

RESEARCH ARTICLE

Deep demersal fish communities respond rapidly to warming in a frontal region between Arctic and Atlantic waters

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Abstract

The assessment of climate impact on marine communities dwelling deeper than the well-studied shelf seas has been hampered by the lack of long-term data. For a long time, the prevailing expectation has been that thermal stability in deep ocean layers will delay ecosystem responses to warming. Few observational studies have challenged this view and indicated that deep organisms can respond exceptionally fast to physical change at the sea surface. To address the depth-specific impact of climate change, we investigated spatio-temporal changes in fish community structure along a bathymetry gradient of 150–1500 m between 1998 and 2016 in East Greenland. Here, the Arctic East Greenland Current and the Atlantic Irminger Current meet and mix, representing a sub-Arctic transition zone. We found the strongest signals of community reorganizations at depths between 350 and 1000 m and only weak responses in the shallowest and deepest regions. Changes were in synchrony with atmospheric warming, loss in sea ice and variability in physical sea surface conditions both within our study region and North of the Denmark Strait. These results suggest that interannual variability and long-term climate trends of the larger ecoregion can rapidly affect fish communities down to 1000-m depth through atmospheric ocean coupling and food web interactions.

KEYWORDS

Arctic, Atlantification, borealization, deep sea, East Greenland, ecosystem change, fish communities, fisheries

1 | INTRODUCTION

The most prominent impact of climate warming on marine ecosystems are distributional shifts in fish, which influence species interactions and food web organization. For shallow continental shelf seas, this usually implies a poleward shift or movement to deeper waters to retreat in cold water refuges (Dahlke et al., 2018; Fossheim et al., 2015; Pinsky et al., 2013). Although more than 90% of the habitable oceans' volume lies below 200 m, long-term studies of biodiversity

in slope and deep-sea regions are rare (Danovaro et al., 2020; Howell et al., 2020; Levin and Bris, 2015). It has often been proposed that the rapidity of species' responses to climate change decreases with depth because deeper waters are thermally more stable (Levin and Bris, 2015; Van der Spoel, 1994; Yasuhara et al., 2014). However, rapid responses in the abundance of deep-sea biotas, such as fish, nematodes and amphipods, to changing environmental conditions at the surface indicate that processes such as changes in primary productivity can trigger unexpectedly fast responses in the deep

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(Danovaro et al., 2004; Milligan et al., 2020; Soltwedel et al., 2016). Although the number of such observations is limited, they challenge the long-standing perception of a slow response to climate change in the deep sea.

In sub-Arctic and Arctic marine ecosystems, climate change happens faster than in any other region globally (Hoegh-Guldberg and Bruno, 2010). Since the mid-2000s, a loss of sea ice and physical changes of sea surface waters have transformed Arctic waters to more closely resemble North Atlantic and Pacific waters (Huntington et al., 2020; Ingvaldsen et al., 2021; Lind et al., 2018; Mueter et al., 2017). As a result, an increasing borealization of Arctic biota is observed in shallow continental shelf seas, meaning that more southerly distributed species invade these high-latitude ecosystems (Fosheim et al., 2015; Huntington et al., 2020). Along the East Greenland coast, sea ice extent has declined and reached record-lows in the recent two decades (Meredith et al., 2019; Våge et al., 2018), with formerly seasonally ice-covered regions becoming permanently ice-free. The East Greenland ecosystem represents a sub-Arctic transition zone, where the cold East Greenland Current mixes with the temperate Irminger Current and flows southwards following the continental slope (Sutherland and Pickart, 2008). Since the early 2000s, bottom temperatures have decreased on the shelf of East Greenland and increased along the slope, which illustrates the potential influence of different water masses (Emblemsvåg et al., 2020). The dominance of the cold East Greenland Current on the shelf and the influence of the warmer Irminger Current along the slope (Våge et al., 2011) create a front and a transition zone, where boreal and Arctic species live (Emblemsvåg et al., 2020; Jørgensen et al., 2015). According to a recent analysis from more northern regions in east Greenland, which also host fronts between Arctic and Atlantic water masses, this thermal front is highly productive offering beneficial conditions for phytoplankton (Bluhm et al., 2020; Boertmann et al., 2020; Frey, 2018). Such transition areas are expected to represent a hotspot for the impacts of climate change because species often live close to their boundary of thermal affinity, where they respond quickly to changes in the environment (Frainer et al., 2017; Fredston-Hermann et al., 2020; Horta e Costa et al., 2014). The abundance of boreal species, such as haddock (*Melanogrammus aeglefinus*), blue whiting (*Micromesistius poutassou*) or blue ling (*Molva dipterygia*), is associated with periodical increases in temperature in Greenland waters (Hansen, 1949; Post et al., 2020; Tåning, 1949). On global scale, surface waters are currently heating faster than the deeper waters, but the deep-sea is predicted to experience accelerated warming under high carbon emission scenarios (Brito-Morales et al., 2020). Nevertheless, it is unknown how fish communities might respond to climate change across a vertical depth gradient exceeding the typical bottom depth of shelf areas and whether the vertical structuring of water masses of different origins might affect the ecological response.

Knowledge of how fish communities distributed from the continental shelf to the deep sea respond to abrupt environmental changes can provide novel insights into their depth specific vulnerability to

climate change. To investigate temporal changes in demersal fish communities associated with warming in shelf, slope and deep-sea regions ranging from 150 to 1500 m, we compiled data collected for scientific fish stock monitoring during the period 1998–2016. To analyse spatio-temporal variation in fish community structure, we used three-dimensional tensor decomposition, a multivariate method that comprehensively describes the dataset considering the interaction between (1) species composition, (2) depth layers and (3) time (Frelat et al., 2017). The analysis was performed on abundance data for 55 fish species collected at 1389 bottom trawl stations distributed over seven depth layers (Table S1). The time-series associated with the principal tensor summarizing temporal change in fish community abundance was related to environmental data across the large ecoregion of East Greenland and Iceland.

2 | MATERIALS AND METHODS

2.1 | Fish community data

The study area is in East Greenland waters expanding from 63° N to 66° N (Figure S1a). Here, the German Thünen Institute of Sea Fisheries and the Greenland Institute of Natural Resources jointly monitor bottom fish communities. These expeditions are part of annual scientific fish stock monitoring surveys in summer and early autumn. The German survey covers shelf and slope regions down to 400 m and the Greenland survey slope and deep-sea regions from 400 to 1500 m (Figure S1c). Both the German and the Greenland survey use bottom trawl nets and samples are taken based on stratified random survey design, meaning that the whole survey area is divided into strata, in which sample locations are randomly distributed (Kingsley et al., 2004; Rätz, 1996). The Greenland survey uses a rock hopper-type trawl and an average towing speed of 3.0 knots. The German survey uses heavy bottom gear, due to the rough nature of the sea bed on the shelf, and an average towing speed of 4.5 knots (Fock, 2008). This difference in towing speeds might affect the catchability of larger, more mobile individuals, which often have a higher sustained swimming speed, as it was shown for Atlantic cod (*Gadus morhua*) and haddock (Breen et al., 2004; He, 1991). Atlantic cod, which is one of few large, more mobile species within this dataset, is most successfully caught during towing speeds between 2- and 4.5 knots (Winger et al., 2000). Hence, it seems unlikely that trawling speed affected our results. Both surveys use a net with 140 mm mesh size and a small-mesh liner in the codend. After each haul, the catch is sorted, identified to the lowest possible taxonomic level (mostly to species level), counted and weighed. For the Greenland survey, sampling dates changed in 2008 from June (1998–2007) to August (2008–2016). However, such change in the survey timing of 1–2 months can likely not explain the large changes observed in the ecosystem, which started to occur at least 2 years before the change of the survey design and were in synchrony with the environment before and after this change (Figure S2). Moreover, similar, albeit more moderate, changes occurred in shallow waters, where the time of sampling was consistent over the whole time series (Figure S2).

2.2 | Data processing

We used yearly data from 1998 to 2016 except for the year 2001, when there was no Greenland survey in deeper waters (Figure S1c). In total, information collected at 1389 trawl stations were included in this study. Prior to the analyses, data were screened, quality checked and pre-processed; only fish classified to species level were retained. Pelagic species (Froese and Pauly, 2017; Haedrich and Merrett, 1988) were likely caught during the setting and hauling of the trawl and consequentially removed from the dataset. 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 stations) were included in the analyses, which resulted in a final dataset of 55 out of 91 species. These 55 species represent more than 99.9% of the recorded abundance. Catch per unit of effort was calculated as the number of individuals per swept area in km², because the two surveys use different nets and different towing speeds, which affects the area covered with the net. Afterwards, abundances were averaged per species, year and depth stratum. We defined seven depth strata distributed between 150 m and 1050 m. The deepest depth stratum contains all stations carried out between 1050 m and 1500 m depth because this depth layer was less intensively covered by the survey. On average, 10 stations were carried out per depth stratum and year.

2.3 | Temporal and spatial community dynamics

To determine spatial and temporal fish community dynamics and relate these to environmental change, we used tensor decomposition analysis (Leibovici, 2010; Leibovici and Sabatier, 1998). Tensor decomposition analysis is a method to decompose a tensor (3D array), such as the one consisting of observations of abundances of multiple species (first dimension), repeated across multiple depth layers (second dimension) and multiple years (third dimension). The method is similar to traditional multivariate approaches, such as principal component analysis, but extended to more than two dimensions. The aim of tensor decomposition is to summarize the maximum variability of the original tensor in the minimum number of components. This approach allowed us to investigate fish communities as they change over time and simultaneously over space. To reduce the dominance of high abundant species in the analysis, species abundances were log-transformed ($\log(x+1)$) and normalized to zero mean and unit variance. The principal tensor analysis was run using the PTAK package in R (Leibovici, 2010; Leibovici and Sabatier, 1998). We selected the number of components, called principal tensors (PT), based on the screen test, identifying an inflection point in the successive percentage of variance explained (Cattell, 1966). The output of the tensor decomposition indicated the selection of four PTs of the highest explanatory power (Figure S1). The original tensor was shuffled 1000 times and these four PTs explained more variance than was expected by chance (Figure S3). PTs represent the main spatio-temporal dynamics of species, providing scores for all species, depth strata and

years (Figure S2). PTs 1–3 had high variability in-depth scores, but low in temporal scores, whilst the opposite is true for PT4. This is visible in Figure S2—with different colours per row in PT1–3; and different colours per column in PT4. To simplify the interpretation and visualize the results, the scores of species on the PTs were used to conduct hierarchical cluster analysis based on Ward's criterion (Ward, 1963). We used the species scores on these four PTs to compute Euclidean distances between species. Afterwards, we ran hierarchical clustering based on this distance matrix. Based on visual inspection of the dendrogram and the identification of a flattening point on the within-cluster sum of square (Figure S4), we identified six clusters. The identified clusters represented groups of species sharing similar spatio-temporal distribution. We compared the clusters with information about species' biogeography (Mecklenburg et al., 2018).

The dominating temporal trends of the entire community were summarized by the temporal scores of PT4 (Figure S2). We called this dominant temporal trend 'tensor time series', and used this time series for further analysis. The scores of species and depth layers on PT4 indicate the strength of the temporal dynamics for the respective species and depth layer. For example, the abundance of species with a strong positive PT4 score follows the increasing trend of the tensor time series, whilst species with strong negative PT4 score have the opposite negative trend in abundance, and species with PT4 score close to zero do not follow the dynamic shown in the tensor time series. The same applies for depth layers; depth layers with higher absolute PT4 score have stronger temporal trends than depth layers with the score close to zero.

2.4 | Correlation maps

Monthly sea level air temperature with a resolution of 2.5° was obtained from the atmospheric reanalysis of the U.S. National Centres for Environmental Prediction and National Centre for Atmospheric Research (Kalnay et al., 1996; NCEP, 2019). Daily chlorophyll-a data with a resolution of 0.25' from satellite ocean colour observations processed and distributed by ACRI-ST, whilst sea surface temperature (SST) and daily sea ice fraction with a resolution of 3' from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) of the UK Meteorological Office were obtained from the E.U. Copernicus Marine Environment Monitoring Service (Copernicus, 2019a, 2019b), respectively. The monthly temperature, salinity, as well as longitudinal and meridional current velocities with a resolution of 0.25° at depths 150 m and 750 m, were obtained from the global ocean reanalysis ORAS5 (ORAS5, 2019; Zuo et al., 2019). All data have been extracted in the region 55–75°N; 50–10°W, where we tested for correlations with the tensor time series. All data resolutions refer to both latitudinal and longitudinal directions.

Annual averages of length, start and end of annual phytoplankton blooms were calculated from the daily chlorophyll-a data based on Section 2.5 from Soppa et al. (2016). The influence of all environmental variables on the tensor time series was searched spatially and quantified with maps of Pearson correlation coefficients.

Such maps are widely used in meteorology, i.e. (Chelton et al., 2000; Mo and White, 1985), i.e. (Becker and Pauly, 1996; Núñez-Riboni and Akimova, 2017) and marine ecology (Akimova et al. (2016), for instance, to search for non-localized influences like teleconnections. For the case of chlorophyll-a, also correlations with its logarithms were calculated to account for non-linear relations. Only correlations significant within 95% confidence were considered. Autocorrelation in time series can inflate the chance of detecting significant correlations where none exist (Pyper and Peterman, 1998). In order to account for this potential bias, we adjusted the test procedure for testing significance by reducing the effective number of degrees of freedom (increasing the p-value) considering the auto-correlation of the individual time-series and following the methodology of Pyper and Peterman (1998); Pyper and Peterman (2011). This approach does not only consider the long-term trend in the time series but also interannual variability. Correlations were searched for variables averaged inside individual year quarters Q1 to Q4, as well as for the annual average. Averages of Q2 and Q3 were finally chosen for showing maximum correlation with the tensor time series. Correlations were searched for lags -1 to +1 but were significant only for lag zero. Testing for significance at lag -1 follows the notion of studying delayed responses of the ecosystem, whilst testing at lag +1 is a way of verifying that the method does not identify spurious correlations as significant. To illustrate the characteristics of the environmental indices, which are highly correlated with the tensor time series, we defined an area including the study region and regions which are connected through advection (61.2–70°N and 22.6–44°W).

2.5 | Impact of fisheries

Because fishing takes place in the study region and targets bottom fish species investigated in this study, such as Atlantic cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*), we calculated fishing effort given as hours of fishing on the commercial species in East Greenland for the period 1999–2016 (Figure S5). Calculations were based on haul duration in logbooks data obtained from the Greenland Fishery and Hunting License office for all fishing vessels operating in the exclusive economic zone in East Greenland. The fishing effort of commercial species has declined and showed no strong variations during the study period. Hence, it is not likely that commercial fishing activities have affected our results.

3 | RESULTS

3.1 | Fish community structure

The output of the tensor decomposition indicated four PTs accounting for most of the systematic variation in fish abundance (Figure S2). Three of the four PTs described vertical structure, i.e.

differences in fish communities among depth layers, whereas one tensor accounted for temporal variability in abundance (Figure S2). Hierarchical clustering of the Euclidean distances between species scores on the four PTs revealed six clusters (Figure 1; Figure S4), each characterized by a unique subset of species (typical species in Figure 2C; Table S1). The six clusters summarized abundance patterns over depth and time (Figure 1; Table S1).

The species dominant in clusters representing the shallowest (d225) and deepest (d1225) layers suffer only small changes of abundance over the study period (Figure 1). The main temporal developments took place in the intermediate layers, between 350 and 1000 m, covered by the four remaining clusters (Figure 1). For the species members of two of the clusters in intermediate layers, abundance increased (d375+, d675+), but decreased in the other two clusters (d375-, d675-). The temporal changes in abundance were gradual before 2005 and accelerated between 2005 and 2010. Species from cluster d375- retreated to a narrow depth layer, when the abundance of d375+ rose, whereas cluster d375+ expanded its vertical distribution over time. These patterns suggest that ecosystem changes in the deep can be just as strong or stronger compared to shallower waters.

3.2 | Biogeographic affiliation within clusters

Clusters displaying increasing abundances were dominated by boreal and widely distributed fish (Figure 2; Figure S6). In contrast, 63% of species in clusters with decreasing abundance were found to be Arctic or Arctic-boreal (Figure 2; Figure S6). For example, the abundance of Arctic rockling (*Gaidropsarus argentatus*), threebeard rockling (*G. ensis*) and three Arctic species of eelpouts (*Lycodes paamiuti*, *L. pallidus*, *L. squamiventer*) decreased over time (Figure S6). Whereas abundance of boreal species, such as Atlantic argentine (*Argentina silus*), blue ling, witch flounder (*Glyptocephalus cynoglossus*) and round ray (*Rajella fyllae*) increased (Figure S6). The widely distributed deep-sea species snubnosed spiny eel (*Notacanthus chemnitzii*) and black dogfish (*Centroscyllium fabricii*), which are normally limited in their distribution by Arctic waters, increased in abundance (Figure S6).

3.3 | Correlations between fish community responses and climate indices

Whilst the main trend in temporal development in species abundances, captured by PT4 (see PT4 in Figure S2 and S6; Table S2), was likely supported by the increase in bottom temperatures of the Irminger current, community changes were significantly correlated with changes in surface environmental conditions driven by climate warming (Figure 3). We found positive, significant correlations ($p < 0.05$) between the tensor time series and sea surface air temperature, water temperature and salinity and a negative correlation with sea ice concentration (Figure 4). Correlations between environmental variables aggregated over April to July and the tensor time series were strongest without lag, meaning

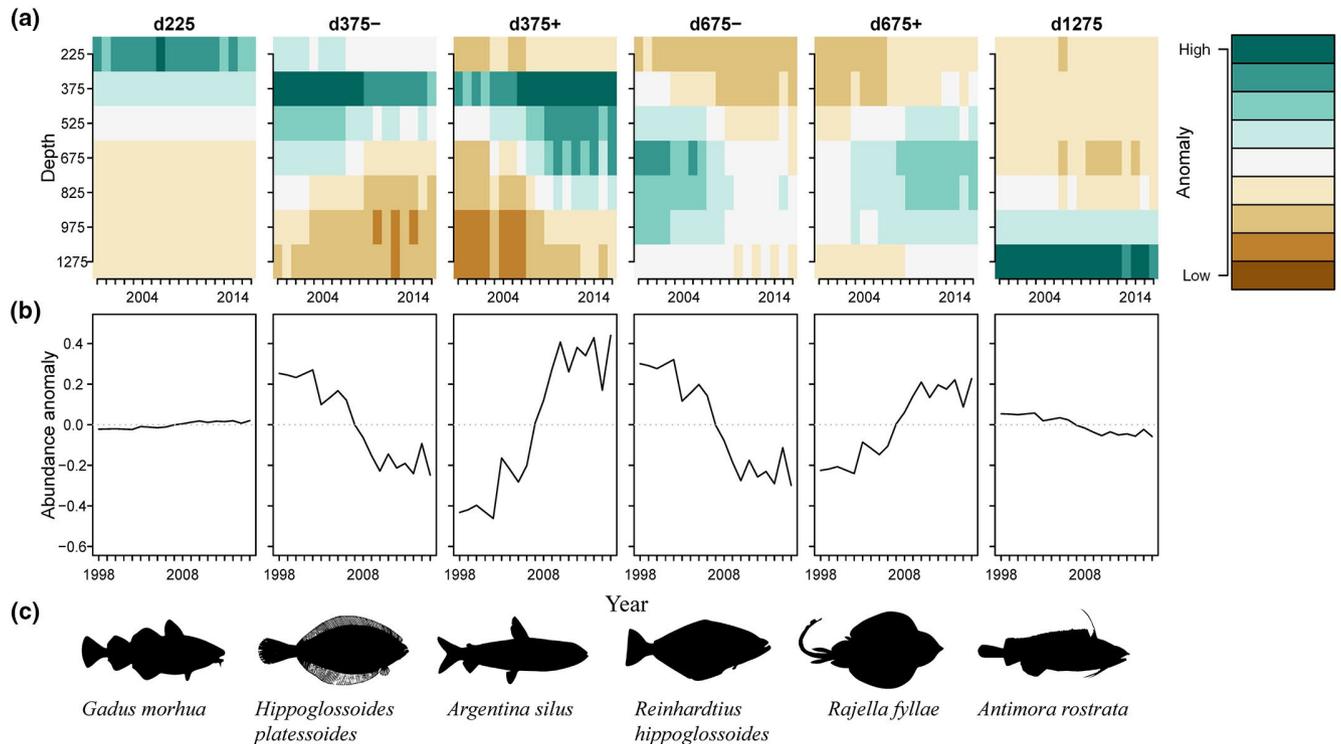


FIGURE 1 Spatial-temporal dynamics in fish abundances. (a) Anomalies in fish community abundance in East Greenland represented in a heatmap showing the six clusters with time on the x-axis and depth on the y-axis. (b) Temporal average of the abundance of each cluster. (c) Indicator species reflecting the main depth of distribution and the temporal trend of the respective cluster. The names of the communities (d225, d375-, d375+, d675-, d675+, d1275) reflect their depth of the main occurrence ('-' for decreasing abundance, '+' for increasing abundance)

that deep bottom fish communities responded within a few months to environmental changes detected through surface oceanographic conditions. The measured environmental conditions were a good indicator of climate variability because the area from which they were sampled is influenced by year-to-year regional climate fluctuations (Figure 4; Figure S7). A spatial analysis of the correlations between environmental conditions and the tensor time series shows the strongest temporal correlations in areas most affected by regional climate variability (Figure 4; Figure S7). The close association of the climate indicators with fish responses is exemplified by the extreme year of 2003 when warm waters expanded onto the slope and over the shelf. The correspondence in year-to-year fluctuations of climate indicators and ecological response were also observed in the last years of the study (Figure S7). The correlations between fish responses and surface processes were highest in an area north of the Denmark Strait (Figure 4).

4 | DISCUSSION

4.1 | Pronounced community changes in deeper layers

Our findings suggest that ecosystem responses to warming in the deep can be just as strong or stronger compared to shallower waters. The dominance of the cold East Greenland Current on the shelf might explain why the response of demersal communities in shallow

waters was weaker. The deeper regions are under the impact of the warmer Irminger Current, which has likely caused the increase in temperatures observed along the slope (Emblemsvåg et al., 2020). This climate signal is largely absent on the continental shelf (Figure 5) and highlights the importance of considering regional and local environmental conditions in analyses and predictions of ecosystem responses to climate change. A second hypothesis as to why shallow regions did not show a strong response could be related to the increasing dominance of Atlantic cod on the shelf (Jørgensen et al., 2015). Atlantic Cod is a highly opportunistic predator and preys upon many fish species present in East Greenland (Werner et al., 2019). Cod was shown to have a strong impact on the fish community in the Barents Sea (Ellingsen et al., 2020), and could diminish the abundance of other smaller species and mask community signals in our region.

4.2 | Borealization

The increasing dominance of boreal fish species, as observed in shallow continental shelf seas, such as the Barents Sea and Bering Sea (Fossheim et al., 2015; Huntington et al., 2020; Ingvaldsen et al., 2021; Mueter et al., 2017), also happened in East Greenland, but in deeper waters (350–1000 m). In shallower regions, such as the Barents sea, borealization has led to an increase in species richness as the northward migrating species are adding to the species pool (Johannesen et al., 2012). These observations would suggest that increasing temperatures

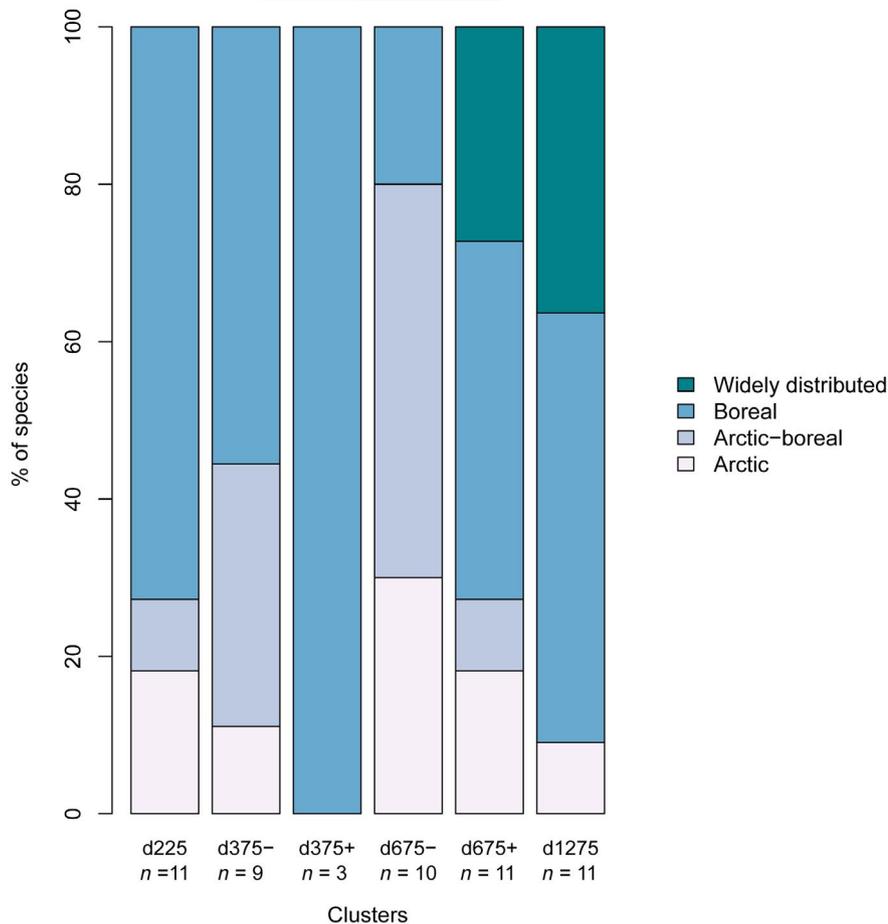


FIGURE 2 Community-specific biogeographic affiliation of demersal fish species in East Greenland. The names of the communities are based on their spatio-temporal characterization. The numbers below the names denote the number of species in each cluster

in deeper waters along the slope might also result in increasing species richness. However, in accordance with Emblemsvåg et al. (2020), we found that the local loss of species is not compensated by the gain of species (Figure S6; Table S1), leading to a decrease in species richness. These results are likely related to regional oceanography, which generates different biodiversity trends than what is observed in other high latitude shelf seas like the Barents Sea (Fossheim et al., 2015; Hiddink and Hofstede, 2008; Johannesen et al., 2012). In the Barents Sea, the Gulf Stream acts as a pathway of transport for species moving northwards, fuelling this shelf Sea with new incoming species. In east Greenland, where the currents are running southward, there is less evidence for extensive horizontal movement of slope and deep-sea species. Further, the depth range and habitat requirements of boreal deep demersal species might prevent them from redistributing to East Greenland. The lack of available habitat has, for example, been shown to inhibit the redistribution of demersal species in the North Sea (Rutterford et al., 2015).

4.3 | Effects of surface climate and extreme events in the deep-sea

The synchronicity of the community response with climate variability is evident in the extreme years of 2003 and 2015 when climate indices and the tensor time series peaked synchronously. Such fast ecological responses are likely mediated by behaviour, with fish species rapidly

redistributing to areas with more favourable physical and biological conditions (Pinsky et al., 2013). The physical conditions affected by climate co-varied, which is in line with the documented Atlantification processes described in the Barents Sea (Ingvaldsen et al., 2021; Lind et al., 2018). Once the sea ice begins to decline, freshwater input declines and salinity rises. These near-surface density changes in spring lead to less stratification, more vertical mixing and increasing surface temperatures, which further prevents sea-ice formation (Lind et al., 2018).

The observations of high SST in East Greenland in 2003 is not restricted to this region, but also recorded elsewhere in the North Atlantic up until the Arctic Circle (Feudale and Shukla, 2011) and caused a record-breaking heatwave with the centre of action in central Europe (Feudale and Shukla, 2011; Schär et al., 2004). This event may have caused preconditioning, which promoted the transitional change observed between 2005 and 2010.

The high correlation between fish responses and surface processes located northwest of Iceland indicates that atmospheric processes taking place in this region play a key role in shaping the food web downstream. A sudden and large inflow of cold and fresh Arctic water through the Strait has been linked to the so-called 'Great Salinity Anomaly' in the late 1960s when Arctic water masses were exported to the entire open North Atlantic and traceable for more than a decade (Dickson et al., 1988). This event was linked to a low abundance of zooplankton in Southwest Greenland, indicating that a change in

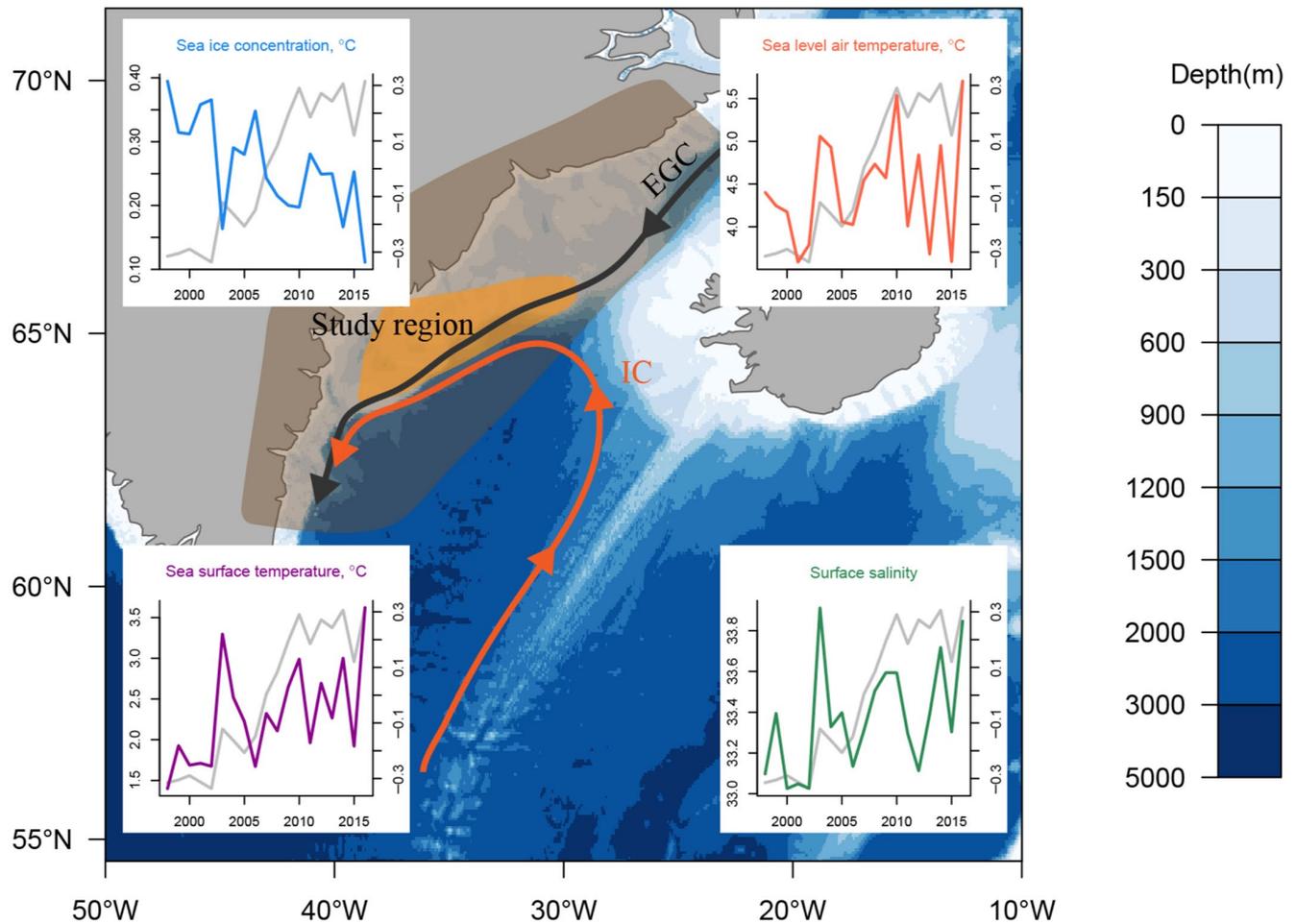


FIGURE 3 Time series correlations between fish abundances and climate events. Time series of the four significantly correlated environmental parameters in relation to fish community abundance summarized by the tensor time series (grey line). The shaded orange area shows where fish samples were collected whereas the larger brown shaded polygon shows the area from where the environmental time series were collected. Arrows on the map show the position and direction of the two main currents in the region (IC = the warm Irminger current; EGC = the cold East Greenland Current)

oceanographic conditions North of the Denmark Strait can affect food web processes in our study region (Pedersen and Rice, 2002).

Whilst Brito-Morales et al. (2020) predicted that a change of speed and direction in climate velocities in the deep might decouple vertical connectivity in the future, our results show that bottom fish can immediately respond to larger climate processes, evident in surface indices. Although our evidence is regionally limited, this challenges their conclusion and shows that not only ambient thermal niches but also wider ecosystem considerations differing on regional level should be taken into consideration, when predicting biodiversity responses to climate change.

4.4 | Productivity and ocean coupling

The rapid ecological responses to surface climate variables suggest that fish experienced changing environmental conditions. The lack of time lag indicates that processes such as recruitment or mortality cannot be the causal driver, especially because most of the species

involved in this study are slow-growing and late maturing, such as redfish (*Sebastes* sp.) and Greenland halibut. Hence, the observed rapid responses most likely reflect fish movement.

Although there is no comprehensive information on the relationship between the physical environment and low-trophic levels in East Greenland, evidence from other similar regions suggests that the Atlantification observed in East Greenland likely had an impact on plankton production, plankton composition and sedimentation (Soltwedel et al., 2016; Weydmann et al., 2014). These bio-physical changes in sea surface layers induced by ocean warming and a loss of sea ice might affect the resources of deep-sea fish communities through changes in primary production and in sinking rates of organic matter (Danovaro et al., 2004; Møller and Nielsen, 2019; Ruhl and Smith, 2004; Smith et al., 2008; Soltwedel et al., 2016). Such connections have previously been suggested to be one of the most likely mechanisms through which surface conditions can affect the abundance of deep-sea fish (Bailey et al., 2006; Levin et al., 2020; Ruhl and Smith, 2004). In the Fram Strait, warming and changes in low trophic levels led to an increase in phytodetritus

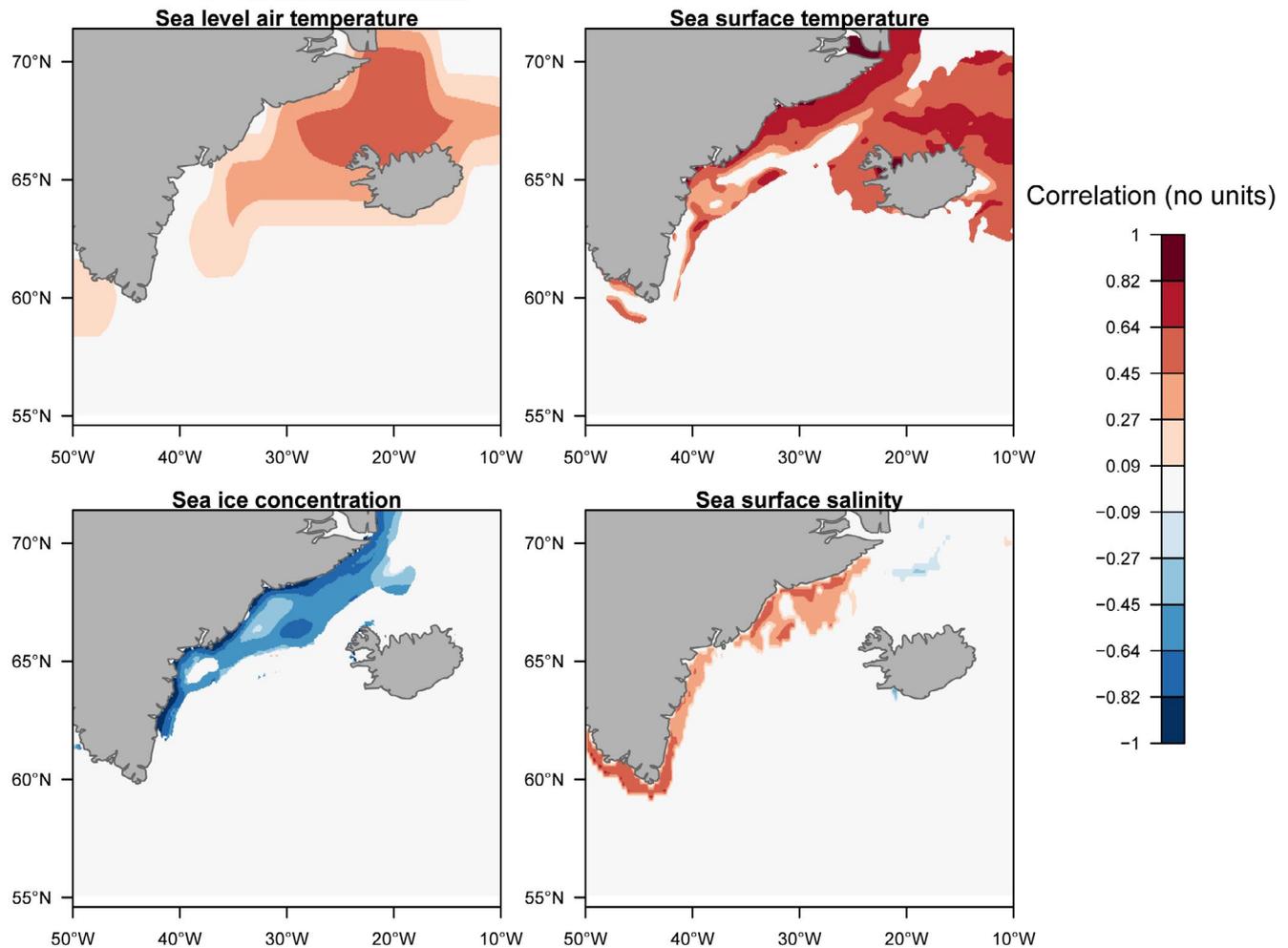


FIGURE 4 Correlation maps. Maps of significant correlation coefficients between the tensor time series and the four environmental indices in the larger East Greenland-Iceland ecoregion

biomass, the main food source for benthic organisms in the deep (Soltwedel et al., 2016). Behavioural responses of deep-sea fish communities to interannual changes in particulate organic carbon flux to the seafloor was recently documented in the South East Atlantic (Milligan et al., 2020). A possible change in the transfer of the organic matter to deep habitats in our region may further have been caused by the intensification of winter convection events observed in the North Atlantic (Piron et al., 2017; Yashayaev and Loder, 2017). Recently, unforeseen convection was observed upstream from the study region, along the ice edge, where the sea ice retreat is linked to the deep mixing of cold surface waters (Våge et al., 2018). However, given the broad spectrum of species involved, both bottom-dwelling specialists and generalists, displaying both decreasing and increasing temporal changes in community abundances, this simplistic hypothesis calls for a more mechanistic investigation.

Both in the Fram Strait and West of Spitsbergen, warm-water anomalies caused a change from the cold-water Arctic to warm-water boreal dominated zooplankton communities in the early 2000s (Soltwedel et al., 2016; Weydmann et al., 2014). Similarly, a reduction in sea ice cover was associated with a borealization and an

increase in lipid-poor zooplankton communities in West Greenland (Møller and Nielsen, 2019). Increased pelagic productivity attracts zooplankton, forage fish and ultimately higher trophic level predators such as the boreal and widely distributed species, Atlantic argentine, black dogfish (*Centrocyllium fabricii*) and black scabbardfish (*Aphanopus carbo*), with a broad diet that includes pelagic prey (Frainer et al., 2017; Pecuchet et al., 2020). The decrease in Arctic species might be explained by their low affiliation to the pelagic zone, low tolerance to increasing temperatures and increased predation from—and competition with the increasingly abundant boreal species. These are in general of larger body size, opportunistic, highly migratory and often more adaptive in a changing environment (Aune et al., 2018; Sunday et al., 2015). Many of these boreal species practice vertical diel migrations and feed in the upper water column, which connects them to changes in surface processes. Their migratory and generalist behaviour might characterize these species as connectors within the food web and between the pelagic and deep demersal zone (Kortsch et al., 2015). In such ways, the response of an ecosystem can be gradual and evolve through the food web, or rapid through abrupt behavioural responses that change species distribution.

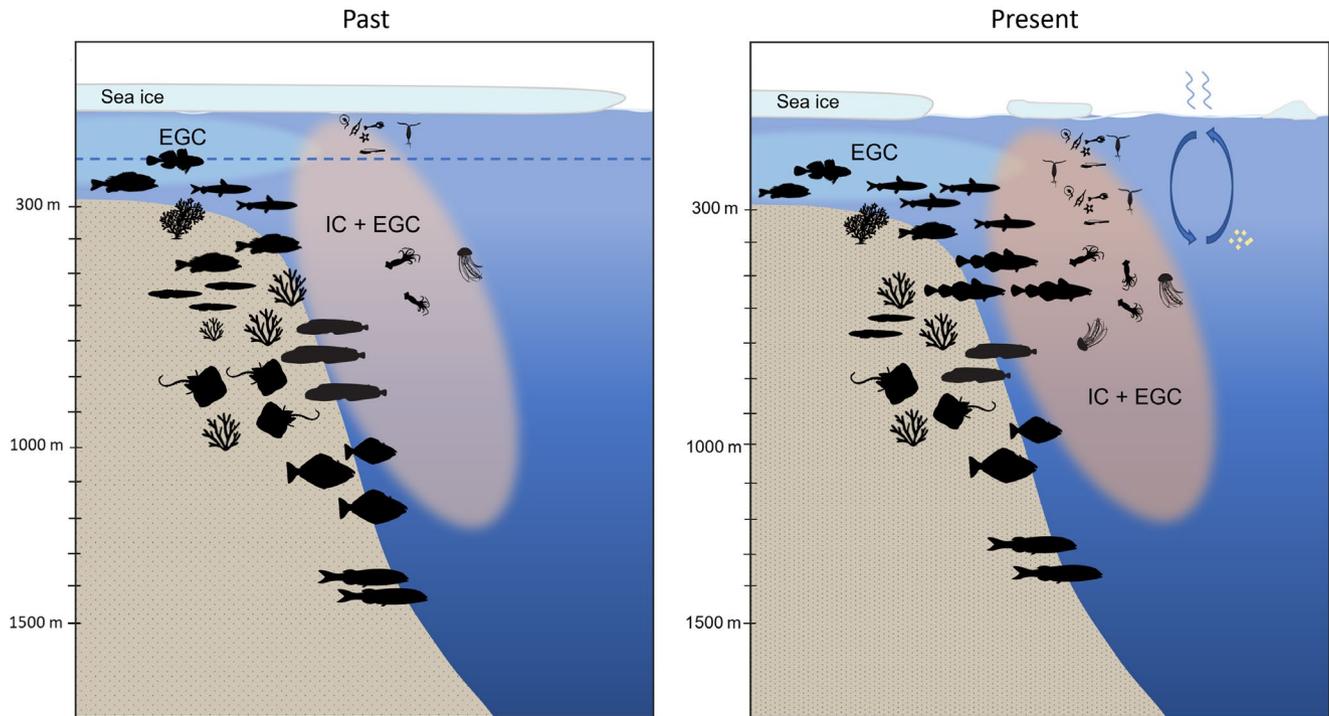


FIGURE 5 Conceptual Illustration of past and present community structure in the East Greenland ecosystem along the continental margin. During the two last decades, sea surface temperatures increased whereas sea ice concentration decreased in the area. The changes in surface climate conditions likely led to the Atlantification process including less stratification and more mixing of the water column (as indicated by the blue dotted line in the left figure and the blue vertical arrows in the right figure). Fish symbols illustrate that the abundance of Arctic benthivore species decreased and the fish community became increasingly dominated by boreal generalists as a response to these environmental changes. This mainly happened at depths between 300 and 1000 m where the warm Irminger Current (IC) mixes with the cold East Greenland Current (EGC)

5 | CONCLUSION

The abrupt changes we observed in deep demersal fish communities and the significant correlations with climate events provide a new perspective on the dynamics and energetic connectivity across a depth range covering continental shelf, slope and deep-sea habitats. Our results indicate that deep-water species, adapted to stable environments, respond strongly to environmental change. In addition to a response to gradual warming, deep fish communities can be affected by climate events, given the rapid behavioural nature of the responses observed in this study. If the ocean keeps warming with more extreme events, such as the one observed in 2003, the borealization of these Arctic communities is likely to accelerate, partly due to fast behavioural responses that will affect food web structure and species interactions. It is, therefore, important that the ongoing climate-driven ecological changes in deep water communities are considered in ecosystem management and climate adaptation plans.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

M.E., K.M.W., H.O.F., and R.P. conceived the study. All authors designed the study. R.F., I.N.R., M.E., and K.M.W. conducted the analysis of the data. H.T.C. and H.O.F. contributed fish data collections. M.E., K.M.W., and R.P. drafted the manuscript. All authors critically revised the manuscript.

DATA AVAILABILITY STATEMENT

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Data needed to reproduce the analysis, the script and the correlation maps are available at: <https://github.com/rfrelat/GreenlandFish> and <https://doi.org/10.5281/zenodo.5904328>. Further data may be made available from the corresponding authors on reasonable request. Environmental data were downloaded from freely available data sources.

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