

RESEARCH ARTICLE

Rapid climate change increases diversity and homogenizes composition of coastal fish at high latitudes

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Abstract

Rapid warming at high latitudes triggers poleward shifts of species' distributions that impact marine biodiversity. In the open sea, the documented redistributions of fish lead to a borealization of Arctic fauna. A climate-driven borealization and increased species diversity at high latitudes are also expected in coastal fish communities, but they have not been previously documented on a large, biogeographic scale. Here, we investigate the impact of temperature change over the last 25 years on fish communities along the coast of Norway. The study area, spanning different ecoclimatic zones between 62° and 71° N, harbors over 200 species of boreal and Arctic fish. Several of these fish species are harvested by coastal and indigenous communities, influencing settlement geography and livelihood. The long-term data on coastal water temperatures and fish species were obtained from monitoring stations and scientific surveys. Water temperature measured at three fixed sampling stations distributed along the coast show increased temperatures during the study period. The fish species distribution and abundance data were obtained from the annually standardized scientific bottom trawl survey program. Fish species richness, which was highest in the south, increased with warming first in the south and then, gradually, further north, eventually affecting biodiversity in the whole study area. Fish community composition showed a distinct latitudinal pattern early in the study, with Arctic fish species confined to the north and boreal species dominating the south. The poleward shifts eventually eroded this zoogeographic pattern, resulting in more boreal fish species in the north and an increased homogenization of species composition along the Norwegian coast. The climate-driven reorganization of fish communities affects coastal ecosystems that are exposed to fisheries, aquaculture, and other rapidly expanding human activities, stressing the urgent need for a climate adaptation of integrated coastal management.

KEYWORDS

alpha diversity, biodiversity, biogeography, climate change, species distribution, sub-arctic, zoogeography

1 | INTRODUCTION

Rapid climate warming at high latitudes is leading to changes in species' distribution, abundance, and phenology, affecting biodiversity and ecosystem organization (IPBES, 2019; Ingvaldsen et al., 2021; Pecl et al., 2017; Pörtner et al., 2022). Climate-induced poleward shifts in marine species distributions are expected to modify biogeographic patterns of diversity and composition (Alabia et al., 2023; Cheung et al., 2009; Kjesbu et al., 2022). At a global scale, marine biodiversity declines with latitude, being lowest towards the North Pole (Chaudhary et al., 2016), and the observed distinct biogeographic regions can be associated with different climatic zones (Costello et al., 2017). Evidence for the expected climate-driven increase in diversity at higher latitudes, and for the reshuffling and shifting of species compositions, is rapidly accumulating (Fossheim et al., 2015; He & Silliman, 2019; Kjesbu et al., 2022). Poleward shifts have been documented for fish, birds, and mammals, with northward expansions that can keep track of temperature changes in mobile species (Grebmeier et al., 2006; Orgeret et al., 2021; Pinski et al., 2013; Poloczanska et al., 2016; Sorte et al., 2010; Sydeman et al., 2015). The evidence for redistributions of marine species at high latitudes comes primarily from studies on fish in the open ocean (e.g., Fossheim et al., 2015; Yasumiishi et al., 2020), with coastal areas being understudied. The lack of similar large scale, comprehensive studies in coastal areas is concerning, considering the important ecological and socio-economic role played by fish species, which have contributed to shape the geography of coastal settlements and the livelihood of local and indigenous communities over many centuries (Collie et al., 2008; Pedersen et al., 2022; Perdikaris, 1999; Varpe et al., 2005). Documenting and understanding the impact of climate change on coastal biodiversity at high latitudes, where the rate and magnitude of change are expected to be greatest, is urgently needed to inform climate adaptation and integrated management of expanding human activities (IPBES, 2019; Harley et al., 2006; Pörtner et al., 2022).

In marine ecosystems, fish display some of the most rapid and substantial ecological responses to climate warming, with documented reorganizations of biodiversity and ecosystems (Ingvaldsen et al., 2021; Pörtner et al., 2022). Poleward distributional shifts in fish have been documented in the arctic (Fossheim et al., 2015), temperate (Perry et al., 2005), and tropical waters (Fodrie et al., 2010; Fujiwara et al., 2019). The speed of fish redistributions, which can track climate velocities (Brito-Morales et al., 2018), suggests that behavior often mediates the ecological response in the short term (Fossheim et al., 2015; Pinski et al., 2013). The importance of a behavioral component is evident in distributional responses to extreme climatic events, such as heatwaves (Husson et al., 2022; Lonhart et al., 2019). In response to species' poleward distributional shifts, shelf and open sea fish diversity at high latitudes tends to increase, at least temporarily (Alabia et al., 2023; Hiddink & ter Hofstede, 2008; Ingvaldsen et al., 2021; Wiedmann et al., 2014). Poleward shifts modify biogeographic patterns, reshuffling species and leading to a homogenization of assemblages across regions with previously distinct composition (Fossheim et al., 2015; Frainer et al., 2017; Mueter et al., 2021).

Coastal marine ecosystems are among the most diverse and productive ocean areas in the world and provide many ecosystem services (Barbier et al., 2011). The warming trends observed in the open ocean also affect coastal marine ecosystems, compounding cumulative risk (Bindoff et al., 2019; He & Silliman, 2019; McCarthy et al., 2001; Pörtner et al., 2022). The main climate-driven hydrographic changes affecting coastal environments, including increasing water temperatures, changes in salinity, and alterations of current systems, are all expected to influence coastal ecosystems and their biodiversity (He & Silliman, 2019; Pörtner et al., 2022). However, climate-induced biodiversity alterations in coastal ecosystems are poorly studied, particularly at large biogeographic scales (Collie et al., 2008; He & Silliman, 2019). Rapid distributional responses by fish are also expected in coastal ecosystems, despite the greater spatial heterogeneity of habitats compared to open oceans (Barry & Dayton, 1991; Last et al., 2011). Fish play an important role in coastal ecosystems, both as prey for upper trophic levels such as marine mammals and sea birds, and as consumers of benthic and pelagic prey. Coastal regions host one-third of the world's human population (Mehvar et al., 2018), and the socio-economic implications of climate change in coastal ecosystems are expected to be particularly severe considering coastal communities' strong dependency on marine resources (He & Silliman, 2019; Pörtner et al., 2022). In addition, coastal ecosystems are exposed to human activities across multiple sectors, including fisheries, aquaculture, tourism, and extractive industries (Halpern et al., 2019). However, climate change impact on fish is of particular concern considering their key ecological and socio-economic role in coastal areas (Seitz et al., 2014), and fish redistribution calls for climate adaptation of coastal management (Leith et al., 2014; Pham et al., 2021).

The impact of climate warming on high-latitude coastal ecosystems is poorly documented, but is expected to be equally rapid and substantial as observed in the open ocean (Pörtner et al., 2022). In the present study, we assess the impact of warming on fish biodiversity along the Norwegian coast (62°–71°N), which harbors over 200 fish species and encompasses several ecoclimatic zones. We document the effects of rapid distributional shifts for species diversity and composition by analyzing a 25-year long time-series of demersal trawl survey data. We expected climate-driven poleward shifts to increase species richness, affect the latitudinal diversity gradient, and homogenize species composition along the Norwegian coast. We discuss the implications of the observed climate-driven changes in fish diversity and composition for these high-north coastal ecosystems and for the associated goods and services.

2 | MATERIALS AND METHODS

2.1 | Study area

The Norwegian coastline spans from 58° to 71°N and has a pronounced latitudinal gradient of water temperature (Figure 1) of about eight degrees difference from South to North in summer. The coastline is characterized by fjords and islands creating

diverse and spatially heterogeneous habitats. Fish species play an important ecological and socio-economic role and have contributed to shape coastal settlements and the livelihood of local and indigenous communities over many centuries (Collie et al., 2008; Pedersen et al., 2022; Perdikaris, 1999). Coastal habitats also form the spawning grounds for several large fish populations

that are migratory and with oceanic and pelagic distributions for parts of the year (Kjesbu et al., 2022). Norwegian coastal areas north of 62°N (statistical areas 0 and 3–7, extending maximum ca. 230 km from the coastline) support fisheries targeting over 70 taxa. Average annual landings during the last decade (2014–2023) were close to 1 million tons, which corresponds to an average

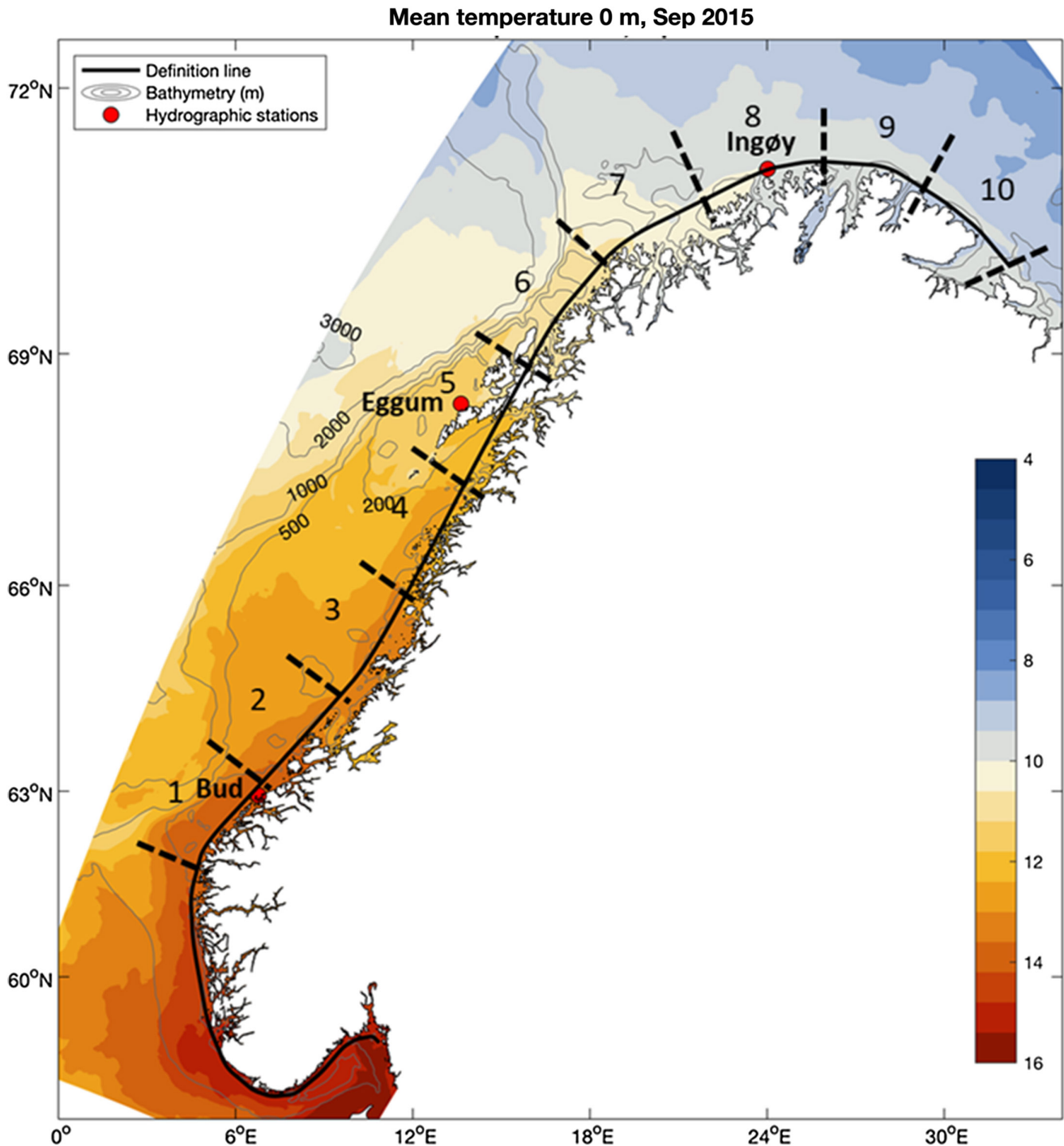


FIGURE 1 Map of the study area illustrating the latitudinal gradient in water temperature (°C) in the upper 10m (September mean) off the Norwegian coast, simulated with a numerical ocean model (NorKyst800, Asplin et al., 2020). The black solid line is a reference line used to specify trawl sample positions along the Norwegian coast in this study (from 61°N, 4°E to 71°N, 32°E). The reference line was divided into 10 equally long segments (167 km), with orthogonal delimitation borders (stippled lines) defining sampled areas along the coast. Bathymetry is shown by gray isobath lines marked with depths (m).

annual value of ca. 0.8 billion euros (calculated based on freely accessible fishery statistics data downloaded from the Norwegian Directorate of Fisheries webpage, www.fiskeridir.no).

The ocean climate along the Norwegian coast depends on the amount of warm and saline Atlantic water (AW) that flows into the Nordic Seas (e.g., Skagseth et al., 2011) with the North Atlantic Current (NAC), and the properties of the lower-salinity coastal water flowing northwards along the Norwegian coast as the Norwegian Coastal Current (NCC; Sætre, 2007). The NCC carries large volumes of fresh and brackish water from the Baltic Sea and is receiving runoff from land, fjords, and rivers along the Norwegian coast. The Atlantic water becomes gradually cooler and less saline as it flows towards the north along the coast, due to mixing with the coastal water, freshwater discharge, precipitation, and atmospheric cooling. The temperature of the AW has varied in the past with warm and cold periods (Sutton & Hodson, 2005), and since 1981 there has been a period of increasing temperatures until circa 2012, whereafter the heating culminated (Sandø et al., 2022). Albreten et al. (2012) have shown that the ocean temperatures increased in both upper and deeper layers along the Norwegian coast between 1990 and 2009 and attributed this to a reduction of the North Atlantic Subpolar Gyre (Hátún et al., 2005) combined with the reduced (normalized) NAO, and possibly also large-scale hemispheric warming. Skagseth et al. (2022) have recently identified another oceanographic change that may affect the marine ecosystems along the Norwegian coast: a redistribution of the Arctic Intermediate Water masses (AIW) at depth (below AW) in the Norwegian basin has led to a shift after 2006 with less advection of new nutrients and nutrient-rich Arctic zooplankton to the eastern side of the Norwegian basin and towards the Norwegian shelf break (Skagseth et al., 2022).

2.2 | Data collection

The present work is based on yearly scientific survey data from 1995 to 2019, collected by the Norwegian Institute of Marine Research (IMR), consisting of trawl samples of fish along the Norwegian coast. Water temperature profiles were obtained from three monitoring stations Bud, Eggum, and Ingøy (Figure 1), located in the southern, central, and northern regions visited by the survey.

2.2.1 | Survey description

The coastal survey is a standardized scientific combined acoustic-bottom trawl survey program. In autumn each year, the coastal survey covers the Norwegian coast, from approximately 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 nm (120 km).

2.2.2 | Fish sampling

Demersal fish were sampled with shrimp trawls, with a typical towing speed of approximately three knots. In total, the data set included 3969 bottom trawl samples with acceptable sample quality and gear condition. Sampling stations for which fish abundance data ($n=130$) were not available for all species were not included in the study. Further, trawling stations that covered less than 0.5 nm ($n=222$) or more than 2.1 nm ($n=34$) were removed from the dataset to reduce sampling bias. We also excluded stations deeper than 500 m ($n=52$), as there were very few samples from deep stations, restricted to a few deep fjords. The total number of trawl samples included was 3529.

Fish were identified to the lowest feasible taxonomic level, and the majority were identified to species level. Of the 127 taxa registered in the dataset, we selected the 60 most widely distributed and abundant (Table S1). Among the 60 included taxa, some have a lower taxonomic resolution being aggregated genus (redfishes *Sebastes* sp.), or order level (Lanternfishes Myctophiformes). For skates (*Rajidae*), only individuals identified to species were kept in the dataset. The final 59 taxa included in the analyses were present during all survey years and account for more than 99.9% of the total abundance by count of the catch.

Biogeographic information was obtained from classifications in Arctic seas (Andriyashev & Chernova, 1995; Mecklenburg et al., 2018), complemented by classifications from the North Sea (Yang, 1982). Included biogeographical groups, from the most southern to the most northern, are: South Boreal (SB), Boreal (B), Northern Boreal (MB, referred to as Mainly Boreal in Andriyashev & Chernova, 1995), Widely Distributed (WD), Arcto-Boreal (AB), Mainly Arctic (MA), and Arctic (A). Habitat preference data were obtained from the literature expanding on the trait dataset by Wiedmann et al. (2014).

2.2.3 | Environmental data

Time series of water temperature measurements were obtained from fixed hydrographic monitoring stations along the Norwegian coast (Albreten et al., 2012; Aure & Østensen, 1993; Eggvin, 1938), where vertical profiles of temperature and salinity have been measured 1–4 times per month since 1935 by the Institute of Marine Research (IMR). The time series can be accessed at <http://www.imr.no/forskning/forskningsdata/stasjoner/index.html>.

Temperature data from depths 10 and 200 m, representing surface and deeper layer water masses, from the stations Bud (62°56' N), Eggum (68°22.8' N), and Ingøy (71°08' N) (Figure 1), were extracted for the period 1980–2023. For a longer time series of surface temperature at these stations, see Skagseth et al. (2015). Measurements for the months July to September were extracted and averaged to obtain mean summer temperatures, and the temperature trends were estimated using generalized additive models (GAM).

2.3 | Data analyses

2.3.1 | Pre-processing

Geographic location was likely to influence fish diversity and composition, given the latitudinal gradient in water temperature and productivity. Since the studied coastline is only partially aligned with the latitudinal gradient, we used a simplified, coarse line following the coast as a reference for geographic position instead of geographic coordinates (Figure 1). The position of the southernmost station (62°00' N, 4°15' E) along our reference line was set to 0, and all other stations' positions were measured as the distance (km) along the simplified line from this point. The coast was divided into 10 equally long segments (167 km long), and summary statistics are presented for each of these coastal intervals (Table S2). Fish abundance per trawl sample was standardized to counts per nautical mile trawled (1.852 km).

2.3.2 | Spatio-temporal variation in diversity

As our primary measure of diversity, we use species richness (S), measured as the number of taxa identified in each trawl (alpha richness). We also include results based on the Shannon's diversity index (Shannon, 1948), which takes relative abundances into account. Shannon's diversity index is constrained between 0, where only one species is present, and $\ln(S)$, where all species are present with equal abundances. In addition, we used Pielou's evenness index (J) (Pielou, 1966), ranging from 0 to 1, with values increasing as the abundances of species become more evenly distributed.

The spatial and temporal variation in species richness was modeled using a generalized linear model (GLM) with a Poisson error distribution (Zuur et al., 2009). Model specification was informed by diagnostic regression using a generalized additive model (GAM) that helped detect nonlinear relationships between species richness and the predictor variables geographic location, year, depth, and trawled distance (Figure S1). Trawled distance did not influence species richness, and was not included in the GLM model. The nonlinear, dome-shaped relationship with depth was accounted for by a quadratic term in the GLM. An interaction term between geographic location and year was included in the GLM to account for temporal change in species richness profiles along the coast. The GLM model assumptions were inspected using regression diagnostics. A semivariogram of residuals from the selected model showed no evidence of spatial auto-correlation unaccounted for by explanatory variables. There was only weak collinearity between predictors (all Pearson correlation coefficients $|r| < .5$). The selected model was chosen from a set of candidate models, including all possible combinations of the three predictors and their pairwise interactions, based on the Akaike information criterion (Table S3).

2.3.3 | Spatio-temporal variation in composition

To investigate changes in the composition of fish assemblages along the coast, we first identified the main zoogeographic clusters with distinct fish assemblages in the early study period (1995–2002) by applying hierarchical clustering (Bray–Curtis dissimilarity and Ward linkage) to log-transformed abundance (\log_{10} ind/nm) data. The two main clusters, corresponding to a northern and southern fish assemblage with distinct species composition, were then used to train a random forest classification (R-package “randomForest”). The random forest classification was trained on 75% of the sampled stations in the first period and validated on the remaining 25%. The resulting model correctly assigned 97% of the stations to fish assemblage type, with similar results for the northern and southern clusters. The random forest classification was then used to assign all trawl samples during the study period to the two main zoogeographic clusters (southern and northern assemblages), based on species composition. The classification results allowed us to track changes in the spatial distribution of northern and southern fish assemblages over time.

Homogenization of fish community composition along the coast was assessed by comparing annual distance-decay patterns across years. Community dissimilarity was expected to increase with geographic distance. With the northward displacement of southern species, dissimilarity over larger geographic distances was expected to decrease. We addressed this expectation by first calculating community dissimilarities as the Jaccard distance between trawl stations, and the associated geographic distance between trawl stations as the shortest distance in meters. Second, we used quantile regression to estimate the intercept and slope of quantile trend lines (0.50, 0.75) relating community dissimilarity to geographic distance each year, thereby obtaining the rates at which compositional dissimilarity increases with geographic distance. The higher quantile (0.75) of compositional dissimilarity between stations should be affected by compositional homogenization due to the poleward expansion of species distributions. Geographic homogenization of communities over time is indicated by a temporal decrease in the slopes of regression lines.

To elucidate individual species' roles in the observed changes in fish diversity and composition, we explored trends in average annual abundance (count/nm) and northern distribution limit (90% quantile of position along the coast). Ordinary linear regressions were applied to each species, allowing us to identify species displaying significant ($p < .05$) trends in abundance or distribution throughout the study period.

Spatial and temporal variation in total fish density (count/nm) was modeled using a GLM with a Gaussian error distribution (Zuur et al., 2009). Total fish densities were log-transformed to reduce the skewness of abundance distributions. The model specification was informed by a GAM that helped detect nonlinear relationships between total density and the predictor variables geographic location, year, depth, and trawl distance (Figure S2). The nonlinear, S-shaped relationship with depth was accounted for by a cubic term in the

GLM. An interaction term between geographic location and year was included in the GLM to account for between-year differences in fish density profiles along the coast. The GLM model assumptions were inspected using regression diagnostic plots and statistics.

3 | RESULTS

3.1 | Increasing water temperatures

The measurements from the coastal monitoring stations show that the water temperature along the Norwegian coast has increased during the last four decades (Figure 2). The temperature increase was most pronounced near the surface and at the two southernmost locations, Bud and Eggum, where the interpolated mean surface (10m depth) temperatures during summer (July–September) have increased by c. 2.5°C since 1980. In contrast, the interpolated mean temperature in the northernmost location (Ingøy) increased by circa 1°C in the period 1980–2010, then declined slightly (ca. 0.3°C) in the last decade. At 200m depth, the temperature increased by about 1°C at the two southernmost locations, whereas it increased by ca. 0.7°C at the northernmost location. The most pronounced temperature increase was during the eighties and nineties, whereafter the temperature stabilized or slightly decreased after 2010, in accordance with Albretsen et al. (2012) and Sandø et al. (2022).

3.2 | Species richness increases gradually northward

Fish species richness, which was highest in the south, increased first in the south and then, gradually, further north, eventually affecting biodiversity along the entire study area (Figure 3; Table S3). In the southernmost coastal interval (interval 1), annual mean richness increased from the minimum observed nine species per trawl haul in 1999 to 18.3 in 2019 (Figure 3b). In the northernmost interval (interval 10), the lowest average richness, with 5.8 species, was observed in 1998, and increased to 14.4 in 2017 (Figure 3b). On average, richness increased by 21% per decade, with a significant difference in rate of increase between the south, increasing by 14% per decade, compared to the north, increasing by 29% per decade (Table S4; Figure S3). Thus, the initially large difference (43%) in richness between the south and north became smaller (22%) by the end of the study period.

The temporal changes in species distribution and abundance were associated with alterations in Pielou's evenness index and Shannon diversity index that differed between south and north (Figures S4 and S5). Initially, evenness was low in the south and high in the north. As new species entered northern areas, evenness first declined and then increased. The Shannon diversity index eventually increased along the whole coast, first in the south, then gradually northward (Figure S5). The initial decline and fluctuation in Shannon index in the north reflect the shifting balance between an increasing richness and declining evenness.

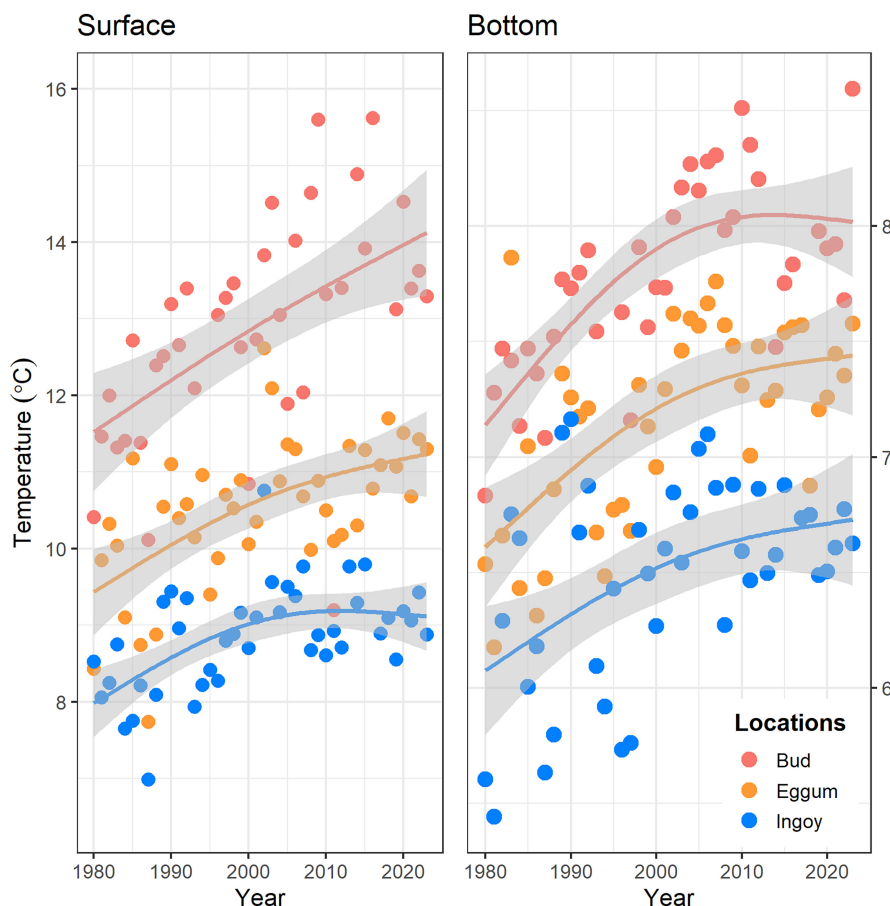


FIGURE 2 Mean summer (July–September) temperatures in surface (10m; left panel) and bottom (200m; right panel) water at three locations (Bud, 62°56' N; Eggum, 68°22' N; Ingøy, 71°08' N) along the Norwegian coast in the period 1980–2023. The trend lines (GAM smoothers) are plotted with 95% confidence bands (grey bands). Note the different scale of the two y-axes. Fish community data cover the period from 1995 to 2019.

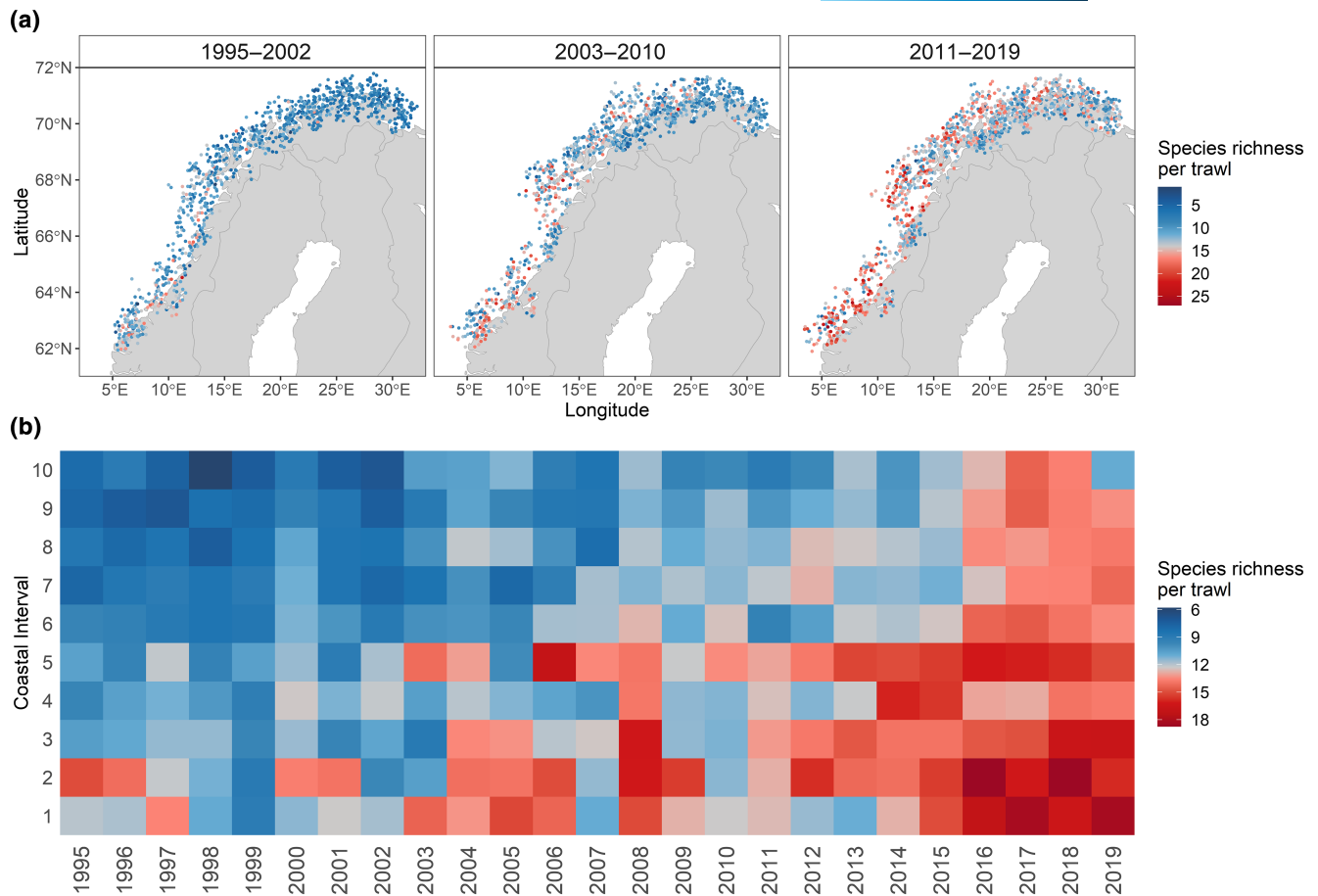


FIGURE 3 (a) Species richness per trawl along the coast of Northern Norway in the early (left panel), intermediate (mid panel), and late (right panel) study periods. (b) Species richness averaged over coastal intervals (Figure 1) and year. Numbers on the y-axis refer to the 10 coastal intervals (see Figure 1), numbered from southernmost (1) to northernmost (10).

3.3 | Species compositions are reshuffled eroding the latitudinal biogeographic pattern

During the colder, early phase of the study, fish species distributions showed a zoogeographic transition zone at about 70°N, separating a southern and northern assemblage with distinct species composition (Figure 4 and Figure S6). The northern assemblage had a greater proportion of Arctic, Arcto-Boreal, and northern Boreal species (Figure 5), and was characterized by a higher abundance of the Arcto-Boreal capelin (*Mallotus villosus*), and northern Boreal species such as haddock (*Melanogrammus aeglefinus*), Atlantic cod (*Gadus morhua*), European plaice (*Pleuronectes platessa*), and spotted snake blenny (*Leptoclinus maculatus*). The southern assemblage was characterized by higher abundances of several South Boreal and Boreal species, typically lacking in the northern assemblage, such as sprat (*Sprattus sprattus*), blackmouthed dogfish (*Galeus melastomus*), silvery pout (*Gadiculus argenteus*), poor cod (*Trisopterus minutus*), argentine (*Argentina sphyraena*), and European hake (*Merluccius merluccius*).

The random forest classification showed a gradual erosion of the area covered by the northern fish assemblage during the study period (Figure 4). The spatial distribution of the northern fish assemblage displayed a contraction, retracting toward the northeast and

into fjords of the northern coast (Figure 4a). Accordingly, the proportion of stations with northern assemblages in the northernmost region (coastal intervals 9 and 10) decreased by 52% between the first and last 5-year period (Figure 4b). The poleward shifts in fish distributions have led to a homogenization of fish species composition along the entire Norwegian coast north of 62°N, as indicated by the reduced slope of the distance-decay regressions over time (Figure S8).

3.4 | Abundance increases mainly in the north

Total fish abundance was generally higher in southern compared to northern areas (Figure S9). During the study period, total abundance increased only in the northern areas, reducing differences in overall fish abundance between the south and north toward the end of the study (Figure S10; Table S5). Several species with different biogeographical affinities increased in abundance ($n=30$) and/or expanded their northern distribution limit ($n=19$) during the 25-years study period, contributing to the observed increasing trends in species richness (Table S1). The majority of the nine species displaying both a northward expansion and an increase in abundance were classified

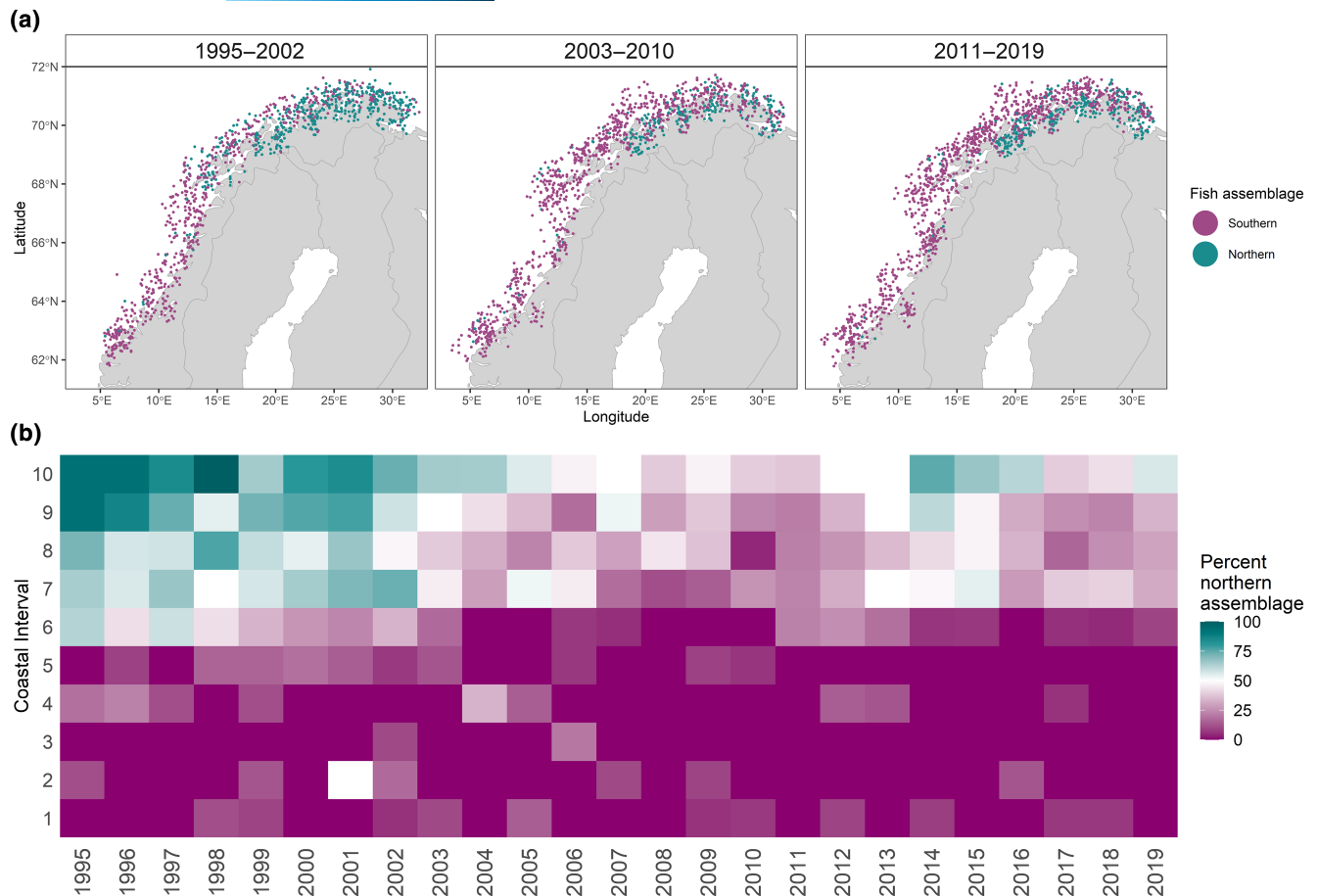


FIGURE 4 (a) Spatial distribution of two main fish assemblages identified by random forest classification in the early (left panel), intermediate (mid panel), and late (right panel) study periods. (b) Spatio-temporal variation in percentage of “northern” fish assemblage among trawl stations within each coastal interval (Figure 1). Numbers on the y-axis refer to the 10 coastal intervals (see Figure 1), numbered from southernmost (1) to northernmost (10).

as South Boreal or Boreal ($n=7$) and were both pelagic ($n=4$) and demersal ($n=5$) species (Table S1).

4 | DISCUSSION

4.1 | Climate-driven change in fish biodiversity along the Norwegian coast

Our findings show how the increase in water temperature registered along the Norwegian coast over the last decades was accompanied by poleward redistributions of fish, affecting latitudinal patterns of diversity and composition. Species richness initially displayed a sharp latitudinal gradient, with the highest diversity in the south. Over the study period, species richness gradually increased northward, resulting in a twofold increase in mean species richness in the south and a threefold increase in the north. The latitudinal pattern in species composition, with Arcto-boreal fish species confined in the north and primarily boreal species in the south, was gradually eroded as boreal species expanded their distribution northward. The fish communities became more diverse and increasingly homogenized

along the entire Norwegian coast, with important implications for ecosystem structure and function, and for the goods and services exploited by coastal human communities.

4.2 | Increasing fish diversity

Fish species richness displayed an initially sharp latitudinal gradient, with average diversity in the south of the study area being about 43% higher than in the north. The expected latitudinal gradient in diversity can be explained by differences in the duration of the productive season and in overall productivity (Alabia et al., 2023; Hillebrand, 2004). The increase in richness started in the south and then propagated gradually northward, a clear manifestation of the community-level implications of climate-driven poleward shifts. The poleward shifts affecting species richness were accompanied by changes in relative abundance that affected evenness and diversity indices. Initially, evenness was low in the south and high in the north. As new species entered northern areas, evenness first declined, due to low abundances of incoming species, and then increased as abundances of incoming and resident species evened out.

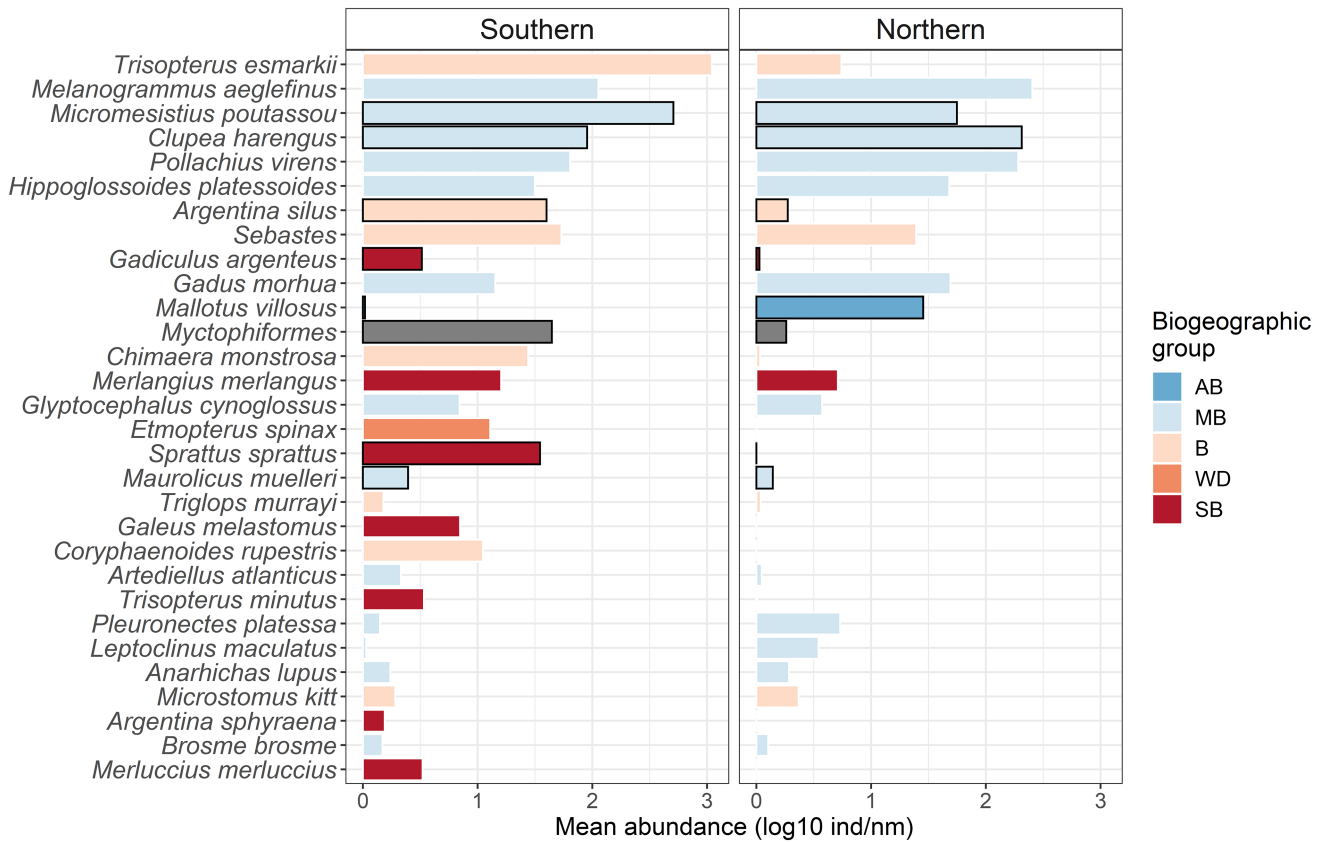


FIGURE 5 Species composition in each of the two fish assemblages in the first time period 1995–2002, based on Bray–Curtis dissimilarities and hierarchical ward clustering. Biogeographical groups are from the most southern to the most northern: South Boreal (SB), Boreal (B), Northern Boreal (MB), Widely Distributed (WD), Arcto-Boreal (AB), Mainly Arctic (MA), and Arctic (A). Myctophiformes (lantern fishes) includes several species with different biogeographic affiliations and is shown in gray. Pelagic species are indicated by a black frame around the bars. The figure shows the 30 most common species; all species are shown in Figure S7.

Increased species richness at high latitudes as an outcome of climate-driven poleward shifts has not previously been documented in coastal fish communities, but has been observed in shelf ecosystems (Alabia et al., 2023; Frainer et al., 2021; Jones et al., 2023; Mueter et al., 2021). In the northeast Atlantic, southerly species have expanded their distributional range northwards, coinciding with rising water temperatures (Brander et al., 2003; Hiddink & ter Hofstede, 2008; Poulard & Blanchard, 2005). Consequently, shelf and open sea fish diversity at high latitudes increases (Frainer et al., 2021; Hiddink & ter Hofstede, 2008; Ingvaldsen et al., 2021; Jones et al., 2023; Wiedmann et al., 2014). Our findings on coastal fish communities are consistent with the growing evidence of rapid borealization and diversity increase reported from various high-latitude shelf ecosystems (Ingvaldsen et al., 2021).

4.3 | Compositional homogenization, boreal species move north

During the colder, early phase of the study period, fish species distributions showed a zoogeographic transition zone at about 70°N, separating a southern and northern assemblage with distinct species

composition. In this area, the shelf slope diverts from the coast and continues northward (Figure 1). This type of steep topography typically traps currents and creates biogeographic boundaries and fronts (Holligan, 1981). The North Atlantic Current, carrying warm and saline water northward, also splits into two branches in this region (Furevik, 2001; Helland-Hansen & Nansen, 1909; Hopkins, 1991; Skarðhamar & Svendsen, 2005). Poleward shifts by southerly species eventually eroded the zoogeographic transition zone, which led to a compositional homogenization of fish assemblages along the entire coast and a contraction of the area covered by northern fish assemblages, which retracted northeast and into the fjords.

Climate-driven compositional change in other high-latitude coastal ecosystems is poorly documented. However, in North Atlantic shelf seas, rapid poleward shifts have been observed (Campana et al., 2020; Fossheim et al., 2015; Frainer et al., 2017; Mueter et al., 2021), leading to increased biodiversity and reshuffling of species compositions. Climate change, and particularly water temperature, was identified as the main driver of fish community composition in a recent large-scale study across the Northeast Atlantic shelf seas (Rutterford et al., 2023).

Poleward distributional shifts of southern fish species were observed both through the northward range expansion of the

southern fish assemblage and by range shifts in individual species. Like more open shelf systems, northward expansion was most pronounced in fish species associated with southern ecoregions (e.g., Beare et al., 2004; Fosshem et al., 2015; Mueter et al., 2021; Pawluk et al., 2021). In the present study, mainly South boreal and boreal fish species (68%) expanded their distribution northwards. Among the 19 species expanding northwards, there were both pelagic and demersal species (e.g., whiting *Merlangius merlangus* and greater argentine *Argentina silus*). However, a larger proportion of the pelagic species showed a northward expansion (58%), compared to demersal species (26%), as expected based on the greater mobility of the pelagic compared to most demersal species (Sunday et al., 2015).

The fish species included in this study did not respond equally to climate warming. Some species showed rapid northward distributional expansion, whereas other species did not display northward range edge shifts. As an example of species rapidly moving north, the commercially important Atlantic mackerel (*Scomber scombrus*) appeared during the last decade in all areas but the northernmost coastal ones (west of 25°E). This boreal, pelagic species has, since the mid-2000s, also been observed more commonly in Icelandic waters and around Svalbard (Berge et al., 2015; Olafsdottir et al., 2019). Other species, such as the greater forkbeard (*Phycis blennoides*), were present only in the southern part of the study area at the beginning of the study period and appeared further north only in later years. The latter may be explained by the fact that this demersal, south boreal species has a higher temperature affinity and does not keep track of climate velocities. As such, the species appeared progressively further north and increased in abundance throughout the study period, even though the temperature curves flattened during the last decade. In contrast, the boreal snake pipefish (*Entelurus aequoreus*) was absent from the study area most of the study period but appeared along the entire coast during the warm years 2005–2007. The transient appearance of this weak swimmer has previously been explained by a temperature-driven enhanced reproduction and a northwards transportation by the warm North Atlantic current (Fleischer et al., 2007).

Observations of rapid redistributions of fish related to water temperature changes, suggest that environmental tracking behavior often mediates the response (Fosshem et al., 2015; Pinski et al., 2013). However, distributional shifts and range expansion may, in addition, be affected by changes in population size. It is expected that the geographic range of a species will increase with increasing population size, which could lead to expanding the northern distribution limit also without temperature tracking (e.g., Adams et al., 2018; McCall, 1990; Simpson & Walsh, 2004). This could be the case for nine species in the present study, which showed coinciding increase in abundance and northward range expansion during the study period. However, there were also 14 species that increased in abundance without northward expansion, and 10 species moving northward without a significant increase in abundance. Thus, it seems likely that there are different causal explanations for individual species' poleward range expansion.

In addition to the observed long-term trend in water temperatures and associated changes in diversity and composition in the coastal fish communities, the results indicated the occurrence of more abrupt changes in diversity and composition in the early 2000 (Figures 3b and 4b). This corresponds in time with observations of increasingly higher temperatures across the North Atlantic in more offshore systems (Husson et al., 2022; Mohamed et al., 2022; Skagseth et al., 2022). Climatic shifts, with an amplified warming trend, were identified around 2004 across the entire Barents Sea (Mohamed et al., 2022), and a change in the ecosystem dynamics was identified by Johannesen et al. (2012) after 2006–2008. In the period from 2002 to 2004, there was also a substantial increase in the volume of relatively warm Atlantic water transported into the Barents Sea (Myksovoll et al., 2013), which may influence the distribution of different fish species. Water temperature measurements along the coast (Figure 2) indicate a warmer period than previously around this time also in coastal areas.

4.4 | Ecological reorganization and its implications

The documented rapid increase in fish biodiversity and the homogenization of species composition are likely to have important ecological implications. Poleward range expansion of southern species and the resulting borealization of Arctic fish communities are associated with functional change and food web reorganization (Ingvaldsen et al., 2021). The newly established co-occurrences of boreal and Arctic species along the North Norwegian coast indicate the climate-driven emergence of new ecological interactions that can impact population dynamics and reorganize the food web. The addition of new species and feeding links modifies the structure of the coastal food web, possibly affecting its robustness to perturbation, as seen in the adjacent Barents Sea (Ingvaldsen et al., 2021; Kortsch et al., 2015; Pecuchet et al., 2020).

The exact impact on the northern coastal ecosystems will depend on the characteristics and traits of the arriving fish species. In the Barents Sea, redistribution of species with boreal traits, such as generalism and large body size, has been suggested to negatively affect resident Arctic species by increasing competition and predation (Kortsch et al., 2015; Pecuchet et al., 2020). The increasing abundance of these incoming species is also expected to enhance top-down regulation in the existing ecosystem (Kortsch et al., 2015). In other systems, northward distribution shifts were also observed in small-sized fish species (Perry et al., 2005), which may serve as prey for higher trophic levels such as seabirds, marine mammals, and predatory fish.

In addition to the ecological impact of the newly established boreal species coming from the south-west, Norwegian coastal ecosystems are exposed to ongoing expansions of introduced species from the east (red king crab *Paralithodes camtschaticus* and pink salmon *Oncorhynchus gorbuscha*), and human activities across multiple sectors. Climate-driven fish redistributions and associated changes to coastal ecosystems are likely to affect coastal human communities

that strongly depend on marine resources (He & Silliman, 2019; Pörtner et al., 2022), which entails the need for climate adaptation in coastal management.

4.5 | Limitations of the study

Our findings document substantial and rapid change in fish diversity and composition along the coast of Norway. Whereas the main trends and patterns shown are reliable, our estimates are affected by the survey sampling design. Variation in sampling effort and catchability, particularly the difference between pelagic and demersal species, may have affected the results. The same sampling gear was used throughout the study, and although the used gear is not tailored for pelagic species, there is no reason to expect a systematic change in the likelihood of pelagic species being caught throughout the study period. As pelagic species have lower catchability and displayed a greater propensity for northward expansion than demersal species, it is possible that we underestimate the magnitude of the community responses to climate warming.

4.6 | Conclusions

We have documented a rapid increase in diversity and homogenization of fish communities along the Norwegian coast over the last 25 years, coinciding with increasing sea water temperatures.

Such changes of coastal fish biodiversity are expected to have important implications for ecosystem structure and function, with possible impacts on ecosystem robustness. Changes in coastal ecosystems due to climate-driven fish redistributions are likely to impact coastal human communities reliant on marine resources. The observed poleward redistributions of fish affecting diversity and composition stress the urgent need for a climate adaptation of integrated coastal management.

AUTHOR CONTRIBUTIONS

Anna Siwertsson: Conceptualization; data curation; formal analysis; visualization; writing – original draft; writing – review and editing. **Ulf Lindström:** Conceptualization; data curation; funding acquisition; visualization; writing – original draft; writing – review and editing. **Magnus Aune:** Writing – original draft; writing – review and editing. **Erik Berg:** Data curation; writing – review and editing. **Jofrid Skarøhamar:** Data curation; visualization; writing – review and editing. **Øystein Varpe:** Writing – review and editing. **Raul Primicerio:** Conceptualization; formal analysis; funding acquisition; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at DRYAD: <https://doi.org/10.5061/dryad.zs7h44jhf>. Water temperature data is publicly available at: www.imr.no/forskning/forskningsdata/stasjoner/view/initdownload.

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