RESEARCH ARTICLE

Diversity and Distributions **WILEY**

Recent warming causes functional borealization and diversity loss in deep fish communities east of Greenland

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Abstract

Aim: We assessed temporal trends in functional diversity of the deep-sea demersal fish communities of East Greenland to characterize ecological responses to rising sea temperatures.

Location: The study region encompasses a shelf and slope area located offshore between 63°N and 66°N, east of Greenland.

Methods: A unique dataset of demersal fish abundance covering a depth range of 1500 m over 18 years was combined with a fish trait dataset which included a mix of quantitative and categorial traits that characterized species' morphology, feeding strategy, habitat, and life history. We analysed the species by trait matrix using principal component analysis (PCA). To investigate trait patterns across the communities (sites), community weighted mean (CWM) traits were calculated and analysed using PCA. Further, depth specific and temporal trends in functional diversity indices were calculated.

Results: We found signs of a taxonomic and functional borealization, associated with a loss in functional diversity, down to 1000 m, characterized by an increase in mobile generalists and a decrease in bottom dwelling benthivores.

Main conclusions: The increased dominance of boreal species traits was not sufficient to compensate for the loss of Arctic species traits leading to declining functional diversity. The decrease in functional diversity may negatively affect ecosystem robustness to environmental change. These responses are most likely not unique to this study area and call for more attention to ecosystem considerations in climate change management strategies in the deep-sea.

KEYWORDS
Arctic, continental slope, deep-sea, functional diversity, traits

1 | INTRODUCTION

Rapid warming in the Arctic is causing changes in ocean processes that affect species distributions, ecological interactions, and ecosystem functioning (Fossheim et al., 2015; Ingvaldsen et al., 2021; Meredith et al., 2019; Mueter & Litzow, 2008; Pecuchet et al., 2020). In Arctic marine ecosystems, such as the Barents Sea and the Bering Sea, boreal fish species are quickly redistributing poleward as a response to warming (Alabia et al., 2020; Fossheim et al., 2015; Hiddink & Ter Hofstede, 2008; Mueter & Litzow, 2008; Pinsky et al., 2013; Stevenson & Lauth, 2019; Sunday et al., 2012). This process is called "borealization" of Arctic communities. At these high-latitudes, marine ecosystems encompass transition zones between Arctic and boreal biota that are undergoing some of the most pronounced climate-driven changes in biodiversity (Blowes et al., 2019; Burrows et al., 2019; Horta e Costa et al., 2014). As boreal species shift poleward in high-latitude seas, species richness tends to increase in accordance with general predictions (García Molinos et al., 2016; Johannesen et al., 2012). The few studies that address the functional diversity implications of ongoing species redistribution in the high-latitude seas find an increasing trend in local diversity with warming (Frainer et al., 2021, 2017; Wiedmann, 2014). Larger, more motile generalist species, for example Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), are able to undergo rapid range-shifts and have been entering Arctic regions, increasing functional diversity there (Frainer et al., 2021).

The rapid changes in functional diversity and composition observed in Arctic biogeographic transition areas are due to the distinct functional traits of boreal versus Arctic fish species (Frainer et al., 2021, 2017). Boreal species entering the Arctic are typically large mobile generalists, as opposed to the Arctic specialist benthivores (Kortsch et al., 2015; Pecuchet et al., 2020). Functional diversity is also influenced by the number of species in a community (species richness), with traits richness (functional richness) typically increasing with species richness. In the Arctic, climate warming may lead to loss of Arctic species which experience temperatures exceeding their thermal tolerance and unfavourable environmental conditions (Ingvaldsen et al., 2021). Such species loss could negatively impact functional diversity if the increase of boreal species functional traits does not compensate for the loss of Arctic species functional traits (Danovaro et al., 2008; Pinho et al., 2011). However, if the species that are lost are functionally redundant and new immigrating species are functionally unique, functional diversity could increase despite a decline in species richness. Such trends in functional diversity provide important insights into the implications of climate warming for assembly processes and for ecosystem functioning and vulnerability (Buisson et al., 2013; Frainer et al., 2021; Violle et al., 2014). Given the substantial impact of warming on fish functional characterization and diversity in Arctic shelf seas, deep-sea fish communities (>200 m), which are adapted to deep-sea stable environmental conditions, might have also been affected by changes in sea temperatures.

The deep-sea has been warming more slowly than the sea surface (Cheng et al., 2019; Desbruyères et al., 2017; Meinen et al., 2020), resulting in a delayed ecological response (Yasuhara & Danovaro, 2016). However, regional differences exist, with higher rates of warming reported in the sub-Arctic (Emblemsvåg et al., 2020), Arctic (Bergmann et al., 2011), and Antarctic (Smith et al., 2012). A future increase of climate velocities in the deep-sea has been predicted by Brito-Morales et al. (2020). Such rapid warming would greatly affect a vast and valuable deep-sea ecosystem (Armstrong et al., 2012; Ramirez-Llodra et al., 2010) considered more vulnerable to environmental change due to species' slow life history traits (longevity, slow growth, late maturing, low fecundity) and specialized life style (Drazen & Haedrich, 2012; Wiedmann et al., 2014b).

In the deep-sea, species are filtered by the environment which favours a narrow set of traits to cope with limited food availability, light scarcity, and harsh environmental conditions (Danovaro et al., 2008; Drazen & Haedrich, 2012; Keddy, 1992). Thus, functional diversity would be expected to decrease with depth. However, taxonomic and functional richness of demersal fish along the continental slope of Rockall Trough, in the East Atlantic, were shown to increase with depth down to 800 m, below which functional richness started to decrease as a result of increasing specialization to the deep-sea habitat (Mindel et al., 2016). This is in congruence with a recent study from New Zealand where increasing functional diversity of fish species was found to decrease with depth ranging from 50 to 1200 m (Myers et al., 2021). Functional redundancy, defined as the traits overlap between species, also followed a decreasing trend with depth, in the Mediterranean Sea (Farré et al. 2016). This suggests that even if functional diversity is relatively high in the deep-sea, there are few species sharing similar traits. This makes the deep-sea vulnerable to environmental stressors and fisheries, as the loss of species will cause a loss of ecosystem functions.

Recent warming has impacted deep-sea fish communities in East Greenland, south of the Denmark Strait, in a transition zone between the Arctic and the Atlantic Ocean. Since the late 1990s, bottom temperatures have increased by 0.2–0.5°C (Emblemsvåg et al., 2020; Post et al., 2020), and sea surface temperatures within the Irminger Current have increased by approximately 1°C (Jansen et al., 2016). This region has likely gone through a process of Atlantification, with stronger influence of Atlantic water (Irminger Current) causing a reduction of sea ice, less stratification, higher surface salinity and higher mixing of the water column (Ingvaldsen et al., 2021; Lind et al., 2018; Vihtakari et al., 2018). In this transition zone, many species are living close to their upper or lower limits of temperature tolerance and should thus be strongly affected by climate change. In other transition seas at this latitude, Atlantification of water masses causes borealization of fish communities, followed by a general rise in species richness (Chaudhary et al., 2021; Frainer et al., 2017; Hiddink & Ter Hofstede, 2008; Johannesen et al., 2012). Surprisingly, contrary to the expected rise in species richness which is found elsewhere in the North Atlantic, there has been a decrease in species richness and total abundance in deep-sea

demersal fish communities (400–1500 m) between 1998 and 2016 in East Greenland (Emblemsvåg et al., 2020). A restructuring of the fish community with an increased importance of boreal species took place in the mid-2000s with rapid changes at depths between 350 and 1000 m, where the warm Irminger Current mixes with the cold East Greenland Current. These changes in species composition are expected to affect functional composition and diversity, with important implications for local fishery and ecosystem management.

Here we assess changes in fish functional composition and diversity associated with warming off East Greenland. We investigated spatio-temporal changes in fish communities based on a unique dataset of demersal fish abundances, covering a depth range of 1500 m over 18 years, combined with an extensive fish trait dataset. We expected a borealization of functional composition driven by increasing occurrence of boreal species. Further, the documented loss in species richness (Emblemsvåg et al., 2020) is expected to affect negatively functional diversity, raising the question of whether the addition of boreal traits can compensate for the loss of Arctic ones, thereby maintaining functional diversity. We also expected that trends in functional composition and diversity would differ between depths due to different oceanographic features and different rates of warming.

2 | METHODS

2.1 | Study area

The East Greenland marine ecosystem encompasses a shelf and slope area located offshore between 63°N and 66°N. The mean depth of the shelf is about 350 m, whereas the continental slope extends to approximately 3000 m. The region is influenced by cold water originating in the Arctic and flowing southward (East Greenland current) through the Denmark Strait along the shelf break and slope (Våge et al., 2011). South of the Denmark strait, the cold water meets and mixes with the warm Atlantic waters (Irminger current), which creates a vertical front of different water masses at the shelf break and upper slope (Figure S1).

The study area is an international fishing ground where several nations (Norway, Germany, Greenland, and Russia) have been targeting Greenland halibut (*Reinhardtius hippoglossoides*), two redfish species (*Sebastes norvegicus* and *S. mentella*), and Atlantic cod for decades. Due to climate warming, new species have entered the area and are being fished, including mackerel (*Scombrus scombrus*) that has shifted its distribution westward into Greenland waters (Jansen et al., 2016).

2.2 | Sampling design

Abundance data on demersal fish species were obtained by combining 18 years of data (1998–2016, except 2001 due to lack of data) from two surveys. Sampling of the shallow shelf areas (0–400 m)

was conducted by the Thünen Institute of Sea Fisheries, Germany, whereas the Greenland Institute of Natural Resources covered the slope and deeper parts of the shelf and slope (400–1500 m) between the 3 nm line (baseline) and the 200 nm (Exclusive Economic Zone) or middle line to Iceland. The German survey uses a random stratified sampling design, whereas the Greenlandic survey uses a buffered random stratified sampling design (Kingsley et al., 2004). Both surveys use bottom trawl nets of the rock hopper type and heavy bottom gear. Towing speed was 4.5 knots for the German survey and 3 knots for the Greenlandic survey. This difference in towing speeds might affect the catchability of larger, more mobile individuals with the ability to avoid the net, as for example Atlantic cod and haddock (Breen et al., 2004; He, 1991). Atlantic cod, which is one of few large mobile species within this dataset, is most successfully caught under towing speeds between 2 and 4.5 knots (Winger et al., 2000). Hence, it seems unlikely that the difference in trawling speed affected our results significantly. Both surveys use a net with 140 mm mesh size and a small-mesh liner in the codend. Since the same species were caught in the two surveys consistently over time and the two surveys do not overlap in depth, we consider the data from the two surveys to be comparable. For the Greenland survey, sampling dates changed in 2008 from June (1998–2007) to August (2008–2016). A change in sampling time could have caused a shift in species abundances and thereby affected the results. However, after thorough checking, both descriptively and by use of statistical tests (change point analysis), we conclude that the change in survey time did not likely influence the observed changes in species composition (Emblemsvåg et al. 2022). The catch was sorted, identified to the species level, weighed, and counted. A total of 1303 sites (sampling stations) were used for further analyses, hereof, 590 sites from the shallow German survey and 713 sites from the Greenlandic deep-water survey (Figure S1).

2.3 | Selection of species and traits

Because the dataset consisted of a large number of rarely occurring species, only species present in more than 1% of the stations (i.e., more than 13 sites) were included in the analyses, which resulted in a final dataset of 55 species out of the total 91 recorded species (Table S1). The 55 species included in the analyses represent more than 99.9% of the total recorded abundance. Catch per unit of effort was standardized to the number of individuals per swept km^2. The sampled area was divided into six strata, each of 150 m depth range, between 150 and 1050 m (150–300 m, 300–450 m, 450–600 m, 600–750 m, 750–900 m and 900–1050 m), and a deepest stratum between 1050 m and 1500 m depth, which was less intensively covered by the survey. The chosen depth strata balanced the need for high depth resolution and for sufficient sample size within each stratum to ensure statistical robustness. Hereafter we refer to results concerning multiple consecutive strata by writing the minimum and maximum range (e.g., 300–750 m instead of 300–450 m, 450–600 m, 600–750 m).

The fish traits dataset was compiled based on an online database of traits of marine fish species from the North Atlantic and Northeast Pacific (Beukhof et al., 2019) and from Fishbase (Froese & Pauly, 2017). We selected 19 traits, related to habitat affinity, feeding ecology, life history, and mobility, that influence responses to environmental change and ecosystem function of fish species (Frainer et al., 2017; Wiedmann et al., 2014a). Life history traits included offspring size, fecundity, maximum length and longevity (as maximum registered age; Table S1) (Wiedmann et al., 2014a). Mean trophic level was calculated based on species prey items (Froese & Pauly, 2017), and fish were categorized into piscivorous, benthivorous, planktivorous, and generalist. Affinity to feeding habitat was included to define whether species feed at or near the bottom or in the pelagic, distinguishing them as demersal, pelagic, bathypelagic or benthopelagic. The shape of the body and aspect ratio of the caudal fin can inform about fish lifestyle and relate to functions such as mobility, feeding strategy, and habitat use (Friedman et al., 2020; Martinez et al., 2021). Body shape is herein described as eel-like, fusiform, elongated, flat, and short and/or deep, whereas aspect-ratio is a measure of the fin shape (Aspect ratio = h^2/s; where h is height of the caudal fin, and s is surface area of the fin) (Pauly, 1989). High-aspect ratio fins have lower drag and higher lift than lower aspect-ratio fins and therefore yield higher swimming speed. Species biogeography (Arctic vs boreal) was based on the Atlas of Marine Fishes of the Arctic Region (Mecklenburg et al., 2018).

2.4 | Data analysis

Taxonomic and traits data were used for the functional characterization of taxa and to estimate community weighted mean (CWM) and functional diversity. Three measures of functional diversity were estimated: functional richness, the amount of trait space occupied by the species within a community and based on species presence/absence; functional evenness, the regularity of the distribution of species abundances and dissimilarities in functional space; and functional dispersion, the mean distance of all species to the abundance-weighted centroid of the community in the trait space. Before the analysis, the quantitative traits were log transformed (log^{10}) due to right skewness, whereas categorical variables were coded as binary. The trait dataset was scaled (zero mean and unit variance), before running multivariate analysis. To investigate how species are characterized by their traits, we analysed the species by trait matrix using principal component analysis (PCA). To investigate trait patterns across the communities (sites), community weighted mean (CWM) traits were calculated using the R package *FD* (Laliberté et al., 2014), providing the average trait values in a community weighted by species abundances (Lavorel et al., 2008). The 1303 sites by 19 CWM traits' matrix were first analysed using PCA and summarized with a biplot visualizing the centroids of depth strata by year in trait space. An ANOVA was run on the scores of the first four principal components as function of depth and year, including an interaction term. Mean scores for depth stratum were

plotted to visualize the spatial patterns of CWM functional traits. The CWM traits matrix was further analysed by redundancy analysis (RDA) with depth-strata and year as explanatory variables. An interaction term was included to determine depth strata-specific temporal trends in traits characterization. The RDA results were summarized by a tri-plot, and the inferential statistics were performed by permutation (Appendix S1).

To calculate functional diversity indices, the binary traits sharing similar biological or functional information were rearranged into three groups: a group describing feeding habitat (benthopelagic, demersal, bathydemersal, bathypelagic), a group for feeding ecology (generalist, benthivorous, piscivorous, and planktivorous), and a group for body shape (fusiform, eel-like, short and/or deep, flat and elongated). We used the modified Gower dissimilarity function 'gawdis' (R package *gawdis*; de Bello et al., 2021) on the trait list (feeding habitat (group), feeding ecology (group), body shape (group), trophic level, aspect ratio, offspring size, fecundity, maximum length, and maximum age) to ensure more uniform contributions of each of the traits and groups when calculating the multi-trait dissimilarity. The trait weights were optimized within- and between-groups by the "gawdis" function to equalize their contribution in the calculation of the dissimilarity matrix (de Bello et al., 2021). Species richness was calculated as the number of unique species at each site and species evenness was measured as Pielou's index. To evaluate changes in diversity and functional diversity over time and across depth, the taxonomic and functional diversity indices were modelled using generalized additive models (GAM). Models addressing temporal development were run for three depth strata (150–350 m, 350–1000 m and 1000–1500 m), and models of depth profiles for three different time periods (1998–2004, 2005–2010 and 2011–2016). The three depth strata and time periods were based on results from Emblemsvåg et al. (2022), which showed that most temporal changes in fish community structure were observed in depths between 300 and 1000 m from 2005 until 2010, whereas little temporal change was observed in the shallower and deeper strata and before 2005 or after 2010.

Data were analysed using software R version 4.0.3 (R Core Team, 2020). The PCA, RDA, and permutation analyses were computed using the package *vegan* (Oksanen et al., 2020). Functional richness, functional dispersion, and functional evenness were calculated using the R package *FD* (Laliberté et al., 2014). R package "mgcv" was used for GAMs (Wood, 2011). The results were plotted using the R package *vegan* (Oksanen et al., 2020) *and ggplot2* (Wickham et al., 2016).

3 | RESULTS

3.1 | Functional characteristics of fish species

The East Greenland demersal fish traits displayed co-variation illustrated by the PCA results (Figure 1). The first axis of variation (PC1), accounting for 14.2% of the fish traits variation, depicted a
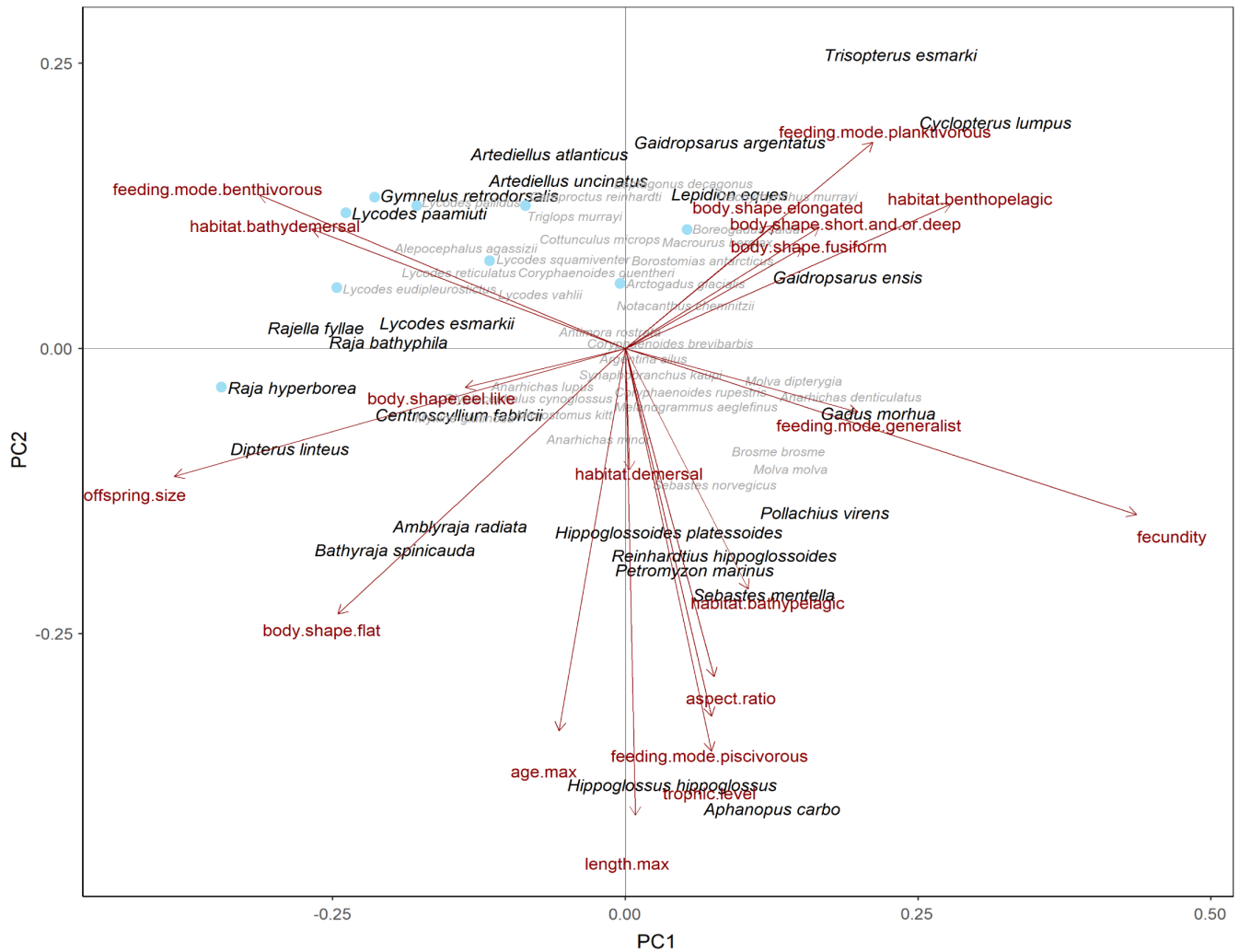
FIGURE 1 Biplot of principal component analysis (PCA). Results for East Greenland fish functional traits. Red labels represent traits and black labels represent the species. Blue dots mark the Arctic species characterized by Mecklenburg et al. (2018)
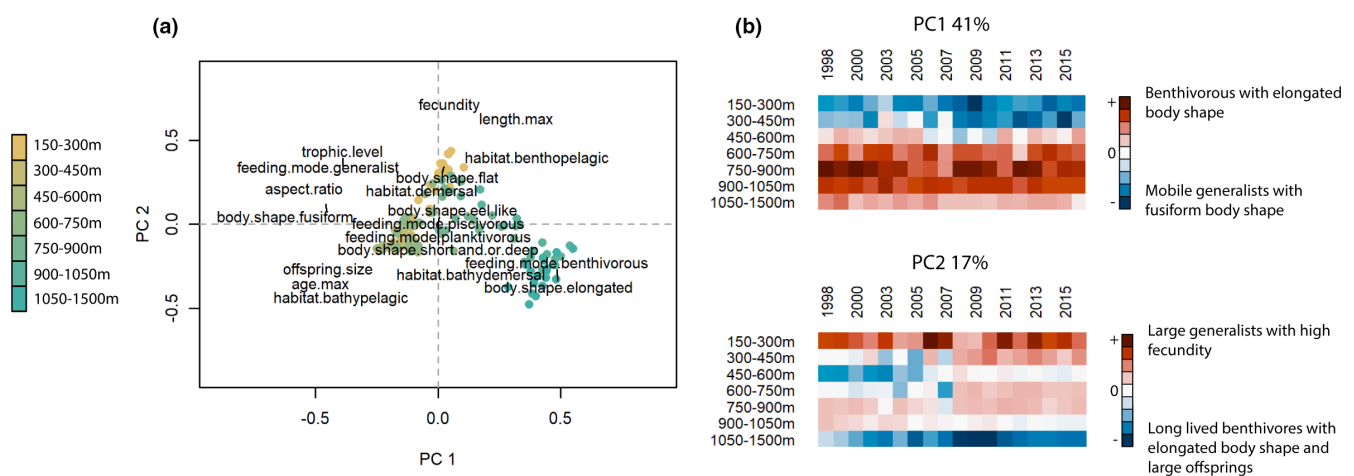

FIGURE 2 Principal Component Analysis (PCA) of Community Weighted Mean traits (CWM). (a) PCA biplot of PC1 and PC2. The dots represent centroids of depth stratum/year and colour coded accordingly, yellow being the shallowest stratum and turquoise being the deepest stratum. (b) Heatmaps of the two PCs with year on the x axis and depth on the y-axis. Colours of the heatmap represent PCA axis mean scores. Schematic bars describe which main traits drive the gradient. Percentages indicate proportion of variance explained
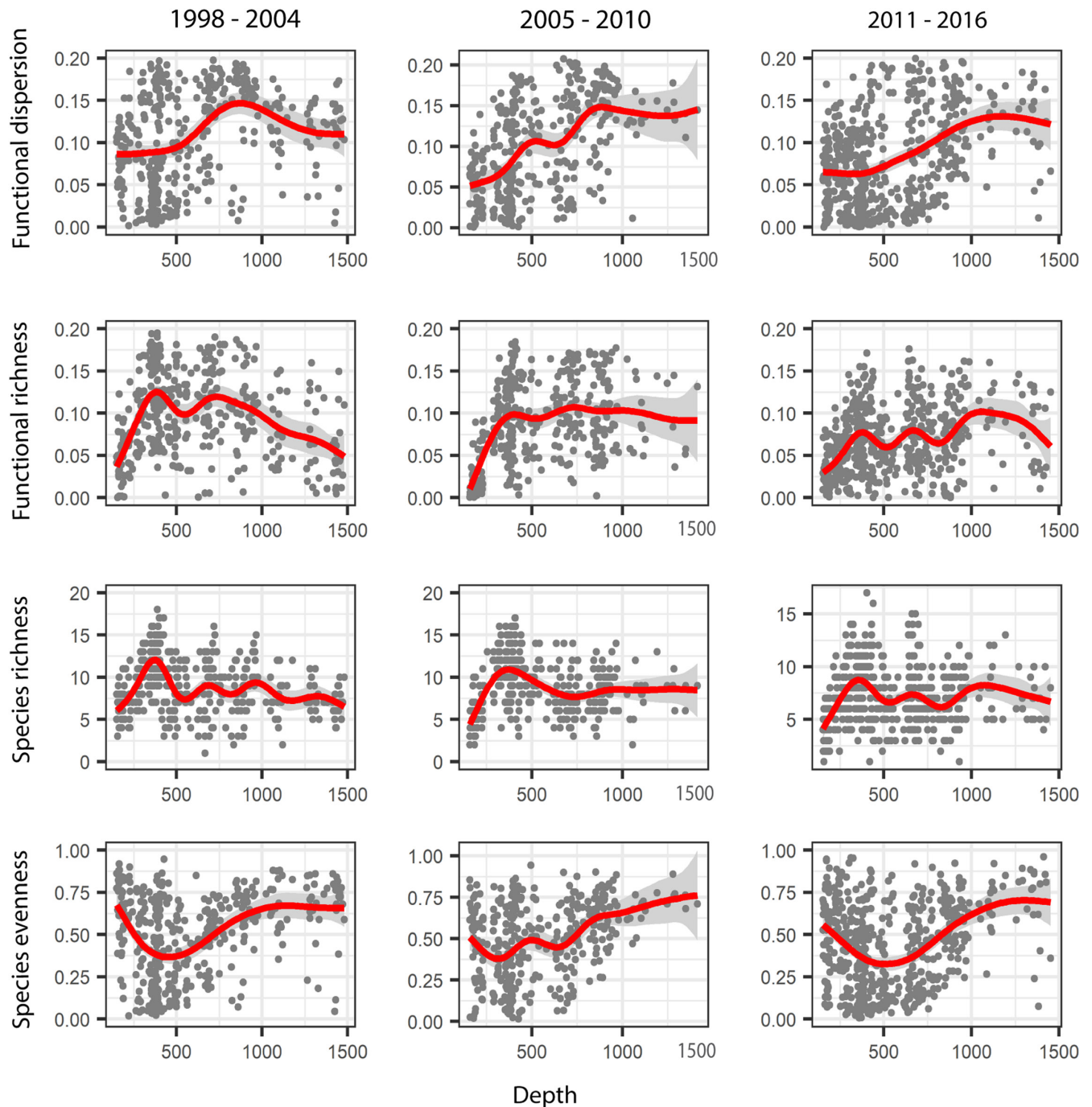
FIGURE 3 The depth profiles of diversity indices in three time periods. From top to bottom: functional dispersion, functional richness, species richness, and species evenness. From left to right: 1998–2004, 2005–2010, and 2011–2016. The red lines represent the smoother from a GAM model, grey dots represent each sample/site

gradient from bathydemersal benthivores species with large off-spring size and low fecundity to generalist species with high fecundity (Figure 1). The latter traits are typical of boreal species such as Atlantic cod, pollock, (*Pollachius virens*), and blue ling (*Molva dypterygia*), whereas the former are typical of bottom dwelling and smaller Arctic species such as eelpouts (*Lycodes* ssp, *Gymnelus retrodorsalis*). The second axis (PC2), accounting for 13.7% of traits variation, captured a slow-fast life history continuum, going from species with a large body size that are long lived, typically redfish, Atlantic halibut (*Hippoglossus hippoglossus*), and Greenland halibut (*Reinhardtius hippoglossoides*), to species that are fast growing and maturing early, such as Norway pout (*Trisopterus esmarkii*), lumpfish (*Cuclopterus lumpus*), and Arctic rockling (*Gaidropsarus argentatus*). Species with negative loadings on PC1 and PC2 were flatfishes (mainly rays), whereas species with positive loadings on PC1 and PC2 were species with fusiform, elongated, and short/deep body shapes.

3.2 | Functional characterization of fish communities

The fish communities displayed clear spatial patterns and temporal trends in CWM traits, as seen in the ANOVA results for the four principal components (PCs). The two first PCs are displayed in Figure 2, whereas PC 3 and 4 are displayed in Figure S2. Statistics are given in Table S2. Depth had significant effects on all four principal components (Table S2). Depth dependent changes in time (interaction term) were significant for PC2-PC4, whereas time alone was significant for PC1, PC2, and PC4. Based on visual inspection of the plots, PC1 separates fish communities in the shallower strata (150 m - 450 m), with higher abundance of mobile generalists and species with a fusiform body shape, from fish communities in the deeper strata (450–1500 m) with higher abundance of benthivores with an elongated body shape. PC2 spatially separates fish communities with higher abundance of shallow-living large generalists with high fecundity from communities with long lived benthivores with elongated body shape and large offspring (egg size). At intermediate depths (450–750 m), there seems to be an increasing and decreasing trend of these traits, respectively (Figure 2). PC3 and PC4 displayed temporal trends in the loading values at depths between 300 and 750 m (Figure S2). PC3 distinguishes shallow (150–300 m) and deep (750–1500 m) communities with higher abundance of large flatfishes, feeding in the benthopelagic from mobile demersal with high fecundity in intermediate depths (300–750 m), showing a decreasing trend (Figure S2). In PC4, the gradient is driven by demersal flatfishes with large offspring size, present at all depths, versus mobile species with high fecundity, feeding in the bathypelagic at intermediate depths (450–600 m). The latter were decreasing through time (Figure S2). The RDA results also showed significant spatio-temporal effects in CWM, summarized by a tri-plot (Figure S3). Description of RDA results and statistics are given in the Appendix S1 and Table S3.

3.3 | Depth gradients of functional diversity

Functional dispersion was highest at depths between 800 and 1000 m across the three time periods (Figure 3). In the first period, 1998–2004, functional dispersion was fairly stable until 500 m then increased until 900 m and decreased again in the deepest sites. Functional richness displayed different shallow depth profiles across the three periods. During 1998–2004, species richness was lowest in the shallower depths and highest between 400 and 700 m before gradually decreasing towards 1500 m. From 2005 and onwards the peak at 400 m was replaced by a steady increase in functional richness down to around 900 m, below which it decreased again (Figure 3). Species richness was highest around 350–400 m in all three periods, but most distinctly in the first period. For all time periods, the profile of species evenness declined with depth to about 500 m, to increase again, reaching the highest values in the deepest sites. It is to be noted that the deepest depth layer was less sampled compared with the shallower depth layers, which may have caused

the observed lower functional diversity at this depth. Trends in functional diversity and species richness across depth were significant in all three time periods. Model statistics are given in Table S4.

3.4 | Temporal changes in functional diversity

In the two shallower depth strata (150–350 m, 350–1000 m), functional dispersion decreased after 2005, and functional richness displayed a decreasing trend throughout the study period (Figure 4). Species richness decreased throughout the study period in the shallower depth strata and after 2005 in the intermediate depth strata. The temporal development in species evenness resembled that of functional dispersion in the two shallower depth strata. Temporal trends in functional diversity and species richness were significant, except in the deepest strata (1000–1500 m; Figure 4, Table S5).

4 | DISCUSSION

The functional traits of demersal fish species in East Greenland displayed ample variation both across species, with trait values distinguishing boreal and Arctic species, and across space, with depth habitat preferences. In shallower, colder waters, we found few species with only moderate functional traits variation; functional dispersion increased with depth. The functional characterization of fish communities changed with warming, resulting in an increased prominence of boreal fish species. At intermediate depths, the numerical importance (abundance) of benthivores decreased, whereas that of generalists increased over the study period, reflecting possible changes in productivity and available resources associated with sea warming and Atlantification. Taxonomic and functional richness decreased over the study period at depths above 1000 m, due to the loss of species with a specific set of traits and insufficient compensation by boreal traits. The relatively slow colonization rate by boreal species might be explained by the complex regional oceanographic system and by topographical constraints (Emblemsvåg et al., 2020; Rutterford et al., 2015). The functional reconfiguration and loss of diversity are likely affecting ecosystem functioning and vulnerability and need to be accounted for by fisheries management.

4.1 | Functional characteristics of fish species

The distinction in functional characteristics between Boreal and Arctic species concerned traits related to life history, foraging, and mobility. Boreal species had larger body size, higher fecundity, broader diets and greater preference for pelagic resources than bottom dwelling Arctic species, reflecting adaptations to different environmental conditions (Frainer et al. 2017). Arctic species live in a strongly seasonal and harsh environment where specialization in benthic prey, relatively low fecundity, and greater investment in individual offspring of larger size help to increase their chance of
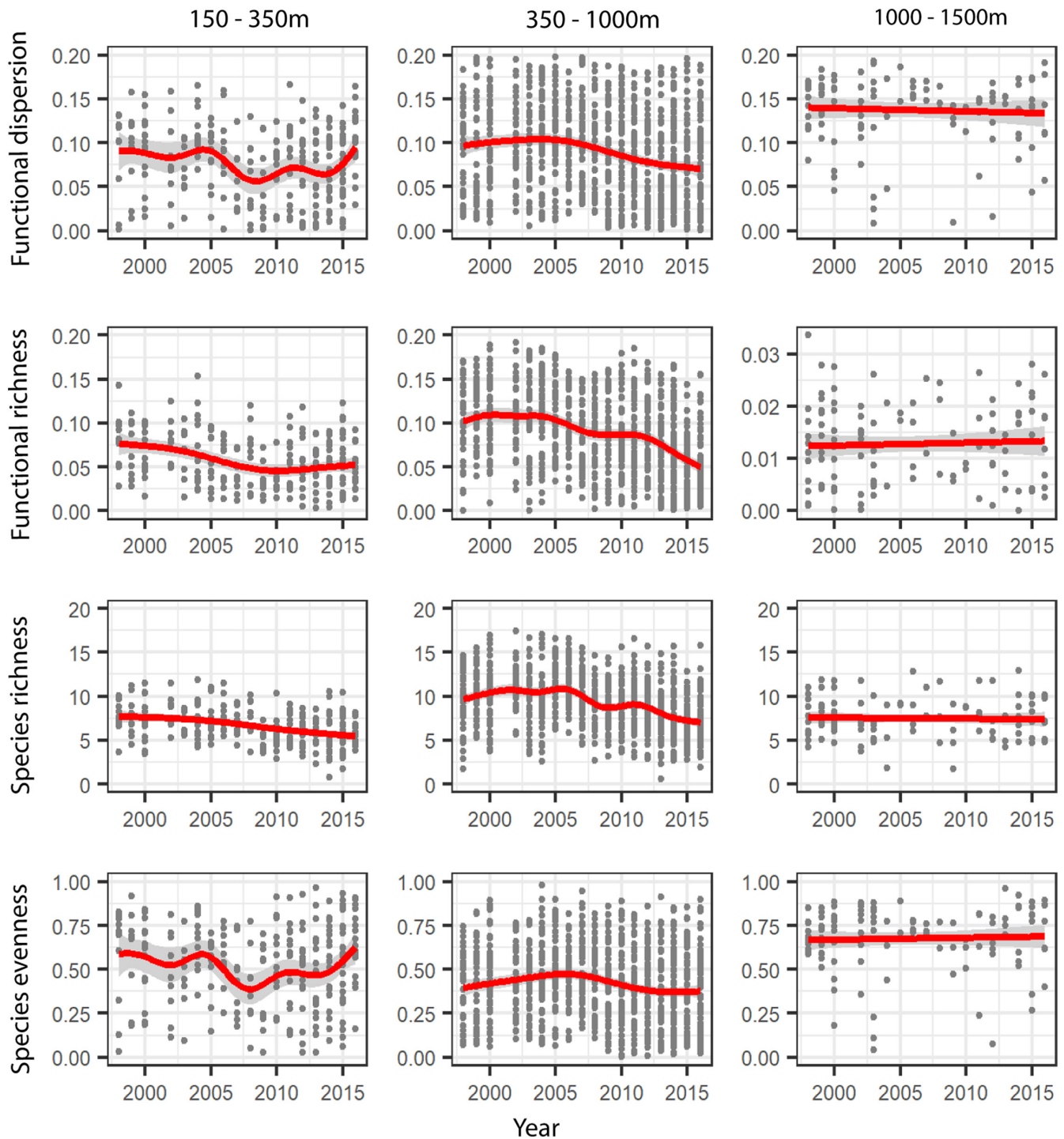
FIGURE 4 Temporal developments of diversity indices in three depth strata. From top to bottom: functional dispersion, functional richness, species richness, and species evenness. From left to right: 150–350m, 350–1000m, and 1000–1500m. The red lines represent the smoother from a GAM model, grey dots represent each sample/site

survival (Marshall, 1953). A larger larva is generally a better swimmer with higher lipid storage capacity, and therefore it may better cope with low or heterogeneous food supplies (Allen et al., 2008; Bashey, 2008; Marshall & Burgess, 2015). As documented in other Arctic marine ecosystems (Wiedmann et al. 2014), Boreal and Arctic species were also separated along the slow—fast life history continuum, with boreal species such as Atlantic cod, tusk (*Brosme brosme*),

and haddock (*Melanogrammus aeglefinus*) having slow life histories, maturing later at a larger size and living longer than Arctic species such as the eelpouts (*Lycodes* spp.; Wiedmann et al., 2014a).

Boreal species, like Atlantic cod or redfish, could also be distinguished in terms of foraging behaviour. They are generalists feeding on both benthic and pelagic prey, as opposed to Arctic species more specialized on benthic prey. Boreal demersal species have adapted to

environments with higher and less pulsed pelagic productivity, and thereby they may rely on pelagic prey (van Denderen et al., 2018). However, some feed on prey close to the sea floor (e.g., wolffishes) and others practice diel vertical foraging migrations (e.g., Greenland halibut), so that food availability higher or lower in the water column can determine the occurrence and success of these predators (van Denderen et al., 2018). Arctic fish have specialized on a rich community of benthic prey, sustained by organic deposition from a pelagic compartment that is not depleted by pelagic consumers, as also seen in bottom communities of the Bering Strait (Waga et al., 2020). Foraging-related traits also varied with depth, with generalist species living deeper than the typical benthivores which are less mobile, as indicated by distinctions in morphological traits (low aspect ratio and elongated body shape). Higher swimming capacities are common in generalists that often feed on both benthic and pelagic prey, providing them with an advantage in deeper waters where the food supply might be scattered and unstable and sometimes limited (Drazen & Sutton, 2017). A similar relationship with depth was found in the North Atlantic, where there was higher dominance of pelagic feeders at 900–1700 m (Mindel et al., 2016).

4.2 | Depth gradient in functional diversity

We found the highest species richness between 300 and 400 m depth, coinciding with the depth of the shelf-break. Relative to the shelf, the area above and off the shelf break and upper slope is considered highly productive as this is where the colder and less saline East Greenland Current meets and mixes with the warm and saline Irminger Current (Boertmann et al., 2020). High nitrate concentrations, controlling phytoplankton production, were found in surface waters above the shelf along northeast Greenland, corresponding with the frontal zone between water masses and higher mixing of the water column (Boertmann et al., 2020). The shelf break should thereby provide abundant food supply for copepods and other invertebrate herbivores, especially during late summer, supplying energy to higher trophic levels such as fish, benthos, marine mammals, and seabirds (Boertmann et al., 2020). Contrary to other findings in the Northeast-Atlantic, showing a steady increase in species richness down to 1500 m (Mindel et al., 2016), species richness in East Greenland declines after 400 m and stabilizes at around 500–600 m. This pattern is more evident in the first time period (1998–2004) considered and least pronounced in the last time period (2010–2016), indicating a temporal development in depth profile with warming, a development also seen in functional richness. This causes the depth profile of functional dispersion to shift from having a peak at around 900 m in 1998–2004 to an increasing trend with depth throughout the investigated depth range in 2010–2016, an outcome also influenced by species evenness increasing with depth. The transition phase in 2005–2010 is consistent with rapid changes in fish community abundances reported within this period (Emblemsvåg et al., 2022). Lower species richness and functional richness at 400 m depth in the years after 1998–2004 and the

concomitant increase in these indices below 400 m depth could indicate redistribution towards deeper waters, as suggested for sub arctic species in west Greenland (Lekanda et al., 2021). Such a vertical redistribution in response to warming waters is expected (Dulvy et al., 2008), especially when the depth-related temperature gradient is strong (Burrows et al., 2019), and latitudinal redistributions are restricted (Pinsky et al., 2013).

4.3 | Functional borealization

The increasing dominance of boreal traits detected in the deep-sea (300–900 m) indicates a likely shift in habitat characteristics and food availability driven by warming. The observed functional borealization is partly explained by environmental filtering acting on the temperature tolerance of fish (Sunday et al., 2012). As temperatures rise, the Arctic fish species will experience suboptimal thermal conditions that may eventually cause local population declines, whereas boreal species will benefit from warming given their higher temperature affinities (Fossheim et al., 2015; Frainer et al., 2017; Mueter & Litzow, 2008). However, the species with declining abundance were not exclusively Arctic ones, rather they were species of mixed biogeographic affiliation that share the benthivore feeding mode and low motility, indicating that thermal tolerance is not the only factor involved in the documented functional borealization. In addition to sea warming, the Atlantification of the Greenland sea may have caused increased pelagic production and altered environmental conditions in favour of boreal species (Ingvaldsen et al., 2021). The resulting biogeographic changes affect ecological interactions such as predation and competition that trigger further changes in the Arctic communities (Kortsch et al., 2015; Pecuchet et al., 2020).

The lack of temporal change in functional traits in the shallowest strata (150–300 m), representing the shelf region, is in accordance with the similar lack of response in fish community abundances (Emblemsvåg et al. 2022a). A likely explanation for these observations is the lack of influence of the warm Atlantic Irminger current on the shelf, which is manly dominated by the cold East Greenland Current. Along the slope, these two currents meet and mix, with the Irminger current being the likely source of a warming trend (Emblemsvåg et al., 2020). Such fronts between different water bodies are known to create favourable environments for primary production, foraging fish, and generalist feeding behaviour.

4.4 | Increasing dominance of generalists

The decline in species richness in East Greenland (Emblemsvåg et al., 2020, 2022) is largely driven by benthivores with low fecundity and motility, such as eelpouts (*Lycodes* spp.) and wolffishes. Boreal generalists may reduce the biomass of benthivores by increasing competition and predation pressure (Frainer et al., 2021). Further, changes in pelagic production and deposition brought about by the Atlantification may negatively affect food availability for benthivores

while improving conditions for pelagic feeders. Although long-term measurements of primary production are not available in East of Greenland, climate-related changes in pelagic production have been documented in the Fram Strait and West Greenland, with fast responses throughout the water column (Møller & Nielsen, 2019; Soltwedel et al., 2016). Such effects of warming and Atlantification have been described in other Arctic marine ecosystems experiencing changes in fish functional characterization similar to those documented in the east of Greenland (Frainer et al., 2021, 2017).

The documented functional reorganization of fish east of Greenland suggests an increased importance of the pelagic food-web compartment, as also seen in the Barents Sea (Oziel et al., 2020) and projected for the Bering Sea (Alabia et al., 2020). Higher dominance of demersal generalist species with the ability to utilize pelagic resources might increase food-web connectivity and benthic-pelagic coupling. Additionally, the loss of benthivores reduces the importance of the benthic compartment, resulting in a rewired food-web with altered energy pathways (D'Alelio et al., 2019; Kortsch et al., 2015). The food-web reorganization driven by fish functional borealization is thus likely to affect ecosystem functioning and vulnerability towards environmental stressors. An increased food-web connectivity and reduced modularity may promote the spread of perturbations across the food-web (Kortsch et al., 2015). If so, the eastern Greenland Sea might lose adaptive capacity due to declining functional diversity and experience reduced ecosystem robustness to perturbations due to increased food-web connectivity.

4.5 | Impact of fisheries

Fisheries can impact ecosystems by increasing mortality of target species and bycatches and by disrupting habitats with the use of destructive fishing gears such as bottom trawl (Gianni, 2004; Goñi, 1998; Rijnsdorp et al., 2020). Although fishing effort has decreased in this region over the study period (Emblemsvåg et al., 2020) and can thus not be considered a main driver of the observed diversity loss, it is important to consider the impact of fisheries and particularly the possible additive effect of warming (Levin et al., 2020). For Arctic species already suffering from sea warming, the additional pressure of fisheries may lead to local species loss. As warming drives borealization and diversity loss, the ecosystem becomes less resilient to fisheries and other human pressure. A precautionary approach to fisheries management may thus be appropriate under warming, particularly in deeper waters undergoing rapid changes. The same considerations would apply to similar biogeographical transition zones expected to respond rapidly and strongly to the effects of climate change.

4.6 | Decrease in functional diversity

The observed decline in functional diversity indicates that the addition of functional traits by boreal species entering the area is not sufficient to compensate for the observed local loss of species. The loss in species richness was accompanied by a decline in functional richness. Functional dispersion did not decline initially due to a compensation by increasing species evenness driven by higher abundance of boreal species. But after 2005, functional dispersion also declined. The shift in 2005 might have been caused by a loss of species with redundant traits up until this point. After 2005, there is no more redundancy of traits among species lost, which causes dispersion to decrease. The overall decreasing trend in diversity is contrary to findings in the Barents Sea, where functional diversity has increased with warming due to the addition of novel traits brought by range shifts of the boreal species (Frainer et al., 2021). Regional oceanographic and topographic constraints east of Greenland may limit the immigration of new boreal demersal species, making the area "semi enclosed" (Emblemsvåg et al., 2020), effectively reducing species redistribution. The loss of functional diversity threatens the maintenance of ecosystem function in an area undergoing rapid environmental change (Cadotte, 2017).

5 | CONCLUSION

The rapid, climate-driven functional borealization of the East Greenland fish community did not compensate for the local loss of Arctic fish species and their specific traits, and functional diversity thus declined. The documented decline in taxonomic and functional diversity warns of a reduced adaptive capacity that may negatively affect ecosystem robustness to environmental change and fisheries. This study emphasizes that regional conditions such as oceanography, topography, and depth are important determinants of species responses to warming. The observed impact of climate change on deep-sea demersal fish communities is most likely not unique to this study area and calls for higher focus on understanding the climate change impacts on deep-sea fish and their associated fisheries.

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BIOSKETCH

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Author contributions: M.E. and R.P. conceived the study. All authors designed the study. M.E., R.P. and L.P. conducted the data analysis and drafted the manuscript. All authors critically revised the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.