (e.g. red fishes to *Sebastes* sp.) or order level (e.g. lanternfishes to *Myctophiformes*).

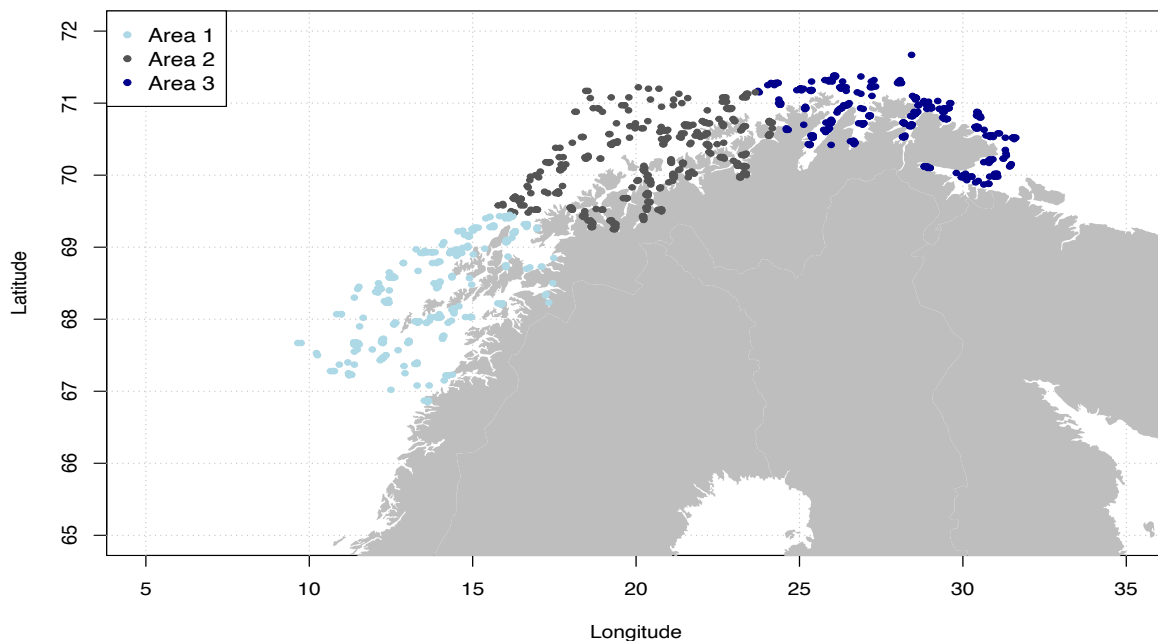


Figure 2: Map over the North Norwegian coast showing the positions of the sampling stations for the IMR trawling survey. The areas 1 (light blue), 2 (brown) and 3 (blue) are each 334 km long. The study area stretches from approximately 67° N (10° E) to 71° N (32° E). The depth of the trawling samples included in the study ranged between 32 and 489 meters.

## 2.3 Metaweb and coastal food webs

Food webs represent different trophospecies – i.e. individual species or groups of species that share the same predators and prey - and their feeding links. We compiled six food webs, one for each of the three studied areas in the two periods 1995-2000 and 2014-2019. The three areas were specified based on ten already defined coastal intervals from south to north, each 167 km long (Fig 1, Siwertsson et al. (2024)). I aggregated coastal intervals 5 and 6 into area 1, 7 and 8 into area 2, and 9 and 10 into area 3 (see Fig 1 for coastal intervals' number from Siwertsson et al. 2024). For the food web data compilation, we further selected 34 out of the 59 fish species for which metaweb data were available (Table A4). The food web data were obtained from the

metaweb dataset published by Planque et al. (2014), revised according to Kortsch et al. (2019) and Pecuchet et al. (2020), encompassing trophospecies and feeding links documented in the region (primarily Barents Sea).

The area and period-specific food webs were compiled by combining compositional and metaweb data (Fig 3). Field observations were used as a basis for creating the food webs. To select which fish species were present in each of the six food webs, I used presence-absence data processed from the survey trawl data from IMR. I used a 5 % threshold for species prevalence to determine if the fish species were considered present or absent in each area for each period. Zooplankton and benthos trophospecies were aggregated into functional groups defined by body size and feeding categories. The functional groups were *large predator*, *small predator*, *large suspension feeder*, *small suspension feeder*, *large deposit feeder*, and *small deposit feeder*. Sea bird and sea mammal species living and feeding along the coast of Northern Norway were also selected from the original metaweb.

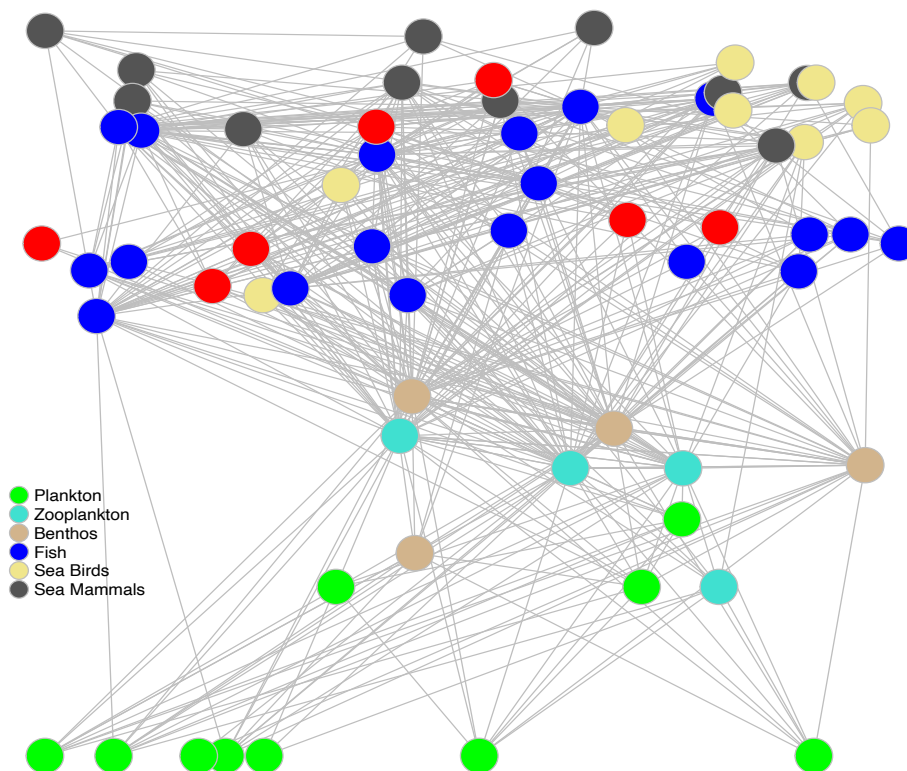


Figure 3: Meta-web used in the study highlighting the incoming fish species (red symbols). The trophospecies are depicted as colored circles (color code for functional groups - green, phytoplankton; turquoise, zooplankton; light brown, benthos; blue and red, fish; sandbrown, sea birds; dark brown, sea mammals) and the feeding links are shown as grey lines.

The original metaweb comprised 180 trophospecies with 1424 links, and the aggregated metaweb used in this study contained 72 trophospecies with 542 links.

## 2.4 Data analysis

The fish presence-absence data and the metaweb data were compiled and processed to cover the three study areas over the two periods 1995-2000 and 2014-2019 (Fig 4).

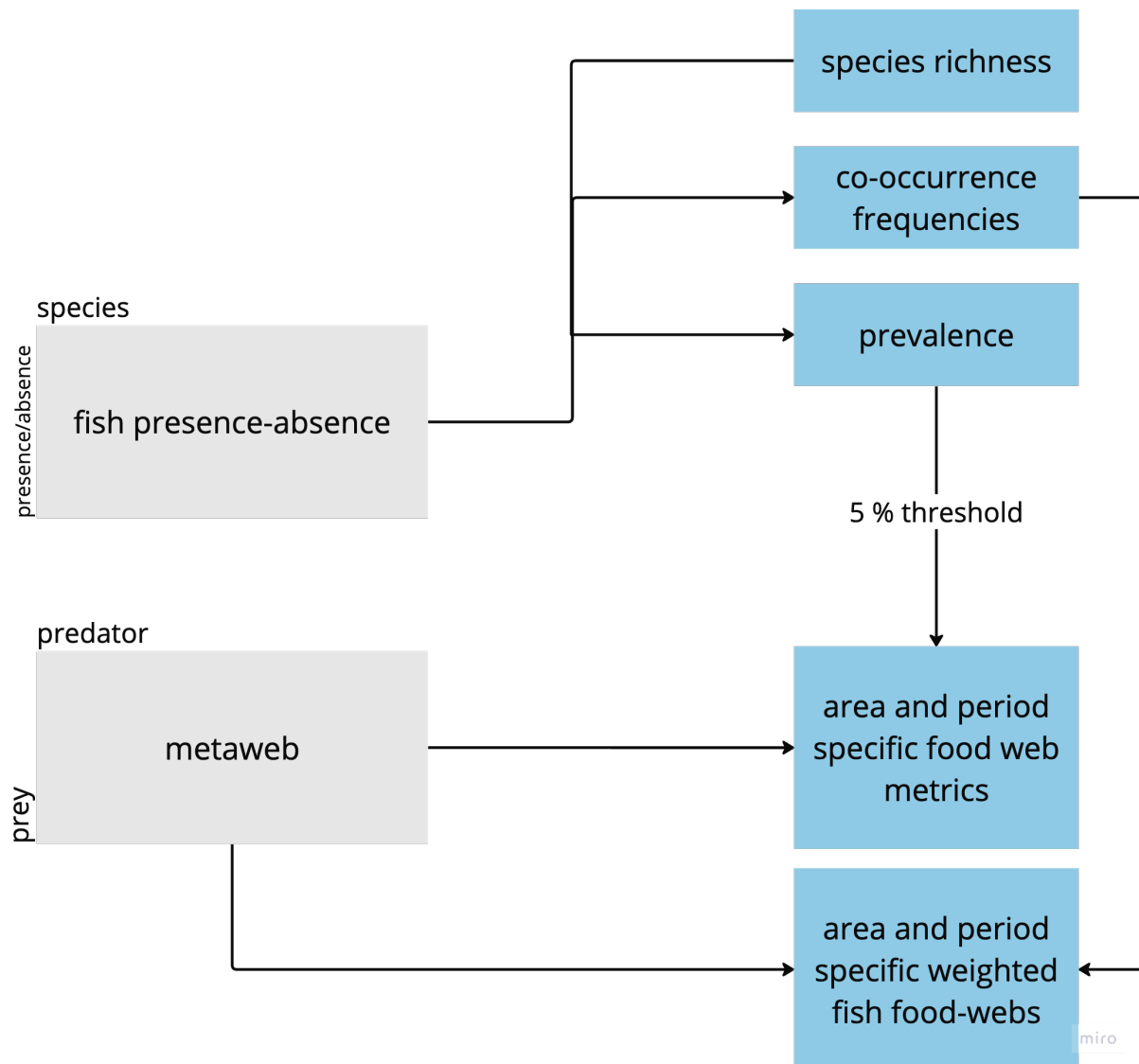


Figure 4 Diagram describing data used to produce the different study outcomes (blue boxes). We used 1) fish presence-absence data to produce species richness, prevalence, and co-occurrence frequencies for all areas and periods. 2) The presence-absence data were further used to compile area and period specific food webs by identifying fish species present, using a 5 % prevalence threshold, and by adding these to the other trophospecies and relevant links in the metaweb. 3) The co-occurrence frequencies were used to produce area and period specific weighted fish food webs, using relevant links from the metaweb.

### **Species richness and prevalence**

The IMR trawling survey data for the studied region were processed and coded to presence-absence, to calculate species richness for each trawling sample, a measure of alpha diversity. Alpha diversity is measured in this study as species richness, i.e. number of species in one sample (Colwell, 2009). Species richness was summarized graphically in a boxplot and analyzed using a generalized linear model (GLM) relating *species richness* (count data) to the categorical predictors' *period* and *area*, using a Poisson error distribution. Species prevalence for each period was calculated as the proportion of sampled stations occupied by a species (Sor et al., 2017).

### **Species co-occurrences**

Co-occurrence frequencies for each area and period were computed as the number of trawling samples in which two species co-occurred divided by the total number of samples. The co-occurrence frequency provides an estimate of spatial overlap at the local (trawling sample) scale at which ecological interactions take place and is a measure of the likely contact frequencies between species in a given area and period (Cazelles et al., 2016; Morales-Castilla et al., 2015). To estimate temporal changes in fish species co-occurrences for the whole region and for each study area, I subtracted the co-occurrence frequency matrix for the later period from that of the early period.

### **Food webs and structural metrics**

Food web diagrams were produced to visualize food web configurations and differences thereof across areas and periods (Fig 3). Food web metrics (Table 1) were calculated to characterize the topological structure of the six compiled food webs. The main focus will be on seven of the total 16 calculated food web metrics listed in Table 1, specifically the number of species, number of links, connectance, clustering, compartmentalization, the proportion of intermediate species, and mean shortest path length, which captures distinctive features of marine ecosystems (Dunne et al., 2004; Thompson et al., 2007).

Table 1: Overview of food web metrics, their definition, and potential ecological implications.

<b>METRIC</b>	<b>DEFINITION</b>	<b>ECOLOGICAL IMPLICATIONS</b>
<b>NUMBER OF SPECIES</b>	Number of nodes in the food web.	The greater the species richness, the more persistent an ecosystem is. An increase in species richness may support processes such as productivity and stability.
<b>NUMBER OF LINKS</b>	Number of trophic interactions in a food web.	The more links, the more complex a food web is, e.g. more pathways for energy to flow through.
<b>LINK DENSITY</b>	Number of trophic interactions (links) per species.	An increase in link density reflects how connected species are within the food web.
<b>CONNECTANCE</b>	Calculated as $\text{link}/\text{species}^2$ – the proportion of all possible interactions (links) between taxa observed in the food web.	Connectance can both be positively and negatively associated with food web robustness (random vs. non-random).
<b>CLUSTERING</b>	The probability that two taxa that are linked to the same taxons are also linked together.	The more clustered a food web is, the more trophospecies are highly interlinked, and could influence the stability of the food web.
<b>MODULARITY</b>	The degree of distinct modules within the food web that have few or no interactions between them. High modularity indicates food webs that are highly compartmented.	High modularity can increase robustness to perturbation by localizing its effects.

<b>PROPORTION OF OMNIVORY</b>	Proportion of taxa that feed on resources from more than one trophic level.	Can negatively or positively influence stability of community, based on strength of interactions between taxa.
<b>PROPORTION OF CANNIBALISM</b>	Proportion of taxa that feed on themselves.	Moderate levels of cannibalism e.g., in fish, can reduce inter-cohort competition, enabling coexistence of many cohorts. It can also be destabilizing and lead to other alternative stable states.
<b>PREDATOR/PREY RATIO</b>	The mean numbers of predators per prey.	The vulnerability for predation increases with the number of predators per prey species.
<b>PROPORTION OF BASAL SPECIES</b>	Proportion of taxa that has zero preys.	Often under-represented in marine food webs as primary producers are disproportionately abundant, creating a funnel shape.
<b>PROPORTION OF TOP SPECIES</b>	Proportion of taxa that has zero predators.	Top predators exert top-down control on ecosystems and can initiate trophic cascaded through lower trophic levels.
<b>PROPORTION OF INTER-MEDIATE SPECIES</b>	Proportion of taxa that are both prey and predators to other species.	Represents the portion of taxa that serve as both predator and prey, linking lower and upper trophic levels, and correlated with higher connectance.

<b>GENERALITY SD</b>	A normalized SD of the number of resources per taxa (generality) present in the food web.	An increase in GenSD reflects the variability in the number of different prey species (“in-degree”) a particular predator has.
<b>VULNERABILITY SD</b>	A normalized SD of the number of consumers per taxon (vulnerability) in the food web.	An increase in VulSD reflects the variability in the number of different predators (“out-degree”) a particular prey has.
<b>MEAN SHORT-WEIGHTED TROPHIC LEVEL</b>	The mean for all short-weighted paths from the base to each taxa.	The vertical structure of the food web is determined by the number of trophic levels and is related to the length of the food chains. The height of trophic levels mirrors ecological mechanisms that support top predators.
<b>MEAN SHORTEST PATH LENGTH</b>	The mean of shortest food chain connecting each pair of taxa in the food web.	The length of food chains affects their stability. Shorter chains are often more stable than long chains. The length of food chains is often longer in more productive ecosystems.

The graphical summaries and data analyses included in the thesis were performed in R (RStudio version 2023.06.1-524). Species richness, prevalence and co-occurrence frequencies were computed from the presence-absence fish survey data via dedicated algorithms. Food web metrics and trophospecies’ positions and roles were computed with the support of R packages NetIndices (trophic level and omnivory) and igraph (centrality measures and spinglass algorithm for modularity estimates).

### 3 Results

#### 3.1 Fish species richness and prevalence

Species richness increased substantially from the early period (1995-2000) to the later period (2014-2019) across all three areas (Fig 5). The median number of species per sampled station for the three areas rose from 12, 9, and 8 respectively in the early period to 16, 13, and 13 in the later period, a 33.33 % increase in area 1, a 44.44 % increase in area 2 and a 62.50 % increase in area 3.

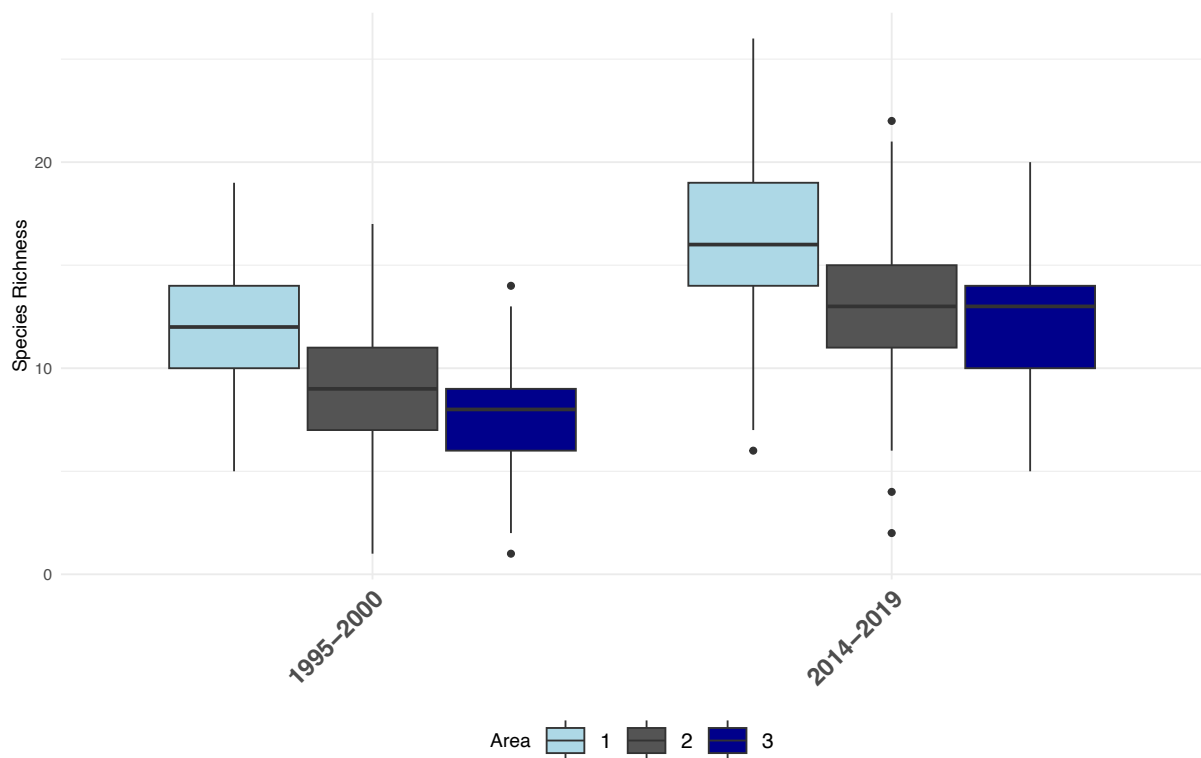


Figure 5: Species richness in the study areas during the early, cold period 1995-2000, and during the warmer period 2014-2019. The boxplot indicates a distinct temporal increase in species richness across areas along the North Norwegian coast.

The Generalized Linear Model (GLM) revealed a considerable and significant increase in species richness in the later period (2014-2019) ( $p < 2^{-16}$ , see Table A1 in Appendix for GLM output). Additionally, there was a significant decrease in mean species richness from area 1 to areas 2 and 3, both being statistically significant ( $p < 0.0001$ , Table A1).



The overall prevalence increased for almost all species from the early period to the late period (Fig 6). Species exhibiting a noteworthy increase in prevalence include the boreal species *Trisopterus esmarkii* (+32.22 %), *Enchelyopus cimbrius* (+228.72 %), *Merlangius merlangus* (+162.79 %) and widely distributed *Etmopterus spinax* (243.51 %), but also the mainly boreal *Lycodes gracilis* (163.24 %) and arcto-boreal *Mallotus villosus* (140.13 %). *Sebastes* showed an increase of 4.67 % with a prevalence proportion of 0.89 in the later period, being the third most prevalent after *Gadus morhua* (0.93), and *Melanogrammus aeglefinus* (0.94), displaying only small decreases (<2%).

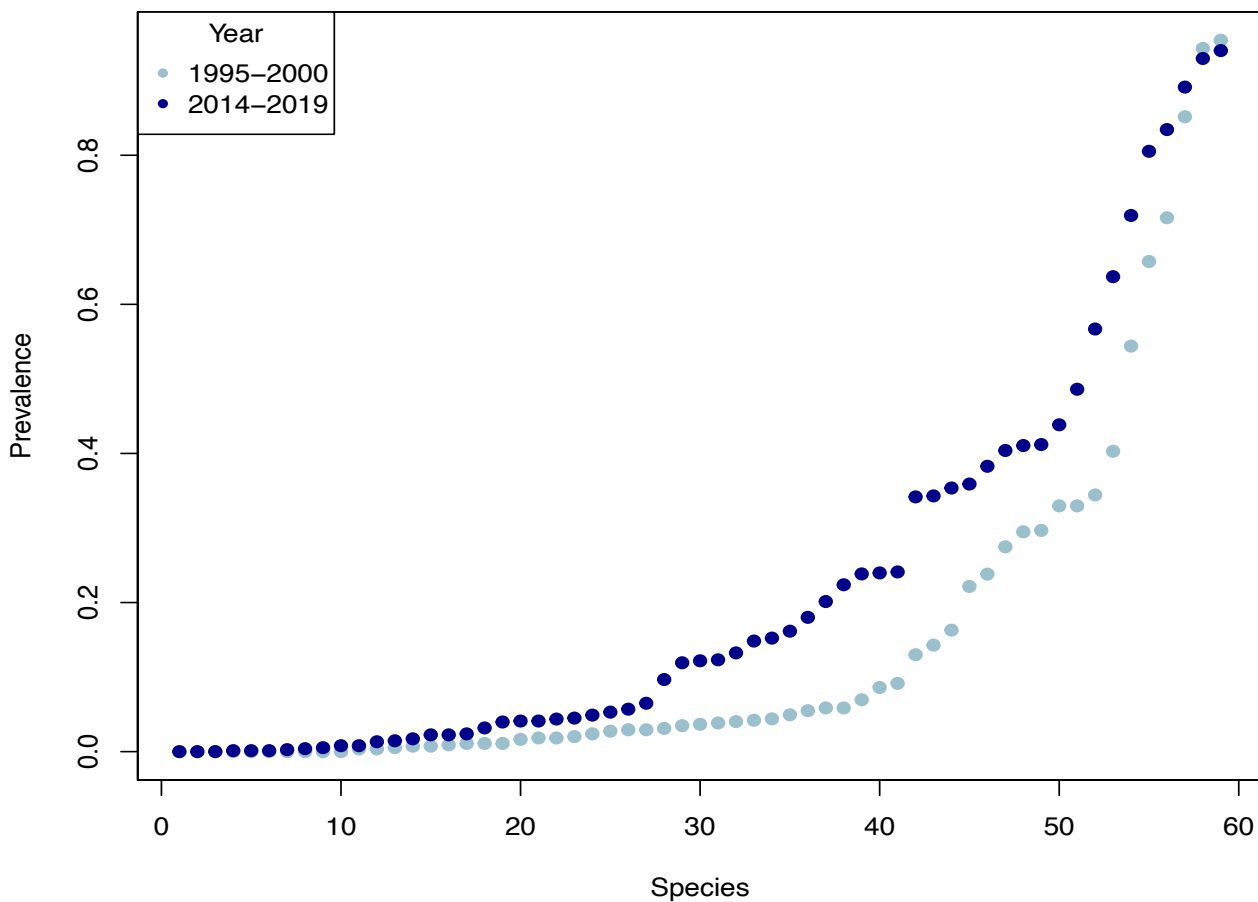


Figure 6: Prevalence of fish species in the studied region during the early period (1995-2000, light blue circles) and late period (2014-2019, dark blue circles). Each point represents the prevalence of a species, calculated as the proportion of trawl samples in which the species was present. Most species show an increase in prevalence from the early, cold period, to the later, warmer period.

### 3.2 Species co-occurrences

Co-occurrence frequencies increased in the warmer period for most species' pairs (Fig 7). The change in co-occurrence frequencies ranged between a minimum of -0.06 to a maximum of 0.40, with an average change of 0.04 and a median of  $< 0.0001$ . The right tale of the frequency distribution depicting sharp increases in co-occurrence frequency shows that for many species pairs the frequency of co-occurrence increased by more than 5%.

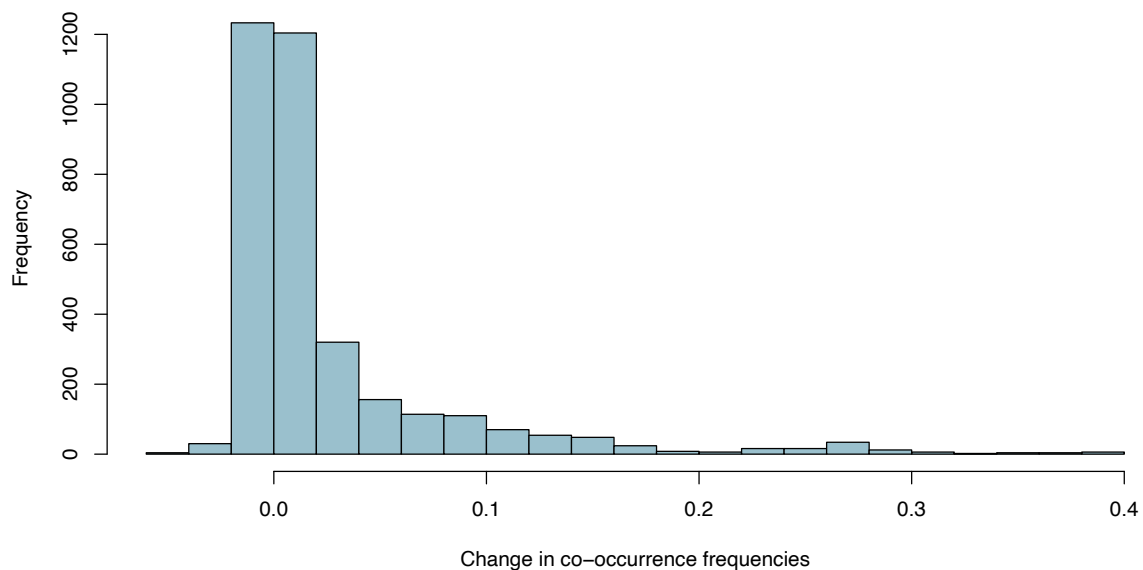


Figure 7: Histogram showing the overall changes in co-occurrence frequencies from the 1995-2000 period to the 2014-2019 period. Positive values indicate a temporal increase in co-occurrence frequencies.

The magnitude of increase in co-occurrence frequencies within areas 1, 2, and 3 was even greater given that the estimates are less diluted over a larger area (Fig 8). Area 1 displayed a substantial range in variation in co-occurrence frequencies, with the minimum change observed at -0.11, a considerable maximum change of 0.49, mean change of 0.03 and median change of  $< 0.0001$ . Area 2 showed a minimum change in co-occurrence frequencies of -0.07, a maximum change of 0.42, a mean change of 0.03 and median change of 0. In Area 3, the minimum change

in co-occurrence frequencies was -0.07, the maximum change 0.48, the mean change 0.03 and the median change 0.

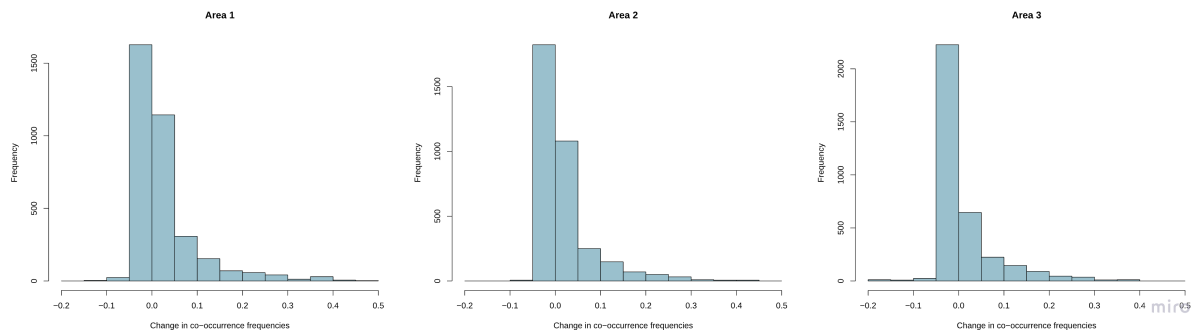


Figure 8: Histogram showing the change in co-occurrence frequencies between the early and late period for each study area. Positive values indicate a temporal increase in co-occurrence frequencies.

### 3.3 Food web reconfiguration

The 5 % prevalence threshold for each area and time used to determine which of the 34 fish species were present in the study area resulted in the introduction of, in total, 13 fish species in the later period for all three areas combined, whose roles and positions in the food web are summarized in Table 2. The biogeographic affiliation of the incoming species is South-Boreal, Mainly Boreal, Boreal, and Widely Distributed, as specified in Siwertsson et al. (2024). The mean trophic level for the incoming species is 3.65, their omnivory index ranges from 0 to 0.77, with a mean of 0.28, and ten out of 13 species have less than 10 in-degrees (number of prey) and overall low out-degrees (number of predators). *Merlangius merlangus* and *Scomber scombrus* display high trophic level and values in the omnivory index, with the highest in-degrees of 25 and 17 respectively, and eight out-degrees, and with their many links have a large potential to affect food web topology. On the other hand, species such as *Enchelyopus cimbrius*, *Lycodes gracilis*, and *Leptoclinus maculatus* all exhibit minor in- and out-degrees, with low omnivore indices, indicating relatively minor impact on the ecological networks.

Table 2: Ecological summary of role and position in the food web for incoming fish species in the study region. Biogeographical groups are marked as: South Boreal (SB), Mainly Boreal (MB), Boreal (B) and Widely Distributed (WD).

<i>Latin name</i>	<b>Common name</b>	<b>Trophic level</b>	<b>Omnivory index</b>	<b>In-degree</b>	<b>Out-Degree</b>
<i>Enchelyopus cimbrius</i> (B)	Fourbeard rockling	3.6	0.39	2	1
<i>Etmopterus spinax</i> (WD)	Velvet belly lanternshark	4.1	0.51	6	0
<i>Gadiculus argenteus</i> (SB)	Silvery pout	3.9	0.37	10	4
<i>Hippoglossus hippoglossus</i> (MB)	Halibut	3.9	0.77	17	1
<i>Leptoclinus maculatus</i> (MB)	Daubed shanny	3.0	<<0	2	2
<i>Lumpenus lampretaeformis</i> (MB)	Snakeblenny	3.3	0.32	9	6
<i>Lycodes gracilis</i> (MB)	Vahl's eelpout	3.0	<<0	3	2
<i>Maurolicus muelleri</i> (MB)	Silvery lightfish	3.2	0.05	4	7
<i>Merlangius merlangus</i> (SB)	Whiting	4.1	0.39	25	8
<i>Molva molva</i> (B)	Common ling	4.3	0.36	10	1
<i>Rajella fyllae</i> (MB)	Round ray	4.1	0.04	7	1
<i>Scomber scombrus</i> (B)	Mackerel	4.0	0.37	17	8
<i>Triglops murrayi</i> (B)	Moustache sculpin	4.0	0.12	7	4

Food web structure changed over time within areas due to the incoming fish species and links, but also differed between areas in the early, cooler period due to compositional differences (Table 3, see Table A3 in Appendix for all 16 metrics). From the early to the late study period there was an increase in the number of links for all areas by 10.33 %, 8.35 %, and 16.13 %, respectively. The connectance decreased in all three areas, with the greatest effect in area 3 with -15.38 %, and the same goes for the clustering coefficient. Modularity decreased with 5.26 % in area 1, increased with 5.88 % in area 2 and exhibited no change in area 3. The proportion of intermediate species rose in the whole region, markedly with 8.47 % in area 3. Mean path length also increased for all three areas, with almost double the effect in area 3 (10.68 %) compared to area 1 (5.50 %).

*Table 3: Food web metrics for the three study areas during the two periods 1995-2000 (indicated as 1995) and 2014-2019 (indicated as 2019).*

	<b>1995</b>	<b>2019</b>	<b>1995</b>	<b>2019</b>	<b>1995</b>	<b>2019</b>
	<b>AREA 1</b>	<b>AREA 1</b>	<b>AREA 2</b>	<b>AREA 2</b>	<b>AREA 3</b>	<b>AREA 3</b>
<b>SPECIES</b>	61	66	61	67	56	64
<b>LINKS</b>	426	470	455	493	403	468
<b>CONNECTANCE</b>	0.11	0.10	0.12	0.11	0.13	0.11
<b>CLUSTERING</b>	0.42	0.40	0.44	0.42	0.45	0.42
<b>MODULARITY</b>	0.19	0.18	0.17	0.18	0.18	0.18
<b>INTERMEDIATE SPECIES</b>	0.61	0.63	0.62	0.64	0.59	0.64
<b>MEAN PATH LENGTH</b>	2.18	2.30	2.20	2.29	2.06	2.28

### 3.4 Changes in interaction strength in food webs

There was substantial change in spatial overlap among several interacting species, depicted by link width representing changes in co-occurrence frequencies in the food web diagrams (Fig 9, 10, and 11).

The increase in co-occurrences over time for area 1 was greatest between *Sebastes* and *Scomber scombrus*, and *Sebastes* also exhibited a smaller but still evident increase in co-occurrence with *Hippoglossus hippoglossus* (Fig 9). *Gadus morhua* showed an increase between *Lycodes gracilis* and *Leptoclinus maculatus*, but a reduction in co-occurrences with *Pollachius pollachius*, which in turn showed an increase in co-occurrences with *Anarchichas lupus*.

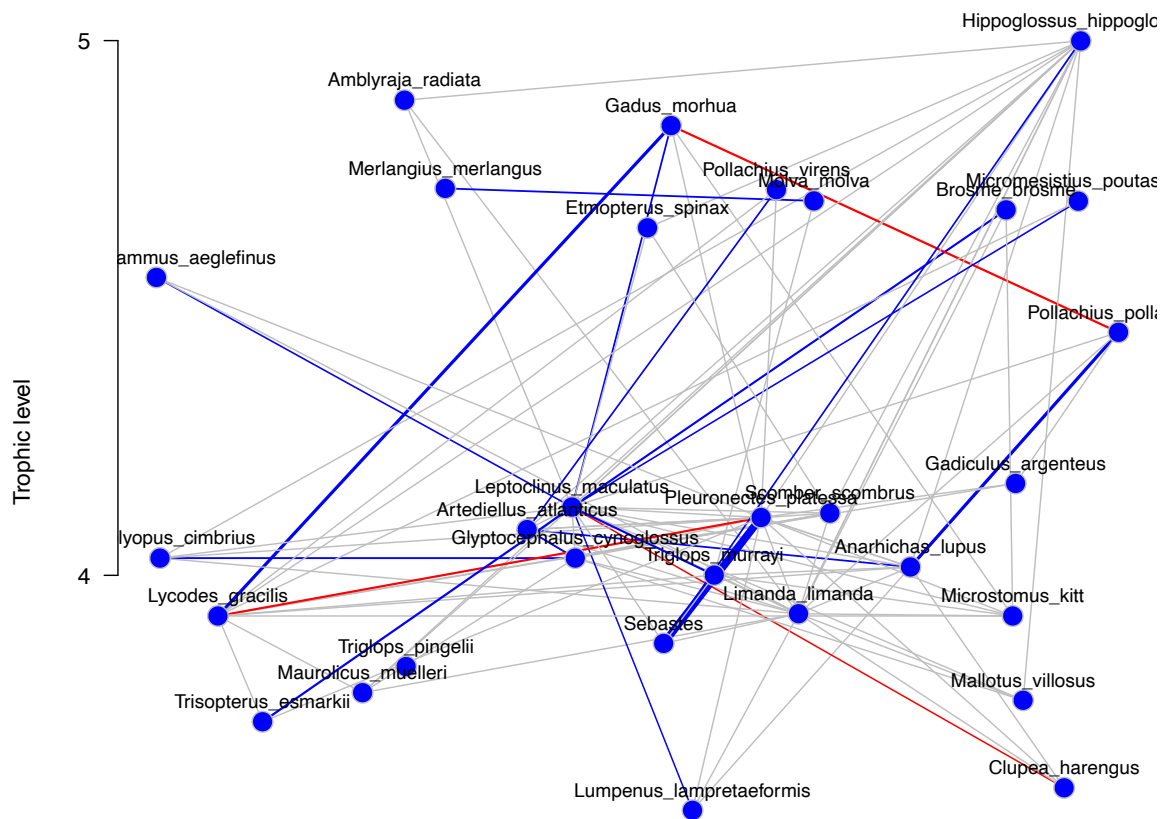


Figure 9: Fish food web in area 1, with link width and color illustrating change in co-occurrence frequencies between the two study periods (blue, positive values; red, negative values, grey no change). The incoming species in this area are *Enchelyopus cimbricus*, *Hippoglossus hippoglossus*, *Maurolucus muelleri*, *Rajella fyllae* and *Scomber scombrus*.

In area 2, the increase in co-occurrence, and inferred contact frequencies, between fish predators and prey was pronounced (Fig 10), and larger than in area 1, such as the positive co-occurrences between *Gadus morhua* and *Pollachius pollachius*. *Melanogrammus aeglefinus* and *Clupea harengus* also showed a substantial increase in co-occurrences, with the latter also exhibiting an increase from negative to positive frequencies with *Leptoclinus maculatus*.

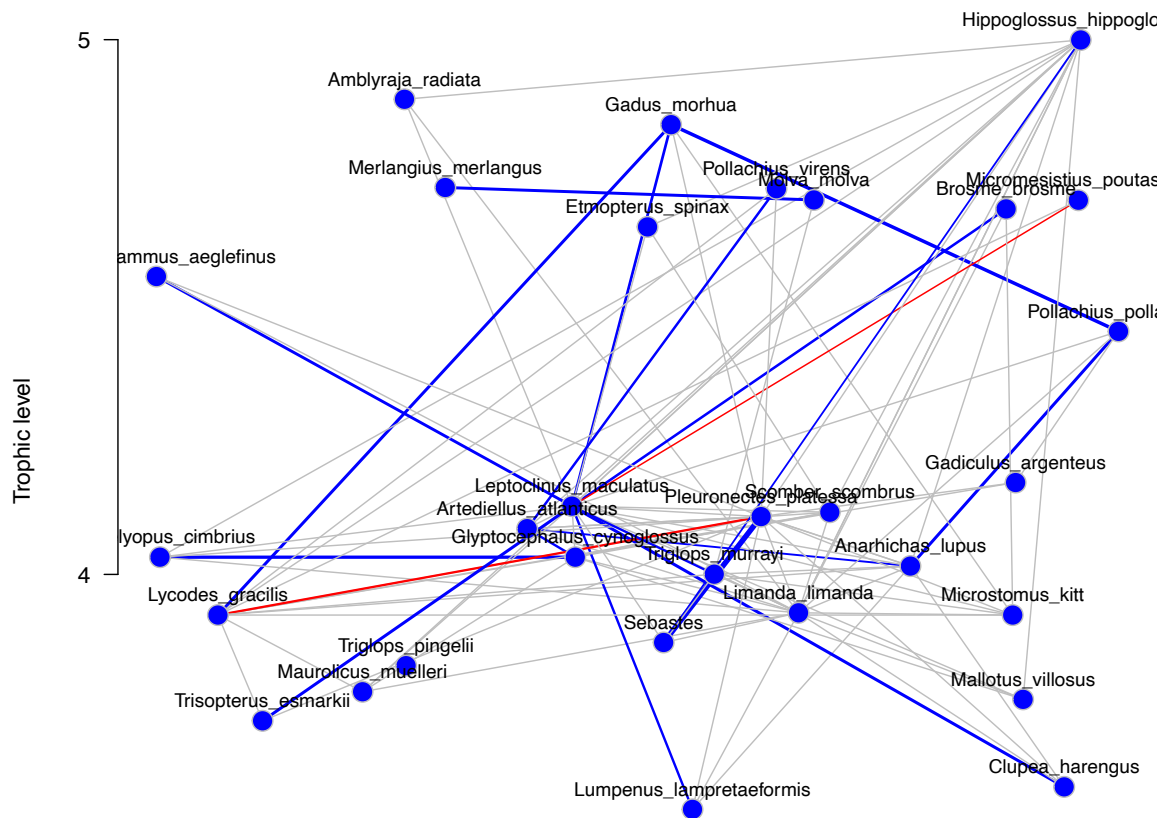


Figure 10: Fish food web in area 2, with link width and color illustrating change in co-occurrence frequencies between the two study periods (blue, positive values; red, negative values, grey no change). The incoming species in this area is *Etmopterus spinax*, *Leptoclinus maculatus*, *Lumpenus lampretaeformis*, *Lycodes gracilis*, *Molva molva* and *Rajella fyllae*.

*Merlangius merlangus* and *Molva molva* exhibited a substantial increase in co-occurrence in area 3 (Fig 11), along with a marked increase between *Hippoglossus hippoglossus* and *Sebastes*. *Melanogrammus aeglefinus* and *Clupea harengus* also continue to show this increase in inferred contact frequencies, together with *Gadus morhua* with *Pollachius pollachius* and *Lycodes gracilis*. Notably, in area 2 and 3 – the strong positive co-occurrences between *Sebastes* and *Scomber scombrus* are slightly decreasing.

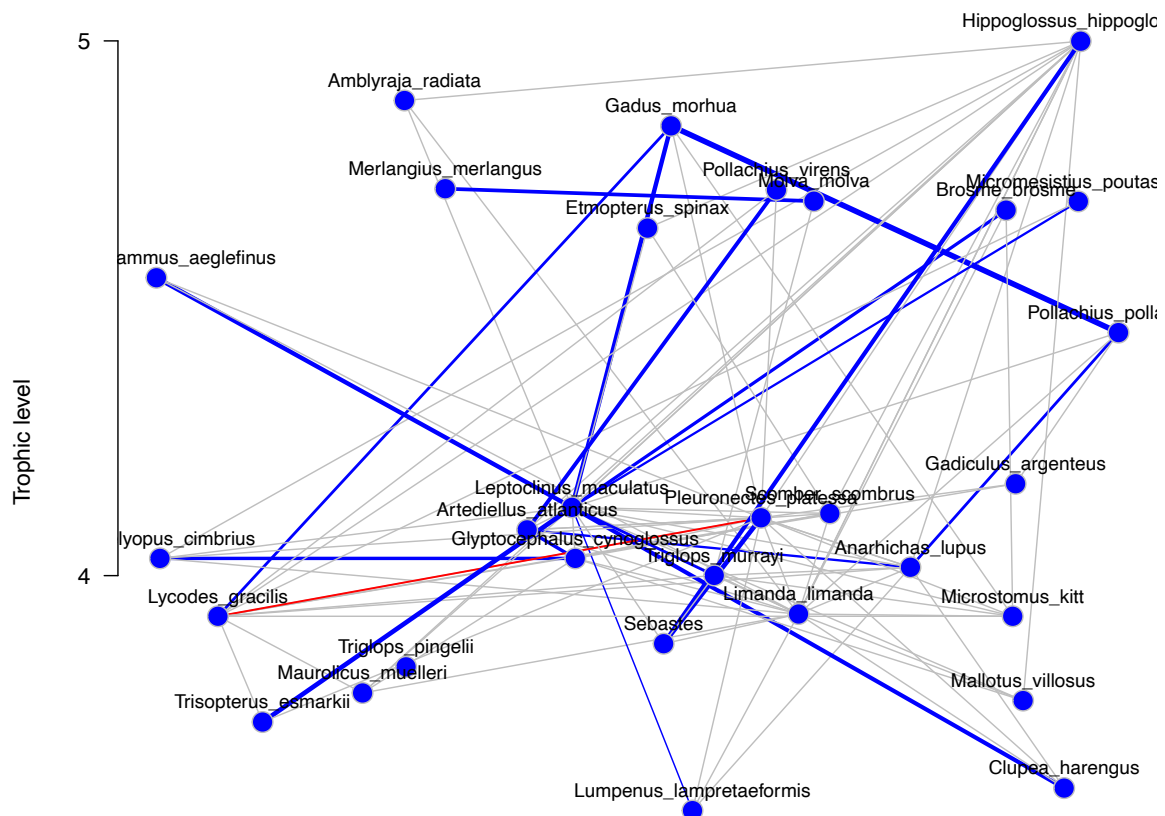


Figure 11: Fish food web in area 3, with link width and color illustrating change in co-occurrence frequencies between the two study periods (blue, positive values; red, negative values, grey no change). The incoming species in this area are *Enchelyopus cimbricus*, *Gadaculus argenteus*, *Hippoglossus hippoglossus*, *Leptoclinus maculatus*, *Maurolicus muelleri*, *Merlangius merlangus*, *Rajella fyllae* and *Tripglops murrayi*.



## 4 Discussion

In this study, I document a climate-driven increase in fish species richness, prevalence, and co-occurrence frequencies along the North Norwegian coast. These changes in fish biodiversity are strongly influenced by climate induced poleward shifts of boreal species. The fish redistributions bring new nodes (i.e., species) and links (i.e., interactions) to the coastal ecosystems, leading to a food web reconfiguration in the three study areas. The observed changes in food web metrics over time include an increase in the number of links, due to the addition of new feeding links by incoming species. An observed decrease in connectance can be attributed to most of the 13 incoming species being more specialists than generalists, reflected in their low number of prey and predators and their low omnivory index. Similarly, the decrease in clustering suggests that the incoming species also disrupt already existing species clusters. Furthermore, an increase in intermediate species and an increase in the mean path length indicates that the incoming species occupy intermediate trophic levels relatively, effectively lengthening the food chains. The effects are especially strong in area 3 for all metrics except modularity. Modularity shows a decrease in area 1, an increase in area 2, and no change in area 3. The weak trend in modularity is likely because the main module connector *Gadus morhua* was already present in all three areas in the early study period. Sharp changes in fish species co-occurrences modify the interaction strength in fish food webs and indicate potential changes in local species' roles and positions. The observed climate-driven reconfiguration of coastal fish biodiversity and food web organization invites considerations on ecosystem changes and climate adaptation of management practice.

### 4.1 Fish species richness and prevalence

From 1995 to 2019, the median fish species count in trawl samples has risen markedly along the North Norwegian coast, with a 33.33 % increase in area 1, a 44.44 % increase in area 2, and a 62.50 % increase in area 3. These trends are consistent with climate-driven redistributions, and a poleward shift of boreal species. A recent study of coastal fish in my study area documents the poleward migration of marine species in response to the increase in sea surface temperatures (Siwertsson et al., 2024). As such, the study adds to the growing literature on biogeographical shifts in northern marine ecosystems (Pinsky et al., 2020), with boreal species driven northward toward suitable habitats (Fossheim et al., 2015; Ingvaldsen et al., 2021). The documented increase in coastal fish biodiversity occurs at a higher rate than observed in the adjacent Barents Sea and other shelf seas bordering the Arctic Ocean (Fossheim et al., 2015; Ingvaldsen et al.,

2021; Mueter et al., 2021). In addition to climate-driven poleward redistributions, the increasing coastal fish biodiversity in Northern Norway may be affected by ecological interactions (Cody & Diamond, 1975). Also, shifts in fishing pressure and management practices over the years might have an impact on species distributions and diversity.

Species prevalence also increased across all three study areas in the later, warmer period. Our results showed a significant rise in prevalence in the later period for boreal species like *Trisopterus esmarkii*, *Sebastes*, *Enchelyopus cimbrius*, *Merlangius merlangus*, and *Etmopterus spinax*. *Mallotus villosus* and *Lycodes gracilis* also showed increased prevalence with the latter having further implications for food web structure, the two species being classified as Arcto-boreal and northern-boreal species (Siwertsson et al., 2024). The minor decrease in prevalence of the two ecologically important species *Gadus morhua* and *Melanogrammus aeglefinus* might be influenced by their prevalence being historically high in the region (Link et al., 2009). The increase in Arcto-Boreal and northern boreal species could be influenced by westward expansions of cold-water species living along the Russian coast.

The observed fish species redistributions can be attributed to increasing temperatures, but also to the higher primary production supporting more productive areas in the north, resulting in increased population sizes and density-dependent dispersal (Quinn, 1991). Although prevalence is not a direct measure of species abundance, it is often related to an increase in population size as individuals of a species are more likely to be caught if the species is more abundant, and are expected to spread out more widely due to density-dependence. Siwertsson et al. (2024) document an increase in both fish species richness and mean abundance of mostly southern boreal species along the north Norwegian coast. The coastal ecosystem is thus becoming more species-rich while species abundances are also increasing, leading to higher prevalence. The comprehensive and substantial rise in prevalence among coastal fish species in the study, combined with a general increase in species richness strongly suggest an increase in coastal fish alpha biodiversity in the north. Poleward shifts and increased prevalence also drive the recently documented homogenization of coastal fish communities, eroding biogeographic patterns along the coast of Norway (Siwertsson et al., 2024).

## 4.2 Species co-occurrences

The interplay between increased species richness and prevalence has led to an observed increase in co-occurrence frequencies across all three study areas (Fig 7). The magnitude of increase in co-occurrence frequencies due to redistributions was generally large, with a mean change of 0.04 and a maximum change of 0.40, and for many species-pairs was larger than 5%, indicating a substantial increase with implications for contact rates between species in the study area. Similar increases in co-occurrences among fish species have been observed in the Pacific and Atlantic Arctic inflow shelves over the last two decades due to increasing ocean temperatures and loss of sea ice (Alabia et al., 2023).

Species must co-occur on a local scale to interact ecologically. Therefore, the documented increase in co-occurrence frequencies can potentially increase the likelihood of predation and competition among species, depending on the food web position and role of the co-occurring species. This can lead to the exclusion of less competitive species or prey species and alter community composition over time (Cody & Diamond, 1975). Fossheim et al. (2015) suggest that Arctic fish species may be already suffering from increased competition and predation by boreal species, effectively retracting northward and eastward in the Barents Sea. A closer examination of the possible impact of *Gadus morhua* moving into Arctic communities supports the above claim (Johannesen et al., 2020; Pecuchet et al., 2020). This indicates an ecosystem responding directly and indirectly to climate-driven environmental changes. The analyses of co-occurrence frequencies and related ecological interactions can provide an early indication of broader ecological change indirectly mediated by predation and competition.

## 4.3 Food web reconfiguration

The 13 incoming fish species are reconfiguring food web structure along the North Norwegian coast. Specifically, the newly introduced feeding links increased the total number of food web links by 10.33% in area 1, 8.35% in area 2, and by a more substantial 16.13% in area 3. The results also demonstrate an overall decrease in connectance, with area 3 showing the most significant decline of -15.38%, reflecting a greater gap between potential and realized links. This suggests that while the food web structure is more complex, the individual species interactions are not as dense as before. This is corroborated by a generally low omnivory-index among the incoming species, with a mean of 0.28 indicating that most of them have fed from few trophic levels. Furthermore, the clustering coefficient also decreased in all areas by around 5 %, indicating a decline in the density of interconnected species clusters. This could be due to

the incoming species disrupting existing clusters. Meanwhile, the mean path length exhibited an increase of 5.50 % in area 1, 4.09 % in area 2, and 10.68 % in area 3, suggesting that food chains have become longer because incoming fish occupy intermediate to high trophic levels, as corroborated by the slight increase in the proportion of intermediate species. Also, more productive ecosystems can foster longer food chains and path lengths (Takimoto & Post, 2013), and increased primary production has been documented in the Norwegian sea ecoregion (ICES, 2021).

Interestingly, modularity displayed different changes over time between areas, with a decrease of 5.26 % in area 1, an increase of 5.88 % in area 2 and no effective change in area 3. Food web modularity is strongly reduced by module-connecting boreal species like *Gadus morhua*, *Melanogrammus aeglefinus*, and *Sebastes*, as observed by Kortsch et al. (2015) for Barents Sea food webs. These species were already present in all three study areas in the early period, effectively limiting modularity in these coastal food webs. These boreal species are habitat generalists facilitating the transfer of energy and matter across habitat boundaries, and may significantly alter food web dynamics and ecosystem functioning as suggested for the Barents Sea (Kortsch et al. 2015; Pecuchet et al. (2020). Other food web impact due to climate-induced fish redistributions has been documented in the Barents Sea, adjacent to my study area (Ingvaldsen et al., 2021; Kortsch et al., 2015; Pecuchet et al., 2020). An increase in modularity is usually coupled with an increase in the proportion of intermediate species and connectance because the intermediate species introduces many new links that usually connect more modules of the food web. This is not the case in this study as we saw no clear trend in modularity and a decline in connectance in all three areas. A possible explanation can lie with the incoming species' in- and out-degrees, where 10 out of 13 have 10 or fewer prey, and all have less than 8 predators. This is also reflected in the minimal changes in link density across all areas (+1.86 %, -1.21 %, +1.53 %), implying that the incoming species are not proportionally introducing many new interactions per species. The minimal changes in link density and the decrease in connectance imply a dilution of direct trophic interactions per species, explained by the added nodes from incoming species without a proportional increase in links. More species interact, but they do so less frequently, reflecting a possible shift towards a more complex but less densely connected food web.

The prevailing trend shows that boreal species are migrating poleward, introducing more generalist species into the Arctic food web, which has fewer links and consists of more specialized species, resulting in a food web that is more interconnected and more modular (Kortsch et al., 2015; Pecuchet et al., 2020). However, it should be noted that most of these incoming fish species along the coast do not fit the generalist category as they have limited predators and prey. *Merlangius merlangus*, a demersal key species in benthic food webs, and *Scomber scombrus*, an important pelagic prey for larger predators, both exhibit high trophic levels and omnivory indices, with the highest in-degrees recorded at 25 and 17, respectively, and both having an out-degree of 8. While these incoming species are positioned to significantly impact both the benthic and pelagic layers of the coastal ecosystem as predators and prey, their influence on food web metrics does not match that of the key species *Gadus morhua*, with an in-degree of 29 and an out-degree of 27. Consequently, their introduction has a less pronounced effect on the structure of the food web than if *Gadus morhua* were absent.

In contrast, *Leptoclinus maculatus* and *Lycodes gracilis*, exhibiting a lower trophic level of 3.0 with omnivory indices close to zero, suggest more specialized trophic roles. These species are often found in the cold, northern and eastern parts of the Barents Sea, suggesting their migration into the region from the east. This geographic origin could explain their low in- and out-degrees in the coastal fish food webs, indicating specialized ecological roles. Accompanying them are *Etmopterus spinax* and *Rajella fyllae*, species that also display a low degree of omnivory and few trophic interactions.

#### **4.4 Changes in interaction strength in food webs**

The co-occurrence frequencies used to visualize the strength in feeding links in the fish food webs show that not only is the increase in the complexity of ecological interactions happening, as reflected in the food web topological metrics, but there is also spatial variability in how the interactions manifest. The modification of contact and interaction probabilities inferred by the link widths, especially in *Gadus morhua*, underscores the ecological response to environmental shifts. In area 1, the negative change in co-occurrence of cod with *Pollachius pollachius* may suggest displacement by competitive interaction, given the overlapping ecological niches of the two fish species. It is a sharp contrast to the positive interactions in areas 2 and 3. This discrepancy can be attributed to a difference in ecological pressure or resource availability in area 1, possibly due to unique environmental conditions or fishing pressure. Conversely, the positive changes for *Gadus morhua* in co-occurrence with species like *Leptoclinus maculatus* and *Lycodes gracilis* in areas 2 and 3 imply a possible increase in overlapping habitats. *Sebastes*

and *Scomber scombrus* also display a substantial increase in co-occurrences over time, with the greatest change in area 1 and little less effect in area 2 and 3, furthermore reflecting the intricate interplay displayed in changing food web interactions.

#### **4.5 Limitations in biological data and data analysis**

The species considered to be incoming in the study areas relative to the early period are not necessarily novel species being introduced to the regions. The 5 % threshold in prevalence based on coastal survey data and used as criterion for presence of a species in a given area is partly responsible for the bias. *Hippoglossus hippoglossus* was reported as not present in both area 1 and 3 in the early period although it is a well-known fish caught along the coast of northern Norway. A possible reason for the low *Hippoglossus hippoglossus* catches is that the species tends to stay in “deep pits on the fishing banks along the coast and fjord areas”, as IMR (2020) reports. If the threshold had been lowered to 1 %, it would have been present in all areas in all periods. Another important consideration affecting estimation of spatial distribution is the seasonal variation in fish stocks, since many are mobile species, for example the migratory *Scomber scombrus*. It typically moves towards deeper waters or southward in October along the Norwegian coast towards the North Sea (dos Santos Schmidt et al., 2023). Since they most possibly are in transition from summer feeding grounds the results can either be under- or overestimated. To further corroborate these findings, there is a need to supplement the survey data with, for example, catch data from fisheries throughout the year.

#### **4.6 Ecosystem changes and implications**

The observed expansion in the number of links across all three study areas suggests an increase in species interactions in the food webs, but connectance—the proportion of potential interactions that are realized—has decreased in all areas. This paradoxically implies that despite more feeding interactions in total, the density of interactions per species is diluted, possibly due to the specialist nature of many incoming species as indicated by their low omnivory index. Intermediate levels of omnivory may stabilize simple food webs (McCann & Hastings, 1997) and together with the decrease in the proportion of top predators across all areas, may diffuse top-down influences through the food webs, thereby reducing the probability of trophic cascades (Baum & Worm, 2009). Yet, this aligns with a reduction in the clustering coefficient suggesting a decline in tightly-knit clusters of interacting species. The slight increase in the proportion of intermediate species accompanied by the observed decrease in connectance and

reduction in clustering suggests that incoming species are not fully integrated into the existing food web structure. This reflects a more complex but less interconnected ecosystem, which could decrease food web robustness (Dunne et al., 2002).

The poleward redistribution of boreal species like the *Merlangius merlangus* and *Scomber scombrus*, which exhibit high trophic levels and omnivory indexes, introduces substantial new interactions into the food web. These species can bridge trophic levels and facilitate energy flow between benthic and pelagic compartments, which may enhance ecosystem productivity and alter the dynamics of existing food chains. Despite the stable prevalence of *Gadus morhua* and *Melanogrammus aeglefinus*, other species like *Enchelyopus cimbrius* and *Lycodes gracilis*, which exhibit low in- and out-degrees, have shown notable increases in co-occurrence frequencies. Specifically, *Gadus morhua* demonstrated increased co-occurrences with both species across all three studied areas, and *Melanogrammus aeglefinus* showed similar patterns with *Lycodes gracilis*. This trend suggests a potential dilution effect, where *Enchelyopus cimbrius* and *Lycodes gracilis* are eroding the effect *Gadus morhua* and *Melanogrammus aeglefinus* have as super-generalist, by integrating them more broadly into the coastal fish food webs. Supporting this interpretation is the decline in the proportion of top predators, coupled with a slight increase in the proportions of intermediate species.

A broader delineation of both the species richness at a local scale but also regional and global (beta and gamma diversity) coupled with abundance data and using climate velocities to predict future changes would give a clearer picture of the biogeographical trends and potential risks of antropogenic impacts (Pinsky et al., 2013).

In summary, the influence of a poleward shift in boreal species due to Atlantic water influx can be seen as a double-edged sword. On the one hand, it has contributed to an increase in species richness and prevalence over time indicating a more heterogenous ecosystem that supports more alpha biodiversity. It is also however driving a greater number of co-occurrences between species, and increased co-occurrences mean an increase in potential ecological interactions between species that can threaten the stability of already existing communities in the Arctic adapted there. This can pilot reduced robustness against environmental perturbation, making it easier for proliferation of matter, energy but also perturbations through the ecosystem (Dunne et al., 2004).

## 5 Conclusion

The climate-driven poleward shifts observed among boreal fish in Northern Norway from 1995-2019 has led to changes in coastal fish food webs. The findings reveal a notable increase in species richness and prevalence, suggesting communities with higher fish alpha biodiversity, alongside a substantial increase in co-occurrences, consistent with observations that warming oceans facilitate expansions of species poleward. This is accompanied by a reconfiguration in coastal fish food webs with increased species links, and a less connected and clustered food web – witnessing more complex but less densely connected food webs. The inconclusive trend in modularity indicates that key species like *Gadus morhua* play a significant moderating role, given their established presence in these regions. Overall, these changes could have far-reaching ecological consequences, particularly in terms of the stability of marine ecosystems. These findings lay the groundwork for further empirical studies and foster a deeper understanding of coastal marine biodiversity dynamics in response to climate change.



## References

- Alabía, I. D., García Molinos, J., Hirata, T., Mueter, F. J., & David, C. L. (2023). Pan-Arctic marine biodiversity and species co-occurrence patterns under recent climate. *Scientific reports*, *13*(1), 4076.
- Albert, O. T. (1994). Ecology of haddock (*Melanogrammus aeglefinus* L.) in the Norwegian Deep. *ICES Journal of Marine Science*, *51*(1), 31-44.
- Albert, O. T., Eliassen, J.-E., & Høines, Å. (1998). Flatfishes of Norwegian coasts and fjords. *Journal of Sea Research*, *40*(1-2), 153-171.
- Albretsen, J., Aure, J., Sætre, R., & Danielssen, D. S. (2012). Climatic variability in the Skagerrak and coastal waters of Norway. *ICES Journal of Marine Science*, *69*(5), 758-763.
- Arronte, J. C., González-Irusta, J. M., Somavilla, R., Fernández-Feijoo, J., Parra, S., & Serrano, A. (2022). Habitat use by *Gadiculus argenteus* (Pisces, Gadidae) in the Galician and Cantabrian Sea waters (NE Atlantic). *Marine ecology progress series*, *694*, 175-191. <https://www.int-res.com/abstracts/meps/v694/p175-191/>
- Asciutto, E., Maioli, F., Manfredi, C., Anibaldi, A., Cimini, J., Isailović, I., Marčeta, B., & Casini, M. (2024). Spatio-temporal patterns of whiting (*Merlangius merlangus*) in the Adriatic Sea under environmental forcing. *PloS one*, *19*(3), e0289999.
- Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological monographs*, *81*(2), 169-193.
- Baum, J. K., & Worm, B. (2009). Cascading top - down effects of changing oceanic predator abundances. *Journal of animal ecology*, *78*(4), 699-714.
- Berg, E., & Albert, O. T. (2003). Cod in fjords and coastal waters of North Norway: distribution and variation in length and maturity at age. *ICES Journal of Marine Science*, *60*(4), 787-797. [https://doi.org/10.1016/s1054-3139\(03\)00037-7](https://doi.org/10.1016/s1054-3139(03)00037-7)
- Bernardo, C. P., Pecuchet, L., Santos, J., Dolgov, A. V., Fossheim, M., Husson, B., & Primicerio, R. (2024). Warming changes the life history composition of marine fish communities at high latitudes. *Marine ecology progress series*, *732*, 119-133.
- Boyce, D. G., Frank, K. T., Worm, B., & Leggett, W. C. (2015). Spatial patterns and predictors of trophic control in marine ecosystems. *Ecology Letters*, *18*(10), 1001-1011.
- Cargnelli, L. M. (1999). Essential fish habitat source document. Pollock, *Pollachius virens*, life history and habitat characteristics.
- Cazelles, K., Araújo, M. B., Mouquet, N., & Gravel, D. (2016). A theory for species co-occurrence in interaction networks. *Theoretical Ecology*, *9*, 39-48.
- Chaudhary, C., Richardson, A. J., Schoeman, D. S., & Costello, M. J. (2021). Global warming is causing a more pronounced dip in marine species richness around the equator. *Proceedings of the National Academy of Sciences*, *118*(15), e2015094118. <https://doi.org/doi:10.1073/pnas.2015094118>
- Cheung, W. W., Lam, V. W., Sarmiento, J. L., Kearney, K., Watson, R., & Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, *10*(3), 235-251.
- Chevolot, M., Wolfs, P. H. J., Pálsson, J., Rijnsdorp, A. D., Stam, W. T., & Olsen, J. L. (2007). Population structure and historical demography of the thorny skate (*Amblyraja radiata*, Rajidae) in the North Atlantic. *Marine Biology*, *151*(4), 1275-1286. <https://doi.org/10.1007/s00227-006-0556-1>
- Cody, M. L., & Diamond, J. M. (1975). *Ecology and Evolution of Communities*. Belknap Press of Harvard University Press. [https://books.google.no/books?id=j\\_idbVxwzpqC](https://books.google.no/books?id=j_idbVxwzpqC)

- Collie, J. S., Wood, A. D., & Jeffries, H. P. (2008). Long-term shifts in the species composition of a coastal fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(7), 1352-1365.
- Colwell, R. K. (2009). Biodiversity: concepts, patterns, and measurement. *The Princeton guide to ecology*, 663, 257-263.
- Dolgov, V., & Drevetnyak, K. (2011). Feeding of three species from the genus *Sebastes* in the Barents Sea.
- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., & Knowlton, N. (2012). Climate change impacts on marine ecosystems. *Annual review of marine science*, 4, 11-37.
- dos Santos Schmidt, T. C., Slotte, A., Olafsdottir, A. H., Nøttestad, L., Jansen, T., Jacobsen, J. A., Bjarnason, S., Lusseau, S. M., Ono, K., Hølleland, S., Thorsen, A., Sandø, A. B., & Kjesbu, O. S. (2023). Poleward spawning of Atlantic mackerel (*Scomber scombrus*) is facilitated by ocean warming but triggered by energetic constraints. *ICES Journal of Marine Science*. <https://doi.org/10.1093/icesjms/fsad098>
- Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5(4), 558-567.
- Dunne, J. A., Williams, R. J., & Martinez, N. D. (2004). Network structure and robustness of marine food webs. *Marine ecology progress series*, 273, 291-302.
- Eldevik, T., Risebrobakken, B., Bjune, A. E., Andersson, C., Birks, H. J. B., Dokken, T. M., Drange, H., Glessmer, M. S., Li, C., & Nilsen, J. E. Ø. (2014). A brief history of climate—the northern seas from the Last Glacial Maximum to global warming. *Quaternary Science Reviews*, 106, 225-246.
- Fjørtoft, S. (2013). *Seas and coastlines - the need to safeguard species diversity*. the Norwegian Ministry of Climate and Environment. <https://www.regjeringen.no/en/topics/climate-and-environment/biodiversity/innsiktsartikler-naturmangfold/hav-og-kyst/id2076396/>
- Fordham, S. (2004). Conservation and management status of spiny dogfish sharks (*Squalus acanthias*). *AC20 Inf*, 22, 1-7.
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature climate change*, 5(7), 673-677.
- Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences*, 114(46), 12202-12207.
- Froese, R., & Pauly, D. (2024a). *Rajella fyllae* (Lütken, 1887)
- Round ray*. Retrieved 8th of May, from <https://www.fishbase.se/summary/7615>
- Froese, R., & Pauly, D. (2024b). *Triglops murrayi* Günther, 1888
- Moustache sculpin*. Retrieved 8th of May, from <https://www.fishbase.se/summary/Triglops-murrayi.html>
- Froese, R., & Pauly, D. (2024c). *Triglops pingelii* Reinhardt, 1837
- Ribbed sculpin*. Retrieved 8th of May, from <https://fishbase.mnhn.fr/summary/4148>
- Froese, R., & Pauly, D. (2024d). *Trisopterus esmarkii* (Nilsson, 1855)
- Norway pout*. Retrieved 8th of May, from <https://www.fishbase.se/summary/1023>

- Geffen, A. J., Albretsen, J., Huwer, B., & Nash, R. D. (2021). Lemon sole *Microstomus kitt* in the northern North Sea: a multidisciplinary approach to the early life - history dynamics. *Journal of Fish Biology*, 99(2), 569-580.
- Gerland, S., Ingvaldsen, R. B., Reigstad, M., Sundfjord, A., Bogstad, B., Chierici, M., Hop, H., Renaud, P. E., Smedsrud, L. H., & Stige, L. C. (2023). Still Arctic?—The changing Barents Sea. *Elementa: Science of the Anthropocene*, 11(1).
- Hátún, H., Sandø, A. B., Drange, H., Hansen, B., & Valdimarsson, H. (2005). Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science*, 309(5742), 1841-1844.
- He, Q., & Silliman, B. R. (2019). Climate change, human impacts, and coastal ecosystems in the Anthropocene. *Current Biology*, 29(19), R1021-R1035.
- Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, 328(5985), 1523-1528.
- Hop, H., & Gjøsæter, H. (2013). Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine Biology Research*, 9(9), 878-894.
- ICES. (2021). *Norwegian Sea ecoregion – Ecosystem overview*. ICES Advice: Ecosystem Overviews. [https://ices-library.figshare.com/articles/report/Norwegian\\_Sea\\_ecoregion\\_Ecosystem\\_overview/18638273](https://ices-library.figshare.com/articles/report/Norwegian_Sea_ecoregion_Ecosystem_overview/18638273)
- IMR. (2020). *Topic: Atlantic halibut*. Retrieved 15 April, from <https://www.hi.no/en/hi/temasider/species/halibut>
- IMR. (2022). *Topic: Blue whiting*. Retrieved 08th of May, from <https://www.hi.no/en/hi/temasider/species/blue-whiting>
- IMR. (2024). *Topic: Capelin in the Barents Sea*. Retrieved April 22, from <https://www.hi.no/en/hi/temasider/species/capelin-in-the-barents-sea>
- Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fosshem, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, 2(12), 874-889.
- IPCC. (2019). *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. Cambridge. C. U. Press.
- IPCC. (2022). *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. <https://www.ipcc.ch/report/sixth-assessment-report-working-group-ii/>
- IPCC. (2023). *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. <https://www.cambridge.org/core/product/415F29233B8BD19FB55F65E3DC67272B>
- Johannesen, E., Yoccoz, N. G., Tveraa, T., Shackell, N. L., Ellingsen, K. E., Dolgov, A. V., & Frank, K. T. (2020). Resource - driven colonization by cod in a high Arctic food web. *Ecology and Evolution*, 10(24), 14272.
- Kammann, U., Lang, T., Berkau, A.-J., & Klempt, M. (2008). Biological effect monitoring in dab (*Limanda limanda*) using gene transcript of CYP1A1 or EROD—a comparison. *Environmental Science and Pollution Research*, 15(7), 600-605. <https://doi.org/10.1007/s11356-008-0048-6>
- Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food - web structure varies along environmental gradients in a high - latitude marine ecosystem. *Ecography*, 42(2), 295-308.

- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), 20151546.
- Källgren, E. K., Pedersen, T., & Nilssen, E. M. (2015). Food resource partitioning between three sympatric fish species in Porsangerfjord, Norway. *Polar Biology*, 38, 583-589.
- Langbehn, T. J., & Varpe, Ø. (2017). Sea - ice loss boosts visual search: Fish foraging and changing pelagic interactions in polar oceans. *Global Change Biology*, 23(12), 5318-5330.
- Link, J. S., Bogstad, B., Sparholt, H., & Lilly, G. R. (2009). Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries*, 10(1), 58-87.
- Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., & Gomis, M. (2021). Climate change 2021: the physical science basis. *Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*, 2(1), 2391.
- McCann, K., & Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264(1385), 1249-1254.
- McGill, L., McDevitt, A., Hellemans, B., Neat, F., Knutsen, H., Mariani, S., Christiansen, H., Johansen, T., Volckaert, F., & Coscia, I. (2023). Population structure and connectivity in the genus *Molva* in the Northeast Atlantic. *ICES Journal of Marine Science*, 80(4), 1079-1086.
- McLean, M., Mouillot, D., Lindegren, M., Engelhard, G., Villéger, S., Marchal, P., Brind'Amour, A., & Auber, A. (2018). A climate-driven functional inversion of connected marine ecosystems. *Current Biology*, 28(22), 3654-3660. e3653.
- Mollet, F. M., Dieckmann, U., & Rijnsdorp, A. D. (2016). Reconstructing the effects of fishing on life-history evolution in North Sea plaice *Pleuronectes platessa*. *Marine ecology progress series*, 542, 195-208.
- Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in ecology & evolution*, 30(6), 347-356.
- Mueter, F. J., Iken, K., Cooper, L. W., Grebmeier, J. M., Kuletz, K. J., Hopcroft, R. R., Danielson, S. L., Collins, R. E., & Cushing, D. A. (2021). Changes in diversity and species composition across multiple assemblages in the eastern Chukchi Sea during two contrasting years are consistent with borealization. *Oceanography*, 34(2), 38-51.
- Murzina, S. A., Nefedova, Z. A., Falk-Petersen, S., Hop, H., Rykolainen, T. R., Meyer Ottesen, C. A., Ripatti, P. O., Berge, J., & Nemova, N. N. (2013). Lipids in the daubed shanny (Teleostei: *Leptoclinus maculatus*) in Svalbard waters. *Polar Biology*, 36(11), 1619-1631. <https://doi.org/10.1007/s00300-013-1381-x>
- Murzina, S. A., Sokolov, S. G., Pekkoeva, S. N., Ieshko, E. P., Nemova, N. N., Kristoffersen, R., & Falk-Petersen, S. (2019). First data on the parasite fauna of daubed shanny *Leptoclinus maculatus* (Fries 1838) (Actinopterygii, Perciformes: Stichaeidae) in Svalbard waters. *Polar Biology*, 42(4), 831-834. <https://doi.org/10.1007/s00300-018-02448-2>
- NASA. (2024). *World of Change: Global Temperatures*. Retrieved 30th of April, from <https://earthobservatory.nasa.gov/world-of-change/global-temperatures>
- Nash, R. D. (1986). Aspects of the general biology of Vahl's eelpout, *Lycodes vahlii gracilis* M. Sars, 1867 (Pisces, Zoarcidae), in Oslofjorden, Norway. *Sarsia*, 71(3-4), 289-296.
- NOAA. (2023). *Daily Sea Surface Temperature*. Climate Change Institute, University of Maine. Retrieved 09th of May, from

- Oosterwind, D., Köhler, L., Paar, M., Henseler, C., Kriegl, M., Gogina, M., Schubert, H., & Arbizu, P. M. (2023). Trophic ecology and seasonal occurrence of two Red List fish species in the Western Baltic Sea—two of a kind? *Marine Biodiversity*, 53(5), 60. <https://doi.org/10.1007/s12526-023-01368-7>
- Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A., & Gjørseter, H. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. *ICES Journal of Marine Science*, 67(1), 87-101.
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., & Evengård, B. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214.
- Pecuchet, L., Blanchet, M. A., Frainer, A., Husson, B., Jørgensen, L. L., Kortsch, S., & Primicerio, R. (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Global Change Biology*, 26(9), 4894-4906.
- Pedersen, T., Nilsen, M., Nilssen, E. M., Berg, E., & Reigstad, M. (2008). Trophic model of a lightly exploited cod-dominated ecosystem. *Ecological Modelling*, 214(2), 95-111. <https://doi.org/https://doi.org/10.1016/j.ecolmodel.2007.12.012>
- Perdikaris, S. (2012). From chiefly provisioning to commercial fishery: long-term economic change in Arctic Norway. In *Arctic Archaeology* (pp. 388-402). Routledge.
- Pinsky, M. L., Selden, R. L., & Kitchel, Z. J. (2020). Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. *Annual review of marine science*, 12(Volume 12, 2020), 153-179. <https://doi.org/https://doi.org/10.1146/annurev-marine-010419-010916>
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine Taxa Track Local Climate Velocities. *Science*, 341(6151), 1239-1242. <https://doi.org/doi:10.1126/science.1239352>
- Planque, B., Primicerio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjørseter, H., Hansen, C., Johannesen, E., & Jørgensen, L. L. (2014). Who eats whom in the Barents Sea: a food web topology from plankton to whales: Ecological Archives E095 - 124. *Ecology*, 95(5), 1430-1430.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature climate change*, 3(10), 919-925. <https://doi.org/10.1038/nclimate1958>
- Polyakov, I. V., Alkire, M. B., Bluhm, B. A., Brown, K. A., Carmack, E. C., Chierici, M., Danielson, S. L., Ellingsen, I., Ershova, E. A., & Gårdfeldt, K. (2020). Borealization of the Arctic Ocean in response to anomalous advection from sub-Arctic seas. *Frontiers in Marine Science*, 7, 491.
- Quinn, T. J. (1991). [Dynamic Geography of Marine Fish Populations, Alec D. McCall]. *Copeia*, 1991(3), 861-863. <https://doi.org/10.2307/1446418>
- Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, 3(1), 168. <https://doi.org/10.1038/s43247-022-00498-3>
- Sanz-Martín, M., Hidalgo, M., Puerta, P., Molinos, J. G., Zamanillo, M., Brito-Morales, I., González-Irusta, J. M., Esteban, A., Punzón, A., & García-Rodríguez, E. (2024). Climate velocity drives unexpected southward patterns of species shifts in the Western Mediterranean Sea. *Ecological Indicators*, 160, 111741.

- Siwertsson, A., Lindström, U., Aune, M., Berg, E., Skardhamar, J., Varpe, Ø., & Primicerio, R. (2024). Rapid climate change increases diversity and homogenizes composition of coastal fish at high latitudes. *Global Change Biology*. <https://doi.org/DOI:10.1111/gcb.17273>
- Skagseth, Ø., Drinkwater, K. F., & Terrile, E. (2011). Wind - and buoyancy - induced transport of the Norwegian Coastal Current in the Barents Sea. *Journal of Geophysical Research: Oceans*, 116(C8).
- Smith, K. A., Dowling, C. E., & Brown, J. (2019). Simmered then boiled: Multi-decadal poleward shift in distribution by a temperate fish accelerates during marine heatwave. *Frontiers in Marine Science*, 6, 407.
- Sor, R., Park, Y.-S., Boets, P., Goethals, P. L. M., & Lek, S. (2017). Effects of species prevalence on the performance of predictive models. *Ecological Modelling*, 354, 11-19. <https://doi.org/https://doi.org/10.1016/j.ecolmodel.2017.03.006>
- Sutton, R. T., & Hodson, D. L. (2005). Atlantic Ocean forcing of North American and European summer climate. *Science*, 309(5731), 115-118.
- Sætre, R. (2007). *The Norwegian coastal current: oceanography and climate*. Fagbokforlaget.
- Takimoto, G., & Post, D. M. (2013). Environmental determinants of food-chain length: a meta-analysis. *Ecological Research*, 28(5), 675-681. <https://doi.org/10.1007/s11284-012-0943-7>
- Tarling, G. A., Freer, J. J., Banas, N. S., Belcher, A., Blackwell, M., Castellani, C., Cook, K. B., Cottier, F. R., Daase, M., & Johnson, M. L. (2022). Can a key boreal Calanus copepod species now complete its life-cycle in the Arctic? Evidence and implications for Arctic food-webs. *Ambio*, 51, 333-344.
- Thompson, R. M., Hemberg, M., Starzomski, B. M., & Shurin, J. B. (2007). Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, 88(3), 612-617.
- Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466(7310), 1098-1101.
- Tyrrell, M., Moustahfid, J. L. H., & Smith, B. (2007). The dynamic role of pollock (*Pollachius virens*) as a predator in the Northeast US continental shelf ecosystem: a multi-decadal perspective. *Journal of Northwest Atlantic Fishery Science*, 38.
- Varela, R., de Castro, M., Dias, J. M., & Gómez-Gesteira, M. (2023). Coastal warming under climate change: Global, faster and heterogeneous. *Science of the Total Environment*, 886, 164029.
- Varpe, Ø., Fiksen, Ø., & Slotte, A. (2005). Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia*, 146, 443-451.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389-395.
- Walther, I. C. W. (2022). *Genetic diversity and differentiation of velvet belly lanternshark (*Etmopterus spinax*) in the Northeast Atlantic*. [UiT The Arctic University of Norway].
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21(2-3), 213-251.
- Yang, M., Qiu, Y., Huang, L., Cheng, M., Chen, J., Cheng, B., & Jiang, Z. (2023). Changes in sea surface temperature and sea ice concentration in the Arctic Ocean over the past two decades. *Remote Sensing*, 15(4), 1095.

- Zhu, Y., Azad, A. M., Kjellevold, M., Bald, C., Iñarra, B., Alvarez, P., Boyra, G., Berntssen, M., Madsen, L., & Wiech, M. (2023). Differences in nutrient and undesirable substance concentrations in *Maurollicus muelleri* across the Bay of Biscay, Norwegian fjords, and the North Sea. *Frontiers in Marine Science*, *10*, 1213612.
- Østerhus, S., Turrell, W. R., Jónsson, S., & Hansen, B. (2005). Measured volume, heat, and salt fluxes from the Atlantic to the Arctic Mediterranean. *Geophysical Research Letters*, *32*(7).
- Aarflot, J. M., Skjoldal, H. R., Dalpadado, P., & Skern-Mauritzen, M. (2017). Contribution of Calanus species to the mesozooplankton biomass in the Barents Sea. *ICES Journal of Marine Science*, *75*(7), 2342-2354. <https://doi.org/10.1093/icesjms/fsx221>

## Appendix

Table A1: Coefficients and their significance for the GLM on species richness.

COEFFICIENTS	ESTIMATE	STD. ERROR	P-VALUE
LOG COUNT OF FISH SPECIES	2.276	0.019	$< 2^{-16}$
SLOPE OF LOG COUNT OF FISH SPECIES IN THE LATER PERIOD (2014-2019)	0.416	0.018	$< 2^{-16}$
SLOPE OF LOG COUNT OF FISH SPECIES IN AREA 2 COMPARED TO AREA 1	-0.111	0.020	$8.67^{-8}$
LOG COUNT OF FISH SPECIES IN AREA 3 COMPARED TO AREA 1	-0.172	0.021	$5.79^{-16}$

Table A2: Food web metrics for all 72 species comprised in the metaweb. Species's role, position, trophic indexed and centrality measures were computed using package "NetIndices" in R

Species	TL	OI	degc e	In- degr ee	Out- degr ee	degc ent1	eigce nt	closecen t	betweence nt
<i>Alle alle</i>	3.7 3	0.11	10	7	3	10	0.23	0.33	9.80
<i>Amblyraja radiata</i>	4.8 9	0.47	22	21	1	22	0.50	0.01	7.25
<i>Anarhichas lupus</i>	4.0 2	0.54	15	8	7	15	0.38	0.01	5.20
<i>Argentina spp</i>	3.8 7	0.03	10	4	6	10	0.24	0.01	0.56
<i>Artediellus atlanticus</i>	4.0 9	0.13	9	5	4	9	0.27	0.01	0.00
Autotroph flagellat	1.0 0	0.00	9	0	9	9	0.23	0.01	0.00



<b>Bacteria indet</b>	1.0 0	0.00	9	0	9	9	0.20	0.01	0.00
<b><i>Balaenoptera acastrutata</i></b>	4.9 8	0.47	11	11	0	11	0.26	NA	0.00
<b><i>Balaenoptera physalus</i></b>	4.8 8	0.56	14	14	0	14	0.35	NA	0.00
<b>BNLarge predator</b>	2.2 0	0.16	10	5	5	10	0.18	0.01	2.50
<b>BNSmall deposit feeder</b>	2.7 2	0.84	36	13	23	36	0.70	0.01	75.47
<b>BNSmall predator</b>	3.1 3	1.19	61	16	45	61	1.00	0.01	765.08
<b>BNSmall suspension feeder</b>	2.9 4	0.92	48	14	34	48	0.82	0.01	127.63
<b><i>Brosme brosme</i></b>	4.6 8	0.39	7	5	2	7	0.17	0.01	1.53
<b><i>Clupea harengus</i></b>	3.6 0	1.20	34	10	24	34	0.55	0.01	95.26
<b>Detritus</b>	1.0 0	0.00	9	0	9	9	0.24	0.01	0.00
<b>Diatom</b>	1.0 0	0.00	8	0	8	8	0.24	0.01	0.00
<b><i>Enchelyopus cimbrius</i></b>	4.0 3	0.01	3	2	1	3	0.11	0.01	0.00
<b><i>Etmopterus spinax</i></b>	4.6 5	0.57	5	5	0	5	0.12	NA	0.00
<b><i>Fratercula arctica</i></b>	4.8 6	0.49	9	8	1	9	0.25	0.01	121.98
<b><i>Fulmarus glacialis</i></b>	4.6 3	0.60	19	17	2	19	0.41	0.50	7.42
<b><i>Gadiculus argenteus</i></b>	4.1 7	0.50	8	4	4	8	0.19	0.01	1.32
<b><i>Gadus morhua</i></b>	4.8 4	0.53	56	29	27	56	0.87	0.01	867.99
<b><i>Glyptocephalus cynoglossus</i></b>	4.0 3	0.01	8	2	6	8	0.16	0.01	1.54
<b><i>Halichoerus grypus</i></b>	5.3 1	0.19	6	6	0	6	0.14	NA	0.00
<b><i>Heterotroph flagellat</i></b>	2.0 0	0.00	11	2	9	11	0.26	0.01	1.72
<b><i>Hippoglossus hippoglossus</i></b>	5.0 0	0.63	10	9	1	10	0.27	0.01	0.00
<b><i>Hippoglossus platessoides</i></b>	4.3 9	0.13	20	7	13	20	0.41	0.01	40.60
<b>Ice algae</b>	1.0 0	0.00	3	0	3	3	0.08	0.01	0.00

<i>Lagenorhynchus albirostris</i>	5.0 6	0.32	8	8	0	8	0.20	NA	0.00
<i>Larus argentatus</i>	4.7 3	0.45	5	5	0	5	0.11	NA	0.00
<i>Larus hyperboreus</i>	4.9 8	0.25	4	4	0	4	0.09	NA	0.00
<i>Larus marinus</i>	4.7 3	0.57	4	4	0	4	0.11	NA	0.00
<i>Leptoclinus maculatus</i>	4.1 3	0.00	3	1	2	3	0.09	0.01	0.00
<i>Limanda limanda</i>	3.9 3	0.03	7	3	4	7	0.18	0.01	0.51
<i>Lumpenus lampretaeformis</i>	3.5 6	0.51	12	6	6	12	0.33	0.01	1.93
<i>Lycodes gracilis</i>	3.9 2	0.04	4	2	2	4	0.11	0.01	0.00
Macroalgae	1.0 0	0.00	2	0	2	2	0.06	0.01	0.00
<i>Mallotus villosus</i>	3.7 7	0.01	30	3	27	30	0.52	0.01	18.35
<i>Maurolicus muelleri</i>	3.7 8	0.01	10	3	7	10	0.23	0.01	2.31
<i>Megaptera noveangliae</i>	4.8 8	0.56	12	12	0	12	0.29	NA	0.00
<i>Melanogrammus aeglefinus</i>	4.5 6	0.54	38	19	19	38	0.69	0.01	209.00
<i>Merlangius merlangus</i>	4.7 2	0.39	24	17	7	24	0.48	0.01	134.73
<i>Micotroph flagellat</i>	2.0 0	0.00	3	1	2	3	0.05	0.01	0.00
<i>Micromesistius poutassou</i>	4.7 0	0.45	30	16	14	30	0.61	0.01	137.84
<i>Microstomus kitt</i>	3.9 2	0.04	4	2	2	4	0.11	0.00	0.08
<i>Molva molva</i>	4.7 0	0.60	8	7	1	8	0.22	1.00	0.00
<i>Orcinus orca</i>	5.2 6	0.47	8	8	0	8	0.17	NA	0.00
<i>Pagophilus groenlandicus</i>	4.7 1	0.56	10	10	0	10	0.28	NA	0.00
<i>Phoca hispida</i>	4.6 1	0.55	11	11	0	11	0.29	NA	0.00
<i>Phoca vitulina</i>	5.2 9	0.22	8	7	1	8	0.15	1.00	1.67
<i>Phocoena phocoena</i>	4.9 8	0.35	25	25	0	25	0.48	NA	0.00

<i>Physeter macrocephalus</i>	4.9 2	0.63	2	2	0	2	0.06	NA	0.00
Phytoplankton indet	1.0 0	0.00	10	0	10	10	0.25	0.01	0.00
<i>Pleuronectes platessa</i>	4.1 1	0.46	13	8	5	13	0.31	0.01	5.14
<i>Pollachius pollachius</i>	4.4 5	0.56	10	9	1	10	0.30	1.00	0.10
<i>Pollachius virens</i>	4.7 2	0.48	32	17	15	32	0.60	0.01	686.71
Protozooplankton	2.4 0	0.24	10	5	5	10	0.21	0.01	11.14
<i>Rajella fyllae</i>	4.0 9	0.13	6	5	1	6	0.20	0.01	0.00
<i>Rissa tridactyla</i>	4.3 8	0.54	6	6	0	6	0.20	NA	0.00
<i>Scomber scombrus</i>	4.1 2	0.59	16	8	8	16	0.33	0.00	8.86
<i>Sebastes</i>	3.8 7	0.03	16	5	11	16	0.35	0.01	40.43
<i>Squalus acanthias</i>	4.7 5	0.48	9	9	0	9	0.24	NA	0.00
<i>Triglops murrayi</i>	4.0 0	0.16	9	5	4	9	0.25	0.01	0.98
<i>Triglops pingelii</i>	3.8 3	0.03	8	5	3	8	0.25	0.01	0.73
<i>Trisopterus esmarkii</i>	3.7 3	0.11	21	7	14	21	0.46	0.01	11.28
<i>Uria lomvia</i>	4.8 2	0.00	2	2	0	2	0.03	NA	0.00
<i>Uria aalga</i>	5.1 0	0.41	6	6	0	6	0.17	NA	0.00
ZPLL large predator	2.0 0	0.00	11	4	7	11	0.18	0.01	5.41
ZPLSmall deposit feeder	2.8 9	1.31	52	14	38	52	0.94	0.01	259.53
ZPLSmall predator	2.7 0	0.67	40	13	27	40	0.77	0.01	117.48
ZPLSmall suspension feeder	2.7 0	0.72	55	14	41	55	0.96	0.01	148.97

Table A3: Food web metrics for both periods and all three areas using metaweb data (72 trophospecies).

	<b>1995</b>	<b>2019</b>	<b>1995</b>	<b>2019</b>	<b>1995</b>	<b>2019</b>
	<b>AREA 1</b>	<b>AREA 1</b>	<b>AREA 2</b>	<b>AREA 2</b>	<b>AREA 3</b>	<b>AREA 3</b>
<b>S</b>	61	66	61	67	56	64
<b>L</b>	426	470	455	493	403	468
<b>LD</b>	6.99	7.12	7.45	7.36	7.20	7.31
<b>C</b>	0.11	0.10	0.12	0.11	0.13	0.11
<b>CLUST</b>	0.42	0.40	0.44	0.42	0.45	0.42
<b>COMP</b>	0.19	0.18	0.17	0.18	0.18	0.18
<b>OMNI</b>	0.35	0.34	0.36	0.35	0.34	0.34
<b>PREDPREY</b>	1.23	1.20	1.20	1.20	1.23	1.19
<b>CAN</b>	0.10	0.09	0.10	0.09	0.11	0.09
<b>BAS</b>	0.11	0.11	0.11	0.10	0.13	0.11
<b>TOP</b>	0.29	0.26	0.26	0.25	0.29	0.25
<b>INT</b>	0.61	0.63	0.62	0.64	0.59	0.64
<b>GENSD</b>	0.79	0.81	0.79	0.82	0.76	0.81
<b>VULSD</b>	1.29	1.34	1.25	1.34	1.22	1.30
<b>MEANSWTL</b>	3.67	3.71	3.74	3.78	3.67	3.76
<b>MEANPATH</b>	2.18	2.30	2.20	2.29	2.06	2.28

Table A3: Food web statistics for both periods and all three areas for 180 species.

	<b>1995- 2000 AREA 1</b>	<b>2014- 2019 AREA 1</b>	<b>1995- 2000 AREA 2</b>	<b>2014- 2019 AREA 2</b>	<b>1995- 2000 AREA 3</b>	<b>2014- 2019 AREA 3</b>
<b>S</b>	169	174	169	175	164	171
<b>L</b>	1260	1324	1293	1342	1217	1306
<b>LD</b>	7.45	7.61	7.65	7.67	7.42	7.63
<b>C</b>	0.04	0.04	0.05	0.04	0.05	0.05
<b>CLUST</b>	0.22	0.22	0.23	0.22	0.22	0.23
<b>COMP</b>	0.31	0.31	0.31	0.31	0.31	0.31
<b>OMNI</b>	0.19	0.20	0.20	0.120	0.19	0.19
<b>PREDPREY</b>	1.08	1.08	1.07	1.08	1.08	1.07
<b>CAN</b>	0.12	0.12	0.12	0.12	0.12	0.12
<b>BAS</b>	0.04	0.04	0.04	0.04	0.04	0.04
<b>TOP</b>	0.11	0.11	0.11	0.11	0.12	0.11
<b>INT</b>	0.85	0.85	0.85	0.85	0.84	0.85
<b>GENSD</b>	1.42	1.41	1.42	1.43	1.44	1.43
<b>VULSD</b>	1.30	1.29	1.29	1.30	1.31	1.23
<b>MEANSWTL</b>	2.83	2.86	2.82	2.85	2.79	2.84
<b>MEANPATH</b>	2.58	2.63	2.60	2.61	2.52	2.61

Table A4: Supplementary table on ecology of all 34 fish species used in the food webs.

<b>Latin name</b>	<b>Common name</b>	<b>Short summary of ecological importance in northern Norway</b>
<i>Amblyraja radiata</i>	Thorny skate	Bottom-dwelling predator, regulate populations of smaller organisms maintaining balance within the food web (Chevolot et al., 2007).
<i>Anarhichas lupus</i>	Atlantic wolffish	Apex predator, control abundance of prey species. Burrowing behaviour also influence sediment dynamics and habitat structure.
<i>Argentina spp</i>	Silver smelt	Prey for larger fish and seabirds, contributing to nutrient transfer.
<i>Arctodiellus atlanticus</i>	Atlantic hookear sculpin/hookhorn sculpin	Found in rocky bottoms in arctic and boreal waters. Eats various invertebrates (Källgren et al., 2015).
<i>Brosme brosme</i>	Cusk/tusk	Demersal species that contributes to diversity in benthic community. Preys on fish, invertebrates.
<i>Clupea harengus</i>	Atlantic herring	Key species in Northern Norway. It serves as a significant food source for larger fish and seabirds, contributing to nutrient transfer.
<i>Enchelyopus cimbrius</i>	Fourbeard rockling	Lives on rocky bottoms and in kelp forest, preying on smaller fish and invertebrates.
<i>Etmopterus spinax</i>	Velvet belly lanternshark	<i>A widely distributed deep-water shark preying on small fish, squids and crustaceans, thus an important link in the food chain (Walther, 2022).</i>
<i>Gadiculus argenteus</i>	Silvery pout	An important forage fish species, and although not much is known for the study area, it likely plays a

		crucial role in energy transfer from lower to higher trophic levels (Arronte et al., 2022).
<b><i>Gadus morhua</i></b>	The Atlantic cod	Commercially important species. Plays significant role in the marine food web, affecting distribution and abundance of other marine species (Link et al., 2009).
<b><i>Glyptocephalus cynoglossus</i></b>	Witch (righteye flounder)	Of some importance as a food fish. Contributes to flux of energy through food web due to its biomass and part of other fish species diet.
<b><i>Hippoglossoides platessoides</i></b>	American plaice/long rough dab	Flatfish species contributing to energy flux, is important part of the diet of large predatory fish species.
<b><i>Hippoglossus hippoglossus</i></b>	Halibut	A significant role as both predator and prey in the North Norwegian coastal ecosystems, with its status reflecting health of groundfish stocks and have commercial value (IMR, 2020).
<b><i>Leptoclinius maculatus</i></b>	Daubed shanny	<i>A common fish species in arctic waters that serve as a vital link between lower trophic levels and many fish, marine mammals, and seabirds. Also considered an important reservoir and host for Arctic marine parasites (Murzina et al., 2013; Murzina et al., 2019).</i>
<b><i>Limanda limanda</i></b>	Common dab	Feeding on crustaceans and small fishes, and acts as a bioindicator for environmental changes due to its sensitivity to pollutants thus playing a crucial role in ecosystem monitoring (Kammann et al., 2008).

<i>Lumpenus lampretæformis</i>	Snake blenny	Preys on small invertebrates and are prey to larger fish. Burrowing behavior also aids sediment mixing and oxygenation (Oesterwind et al., 2023).
<i>Lycodes gracilis</i>	Vahl's eelpout	Integral in benthic ecosystems, feeding on crustaceans and small fish. Serves as indicator species for environmental health due to its sensitivity to habitat disturbances (Nash, 1986).
<i>Mallotus villosus</i>	Capelin	Key species in Arctic and sub-Arctic marine food webs and feed predominantly on krill. Represent high-energy prey for upper trophic levels and their distribution fluctuates based on predator-prey relationships (Hop & Gjørseter, 2013).
<i>Maurolicus muelleri</i>	Silvery lightfish/pearlsides	A mesopelagic fish that exhibit diel vertical migrations, contributing to nutrient cycling between deep waters and surface layers (Zhu et al., 2023)
<i>Melanogrammus aeglefinus</i>	Haddock	Polycheates and bivalves in winter and smaller invertebrates and fish in summer. Undergoes seasonal migrations (Albert, 1994).
<i>Merlangius merlangus</i>	Whiting/merling	A commercially important demersal fish that likely plays a significant role in benthic food webs along the north Norwegian coast (Asciutto et al., 2024).
<i>Micromesistius poutassou</i>	Blue whiting	One of the most abundant fish stocks in the semi-pelagic water masses of the northeast Atlantic, including the Norwegian Sea, and its diet consists mainly of crustaceans (IMR, 2022).
<i>Microstomus kitt</i>	Lemon sole	Commercially valuable species in the northern North Sea. Spawns between early May and



		October, with larvae found in the water column in the North Sea in winter (Geffen et al., 2021).
<i>Molva molva</i>	Common ling	A deep-water gadoid normally found in greater abundance along the coast in the North Sea. Heavily exploited with declining catches. Supports commercial fisheries (McGill et al., 2023).
<i>Pleuronectes platessa</i>	European plaice	Commercially important species that is heavily fished. Proved to be resilient to over-exploitation, spawning biomass is increasing (Mollet et al., 2016).
<i>Pollachius pollachius</i>	Pollack	Important recreational fish, plays a significant role in marine food web (Cargnelli, 1999).
<i>Pollachius virens</i>	Saithe	It preys on blue whiting, Norway pout, sandeel, herring and krill. It is a top predator and feeds on the same trophic level as Atlantic cod and haddock (Tyrrell et al., 2007).
<i>Rajella fyllae</i>	Round ray	A soft seabed-dwelling ray, feeding on bottom-dwelling organisms. It influences prey populations and serves as an indicator species for seabed health (Froese & Pauly, 2024a)
<i>Scombers scombrus</i>	Mackerel	An economically important, highly migratory species that forms large schools near the surface and is key prey item for larger predators (dos Santos Schmidt et al., 2023).
<i>Sebastes</i>	Rose fish	Bentich fish, switching from a semi-pelagic lifestyle in the Barents Sea during its juvenile and

immature phase, to a primarily pelagic existence in the Norwegian sea (Dolgov & Drevetnyak, 2011).

<i>Squalusa acanthias</i>	Spiny dogfish	Small shark found in temperate waters. Slow-growing, long-lived making in particularly prone to over-exploitation and long-lasting depletion (Fordham, 2004).
<i>Triglops murrayi</i>	Moustache sculpin	Benthic fish found on sand bottom, feeds on benthic polychaetas and crustaceans, as well as planktonic crustaceans (Froese & Pauly, 2024b)
<i>Triglops pingelii</i>	Ribbed sculpin	Feeds on various benthos, with a preference for invertebrates (Froese & Pauly, 2024c).
<i>Trisopterus esmarkii</i>	Norway pout	Small gadoid and major prey species for many larger and commercially important predator species in the North Sea, such as Atlantic cod, whiting, saithe, and haddock ((Froese & Pauly, 2024d)

