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Climate warming impact on the deep demersal fish community East of Greenland

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Table of Contents

Original papers

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I dedicate this work to my daughters Noor and Vilma, who were born during this PhD period. You fulfil my life in ways I never had imagined, and you remind me every day of what is important in life.

Summary

This thesis presents a study of the impact of climate warming on deep demersal fish communities East of Greenland, in a transition zone between Atlantic and Arctic waters. Climate change was expected to affect fish community composition and functional characterization via poleward distributional shifts and changes in abundance. To assess the climate driven effects on fish communities, I used long term survey data (1998 – 2016) covering a depth range of nearly 1500m. Data on taxonomic composition and abundance were combined with functional traits information to address temporal changes in diversity, community structure and functional characterization at different depths.

The rapid warming registered during the study period was associated with a decline in both taxonomic and functional diversity, with the sharpest negative trends at depths between 300 and 1000m. Overall, the abundance of boreal species with a generalist diet, like greater argentine (*Argentina silus*) and Tusk (*Brosme brosme*) increased, whereas the abundance of Arctic fish benthivores like *Lycodes* spp. and northern wolffish (*Anarhichas denticulatus*) decreased. Functional reorganization was most pronounced at depths from 300 to 750m. Species living at great depths down to 1000m were affected by climate events detected at the surface, displaying rapid responses that were likely mediated by behaviour. These findings suggest that deep sea demersal species can respond just as fast to environmental change as species living in the shallower waters of shelf seas. The diversity loss was not consistent with the general expectations of a climate driven increase in Arctic marine biodiversity, observed in other high latitude ecosystems. Clearly, regional conditions may decide the climate driven effects on diversity, as the combination of currents and topography East of Greenland seems to inhibit colonization by boreal species. The documented taxonomic and functional

reorganization of the fish communities east of Greenland are likely to affect ecosystem functioning and vulnerability. The increasing importance of generalist species, also feeding in the pelagic food web compartment, changes the main pathways of energy and material flow, and tends to connect more tightly the food web. The increased connectivity of the food web may promote the spread of perturbations within an ecosystem that is losing adaptive capacity due to a decline in diversity. Since the East Greenland Ecosystem seems to be highly vulnerable to environmental change, future monitoring and a precautionary approach to fisheries and ecosystem management is suggested.

Sammendrag

Dette er et studium av hvordan global oppvarming påvirker bunnlevende fiskesamfunn i dypet utenfor Øst-Grønland, et område som representerer en overgang mellom Atlantisk og Arktisk farvann. Klima endringer er forventet å påvirke fiskesamfunn gjennom endringer i sammensetning og funksjonell karakterisering via nordlig forflytting av arter, samt endringer i antall arter og individer. For å undersøke klima-drevne endringer i samfunnene brukte jeg dataserier (1980 – 2016) fra vitenskapelige tokt som dekket en dybde gradient på nesten 1500m. Taksonomiske data ble kombinert med informasjon om artenes funksjonelle karakteristikker for å adressere endringer i diversitet, samfunnsstruktur og funksjonell karakterisering ved forskjellige dybder.

Økte vanntemperaturer, registrert i dette studiet, var assosiert med en nedgang i både taksonomisk og funksjonell diversitet, med tydeligste negativ trend i dybder mellom 300 og 1000m. Det ble observert en generell økning av boreale generalister, som for eksempel vassild (*Argentina silus*) og brosme (*Brosme brosme*) og en nedgang i arktiske bentivore arter som steinbit (*Anarhichas denticulatus*) og *Lycodes* ssp. Funksjonell reorganisering av fiskesamfunnene var størst i dybder mellom 300 og750m. Arter som lever på dybder helt ned til 1000m responderte på klimaendringer i overflaten, med en rask atferdsdrevet redistribusjon. Disse funnene viser at dypvannsarter kan respondere like raskt på miljøendringer som arter i grunnere farvann, som for eksempel i Barentshavet. Tap av diversitet var ikke i tråd med forventninger om klima-dreven økning i diversitet, observert i andre nordlige regioner. Det er tydelig at regionale oseanografiske og topografiske forhold påvirker diversiteten i havet ettersom kombinasjonene av strømmer og bunnforhold øst for Grønland ser ut til å hindre kolonisering av boreale arter og dermed introduksjon av nye

funksjonelle egenskaper. Den taksonomiske og funksjonelle reorganiseringen av fiskesamfunn har sannsynligvis stor betydning for økosystemenes funksjonalitet og sårbarhet. Økningen i antall generalister som spiser i de pelagiske vannmassene, endrer strømmen av energi og materie gjennom en tettere knytting av næringsnettet. Den økte koblingen av dette næringsnettet kan øke spredningen og påvirkningen av klima gjennom et økosystem som stadig blir mer sårbart grunnet redusert diversitet. Ettersom regionen øst for Grønland ser ut til å være svært følsomt for miljøendringer, rådes det til en fremtidig overvåkning av økosystemet og varsomhet i forvaltningen av resursene.

List of papers and contributions

The following papers are included in this thesis:

I: Emblemsvåg M, Núñez-Riboni I, Christensen HT, Nogueira A, Gundersen A, Primicerio R (2020) Increasing temperatures, diversity loss and reorganization of deep-sea fish communities east of Greenland. Marine Ecology Progress Series 654:127-141

II: Emblemsvåg M, Werner KM, Núñez-Riboni I, Frelat R, Torp Christensen H, Fock HO, Primicerio R. Deep demersal fish communities respond rapidly to warming in a frontal region between Arctic and Atlantic waters, *Global Change Biology*. (in press)

III: Emblemsvåg M, Pecuchet L, Velle LG, Nogueira A, Primicerio R. Functional borealization and diversity loss in East Greenland fish communities during recent warming. *Diversity & Distributions*. (accepted for publication)

Contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	**ME**, RP, G	**ME**, KMW, RP	**ME**, RP
Study design, data gathering and methods	**ME**, HTC, INR	**ME**, HTC, KMW, HOF, INR	**ME**, AN
Data analyses and interpretation	**ME**, RP, INR	**ME**, KMW, RF, INR	**ME**, RP, LP
Manuscript preparation	**ME**, RP, INR, HTC, AN, AG	**ME**, KMW, RP, INR, RF, HTC, HOF	**ME**, RP, LP, LGV, AN

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Introduction

Marine ecosystems today are under increasing stress from a rapidly changing environment and anthropogenic exploitation and impact (Hoegh-Guldberg & Bruno, 2010; Worm et al., 2009). At the same time, the demand for ecosystem services is growing concurrently with human population (DESA, 2015). By 2050, the human population is projected to increase by 43%, reaching 10 billion, and the demand for provisioning services to be doubled (U. FAO, 2009). The increasing need for food from the ocean has already led to overexploitation and declining stocks and sustainable management of the ocean resources is urgent (FAO, 2008). Although the overall productivity of ocean fisheries may not decrease during climate warming, large geographical redistribution of fish stocks and fisheries are projected, which presents a great challenge for fisheries management (Brander, 2010; Pörtner & Peck, 2010) and a need for knowledge on both population and community level of marine ecosystems.

Climate change and the impact on marine ecosystems

In the oceans, climate change and rising CO2 levels are contributing to elevated temperatures (Nathaniel L Bindoff et al., 2007), changes in ocean circulation (Alley et al., 2007; Toggweiler & Russell, 2008), altered stratification of the water column (Li et al., 2020; Lind et al., 2018), depletion of oxygen content (Keeling et al., 2010), changes in nutrient levels (Marinov et al., 2010), and acidification (Doney et al., 2009). Ocean warming is affecting marine organisms at several trophic levels, with implications for humans through the impact on fisheries and food productions. Ocean and fisheries governance therefore needs to efficiently adapt to climate change to obtain a sustainable management of ecosystems (N.L. Bindoff et al., 2019)

As marine species are adapted to a specific environment, the temperature and chemical changes influence marine organisms' physiological function, behaviour and traits, affecting population processes. If species are to survive in their new and changing environment, they ned to adapt biologically or behaviourally. The ecological responses of species to climate warming often consist of changes in population biomass, shifts in species distributional range and changes in phenology (e.g. timing of algae bloom, migrations etc.) (Doney et al., 2011) which affect species interactions and ecosystem functioning. Marine fish species often have complex life histories, occupying different habitats at different life stages, each with different exposure and sensitivity to environmental change (Rijnsdorp et al., 2009). The detection and understanding of species responses is therefore difficult, considering the heterogeneity of responses of individuals and populations at local and regional scale. At community level, as in fish assemblages, impact of larger ecological processes can be identified by looking at changes in biomass, species composition and diversity. For example, elevated temperatures tend to alter species composition by favouring warm water adapted species, whereas changes in nutrient levels and primary production tend to affect the biomass ratio of planktivores versus benthivores.

The adaptability of species, the capacity of species to adjust to their immediate environment (Gittleman, 2019), depends on several factors such as thermal tolerance, life history plasticity and functional traits (Frainer et al., 2017; Mouillot et al., 2013). However, other non-biological factors such as oceanography, hydrography and topography of the region may largely affect the species chance of making the necessary adjustments (Emblemsvåg et al., 2020; Pinsky et al., 2013; Rutterford et al., 2015). The sum of different strategies of species adaptability fundamentally determinates ecosystem vulnerability, a measure of how susceptible the system is to environmental stress. Vulnerability is a function of exposure, sensitivity and adaptability of the ecosystem and its components. In this context, exposure means the presence of species or ecosystems in places that could be severely affected, whereas sensitivity denotes to which degree a species or system is affected. The ecosystems in the tropic and Arctic regions are considered most vulnerable to ocean warming as these are the warmest and coldest regions respectively, where species are adapted to relatively narrow thermal windows, living close to their physiological temperature limits. In temperate latitudes, seasonality is strong and temperature excursions are greatest, with species more tolerant to shifts in temperatures (Storch et al., 2014). It is therefore generally expected that temperate and boreal species will increase in abundance in Arctic regions by expanding their northern distributional range (Poloczanska et al., 2016). Such northward distributional shifts are becoming widely documented (Fossheim et al., 2015; Frainer et al., 2017; Hiddink & Ter Hofstede, 2008; Ingvaldsen et al., 2021; Kortsch et al., 2015; Mueter et al., 2021; Ter Hofstede et al., 2010). However, exceptions with west-east, southward and depth redistributions are also found as response to the complexity of climate velocities and topography (Pinsky et al., 2013; Rutterford et al., 2015). Redistributions of species cause regional changes in biodiversity with a documented increase in the Arctic (Johannesen et al., 2012; Poloczanska et al., 2016). The positive trend is shown in the Barents Sea, where elevated temperatures have been beneficial for boreal stocks such as the Atlantic cod (*Gadus morhua*), which have expanded their distribution northward (Wiedmann et al. 2014; Fossheim et al. 2015).

Atlantification and Borealization

The northward shift of North Atlantic and North Pacific biota into the Arctic regions is referred to as borealization (Fossheim et al., 2015; Ingvaldsen et al., 2021), causing shifts in taxonomic composition (Johannesen et al., 2012; Mueter et al., 2021), functional characterization (Frainer et al., 2017) and food web organization (Kortsch et al., 2015). Borealization is largely induced by a process called Atlantification in which Arctic waters are becoming increasingly similar to Atlantic waters as the temperatures are increasing, the sea ice retracts, surface salinity is increasing and the strictly stratified water column is becoming more homogeneous due to higher mixing (Ingvaldsen et al., 2021; Lind et al., 2018; Smedsrud et al., 2013).

Although processes such as Atlantification and borealization induced by climate change are usually regarded as gradual over decades, there is an increasing awareness of the role of extreme climatic events, defined as statistically rare or unusual climatic conditions such as heatwaves (Smith, 2011a), as drivers of pronounced ecological and evolutionary change (Babcock et al., 2019). Extreme events are particularly damaging when affecting sessile habitat forming species such as corals, with loss of habitats being reported (Duke et al., 2017; Thomson et al., 2015; Wernberg et al., 2016). More recently rapid redistributions by motile species such as fish have stressed the ecological importance of extreme climatic events (Cheung & Frölicher, 2020). Years or periods of unusual temperatures or other oceanographic events represent strong pulses that may contribute to push or trigger ecosystem transitions beyond what is expected (Holbrook et al., 2020). Considering that storms and marine heatwaves have doubled in frequency since the 1980s as a result of climate change (IPCC, 2021), and the expected acceleration in the future, extreme events are now one of the main threats facing marine ecosystems (Holbrook et al., 2020). The potential domino effect that they represent throughout an ecosystem calls for collaborative science across disciplines and rapid dissemination of knowledge to stakeholders and management.

The deep Sea

Knowledge of marine biodiversity response to environmental change comes largely from the shallower areas of the ocean, whereas little is known about the responses of the deep-sea, covering regions beyond the edge of the continental shelf (> 200m) (Webb et al., 2010). However, we do know that deep-sea fish are generally more vulnerable to disturbance because of their low fecundity, late maturation, slow growth, and high longevity (Devine et al., 2006; J. Koslow, 1996; J. Koslow et al., 2000; Norse et al., 2012). This is also evident when reviewing past events of deep-sea fisheries. When continental shelf fisheries declined in the second half of the twentieth century, bottom trawling expanded into the deep (Haedrich et al., 2001). Many of these fisheries crashed within one or two decades because of slow recovery and low resilience of deep fish populations (Clark et al., 2007; J. Koslow et al., 2000). If deep sea fish is so vulnerable to fisheries, how are they coping in times of climate change? Deep sea fish are adapted to a stable environment where there is little or no light and seasonal and annual variability. Due to the lesser influence of atmospheric events, the rate of warming is expected to decline with depth (Desbruyères et al., 2017) and it is therefore also assumed that the impact of climate change in the deep-sea will be less and/or that the response of the ecosystem will be delayed. A recent study challenges this expectation by predicting that climate velocities are presently just as fast in the deep as in the surface, and in the future will accelerate far beyond the speed in surface layers (Brito-Morales et al., 2020). Because deep sea species are more vulnerable to environmental change, the consequences may therefore be worse than what is observed for species living closer to the surface. When climate velocities exceed the species ability to adapt, their habitat becomes unfavourable, and in the worst-case scenario, populations might face local extinction. Brito-Morales et al. (2020) also predict that the northward direction of velocities declines with depth indicating a potential vertical decoupling between depth layers in future scenarios.

In the deep, where it is dark, the benthic ecosystem is dependent on the production in the photic zone above. Changes in algal abundance and zooplankton composition and phenology, as already documented in arctic regions (Dalpadado et al., 2020; E. F. Møller & Nielsen, 2019; F. Zhang et al., 2015), will affect the suspension and deposition of organic matter to the sea floor (Brun et al., 2019; Wohlers et al., 2009). This again will affect the abundance of benthivores through food availability, either slowly through metabolism and reproduction, or rapidly through behavioural responses and redistributions. Such cascade of events through trophic levels from zooplankton to benthic macrofauna is documented in the Fram Strait (Soltwedel et al., 2016) and in the North east Pacific (Ruhl, 2007). The deep sea is therefore not only impacted by ambient environmental change, but also by changes happening in shallower depths in a highly connected marine ecosystem.

Knowledge gaps and societal challenges

Climate change impact on ecosystem dynamics, food-web structure and eventually ecosystem services is comprehensive and challenges our understanding of ecological processes. A mean to ensure sustainability of ecosystems and harvesting, is the implementation of ecosystem-based approaches and adaptations towards climate change. However, in practice, this is easier said than done as the interaction of natural processes is highly complex. Climate change is adding to this complexity by causing the systems to constantly change. The question is -are we able to close knowledge gaps and track climate velocities fast enough to adapt management strategies? Or are we loosing natural ecosystems before we can fully study and understand them, and particularly their capacity to withstand pressure and species loss (Holt, 2010)? The ecosystem approach does not translate well to regions where our knowledge is poor. The oceans cover approximately 71 % of the Earth's surface and it is largely unexplored. Spatial biases in sampling are apparent with efforts being highest in mid latitudes, especially in the northern hemisphere, and rapidly decreasing in intensity towards low latitudes and increasing depth (Menegotto & Rangel, 2018). The deep sea is vastly underrepresented and we know little about its biodiversity, ecosystem functioning and the effects of climate change (Costa et al., 2020; Webb et al., 2010).

The East Greenland study region

Oceanography

The study area southeast of Greenland covers both the shelf and the upper continental slope with a depth range of 150 – 1500m (fig 1). The shelf is relatively shallow with average depth of ~300m, with deeper channels and canyons and associated banks formed by glaciers (An et al., 2019). The continental slope is more topographically complex with irregular bathymetry, deep canyons and a steep decent down to the abyssal plane of the Irminger Sea. Just north of the study area between the Greenland and Iceland shelf regions, the narrow Denmark strait connects the extended Arctic Ocean (Greenland Sea) to the Irminger Sea. The main currents dominating the region is the strong cold East Greenland current (EGC) that extends from the Fram Strait and flows southward along the continental slope transporting large amounts of pack ice form the Arctic. South of the Denmark Strait, the EGC meet and mixes with the warm Atlantic Irminger Current (IC) and continues southward along the continental slope (fig 1). The sea ice cover in the Arctic which extends along East Greenland is diminishing and has led to the retraction of the sea ice edge and expansion of ice free time periods during summer (Våge et al., 2018) Environmental conditions in this region are highly influenced by the Sub polar Gyre (SPG), a vortex driven largely by wind movements, and the Atlantic meridional overturning circulation (AMOC). The strength of the SPG determines atmospheric forcing which further has shown to influence marine distributions and abundance of marine fish species (Hátún, Payne, Beaugrand, et al., 2009; Hátún, Payne, & Jacobsen, 2009; Núñez-Riboni et al., 2013; Post et al., 2020).

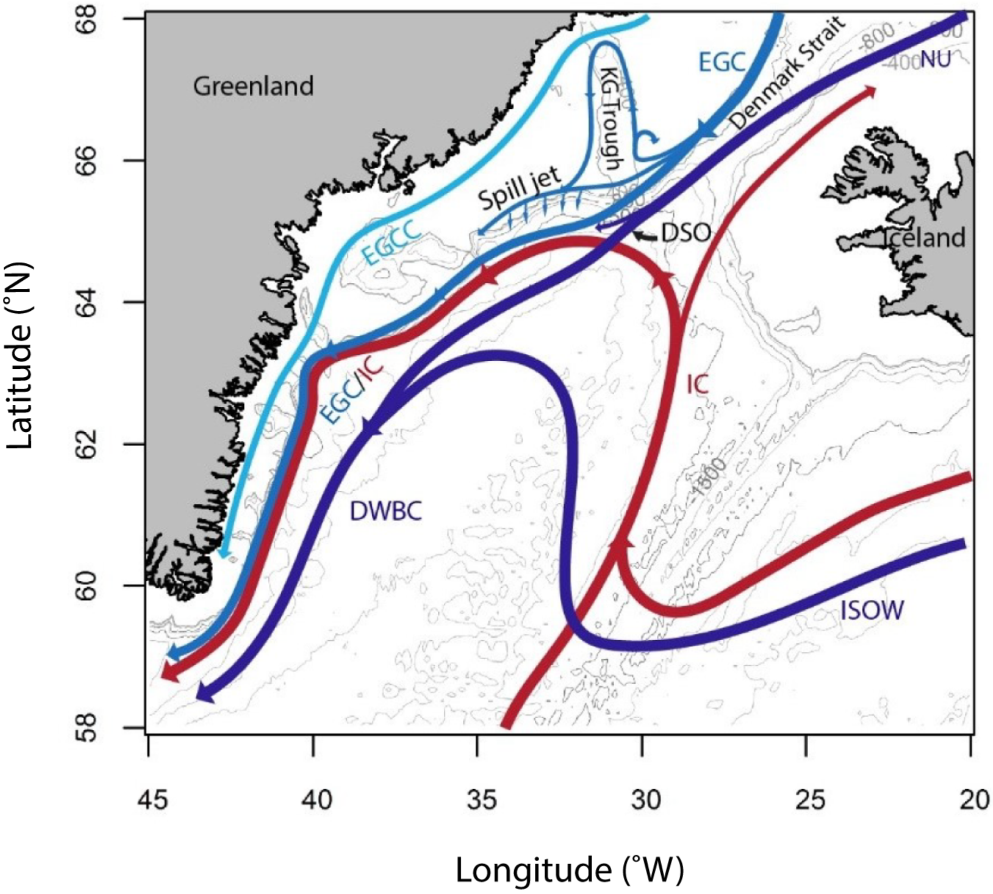

Figure 1: Map of the East Greenland current system. Blue arrows represent cold water masses, whereas red arrows represent warmer waters. EGC = East Greenland Current, IC = Irminger Currrent, DSO = Denmark Strait Overflow, EGCC = East Greenland Costal Current, ISOW= Iceland Scotland Overflow Water, DWBC = Deep Western Boundary Current. The figure is obtained from Emblemsvåg et al. (2020).

Primary production

There are no observation programs of primary productivity along offshore East Greenland, so data is mainly based on remote sensing products. The east coast covers high Arctic to sub-Arctic regions with a southward dispersion of drifting planktonic organisms which is dominated by diatoms in spring, and thereafter flagellated phytoplankton (Richardson et al., 2005). The composition of zooplankton is dependent of the origin of water masses; the cold EGC is dominated by polar copepod species, whereas the warmer IC transports Atlantic copepod species (Falk-Petersen et al., 2007). *Calanus* is the most important and abundant species of the zooplankton groups (Falk-Petersen et al., 2007), whereas the macrozooplankton group mainly consist of krill (*Meganyctiphanes norvegica,Thysanoëssa inermis, Thysanoëssa longicaudata*), amphipods (*Themisto libellula, Themisto abyssorum*) and Chaetognatha. In later years, the reduction of sea ice cover has caused a decline in the Artic species *Calanus hyperboreus* and *Calanus glacialis* and an increase of the Atlantic boreal species *Calanus finmarchius* in west Greenland waters (E. F. Møller & Nielsen, 2019). This shift also represents a significant decrease in lipid content of the main key zooplankton that are likely to have an effect through the food web reaching higher tropic links such as fish, birds and whales (E. F. Møller & Nielsen, 2019). As sea ice concentrations are decreasing also in East Greenland, similar shifts in species composition are likely to be happening also there.

Demersal fish fauna

The demersal fish fauna of the South-East Greenland region composes 182 registered fish species (P. R. Møller et al., 2010) consisting of both Atlantic and Arctic species. Total fish biomass is dominated by few highly abundant species; Greenland halibut (*Reinhardtius* *hippoglossoides*), redfish (*Sebastes mentella* and *Sebastes norvegicus*) and Atlantic cod, whereas the majority of the species are low abundant and considered rare or very rare (P. R. Møller et al., 2010). The number of registered fish species increases every year due to either income of new species or increased fishing and survey effort. The shallow waters have been fished for more than a century, and is more extensively surveyed, so occurrence of unknown species on the shelf can be considered as new species arriving due to climate change. However, in the deeper waters down to 1500m, fishing and survey effort increased considerably after 1988 (Okamura et al., 1995), which naturally led to many new registrations and therefore cannot be considered new species in the area. Also, the biology and distribution patterns of many of the rare species is poorly studied, and it is therefore difficult to determine whether it is in fact a new record, or a seldom appearance of a native species. Hardly any studies have been conducted at depths below 1500m, so with future explorations of the deepest parts, the total species numbers are expected to grow (P. R. Møller et al., 2010).

Fishery

A multinational fishery is currently operating in the East Greenland region (from ICES divisions and subdivisions 12.a3, 14.a, and 14.b2), targeting several species. Except from the Greenland fleet, EU member countries, Faroe Islands, Norway and Russia are fishing in East Greenland waters with the majority of the fishery being conducted south of 70°N (ICES, 2018, 2021; Stedmon et al., 2020). The fishing is mainly operated by large industrial factory ships using a variety of gear, mainly bottom trawl, longliners and pelagic trawl. The demersal fishery is targeting Greenland halibut, Atlantic cod, redfish and Northern shrimp (*Pandalus borealis*). In the early 2000s, following changes in the migration routes of these species

(Jansen et al., 2016), a pelagic fishery of Norwegian spring spawning herring (*Clupea harengus*) and North East Atlantic mackerel (*Scomber scombrus*) has been introduced and since increased to make up the majority of catches today (ICES, 2018, 2021). Since the 1950s, catches of Greenland halibut has fluctuated over time, whereas catches of redfish has generally decreased with interannual fluctuations (Stedmon et al., 2020). The shrimp fishery reached an all-time high during the 80s and 90s before rapidly decreasing to a low level where it has stayed since. The cod fishery collapsed in the 1990s, but the stock has since the middle of 2000s started to rebuild with a following increase in catches (Stedmon et al., 2020). Within the study region, fishing effort of demersal species has decreased since the 2000s (Emblemsvåg et al., 2020), whereas fishing effort of mackerel has increased (Stedmon et al., 2020).

Fisheries within the Greenland exclusive economic zone is managed by the Greenland authority. The widely distributed fish stocks, such as herring and mackerel are managed by the Northeast Atlantic Fisheries Commission, whereas Greenland halibut and redfish is managed bilaterally with Iceland. Although the fishery is regulated through quotas and licenses and several management strategies are in place to achieve a sustainable fishery (e.g. sorting grids to avoid bycatch and protection of spawning areas), there are only one management plan for stocks (cod) and five out of eight stocks were fished above limits for maximum sustainable yield and one is evaluated to be outside its safe biological limit (2019) (Stedmon et al., 2020). Due to lack of data and assessments, species interactions are not considered, and the management is not ecosystem based.

The CLIMA project

This thesis is an output of the CLIMA project funded by the Norwegian Ministry of Foreign Affairs (RER 15/0008). The project addresses long term impact of climate variability on fish diversity, community structure and trophic relationships in the East Greenland Ecosystem and the implications for fisheries and management. Additional funding was provided by the Nordic Council of Ministers.

Objectives

The East Greenland marine ecosystem is largely unexplored. Community studies below the depths of the continental shelf have not previously been performed. The ocean East of Greenland is a transition zone between Atlantic and Arctic water masses. Such transition zones have been shown to be sensitive to climate change with rapid responses of the fish communities (Fossheim et al., 2015; Mueter & Litzow, 2008). Climate driven changes in fish abundances and distribution are likely associated with functional reorganization that will affect ecosystem function and vulnerability. The joint German-Greenlandic monitoring program of demersal fish communities in East Greenland provides a unique opportunity to study fish community responses to climate warming across a vast depth gradient covering the continental margin.

To address the above knowledge gaps, this thesis has the following main objectives:

1: Assess compositional change of demersal fish communities along depth and temperature gradients. (Paper I)

2: Investigate temporal trends in local species diversity and total species abundances. (Paper I)

3: Assess temporal and depth related change in community structure associated with temporal development in climatic conditions of the larger ecoregion. (Paper II)

4: Document changes in functional characterization and diversity with depth and in time. (Paper III)

Material and methods

The community approach

Traditionally, the ecological response to climate change in the marine habitat has been conducted at single species level focusing on phenological and physiological characteristics, as well as distributional patterns and range shifts. However, the responses of single species are dependent on the presence of other species and the interaction with close and adjacent trophic links (Kortsch et al., 2015). Under stress, one species population might be struggling and decrease in abundance, whereas another is thriving and increasing. Therefore, the effect on the community is defined by the "pool" of all single species responses through interactions, distributions, and changes in abundance. The most basic and common approach to measure higher level patterns is species diversity which is the combination of species richness (number of species) (Colwell, 2009) and the evenness (variation in abundance per species) of species (Wilsey & Potvin, 2000). Species diversity is an important ecological property with implications for ecosystem health and productivity, as high diversity promotes ecosystem functions and resilience towards anthropogenic and environmental stress (Bernhardt & Leslie, 2013). However, simple diversity parameters do not consider community compensatory factors, such as species replacements, the uniqueness and importance of individual species and the potential restructuring of the community. To fully understand community ecology aspects and to set the correct conservation and management priorities, associated information on species composition and functional roles is needed (Fleishman et al., 2006). A common quantitative approach to handle such multidimensional information is the use of multivariate statistics to analyse the association between species or study sites (based on distance or dissimilarity measures) and group the ones that share similar properties and further relate variation between species/groups to environmental characteristics.

Even though several studies have documented distributional shifts and changes in abundance as response to environmental change and other disturbances (Alabia et al., 2020; Fossheim et al., 2015; Ter Hofstede et al., 2010), the consequences these community changes have on ecosystem functioning have been less explored (Frainer et al., 2021; Frainer et al., 2017; Sunday et al., 2015). In the last decades, approaches using functional traits as a mean to describe the functional character of ecological communities have been proposed (Violle et al., 2014). Functional traits are morphological, phenological and physiological features that affects individual performance. These are for example body size, fecundity, trophic level, egg size and temperature tolerance. Functional diversity can be measured based on similar indices as taxonomic grouping (richness, evenness and divergence) and provides additional understanding on mechanistic community dynamics and ecosystem function. It is a widely accepted theory, that in general, species rich communities perform better than species poor communities because of complementary niches and multispecies polycultures that buffer towards outer stressors. However, using the traditional methods, we cannot fully investigate which combination of species that optimizes ecosystem functioning and which species play a key functional role in upholding balance. Both the combination of traits, richness of traits and the abundance of each trait (trait redundancy) is important factors in evaluating ecosystem function and vulnerability (Cadotte, 2017). McLean et al. (2019) demonstrates the link between trait redundancy and community sensitivity and how trait redundancy can buffer against disturbance. Which ecological roles that would be affected, highly depends on type of disturbance. For example, temperature increases will affect the ecosystem differently than fishery. In areas where several sources of disturbance are present, which is often the case, it is difficult to analyse and predict responses in functional roles from a single source of disturbance, as interaction effects between disturbances most likely would be present. To my knowledge, there are no study on how environmental change affect functional characterization in the deeper parts of the ocean (>400m). However, from existing findings and theories of what generally determines resilience and vulnerability, some assumptions can be made. The deep sea often consists of many species with low abundance and few highly dominant species. The high abundances of these dominant target species buffer against fisheries, but because these species are few and often live at different depths (for example, Greenland halibut prefers deeper waters than redfish), the loss of these species will cause a loss of that functional role within the ecosystem. As for the many species with low abundance living in deeper waters, there might be a buffering effect in the redundancy of functional traits if the ecosystem consists of species sharing ecologically similar traits. However, in the deep sea, species are highly specialized, segregating in different niches and habitats (J. Koslow, 1996; J. Koslow et al., 2000), which could mean that functional roles do not overlap sufficiently to buffer ecosystem function from species loss. Additionally, if certain important food web interactions are supported by few species (low redundancy), key trophic links may be lost (Kuiper et al., 2015). Distributional shifts in pelagic or demersal species could also affect the deep-sea habitat through connectivity and coupling between the pelagic and demersal compartment. A more direct link between deep and pelagic habitats is the vertical diel migration of many demersal species which feed in the upper water-column. These processes and feeding strategies connect deep demersal species to surface processes and the pelagic compartment.

Fish survey data

Since 1998, the Greenland Institute of Natural resources has surveyed the deep parts (400 – 1500m) of the shelf and slope along East Greenland expanding from 61’5°N to 67°N, targeting Greenland Halibut. The Greenlandic deep water survey data was the basis for analysis in **paper I**. The survey conducted by the Thunen Institute of Sea Fisheries complements the Greenlandic survey by covering depths above 400m depth within the same region. The combination of these two surveys gave a unique dataset of catch data that covers 150 – 1500m of the continental margin over 18 years, used for analysis in **paper II** and **paper III** (fig. 2).

The assessment of species abundances is one of the most important aspects in studies of ecological processes. Groundfish surveys are commonly used to provide an estimate of the abundance of all species present at a certain location. However, no sampling gear successfully captures all individuals in its path. The catchability of species varies considerably, with species behaving differently in front of the trawl. Some species can outswim the speed of the trawl, some are herded into the trawl, and others show net-avoidance behaviour (Bublitz, 1996; Main, 1981; Somerton, 2004). Additionally, timing of sampling affects species catch and composition in the trawl, as many engage in diel and seasonal migrations (Benoít & Swain, 2003). In fish population studies, the catchability of a particular species is normally considered when calculating its abundance and distribution. In a fish community study, which involves numerous species, it is not feasible to make such assessment, as information on catchability is not available for most of the species caught in the survey. Sampling error thus introduces uncertainty in the abundance estimates, and in the analysis of trends and patterns it is assumed that the resulting bias does not vary excessively in space and time.

The selective properties of sampling gear are an important component of study design that influences catch efficiency. Type of gear, trawling length and speed, width of the net and mesh size all influence sampling outcomes (Fraser et al., 2007). In both the Greenlandic and German survey, use of gear and method was consistent throughout the time-series. Although both surveys used similar sampling design and catches were standardized to swept area (abundance/km^2), there was a difference in towing speed between the two surveys which could have caused a difference in catches of certain species. However, considering the strict separation in depth range between surveys and the relative slow swimming speeds of the demersal species within the dataset compared to towing speeds, the effect is considered to be minor.

In the Greenland survey, there was a shift in sampling time from July/August to August/September in 2007. This was related to sea ice conditions at certain stations which made the sampling challenging and inconsistent. The implications of this shift in sampling time were tested statistically and found not to be a driver for the observed temporal changes in this study.

The accuracy of species determination in time series is a concern in temporal diversity assessments as knowledge about species and the taxonomic expertise of personnel typically increases or varies throughout the time series. This especially concerns rare species that are poorly described in literature. I this study, rare species with only few observations were excluded from the analysis to avoid statistical noise. This action would also minimize the effect of a potential bias in species descriptions.

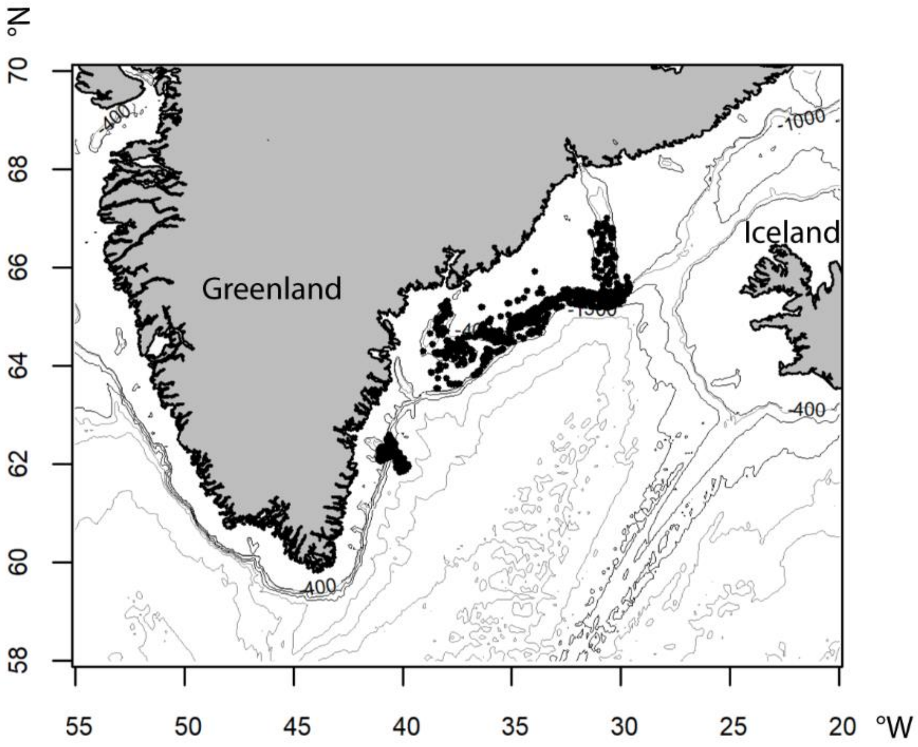

Figure 2: Map of East Greenland study region. Black points mark the survey stations included in the analysis of this thesis.

Environmental data

In all three papers, environmental variables were included to explain spatial and temporal changes in fish communities and the effect of abiotic drivers. In **paper I**, depth and in-situ measured bottom temperature of different depth layers were used to characterize the environment of deep-sea demersal fish communities within the study region. The temperature trend through the study period was assessed using a combination of in situ bottom temperatures and a physical-statistical model of bottom temperatures retrieved from Adjusted Hydrography Optimal Interpolation AHOI (Núñez-Riboni & Akimova, 2015). Sampling year and depth were used to model temporal trends in species richness and species abundance. Calculation of the Subpolar Gyre index was calculated based on sea surface height (SSH) data from satellite altimetry, provided by Archiving, Validation and Interpretation of Satellite Oceanographic Data (AVISO). The first principal component from SSH altimetry from AVISO data in the region 70°−15° W and 47°−68° N was used in the calculations. An index of the Atlantic multidecadal oscillation (AMO) was downloaded from the Earth System Research Laboratory of the National Oceanic and Atmospheric Administration (NOAA, 2018). **In paper II**, time series of sea surface temperature, air temperature, salinity, sea ice concentration and chlorophyll concentration were collected from remote sensing products (Copernicus, 2019a, 2019b) and an ocean reanalysis (ORAS5, 2019), and correlated to fish abundance data (principal tensor time series). Monthly sea level air temperature 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, 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). Monthly temperature, salinity as well as longitudinal and meridional current velocities were obtained from the global ocean reanalysis ORAS5 (ORAS5, 2019; Zuo et al., 2019). All data have been extracted in the region 55-75ºN, 50-10ºW. In **paper III**, depth and time (Year) were used in multivariate analysis and as predictors when modelling spatial and temporal variation in functional diversity.

This study is conducted in a sub-arctic region where Arctic and Atlantic water masses meet across a complex shelf and slope topography. This yields a highly dynamic and versatile environment with movement of the frontal zone between water-bodies and the presence of several oceanographic phenomena such as spill jets over the slope (Pickart et al., 2005) and cyclonic eddies (Bruce, 1995). Due to these characteristics, the in-situ measurements, representing a snapshot of temperature at the site, may not provide reliable information for a larger area. Therefore, when looking at trends within the whole of the study region, data from the AHOI built on data from several remote sensing and in situ products, were used to provide a better picture of temporal variation in environmental conditions. However, as models of environmental data like AHOI are sometimes subject to regional biases, the in-situ temperature observations were used to remove such biases from the long-term averages in **Paper I**. This illustrates the importance of combining modelled and in situ data to achieve best results in studies of the influence of climate, like the present one. Further evaluation of the potential uncertainties in the modelled climate indices and environmental data retrieved from OSTIA and ORAS5 is not considered in this thesis.

Traits data

Traits for all species in **paper III** were obtained from freely available online data (Beukhof et al., 2019), whereas biogeographic characterization of species in **paper II** and **paper III** were based on Mecklenburg et al. (2018). From the traits dataset, we selected 19 traits that describe habitat affinity, feeding ecology, life history and mobility, which affect ecosystem function and fish responses to environmental change (Frainer et al., 2017; Wiedmann et al., 2014). Life history traits included fecundity, maximum length, longevity (as maximum registered age), and offspring size (Wiedmann et al., 2014). Mean trophic level was calculated based on species prey items (Froese & Pauly, 2017), and fish were categorized into piscivorous, benthivorous, planktivorous and generalist. Based on feeding habitat (at or near the bottom, or in the pelagic), species were distinguished as demersal, pelagic, bathypelagic or benthopelagic. The shape of the body and caudal fin was used to gain information about fish life style related to functions such as swimming speed, feeding strategy and type of habitat

(Friedman et al., 2020; Martinez et al., 2021). Body shape is here 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 yield higher swimming speed as they provide lower drag and higher lift than lower aspect-ratio fins. Species biogeography (Arctic vs boreal) was based on the Atlas of Marine fishes of the Arctic region (Mecklenburg et al., 2018).

Not all species within this dataset are equally well studied and described, and for some species availability of traits data is limited. In those cases, information was retrieved from relatively few observations or based on knowledge of similar and related species (Beukhof et al., 2019). The resulting uncertainty in traits data could have introduced error in the estimation of community weighted mean (CWM) trait values and of functional diversity. It is likely that this potential source of error is greater for deep-water and Arctic species, which are generally less studied compared to shallow living species distributed further south.

Statistical methods

To address the objectives of the thesis, I analysed community level properties by applying multivariate methods to multidimensional data and statistical modelling to aggregated data. The complex design of ecological studies based on observational (survey) data of many species over large areas poses statistical challenges that had to be addressed in the papers. Below I list and discuss the choice, strengths and limitations of the statistical methods applied in the three papers of my thesis.

Paper I:

To meet the first objective of paper I, I used **multivariate statistics** so as to describe and classify fish assemblages in relation to temperature and depth in the study area. This was done using hierarchical clustering on species abundance data based on the Bray-Curtis dissimilarity index (Legendre & Legendre, 1998) and Ward linkage. The Bray-Curtis index, expressed in percentages, provides an intuitive measure of community dissimilarity to ecologists, and in combination with Ward linkage allows to identify clusters of structurally homogeneous communities with sharp distinctions in community structure between clusters (Greenacre & Primicerio, 2014).

For the objectives of the study that required inferential statistics, which addressed trends in species richness and total abundance driven by climate warming, I used **Generalized Linear Models (GLMs)**. For trends in temperature, the GLM was applied to in-situ and modelled bottom temperature data, assuming a normal error distribution. For species richness, the GLM assumed a Poisson error distribution because the response variable consisted of count data. For total abundance, the GLM assumed a Gamma or normal error distribution. The GLMs modelled temporal trends, and models of the ecological responses did not include climate variables in the predictors, thereby addressing climate effects on fish communities indirectly.

Species richness is difficult to measure in an unbiased fashion. To estimate species richness reliably, the study area needs to be exhaustively sampled. In a vast region like East Greenland, such exhaustive spatial sampling is difficult to obtain, causing a possible sample size induced bias. This also concerns systematic differences in sample sizes between depths, as the deepest depth layers (1000 – 1500 m) were less intensively sampled than depths above 1000 m. However, precise representative sampling in the marine environment is challenging and hardly ever achieved, especially in the deep ocean. To assess this potential source of bias, a rarefaction technique could have been performed, modelling number of species as function of number of samples (Walker et al., 2008). An option that would limit the above mentioned bias is the use of abundance weighted richness estimates, such as the Shannon’s index or Simpson’s index, but these tend to ignore rare species.

For the data collected over time, used in the trend analyses, there is a chance for the observations to be autocorrelated, meaning that samples closer in time are not independent of each other. Temporal autocorrelation introduces bias in uncertainty estimates, and may produce overly optimistic, narrow confidence bands. The models in this study did not correct for autocorrelation. As the trends were clear, with marked effect sizes, correcting for autocorrelations would not alter the main results and conclusions, but merely affect the uncertainty estimates by increasing the width of the confidence intervals. Mixed modelling would allow to adjust for temporal autocorrelation in secondary analyses of the investigated data.

To summarize the temporal changes of all species within the two regions, a **Redundancy Analysis (RDA)** was performed using time and depth (and latitude) as predictors. Statistical inference relied on (Monte-Carlo) permutation testing, without restrictions on permutation design to account for temporal or spatial autocorrelation. Restricted permutation can accommodate for complex sampling design, and although accounting for spatial autocorrelation without a regular sampling grid can be complicated, adjusting for temporal autocorrelation is feasible and could have helped to mitigate over-optimistic P-values.

Paper II:

In the second paper, an additional data set (survey) covering the depths above 400 m was included in the analyses, which gave the opportunity to assess the entire depth range of the continental shelf and upper slope for temporal and spatial changes in fish community responses to climate change. Traditional multivariate approaches usually analyse temporal and spatial components of variation separately, but risk missing out on important interlinked processes. I therefore decided to use a **tensor decomposition analysis** (Principal Tensor Analysis over k-modes (PTA)), which allowed to assess change across species abundances, depth, and time simultaneously, providing an overview of main patterns and trends. The use of multiway-models does not have a long tradition in biology and ecology, but its value in addressing spatio-temporal variation in multi-species communities has recently been recognized (Frelat et al., 2017). The approach of PTA is the same as with the more familiar Principal Component Analysis (PCA), and involves scaling, selection of components and visual summary and interpretation with a biplot.

To simplify the task of analysing patterns produced by 55 species, hierarchical clustering of PT scores was performed. From the PTA results, the fourth principal component, representing the dominant temporal dynamics of the data, was extracted for further analysis. The clustering of species based on both spatial and temporal scores, could cause a trade-off in weighing of the scores. In other words, two species living in the shallowest strata and the deepest strata respectively, showing similar temporal trends, may be grouped based on depth preferences and not the temporal trend. However, the spatio-temporal pattern of all species within clusters were assessed separately and evaluated to fit well, with few exceptions.

To identify environmental drivers of the observed changes, the **Pearson correlation** between time series of the fourth principal tensor and of various regional climate indices was calculated. A known problem with such analysis is the potential effect of autocorrelation which might inflate the chance of detecting significant correlations where none exist (Pyper & Peterman, 1998). One common way to deal with this is by detrending the time series via linear regression. However, by applying this method, one risk removing an unnecessary amount of information and fail to detect true correlations. Therefore, it was decided to account for autocorrelation by reducing the effective number of degrees of freedom (and, thus, increasing the p-value), following the method of (Pyper & Peterman, 1998). Spatial maps of correlation coefficients were calculated by computing the correlation with each of the time series of the gridded environmental data. Non-significant correlations were not showed in the maps, thus, stressing only the spatial regions where a real relation to the fish tensor time series was highly probable.

Paper III:

To address the underlying ecological processes and functional implications of the changes in fish communities documented in the two previous papers, I relied on functional traits analyses. Specifically, I wanted to investigate which characteristic features of fish species were involved in the response to environmental change. **Multivariate statistics** allows to relate the attributes (traits) of species to the environmental conditions at a site, by using aggregate trait values averaged across species in a community. Such Community Weighted Mean (CWM) approach is widely applied, and assumes that CWM trait values reflect the best traits configuration for given local environmental conditions. The latter notion is challenged by the potentially large interspecific trait variation averaged out in CWM estimates (Muscarella & Uriarte, 2016). It is therefore questioned whether the CWM correctly reflect optimal strategies, especially when few traits are considered. In such cases, the CWM approach may not represent ecologically important niche traits but emphasize the functional composition of dominant species. Therefore, the functional perspective provided by the use of CWM might contain gaps in mechanistic links between the environmental gradients and functional diversity. However, the aim of this study was to reveal main patterns (trends) in traits space in response to environmental change, and therefore smaller local scale dynamics was not the focus. Several traits were included, covering both life history, morphology, and functional attributes, which assures that the findings are reliable. Also, the agreement of the results with expectations, previous findings and literature further strengthens the conclusions. The CWM traits were summarized using PCA and modelled via Redundancy Analysis (RDA) as function of depth, time (year), and their interaction.

Functional diversity indices such as functional richness, evenness and dispersion, are extensively used to effectively assess ecological integrity (Schleuter et al., 2010), and to help infer community assembly processes (Frainer et al. 2021). However, sampling intensity may affect the estimation of these indices and introduce bias (X. Zhang et al., 2021). Functional richness is monotonically increasing with species richness and will therefore be affected by the same sample size bias discussed above for species richness under Paper I. Functional evenness complements functional richness, by measuring the regularity of the distribution of species abundance in functional space. However, functional evenness does not take into account the dispersion (i.e. spread) of species in traits space as it focuses on the distribution of species within a convex hull, independently of its volume (Laliberté & Legendre, 2010). Therefore, a multidimensional index of functional dispersion, accounting for species relative abundances in trait space, was additionally used. Rare species with extreme traits values will not greatly affect the measure (Laliberté & Legendre, 2010).

Before analysis, standardising all traits to mean 0 and unit variance to provide similar weight to all traits is suggested (Villéger et al., 2008). This is done because it is rarely known a priori which traits are more important. However, the broadly applied Gower distance (Gower, 1971) disregard uneven weighing of traits dissimilarity values when using traits with different distributions, such as a mix of continues and categorical variables. Categorial traits and traits coded as dummy variables will contribute more to the multidimensional dissimilarity. Therefore, the gawdis R function was applied to provide to each group of traits (categorial, binary, continues and strongly correlated traits) comparable influence on multi-trait dissimilarity (de Bello et al., 2021).

Species taxonomic and functional diversity were modelled as function of depth and time using **Generalized Additive Models (GAMs)**. The use of GAMs allows to rely on smoothing functions to fit non-linear relationships between variables, and they are therefore widely used in modelling spatial biological and ecological patterns. As the GAMs did not correct for autocorrelation, uncertainty estimates may be overoptimistic. If modelling were to be used for more in-depth analysis and predictions, a more complex ecological mixed model should be applied, allowing to account for complex design considerations.

Summary of results

Paper I:

Margrete Emblemsvåg, Ismael Núñez-Riboni, Helle Torp Christensen, Adriana Nogueira, Agnes Gundersen, Raul Primicerio (2020). Increasing temperatures, diversity loss and reorganization of deep-sea fish communities east of Greenland. *Marine Ecology Progress Series* 654: 127–141

Background: In high latitudes, species are redistributing northwards in response to ocean warming. The invasion of species has led to increased species richness in these regions and new interactions among species. However, so far, no one has yet investigated the effect of warming in depths below the shelf seas (>400m). Climate warming and the response of ecosystems in the deep sea is assumed to be delayed due to more stable environmental conditions, and therefore given less attention. The aim of the paper was to map fish community structure of deep demersal fish communities of East Greenland and to assess temporal changes in biodiversity related to bottom temperature developments.

Material and methods: We investigated and mapped the community structure of 58 deep demersal fish species found in 1060 sites on the continental shelf and slope east of Greenland. Fish communities were determined using various multivariate statistics. Further, sites along the continental slope, divided into two regions (region North and region South) were analysed for temporal trends in local species richness and total abundance. Temporal trend of bottom temperature for both regions were calculated by using in situ measurements and modelled bottom temperature indices.

Main findings: The deep demersal fish assembly of East Greenland consisted of six sub-communities, with the main driver of separation being depth, followed by temperature and latitude. Presence and dominance of species in communities were mainly determined by abundance and not species replacement. Within the two slope regions, species richness and total abundance decreased concurrently to a rise in bottom temperatures.

Paper II:

Margrete Emblemsvåg, Karl Michael Werner, Ismael Núñez-Riboni, Romain Frelat, Helle Torp Christensen, Heino O. Fock and Raul Primicerio. Deep demersal fish communities respond rapidly to warming in frontal region between Arctic and Atlantic waters. *Global Change Biology* (in press).

Background: Climate change affects marine and terrestrial ecosystems all over the world. Although more than 90% of the habitable oceans' volume lies below 200m, long term studies of biodiversity in slope and deep-sea regions are rare. Therefore, it is currently unknown how fish communities respond to changes in the environment across a vertical depth gradient exceeding the typical bottom depth of shelf areas. The aim of this study was to gain knowledge of how fish communities distributed from the continental shelf to the deep sea respond to abrupt environmental changes and provide novel insight into their depth specific vulnerability to climate change.

Material and method: We compiled data from the continental shelf and slope of East Greenland covering a depth range of 150-1500m. We used a multivariate method called principal tensor decomposition followed by hierarchical clustering to identify spatial and temporal developments in fish abundance. The fourth principal tensor displaying the temporal trend were correlated with time series of sea surface temperature, surface salinity, sea level air temperature and sea ice concentration.

Main findings: We identified 7 clusters of species sharing similar spatial and temporal patterns in abundance. A rapid increase of boreal species and a decrease of Arctic species was observed between 2005 and 2010 in the intermediate depth layers of 350 – 1000m, whilst little change was observed in the shallow (150-350m) and deepest depth layers (1000-1500m). This indicates that deep sea fish communities can respond just as fast or faster to environmental change compared to shallow water communities. Year to year fluctuations in community abundances down to 1000m depth were highly correlated and synchronous to surface climate events which suggest rapid behavioural responses to oceanographic climate events.

Paper III:

Margrete Emblemsvåg, Laurene Pecuchet, Liv Guri Velle, Adriana Nogueira and Raul Primicerio. Functional borealization and diversity loss in East Greenland fish communities during recent warming. *Diversity & Distributions* (accepted for publication)

Background: In the last two decades, climate induced local loss in species richness and restructuring of fish communities was observed in depths between 300-1000m depth East of Greenland. Community restructuring have most likely resulted in considerable changes in functional diversity and composition. Knowledge about species functional traits and temporal changes in community functional characteristics is crucial for assessing ecosystem mechanisms and ecosystem vulnerability. The aim of this study was therefore to assess whether functional diversity compensates for the loss of species in maintaining ecosystem function.

Material and Methods: We used species abundance from East Greenland obtained from two surveys covering 150 – 1500m of the continental margin over 18 years. Traits of the total 55 demersal fish species were obtained from freely available online data source. We used

multivariate statistics describe the characteristic of the fish community and to assesses changes in community weighted mean traits in depth and time. Functional diversity indices were calculated to address temporal and spatial changes in community function.

Main findings: Despite a climate driven borealization of the East Greenland fish communities, we found a loss in functional diversity in depths down to 1000m, with most profound decline in deeper waters between 300 – 1000m. There was a general decrease in bottom dwelling benthivores which is typical of Arctic species, and an increase in boreal generalists. These results warn of a decline in ecosystem robustness and ecosystem resilience towards environmental change and the impact of fisheries.

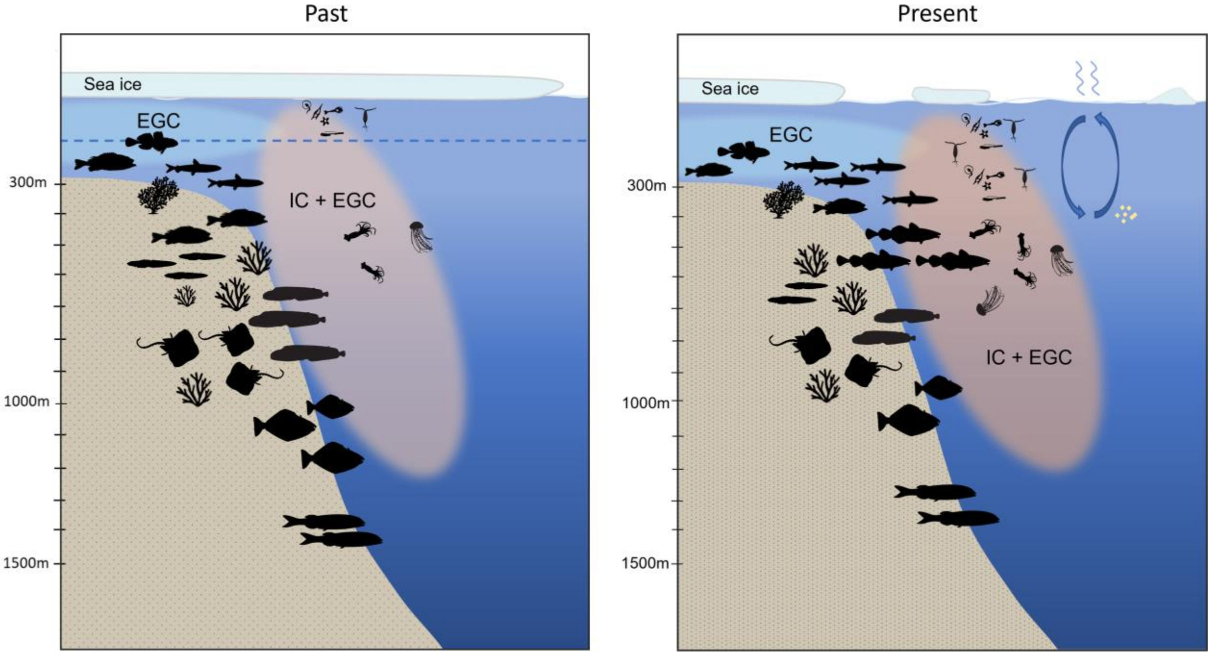

Figure 3: Illustration of past and present community structure in the East Greenland ecosystem along the continental margin. During the two last decades, sea surface temperatures increased whereas sea ice concentration decreased in the area. The changes in surface climate conditions (Atlantification) resulted in less stratification and higher mixing of the water column. Bottom temperatures also increased along the continental slope. As a response to these environmental changes, the abundance of Arctic benthivores species decreased, and the fish community became increasingly dominated by boreal generalists. The transition was mainly happening at depths between 300 and 1000m where the warm Irminger current (IC) mixes with the cold East Greenland current (EGC).

Discussion

This thesis documents how climate change triggers diversity loss and functional reorganization in deep demersal fish communities East of Greenland. Taxonomic and functional diversity declined with sharpest negative trends in depths between 300 and 1000m. The decrease in diversity was mainly caused by an overall loss of Arctic and benthivore specialists and an increasing dominance of boreal generalists. Functional restructuring was most pronounced in in the depths between 350 – 750m between 2005 and 2010. The surprising negative trends in diversity may be explained by regional oceanography and topography inhibiting the redistribution of species. Annual fluctuations in fish abundances were highly correlated to surface climate conditions. Such rapid ecological responses are most likely mediated by behaviour. These findings contradict an expected delayed response in the deep-sea and show that climate driven responses can be just as fast or faster than in shallower waters of shelf seas. The loss in taxonomic and functional diversity and the borealization of deep fish communities alters species interactions and affects ecosystem function and vulnerability.

Loss in biodiversity

During the last two decades, the deep demersal fish community East of Greenland has experienced a rapid loss in species richness and total species abundance (**paper I**). This happened concomitantly with a rise in bottom temperatures probably caused by warming upstream along the Atlantic Irminger current (**paper I**). The loss of species richness is contrary to expectations and observations of a rise in biodiversity in response to warming in high latitude seas (Chaudhary et al., 2021; Cheung et al., 2009; Fossheim et al., 2015; Hiddink & Ter

Hofstede, 2008; Johannesen et al., 2012; Lotze et al., 2019) The surprising results are explained by environmental filtering of Arctic species and by hydrographic and topographic constraints on distributional shifts, discussed in depth below. Findings of **paper I** contradict expectations of a delayed response to climate change in the deep sea and highlight the importance of regional and local considerations when predicting ecological responses. As the community is becoming less diverse, the buffering capacity against perturbations decreases and the ecosystem becomes unstable and less able to recover in a rapidly changing environment. It has been shown that fisheries in species poor ecosystems are collapsing at higher rates than fisheries in species rich ecosystems, indicating the importance of maintaining high taxonomic diversity to support function and ecosystem services (Worm et al., 2006). However, the effect of declining species richness on ecosystem health also depends on whether functional turnover can compensate for the loss of species thereby maintaining ecosystem function.

Borealization

The loss in species richness was part of a larger restructuring of the East Greenland deep demersal fish communities (**paper II**). In accordance with observations in other high latitude seas (Fossheim et al., 2015; Huntington et al., 2020; Kortsch et al., 2015; Post et al., 2020), this restructuring consisted in an increasing dominance of boreal species (**paper II and III**). Borealization took place between 350 and 1000m but not in the shallow (150 – 350m) or deepest (1000 – 1500m) layer. Most rapid change was observed between 2005 and 2010 which is an ecological transition period (**paper II**). The concept of marine borealization has been related to the advection of Atlantic and Pacific origin biota into the Arctic with the expectations of increased taxonomic- and functional diversity (Polyakov et al. 2020, Frainer et al. 2021). As opposite trends in diversity are observed on East Greenland, it is likely that borealization is mainly caused by increased abundance of locally established boreal species and not by the addition of new species. The loss of sea ice and increasing sea temperatures erodes on the Arctic habitat and leaves the Arctic species exposed to challenging environmental conditions. The benthivores are also likely to suffer from the growing importance of boreal species through increased competition and predation pressure. Boreal species are likely benefitting from improved feeding conditions driven by increased pelagic productions (Frainer et al., 2021; Frainer et al., 2017; Kortsch et al., 2015).

In addition to the borealization trend over the study period, an increased importance of boreal species was also observed in association with annual fluctuations in climate conditions. These interannual changes were in synchrony with an Atlantification process (Lind et al., 2018) indicated by surface climate indices such as decreased sea ice concentration, increased SST, air temperature and surface salinity (**paper II**). The rapid changes in community abundances to surface climate indices can only be mediated by behavioural responses through fast redistribution of species. In such, surface climate fluctuations can be used as indicator of community changes, exemplified by the extreme years, such as 2003 and 2015 which resulted in responses down to 1000m.

Functional reorganization

The decrease in species richness was not compensated by functional turnover, resulting in a loss in functional diversity. Functional richness and functional dispersion decreased during the study period, at depths down to 1000m (**paper III**). In general, there was a decline in traits such as benthivory and low mobility, typical of small bottom dwelling specialists, whereas boreal traits such as generalist feeding, and high trophic level became more dominant (**paper III**). As expected, the most rapid functional restructuring was found at depths between 300 and 900m where we also found the highest rate of taxonomic borealization (**paper II**). Specialization is expected to increase the risk of extinction during environmental change (Colles et al., 2009). Generalists with a wide habitat and diet niche are favoured in environments that are more variable and exposed to perturbations (Clavel et al., 2011). As the East Greenland marine ecosystem is a transition zone where Arctic species live close to their upper limits of temperature tolerance, specialists like the Arctic benthivores are likely to be suffering from the change in habitat conditions driven by ocean warming. Boreal species, especially generalists with wide thermal tolerance, are adapting well to increasing temperatures and experience an improvement of the habitat. Generalists are also often more mobile and can therefore respond and redistribute rapidly when the environment and food supply is changing (**paper II and III**).

The observed functional reorganization may lead to changes in food web structure through increased connectivity and shifts in feeding links (Kortsch et al., 2015; Pecuchet et al., 2020). Further, if the warming trend continues, more Arctic and specialist species will be lost, resulting in a more homogenized community. Biotic homogenization, which is the combination of taxonomic and functional homogenization, observed in this study, has been widely documented and acknowledged as indicator of climate change (Clavel et al., 2011). However, the impact of homogenization is less studied. The general expectation is that resistance to environmental change is reduced as the available range of functional characteristics becomes narrower, compromising the regional level of buffering capacity (Olden et al., 2004). When taxonomic diversity declines, the effect on adaptive capacity greatly depends on how many functional traits that are lost, and which remain within the ecosystem. Few studies have documented how marine species loss might affect ecosystem functioning and adaptive capacity. Some of the species that are decreasing in East Greenland, like the Atlantic wolffish (*Anarhichas lupus*) have been shown to play an important structural role as module connector within the food web (Kortsch et al., 2015). Also the Arctic *Lycodes* species seem to play important functional roles, despite their low number of food-web links (Kortsch et al., 2015). It is therefore likely that the decrease and possible loss of these species may have great impact on ecosystem function and services in East Greenland.

Regional responses to climate change

Impact of hydrography

This thesis suggests that deep demersal sea fish communities can respond just as quickly to climate events and climate change as shallow fish communities. The outcome of pressures at different depths is largely defined by local or regional conditions such as waterbody characteristics, direction of currents and bottom topography. The ecosystem East of Greenland is dominated by two main waterbodies: the Arctic East Greenland Current (EGC) on the shelf and a mix the latter and the Atlantic Irminger current (IC) along the shelf break and slope. The borderline between these currents creates a front. The hydrography and characteristics of water masses and the topography of the region seems to be a strong determinant of temporal change in fish community structure that has been observed in this study.

Survey data from continental slope and deep-sea regions collected over extended periods are limited (Maureaud et al. 2020), so the effects of environmental change and fisheries on target species and communities have been difficult to determine. Therefore, evaluation of vulnerability and future responses of fish communities is often based on empirical models of available data, which allow to extrapolate to a broad geographical scale (Alabia et al., 2020;

Cheung et al., 2009; García Molinos et al., 2016; Lotze et al., 2019). Such models provide important information and insight in a situation when data is limited and quantification of future trends is needed, but they are incomplete simplification of the natural world and therefore fails to consider local and regional environmental conditions, which can determine distributional responses of species and communities (Molinos et al., 2017). Although large scale predictions of northward movement of species and increased diversity at high latitudes, is documented to be true for regions such as the Barents Sea (Fossheim et al., 2015), Bering sea (Alabia et al., 2018; Mueter et al., 2017) and North Sea (Hiddink & Ter Hofstede, 2008), this is not true for the fish communities East of Greenland. The explanation for the observed deviation from what is expected can be as nuanced and complex as there are several factors determining and interacting in defining species responses and distribution. These might be characteristics of taxa, such as behavior, life history and phenology, or local and regional conditions such as physical environment and species interactions (Alabia et al., 2018; Nathaniel L Bindoff et al., 2013; Seabra et al., 2015). Depth and oceanographic features of the region is presented in this thesis as a likely important reason for the observed changes in community structure. Contrary to the hydrography of the Eastern Atlantic where the northward flowing warm Atlantic current (gulf stream) is supplying the northern regions with temperate species (Johannesen et al., 2012), currents East of Greenland are flowing southward along the continental slope, and there is no such straight forward northward pathway for deep demersal species to enter the region. Currents as a conveyer of species dispersal and distribution have shown to be important. Marine species may use currents for passive "transport" in early life stages and actively by shifting distribution to reach spawning or nursing area (Bradbury & Snelgrove, 2001), or to find more favourable habitat in a changing environment (Molinos et al., 2017). Berge et al. (2012) discovered that Arctic crustaceans, previously thought to be totally dependent on sea ice, conduct vertical migrations to utilize deep sea ocean currents to transport themselves northward into the high

Arctic. By doing so, they retain their functional role within the Arctic and avoid extinction. The scientists suggest that this is a successful adaptive strategy in a more seasonally ice-covered Arctic, and they call their hypothesis the “Nemo hypothesis” after the Disney movie where Nemo, the clownfish, along with his aquatic friends uses deep-sea currents as a mean of transport across the ocean. However, there is little evidence for an offset of active fish dispersion due to mismatch between current directions and climate velocities. The lack of evidence may be due to scarcity of data from regions where such conditions are pronounced (Molinos et al., 2017). Life history traits related to range expansion are important in such considerations, especially when evaluating demersal deep-sea species which are considered less mobile and restricted to niche habitats (J. Koslow et al., 2000; J. A. Koslow, 1993; Norse et al., 2012).

To put the findings of this thesis in a more global perspective, the decreasing trend in taxonomic and functional diversity might also be true for other shelf and slope demersal communities along East Greenland because of the southward flow of water masses. Similar flow patterns can also be seen along the east coast of Canada and in the west Bering Sea where the southward flowing Kamchatka Current forms the western boundary current. The lack of data series due to the inaccessibility of these cold and ice-covered regions causes a bias in coverage in global studies, whereas the lack of including important climate and oceanographic variables into predictions, causes bias in species distribution models. The negative temporal trend in taxonomic and functional diversity found in this thesis (**Paper I, II and III**) might therefore also take place in other regions with similar characteristics.

Changes in productivity

Climate driven changes in the abundance and species composition of primary productivity can affect higher trophic levels depending on the structure of the ecosystem and the level of top-down or bottom-up control (Frederiksen et al., 2006; Friedland et al., 2012; Šolić et al., 2017). Even though there are no study showing temporal developments of primary production within the study region, the Atlantification process detected in surface indices **(paper II**) are in other regions documented to induce mixing of water masses and trigger primary productivity (Dalpadado et al., 2020; Vernet et al., 2020). High productivity is found along the shelf break along north-East Greenland with increasing algae biomass recorded along the slope of the Greenland Sea (Frey et al., 2018). Here, relatively high concentrations of chlorophyll is induced by sea ice declines and increased light availability (Boertmann et al., 2020; Frey et al., 2018). Considering the resemblance of the regions, it is likely to assume similar high productivity along the shelf edge and slope also in the study region. Cues can also be collected from Arctic regions further away with comparable topography and hydrography. In Eurasian Arctic slopes, the inflow points of Atlantic water are the primary nutrient source that supports gross primary production levels in the upper continental slopes (Randelhoff et al., 2018; Vernet et al., 2020).

Enhanced abundances of secondary producers and consumers are apparent following the blooms, especially around the core of Atlantic inflow, such as in the Fram Strait (Basedow et al., 2018; Gjøsæter et al., 2017). The high active fishery for deep water shrimp (*Pandalus borealis*) in slopes north of Svalbard (Haug et al., 2017) indicate also elevated biomass of higher trophic levels in these inflow regions. The inflow points of Atlantic waters into East Greenland, which is within the study region, might therefore explain the observed elevated species- and functional richness of fish above the shelf break and along the upper slope (**paper III**). The foraging species blue whiting (*Micromesistius poutassou*) is abundant in the upper slope of the study region (Post et al., 2019) which likely reflects high zooplankton prey concentration and high productivity that is usually found along continental slopes and breaks associated with strong frontal zones of Arctic and Atlantic water bodies (Bluhm et al., 2020).

Boundary currents flowing along the slope can transport nutrients, detrital particles, phytoplankton, zooplankton and fish larvae (Bluhm et al., 2020). Therefore, changes in composition and abundances upstream the Irminger current and the East Greenland Current can influence the food web of the study region. In **paper I**, we suggested a warming upstream the Irminger as most likely explanation to the increasing trend in bottom temperatures within the study region. It is therefore likely that changes in nutrients and primary productivity followed this temperature increase and had an impact on the overall food web East of Greenland. Also, winter convections along the retracting ice edge have been registered upstream north of our study region, which induces increased deep mixing of water masses with exchange of organic and inorganic matter (Våge et al., 2018). The above-mentioned observations of productivity patterns and events in similar regions or in regions upstream of the study area can be signs of shifts in energy pathways also within the study region that can help explain the changes in diversity found in this thesis.

Dispersal limitations

Migration patterns of marine fauna is likely to be poleward with warming (Fossheim et al., 2015; Mueter & Litzow, 2008), However, the complexity of interactions between biotic and abiotic factors such as habitat availability and mobility, might cause counter intuitive distribution patterns in some taxa (Hays et al., 2016; Rutterford et al., 2015)**.** Pelagic species can migrate more or less freely across large distances independently of bottom topography.

Demersal species, however, are highly dependent on bottom habitat in terms of feeding, shelter and species interactions and would therefore be more constrained by available habitat of suitable depth and temperature. The dependency on non-thermal variables makes northward dispersal more challenging, especially in areas of varying topography and depth. This assumption is supported in a study by Rutterford et al. (2015) where they predicted little or no future northward distributional shifts of demersal fish species in the North Sea. They found that poleward advances of North Sea demersal fish are not likely to be common due to habitat restrictions. Interestingly they did not find any change in species depth preferences either, indicating that depth associated niches are the main drivers and limitations in demersal fish distributions. These contradictory findings are explained by the underestimation of non-thermal habitat in process-based models that predict large scale northward migrations (Alabia et al., 2020; Cheung et al., 2009; García Molinos et al., 2016). If available habitat is a significant restriction for bottom dwelling fish living in shallow shelf areas such as the North Sea, deep sea demersal species living in continental slopes would be even more restricted due to complex topography (Jakobsson et al., 2012), species narrower niches and adaptation to a deep-sea habitat (J. Koslow et al., 2000; J. A. Koslow, 1993). This thesis shed light on these aspects as **paper I and III** presents decreased mobility of deep demersal species and lack of available suitable habitat as partial possible explanations to why there is a decrease in species richness and functional diversity in the slope regions of East Greenland.

East Greenland sensitivity to climate change.

The region Southeast of Greenland is a complex climatic system. During winter, this is a region of extreme conditions and the stormiest ocean of the world (Sampe & Xie, 2007). It is also an originating point of cyclones that affect other regions of the Nordic and Barents Seas (Papritz, 2017; Sampe & Xie, 2007). The flow of Arctic water through the Denmark strait is the largest transport of Arctic freshwater into the Atlantic (Rudels et al., 2002). The East Greenland current also transport large amounts of sea ice that breaks off in a melting Arctic (Martin & Wadhams, 1999). Further, the warming increases the freshwater runoff from the Greenland sheet and the flux of sea ice into the East Greenland waters (Luo et al., 2016), which undoubtably affects ocean life along its path. Climate modelers are struggling to entangle all variables set in play in this region, exemplified by ongoing discussions about the unusual phenomenon called "the warming hole" southeast of Greenland. In this spot, there has been a cooling -or a less warming than surrounding seas, with its magnitude depending on use of data sources and type of climate models. Although there is a general agreement on existence of this warming hole, the intensity of it and the mechanisms behind it are debated as this is a complex area with multiple drivers (Gervais et al., 2018; Hu & Fedorov, 2020; Keil et al., 2020). In **paper II** we found that sea surface temperatures and the corresponding surface indices were in synchrony with interannual fluctuations in fish community abundances. Sea surface temperature developments in the larger ecoregion revealed that these fluctuations were evident also North of Iceland exemplified by the clear signal of the extreme climate event in 2003. In the front between Atlantic and Arctic waterbodies that run along the slope of the study region, the pulses of warm and cold years cause the frontal belt (climate velocities) to move back and forth over the slope and shelf, or to widen or contract its width (**paper II**). The East Greenland ecosystem might therefore be vulnerable to large scale environmental change and extreme events, which results in strong responses of species living there.

Extreme climate events.

Considering climate change, ocean currents may change, both in temperature and in strength due to alteration in heat balance, wind patterns and freshwater inflow from melting ice. That change is not likely to be gradual and uniform, but periodic and episodic with extreme events (Våge et al., 2018; Våge et al., 2009) or extreme years (Huntington et al., 2020; Somavilla et al., 2016) that could have great local impact on communities and ecosystems through changes in the environment (MacKenzie et al. 2014, Aarflot et al. 2018, Møller & Nielsen 2019). Climate events such as exceptionally warm or cold years could cause a shift in community structure that does not necessarily change back to its previous state the following years. In **paper II**, we identified such an extreme year in East Greenland with effects detected down to 1000m depth. In 2003, sea surface temperature was exceptionally high followed by low ice concentrations and high surface salinity. These large-scale climate events, detected at the surface is also affecting the deep sea through ocean connectivity and by immediate behavioural responses of fish (**paper II**). An extremely warm condition in 2017 was recently observed in the North pacific with a change of state throughout the ecosystem that persisted into 2019 (Huntington et al., 2020). The question is whether these increasing frequencies of extreme event are anomalies or in fact drivers of ecosystem shift through a cascade of sequential changes. The peak in community changes in 2003 presented in **paper II** does not show a complete back transformation in the following years and might therefore be a preconditioning for the rapid changes observed between 2005 and 2010 (**paper II**). The focus in climate change research in marine ecosystem has traditionally been on trends and not events. However, in terrestrial ecosystems, the effect of extreme disturbance events is more widely documented and observed (Jentsch et al., 2007). Severe events such as drought and storms can push an ecosystem beyond dynamic equilibrium, or in a less severe situation, change competitive interactions and reduce variability (Smith, 2011b; Ummenhofer & Meehl, 2017). Although the effect of extreme climate events in time series are important in climate change studies, the challenge lies in statistical identification of such events as the extreme measurements have the characteristics of outliers and therefore considered very unlikely (Schär et al., 2004), especially when such events are local.

The observations of high SST in East Greenland in 2003 (**paper II**) is not restricted to this region, but also recorded elsewhere in the North Atlantic up until the Arctic Circle (Feudale & Shukla, 2011). The warm SST anomalies affected the air temperature field in mid-high latitudes causing a record-breaking heatwave with center of action in central Europe (Feudale & Shukla, 2011; Schär et al., 2004). Effects of high SST in 2003 has been documented in the Mediterranean sea where the extreme temperatures caused mass mortality of benthic macro-invertebrate species in the entire North-West Mediterranean (Garrabou et al., 2009). The 2003 heatwave has been described as “the shape of things to come” and reflects the predictions of summer temperatures at the end of the 21st century (Beniston, 2004; Schär et al., 2004). Studies of global anomalies in sea surface temperatures in 2003 show that the region East of Greenland was strongly affected along with other North Atlantic regions such as the North Sea (Black et al., 2004; García-Herrera et al., 2010). Few or no studies exists on the effect of this extreme year on North Atlantic marine ecosystems, except for a registration of an exceptional abundance peak of dinoflagellates in the English channel (Gómez & Souissi, 2008). With such a strong signal in deep fish communities detected in East Greenland, it is highly likely that the extreme increase in sea surface temperatures also affected ecosystems elsewhere in the North Atlantic. Future warming events, expected to accelerate in frequency, will play an important role in the overall climate driven changes of the marine ecosystems.

Implications of this study

This thesis presents demersal fish assemblage structure and constitutes a first attempt to provide an overview of spatial and temporal trends in deep sea demersal fish communities during the past two decades East of Greenland. This work shows the importance of using a combination of taxonomic and functional diversity to provide key information on ecosystem processes and ecosystem state. Additionally, I also argue the importance of considering regional oceanography, topographic, and hydrographic conditions, as these parameters highly determines the presence and distribution of species in space and through time. Despite living at great depths, species are not isolated from climate events. On contrary, results from this thesis show that such events, detected at the surface, can strongly and rapidly affect deep fish communities, which suggests high oceanographic connectivity.

Oceanic frontal zones, such as the study region, are considered ecological significant regions as biophysical coupling can lead to biodiversity hotspots through the formation of pelagic foraging regions that attract higher trophic level consumers (Cox et al., 2016; Siegelman et al., 2019). Examples of such frontal zones are the North Pacific transition zone, Sub Arctic transition zones, Equatorial fronts, Southern Ocean frontal zones, shelf edge frontal zones and major current fronts (Scales et al., 2014). Although these regions differ in spatial scales and oceanographic characteristics, they are associated with a diverse array of marine vertebrates. This also makes these regions a hotspot of anthropogenic treat through climate change and by attracting fisheries (Scales et al., 2014). During the last decade, increasing amount of research on these regions have provided valuable knowledge, but there are still many unanswered questions. Among these, much is still unknown about the character and nature of species responses to environmental cues in these regions. This study show that fish communities respond rapidly to changes in the environment which are likely related to the back-and-forth movement of the frontal zone (temperature isoline**, paper II**). Due to the special oceanographic features of frontal zones, these regions might respond exceptionally fast to climate change by closely tracking the climate signal.

The immigration of species and borealization of the fish community may result in an increase in commercially interesting species, such as cod and tusk. However, the major community restructuring occurring in East Greenland with a rapid loss of species and functional diversity, clearly indicates a decrease in ecosystem resilience against fisheries impact. As the community is becoming more dominated by borealists and generalists, the effect of overfishing might travel faster though a more closely linked food web and affect species more indirectly (Kortsch et al., 2015). As Benthivores are struggling, demersal trawl known to be destructive to the sea floor, might emphasize the impact of climate change on the benthic habitat.

The deep sea is of the least explored areas of the ocean, and a habitat we know is vulnerable to disturbance (Danovaro et al., 2004; Danovaro et al., 2020). Yet, commercial fishing and other human activities such as mining is occurring at increasing depths (Norse et al. 2012). The biological vulnerability of deep-sea fish combined with little knowledge about deep sea mechanisms, makes deep sea fish or other deep-sea resources exceptionally difficult to manage sustainably. Many would even state that the deep-sea is not suitable for harvesting at all, or that sustainable harvesting is only feasible for a handful of species that meet certain criteria (Norse et al. 2012). It is therefore important for fisheries management to be cautious and closely monitor future developments of the ecosystem, fish community composition and abundances. In evaluating ecosystem health and resilience, it is important to consider both taxonomic and functional diversity. More scientific effort and data collection in recent years yields growing awareness and recognition of a vulnerable deep sea, and hopefully a more precautionary approach will be implemented in future management that also considers the ongoing unpreventable impact of climate change.

Limitations of the study

This thesis present important new insight into the East Greenland ecosystem. Still, I acknowledge the limitations of this study, and do not consider the findings and causal explanations of this thesis as a final description of ecosystem processes. Although the community approach provides valuable insight into the larger processes and drivers of a system, the method is vulnerable to existing knowledge at species level. When knowledge of species is limited, trait information is built on assumptions or information from similar species which would present uncertainty. Incorrect description of species can affect community analysis, especially if those species are relatively abundant within the community. Furthermore, due to limited data and research in other trophic levels the East Greenland ecosystem, causal explanations to the results are reconstructions based on the nature of the observed changes and on cues given from ecosystem studies in similar regions. Questions regarding mechanisms behind the findings of this thesis is therefore still largely unanswered. Through this work, it has become evident just how complex the marine ecosystem is with links and connections in time and space that runs across ecosystems and scientific disciplines. It is therefore important to acknowledge the potential influence of factors not considered in this thesis. I did not consider the importance of critical steps in of early life stages and larval drift, phenology or changes in the abundance of other marine animal groups that may impact fish communities. For example, it is expected that the Arctic mammals will shift northwards following temperature preferences and the retracting ice sheet, whereas the boreal mammals will extend their distribution and the period they spend in East Greenland waters (Ugarte et al., 2020). Considering their high abundance and predatory behavior on most trophic levels, it is likely that abundance shifts of these species might influence the ecosystem through several pathways (Bowen, 1997; Roman et al., 2014).

The potential impact of fisheries on the ecosystem and fish communities was not a focus of this thesis and is therefore not considered in the statistical analysis. However, East Greenland is international fisheries waters with the extraction of many demersal and pelagic species, and it is important to recognize possible direct effects (fishing mortality of target species and use of destructive fishing gear) and indirect effects (mortality of non-target populations and altered biological interactions) on the results. The simplest direct effect of removal of top predators, such as Greenland halibut and redfish, is the potential release of unusual large abundance of prey at lower levels which further might modify trophic links, species composition and interactions (Garcia, 2003). Fisheries my also increase the abundance of other predators by decreasing competition. In light environmental change and the observed redistribution of species within the region, removal of predators could make way for the establishment of species entering the region. Thus, the effect of fisheries in interaction with effects of other stressors such as climate change, might impact the ecosystem and its fish communities.

The majority of the demersal fishery is conducted by the use of bottom trawl, which is known to be destructive to the seabed and the benthic habitat. The ruining of important Vulnerable marine ecosystems (VMEs), such as cold-water corals and sponges (Long et al.; Long et al., 2021), which are abundant along the continental margin of East Greenland, (Blicher & Arboe, 2021), might cause changes to the ecosystem. For example, as coral reefs are considered as important refuge for juvenile fish and often observed to attract several fish species, the decrease in this habitat can affect fish abundances and species richness both locally (at site) and regionally.

Future perspectives

Considering the speed and magnitude of the observed changes in this study, I would recommend future research on climate change impact to focus on deep marine ecosystems. I also strongly recommend considering the effect of regional conditions in assessing ecosystem responses to environmental change. To improve knowledge about the ecosystem east of Greenland, more in-depth knowledge about species and how both single species and species groups contribute to ecosystem functioning, is needed. Such knowledge will be essential to fully understand how the loss and gain of species will affect ecosystem function and ecosystem vulnerability. Further, studies on horizontal movement of species and communities will provide insight into the questions raised about a possible limited redistribution of deep demersal fish. To fully understand the interactions between trophic levels and connectivity between depth layers, it is essential to construct the East Greenland food web to identify prey and predator links specific to this region. Such task require knowledge on trophic levels that might not yet be available. However, because of increased climate related focus on Arctic regions in recent years, the intensity of research in East Greenland is likely to increase. When more data is gathered and compiled, ecosystem models and predictions including biotic and abiotic variables would be a valuable step in the attempt to better understand the effect of ecosystem drivers and responses in present and future climate scenarios.

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Increasing temperatures, diversity loss and reorganization of deep-sea fish communities east of Greenland

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ABSTRACT: In recent years, Arctic and sub-Arctic fish communities have shown extensive reorganization on shelves and in shallow waters, but little is known about the ecological impact of environmental changes in deeper waters. We examined temporal changes (1998–2016) in fish diversity and community structure based on research survey data from East Greenland, over a depth gradient spanning 400 to 1500 m. A northern and a southern continental slope region, 360 km apart, were analysed for temporal changes in water temperature and fish community structure. The bottom water temperature increased by up to 0.2 and 0.5°C, respectively. Contrary to expectations, there was a concomitant loss of species richness of up to 3 and 5 species, respectively, and a decrease in total abundance in both regions. Abundances of individual species displayed different trends between regions, with 3 species of wolf fishes (*Anarhichas* spp.) and American plaice *Hippoglossoides platessoides* decreasing in the north and blue antimora *Antimora rostrata*, Agassiz' slickhead *Alepocephalus agassizii* and the roundnose grenadier *Coryphaenoides rupestris* decreasing in the south. The regional differences may reflect different oceanographic characteristics, as the northern region is more influenced by colder Arctic water, whereas the southern region is primarily influenced by the Subpolar Gyre (SPG). However, the observed temperature increase is expected to be due to an intensifying Atlantic Multidecadal Oscillation and/or anthropogenic climate change and not to SPG changes. The observed changes in biodiversity and community structure associated with warming are likely to affect community dynamics and alter ecosystem functioning.

KEY WORDS: Climate variability · Species richness · Deep sea · Demersal fish · Temporal change · North Atlantic

1. INTRODUCTION

As oceans temperatures rise with global warming, marine species and ecosystems are affected worldwide. The ecological effects of warming are most rapid and pronounced at high latitudes (Wassmann 2011, Fossheim et al. 2015). The Arctic seas are warming more rapidly than the global average (Hoegh-Guldberg & Bruno 2010, Stocker et al. 2013), leading to altered habitats, poleward shifts in species distributions and changes in community organization (Mueter et al. 2009, Doney et al. 2012, Fossheim et al. 2015). Arctic fish communities react quickly to increasing temperatures due to behavioural responses that complement the demographic effects of a changing environment (Fossheim et al. 2015). The direct effects of a changing physical environment in terms of local gain or loss of fish species, and changes in

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abundances, trigger higher-order effects of warming mediated by ecological interactions (Kortsch et al. 2015). The resulting impact of warming on Arctic fish is communitywide, affecting species richness, composition and relative abundances (Mueter et al. 2009, Fossheim et al. 2015). Presently, the impact of climate change on Arctic fish is primarily documented for pelagic and demersal communities living in shallower waters, but little is known about deep demersal communities, for which more marginal effects of warming have been proposed due to the greater environmental stability experienced (Yasuhara & Danovaro 2016). A general prediction of climate change impact on high-latitude fish communities is increased species richness fuelled by poleward shifts in distribution of boreal species (Cheung et al. 2009, García Molinos et al. 2016). The expectation is supported by several recent studies showing how pelagic and demersal species rapidly expand their ranges and increase in abundance when sea ice recedes and water temperature increases (Mueter & Litzow 2008, Fossheim et al. 2015). However, most of these studies were conducted in shallower basins or shelf areas like the Barents Sea (Fossheim et al. 2015) and the North Sea (Hiddink & Ter Hofstede 2008, Ter Hofstede et al. 2010). Shallow marine ecosystems are exposed to daily and seasonal temperature fluctuations and are in general more influenced by changes in the atmosphere. In comparison, the deep-sea environment is considered more stable in space and time, and has therefore often been disregarded as a controlling factor of diversity (Yasuhara & Danovaro 2016). However, several studies indicate that deep-sea bottom temperatures differ between oceans, depths and water masses and can change on both short-term (several years to decades) and long-term (centennial to millennial) time scales (Yasuhara & Danovaro 2016). For example, in the Labrador Sea, deep-water temperatures changed at a rate of up to ~0.5°C decade^{-1} over the last 60 yr (van Aken et al. 2011).

The impact of climate warming on Arctic fish is expected to go beyond changes in species richness, and affect the local composition and abundance of species (Meredith et al. 2019). The vulnerability of a single species to climate-driven pressures, such as increasing water temperatures, is a function of its exposure, sensitivity and adaptability. Fish are adapted to a specific range of environmental conditions that the population is likely to encounter through natural variability. When the environment changes in such way that new conditions emerge and persist, the species needs to either adapt to the new environment, migrate to a new area or face local extinction (Henson et al. 2017). Typically, mobile, short-lived species with a broad tolerance range are better able to adapt in a changing environment than more sedentary, long-lived species with restricted tolerance and habitat range (Perry et al. 2005, Danovaro et al. 2017). At high latitudes, deep demersal fish communities comprise both sedentary species narrowly adapted to local conditions, such as wolfish *Anarhichas lupus*, and highly mobile species with broad tolerance ranges such as Atlantic cod *Gadus morhua*.

The importance of both regional and local processes mediating climate-driven effects on ecological communities is illustrated in waters south and east of Greenland. As a region with adjoining cold and warm water masses, the East Greenland Ecosystem is one of the first to be affected by climatic changes (Bersch et al. 1999, Bersch 2002, Häkkinen & Rhines 2004, Hátún et al. 2005, Bersch et al. 2007, Núñez-Riboni et al. 2013). The main circulation feature in the region is the Irminger Gyre (Våge et al. 2011), which is an integral part of the Subpolar Gyre (SPG). The SPG is a region of strong interaction between ocean and atmosphere and is thus susceptible to the effects of climate change. Natural variation in intensity and geometry of the SPG ranges from inter-annual to multi-decadal time scales, which in turn affects sea temperatures and oceanic fronts (Hátún et al. 2005). Such changes have been shown to influence faunal distribution in the eastern North Atlantic (Hátún et al. 2009a) and, more recently, the geographical distribution of redfish *Sebastes mentella* in the Irminger Sea (Núñez-Riboni et al. 2013). On longer time scales, the whole North Atlantic is subject to a multidecadal oscillation of sea surface temperature, i.e. the Atlantic Multidecadal Oscillation (AMO) (Kerr 2000). Moreover, sea surface temperature is rising due to climate change, and fish species are redistributing (MacKenzie et al. 2014). Cod is re-entering and spawning in the area, the abundance of mackerel *Scomber scombrus* is reaching levels of economic interest, and novel non-commercial species are being reported (ICES Advisory Committee 2018).

In this study, we assessed the effects of climatic variability on deep-water demersal fish communities east of Greenland by investigating temporal changes (1998–2016) in the richness, composition and community structure of species. The time series analysed pertain to an East Greenland Deep Water Survey, conducted by the Greenland Institute of Natural Resources, which covers depths ranging between 400 and 1500 m. Based on predictions for Arctic fish communities (Cheung et al. 2009, García Molinos et al. 2016), corroborated by findings from other areas of the Arctic (Johannesen et al. 2012, Fossheim et al. 2015) and the Northern Atlantic (Hiddink & Ter Hofstede 2008, Ter Hofstede et al. 2010), we expected to find an increase in species richness associated with poleward shifts of boreal species and a compositional and structural reorganization of communities.

2. MATERIALS AND METHODS

2.1. Study area

The study area covers parts of the shelf and slope area of East Greenland expanding from 61° N close to the southern tip of Greenland to 67° N west of the Denmark Strait (Fig. 1). The East Greenland Ecosystem is an area where water masses are brought together by various surface currents. On the shelf, the dominant current is the cold East Greenland Current (EGC), which flows southward carrying polar water (Våge et al. 2011) and is bordered inshore by the meltwater-driven East Greenland Coastal Current (Sutherland & Pickart 2008). Over the deeper parts of the region, the warmer Irminger Current (IC) flows into the Irminger Sea with water temperatures of 3.5–4.0°C (Våge et al. 2011). The IC partly continues northward into the north Iceland Sea region, and partly turns westward to the East Greenland continental slope area. In the north, the Denmark Strait Overflow features the largest transport of dense water from the Nordic seas to the North Atlantic. The dense and cold water known as the Denmark Strait Overflow is forced through the narrow channel of the strait, runs over the sill and sinks into the deep water of the Irminger basin (Dickson & Brown 1994).

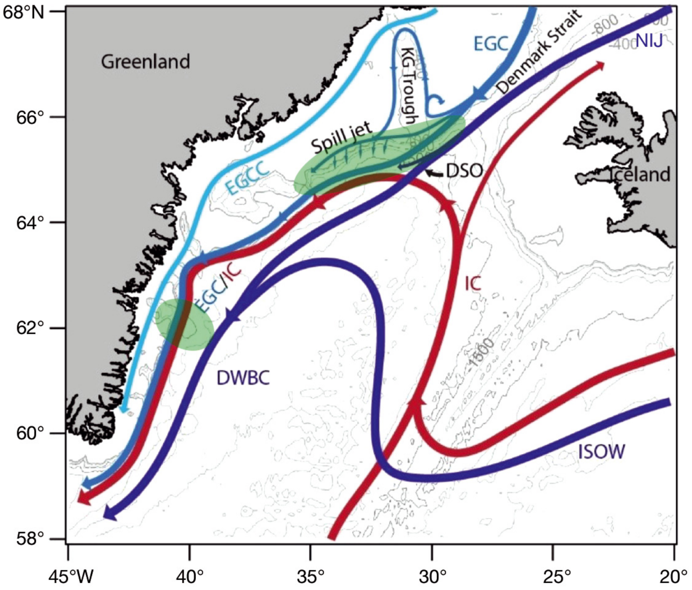

Fig. 1. Water pathways in the Irminger Sea: East Greenland Current (EGC), North Icelandic Jet (NIJ), Denmark Strait Overflow (DSO), Irminger Current (IC), Iceland Scotland Overflow Water (ISOW), Deep Western Boundary Current (DWBC), and Kangerdlugssuaq (KG) Trough. The northern and southern regions used for time series analysis are highlighted in green. ICES area 14b covers almost the entire map. Redrawn from von Appen et al. (2014)

Several countries have been fishing in the study area for decades (e.g. Germany, Greenland, Russia and Norway), primarily for Greenland halibut *Reinhardtius hippoglossoides*, cod and redfish. In recent years, new fisheries have been developed following shifts in fish species distribution, including new and previously unexploited species entering the ecosystem, like mackerel (Jansen et al. 2016).

2.2. Sampling design

We used data from the annual Greenland Deep-Water Survey carried out since 1998 by the Greenland Institute of Natural Resources. The survey covers the International Council for the Exploration of the Sea (ICES) area 14b, between 60° and 67° N and between the 3 nautical mile (n mile) line and the 200 n mile line (midline to Iceland), at depths ranging from 400 to 1500 m. The survey follows a bottom-trawl, buffered, stratified random design (Kingsley et al. 2004). Throughout the time series, an Alfredo III trawl with a mesh size of 140 mm, and a 30 mm mesh liner in the cod-end, was used. The ground gear was of the rock hopper type. Towing time was usually 30 min, but towing times down to 15 min were accepted. Average towing speed was 3.0 knots. After each haul, the catch was sorted and species were counted and weighed to the nearest 0.1 kg. The species determination on the survey is conducted by trained personnel and supported by species experts in case of doubt. Thus the survey was considered consistent throughout the time series. Until 2008, the survey was conducted in June/July, a period when ice cover could challenge sampling. From 2008 onward, to avoid the problems related to ice cover, the survey was postponed to August/September. Also, in 2008 the survey was combined with a new shrimp/fish survey, which led to a change in trawling hours so that most of the stations were sampled during the night. Prior to the change in timing of the survey, a comparative analysis was performed on commercial catch rates which showed only minor effects of changing the sampling period (Christensen & Hedeholm 2016). The change in sampling time is therefore not likely to have affected the results. In the present study, we used yearly data from 1998 to 2016, with the exception of 2001, when no survey was conducted. A total of 1060 stations, ranging from 40 to 100 per year, were included in this study.

Prior to the analyses, the data were screened, quality checked and pre-processed. Only fish classified to species level were retained. Several species were classified as pelagic (Haedrich & Merrett 1988, Froese & Pauly 2017) and were likely caught during setting and hauling of the trawl; these pelagic species were removed from the dataset. As the dataset consisted of a large number of rare species, only species present in more than 1 % of the samples were included in the analyses, resulting in a final dataset of 61 species. Prior to analysis, catches were standardized to numbers per unit area based on the area swept by each haul (numbers km^{-2}). Before analysis on abundance, data were log transformed using natural log base.

As a measure of fishing effect in the area, fishing effort given as hours of fishing was calculated for the commercial species of ICES area 14b. Calculations are based on haul duration in logbook data obtained from the Greenland Fishery and Hunting License office.

2.3. Environmental drivers

Near-bottom temperatures were measured in 0.1°C increments, with a Seamon sensor mounted on the trawl door. In the following, these observations will be referred to as 'trawl temperature observations' (TTOs). To construct climate temperature indices, the TTOs were additionally supported by all available historical temperature observations from conductivity-temperature-depth (CTD) profiles in the study area. A total of 161 000 CTD profiles from the World Ocean Database, ICES, Coriolis and some proprietary data of the Thünen Institute for Sea Fisheries were gathered. Finally, sea surface height (SSH) data from satellite altimetry were provided by Archiving, Validation and Interpretation of Satellite Oceanographic Data (AVISO).

2.4. Data analysis

2.4.1. Oceanographic parameters

In situ hydrography data were gridded with the physical-statistical model Adjusted Hydrography Optimal Interpolation (AHOI; Núñez-Riboni & Akimova 2015). AHOI has been validated by comparing its salinity variations with independent variations of its driving mechanisms in the North Sea (Núñez-Riboni & Akimova 2017). Additionally, for the particular case of the Irminger Sea, temperature output from AHOI has been compared with variations of the current intensity as characterized by the SPG index (Hátún et al. 2005). A drawback of AHOI are regional biases arising from the calculation of the average fields of the Gauss-Markov interpolation (Núñez-Riboni & Akimova 2015). The TTOs can be strongly influenced by sampling location and depth, as well as by important short-term temperature variations at daily and monthly scales, like eddies, tides and current meanders. Thus, the TTOs alone are not suitable for estimating multi-decadal climatic trends. To deal with this, TTOs and AHOI maps were combined as follows: temperature maps were interpolated over central positions on the continental shelf, at each depth stratum, obtaining standardized temperature climate indices. To remove the spatial bias from the long-term average, an off-set was added to (or subtracted from) these AHOI indices based on the time average of the TTOs at each depth stratum. These climate indices were calculated with temperature from the third year quarter (July, August, September).

An SPG index was calculated as the first principal component from SSH altimetry from AVISO data in the region 70°–15° W and 47°–68° N. This index is similar to the SPG index of Hátún et al. (2005), reflecting the current intensity and temperature in the central SPG. The index is sometimes obtained with the second principal component, depending on the altimetry data source and chosen spatial domain (Hátún & Chafik 2018).

An index for the AMO (basically the average sea surface temperature of the North Atlantic) was downloaded from the internet portal of the Climate Time Series at the Earth System Research Laboratory of the National Oceanic and Atmospheric Administration (NOAA 2018).

2.4.2. Community structure

Multivariate analyses were used to describe the spatial organization of fish communities and investigate temporal trends in community structure. Distinct fish assemblages were identified by hierarchical clustering of species abundance data, using Bray Curtis similarity and Ward linkage. Visual inspection of the resulting dendrogram (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m654p127_supp.pdf), and related non-metric multidimensional scaling (nMDS) map (Fig. S2), indicated 6 clusters of distinct fish assemblages that were spatially separated (Fig. S3), due to differences in their depth, TTOs and latitudinal distributions (Fig. S4).

Relative abundance across all assemblages and indicator values of single species within each assemblage were calculated (Figs. S5–S7, Table S1). Indicator species were identified based on the method of Dufréne & Legendre (1997) using the 'labdsv' package in R. This method calculates the probability of obtaining as high an indicator value (fidelity and relative abundance) as observed over specified iterations. Species response curves were calculated for indicator species within each assemblage along gradients of depth and TTOs (Fig. S8). To test for differences between assemblages in depth, TTOs and latitude, an *F*-test was used followed by a Tukey HSD post hoc test (Table S2).

2.4.3. Temporal changes in bottom temperature, species richness and total abundance

For trend analyses of AHOI bottom temperature, species richness and total abundance, only samples from the 2 continental slope areas were included. These areas were sampled consistently and had a similar depth range, allowing a direct comparison of these 2 distinct regions (Fig. 2). In addition, results from the analysis of community structure showed that sites located on the shelf (especially sites located furthest to the north) differ from the other study sites regarding species composition and habitat. The shelf stations were therefore excluded to avoid bias. The 2 slope areas, referred to as northern and southern regions, were analysed separately and compared.

To test for differences in trends over the depth range, 3 depth intervals were specified (400–800, 800–1000 and 1000–1500 m), to balance sampling and obtain a sufficient number of stations per year and depth interval. The AHOI bottom temperature, species richness and total species abundance were modelled as a function of time using generalized linear models (GLMs) (McCullagh & Nelder 1989). An interaction term between time (year) and strata was included to test for differences in trends across depth intervals. Models of species richness and abundance included the covariates longitude and latitude to correct for spatial bias. Statistical modelling parameters are summarized in Tables S3–S5.

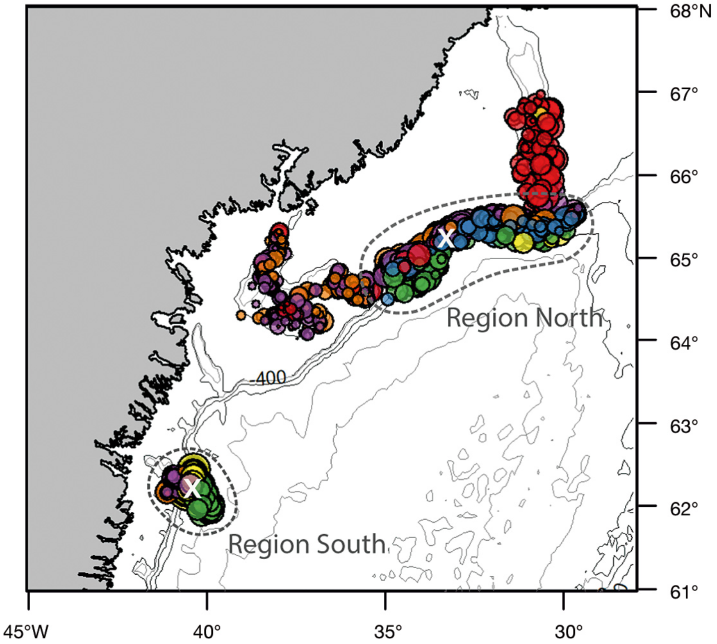

Fig. 2. Study area with sampling sites. Sites are colour-coded according to Assemblages 1 to 6 (red, blue, green, purple, orange and yellow, respectively, as described in Section 3.2). Sizes of points are proportional to species richness at the site. Dashed ellipses mark the northern and southern slope regions used for analysis of temporal change in community structure. The white markings (X) represent the positions where climate indices were calculated for the 2 regions (see Section 2.4.1)

A redundancy analysis (RDA) (Legendre & Legendre 2012) was used to model and summarize changes in abundance of single species in relation with time, TTOs and depth. For the northern region, which covers a larger area along the shelf, latitude was also included in the RDA.

All statistical analyses were done with the software R version 3.3.1 (R Development Core Team 2016). Analyses of fish community data were performed with the package 'vegan' (Oksanen et al. 2017). Indicator species were identified using the package 'labdsv' (Roberts 2016), and species response curves were obtained using the package 'mgcv' (Wood 2017).

3. RESULTS

3.1. Oceanographic parameters

The SPG was in a positive phase at the beginning of the study period, indicating strong currents and low temperatures in the central SPG (Fig. S9), then decreased to a minimum in 1998, indicating weak currents and higher temperatures. Subsequently, the

SPG index oscillated inter-annually until 2010, when it again entered a positive phase similar to the one at the beginning of the study period. The AMO gradually increased through the study period, indicating an increase in temperature (Fig. S9).

3.2. Community structure

A total of 103 demersal fish species were caught during the 18 yr time series; of these, 61 fish species (59% of total) were used in the analysis (species list in Table S1). The clustering resulted in 6 well defined and distinct assemblages (Fig. 2, Figs. S1 & S2), and was mainly driven by differences in abundance between sites and not by the replacement of species (Figs. S5–S7). The different assemblages were associated with different depths, latitudes and temperatures (Table S2). Assemblage 1 (red sites) was separated from the 2 other shelf assemblages (4 and 5) mainly by temperature, which is significantly lower in this area. The main indicator species of this assemblage was polar cod *Boreogadus saida*. Assemblage 2 (blue sites) was located at the edge of the slope and was the shallowest of the slope assemblages. The main indicator species was roughhead grenadier *Macrourus berglax*. Assemblage 3 (green sites) was the deepest assemblage whose main indicator species was the deep-water species Agassiz′ slickhead *Alepocephalus agassizii*. Assemblage 4 (purple sites) was found at warmer and shallow sites on the continental shelf and along the ridge, with the indicator species greater argentine *Argentina silus*. Assemblage 5 (orange sites) was found at the shallowest sites on the shelf and along the ridge of the slope. The indicator species here was the golden redfish *Sebastes marinus*. Assemblage 6 (yellow sites) was located in the middle of the slope and was characterized by the indicator species roundnose grenadier *Coryphaenoides rupestris*. A more detailed description of the depth range, temperature range and listing of indicator species for each assemblage is provided Text S1.

3.3. Temporal changes in bottom temperature, species richness and total species abundance

3.3.1. Bottom temperature

The AHOI bottom temperature increased in all strata in both regions (Fig. 3). As expected, the deepest strata were the coldest, and the shallowest were the warmest. Regional differences were present, with temperatures being generally lower in the northern region by approximately 1°C in all strata.

Over the study period, AHOI bottom temperatures of the northern region increased by 0.14, 0.18 and 0.23°C in the shallow, middle and deep stratum, respectively. In the southern region, the increase was generally larger, with increases of 0.38, 0.40 and 0.45°C in the shallow, middle and deep stratum, respectively (Table S3).

Within the study area, the fastest increase in temperature occurred along the continental slope, with changes of up to approximately 0.5°C in the southern region, whereas the shelf area (<400 m) experienced a slight cooling (Fig. 4).

3.3.2. Species richness

The 2 regions differed with regard to species richness (Fig. 3). Although the difference was not significant, the southern region was slightly more diverse (10.3 ± 0.2 SE) than the northern region (9.4 ± 0.13 SE). In the northern region, species richness was highest in the shallow stratum, whereas in the southern region, the middle stratum was the most diverse and the shallow stratum was the least diverse.

In the northern region, the slope of the temporal trend in species richness was contingent on depth, with a significant interaction term between year and depth stratum in the model ($p < 0.05$). The shallow and middle stratum experienced a local loss of diversity of 2.6 and 3.1 species, respectively, whereas the deep stratum was stable through time. Species richness in the southern region was generally higher than in the northern region, but decreased more rapidly through time, although not significantly. Species richness decreased in the shallow stratum, mid stratum and deep stratum by 2.4, 4.3 and 1.5 species, respectively. Differences in slopes between strata were not statistically significant (Fig. 3, Table S4).

3.3.3. Total abundance

Total species abundance was higher in the southern region, where it also decreased at a higher rate (Fig. 3). In this region, total species abundance decreased through time in all strata, but the rate of change was higher in the middle stratum ($p < 0.05$, Table S5). In the northern region, species abundance also decreased through time in all strata, but did so at a higher rate in the shallow stratum ($p < 0.05$, Table S5).

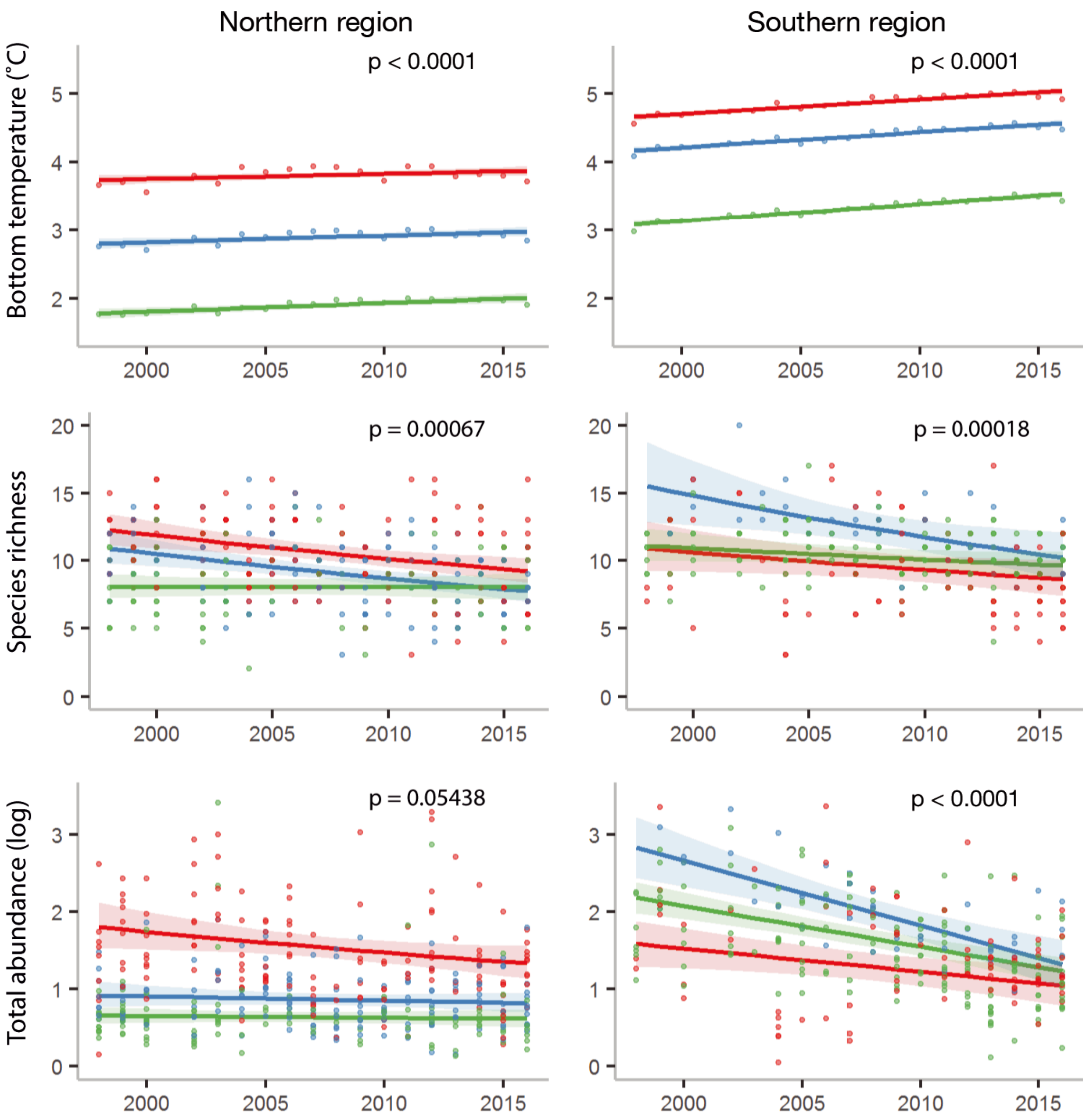

Fig. 3. Temporal trends in Adjusted Hydrography Optimal Interpolation (AHOI) bottom temperature (top panels), species richness (middle panels) and total species abundance (bottom panels) for the northern (left panels) and southern (right panels) regions. Trend lines were obtained by GLM (predicted marginal effects of model terms) and points show raw data (red: shallow strata; blue: middle strata; green: deep strata). Shaded area around trend lines represents confidence intervals, and p-values refer to temporal trends. Only stations from the 2 slope regions indicated in Figs. 1 & 2 were included in these analyses

3.3.4. Individual species abundances

The individual species abundances showed different trends and inter-annual fluctuations through the study period (see Figs. 5 & 6). The RDA ordination summarizes how abundance increased or decreased over time for the different species (Figs. S10 & S11). Species displaying the most rapid changes in abundance differed between the 2 regions.

In the northern region, the species decreasing most rapidly were the Greenland halibut *Reinhardtius hippoglossoides*, 3 species of wolffish (*Anarhichas minor*, *A. denticulatus* and *A. lupus*), American plaice *Hippoglossoides platessoides* and Kaup's arrowtooth eel *Synaphobranchus kaupii* (Fig. 5). In the southern region, the species decreasing most rapidly in abundance were Greenland halibut, blue antimora *Antimora rostrata*, Agassiz' slickhead, Günther's grenadier *Coryphaenoides guentheri*, roundnose grenadier and Murray's longsnout grenadier *Trachyrhynchus murrayi* (Fig. 6).

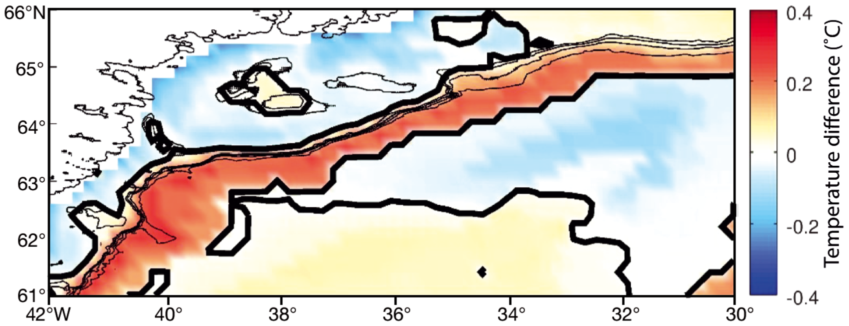

Fig. 4. Adjusted Hydrography Optimal Interpolation (AHOI) bottom temperature differences between 2 averaged periods (2007–2015 minus 1998–2006). Black thick lines indicate regions of no change

Besides tusk *Brosme brosme* and the greater argentine, species increasing in abundance also differed between regions. In the northern region, the main species were roughhead grenadier *Macrourus berglax*, snubnosed spiny eel *Notacanthus chemnitzii* and blue ling *Molva dipterygius*. In the southern region, the main species were lancet fish *Notoscopelus kroeyeri*, smallmouth spiny eel *Polyacanthonotus rissoanus* and northern wolfish *A. denticulatus* (Figs. 5 & 6).

3.3.5. Fishing effort

During the study period, there was a decline in fishing effort of the main commercial species Greenland halibut and redfish after 2004, whereas the effort of catching cod started to increase after 2010 with a small peak in 2015. There were no fisheries targeting the two pelagic species Atlantic herring *Clupea harengus* and Atlantic mackerel *Scombrus scombrus* until 2010 when the fishery started and the effort increased. Fishing effort of the northern shrimp *Pandalus borealis* declined rapidly after 2004 and reached zero by 2016 (Fig. S12).

4. DISCUSSION

We found local decreases in species richness and total abundance in East Greenland deep-water demersal fish communities, concomitant with a rise in

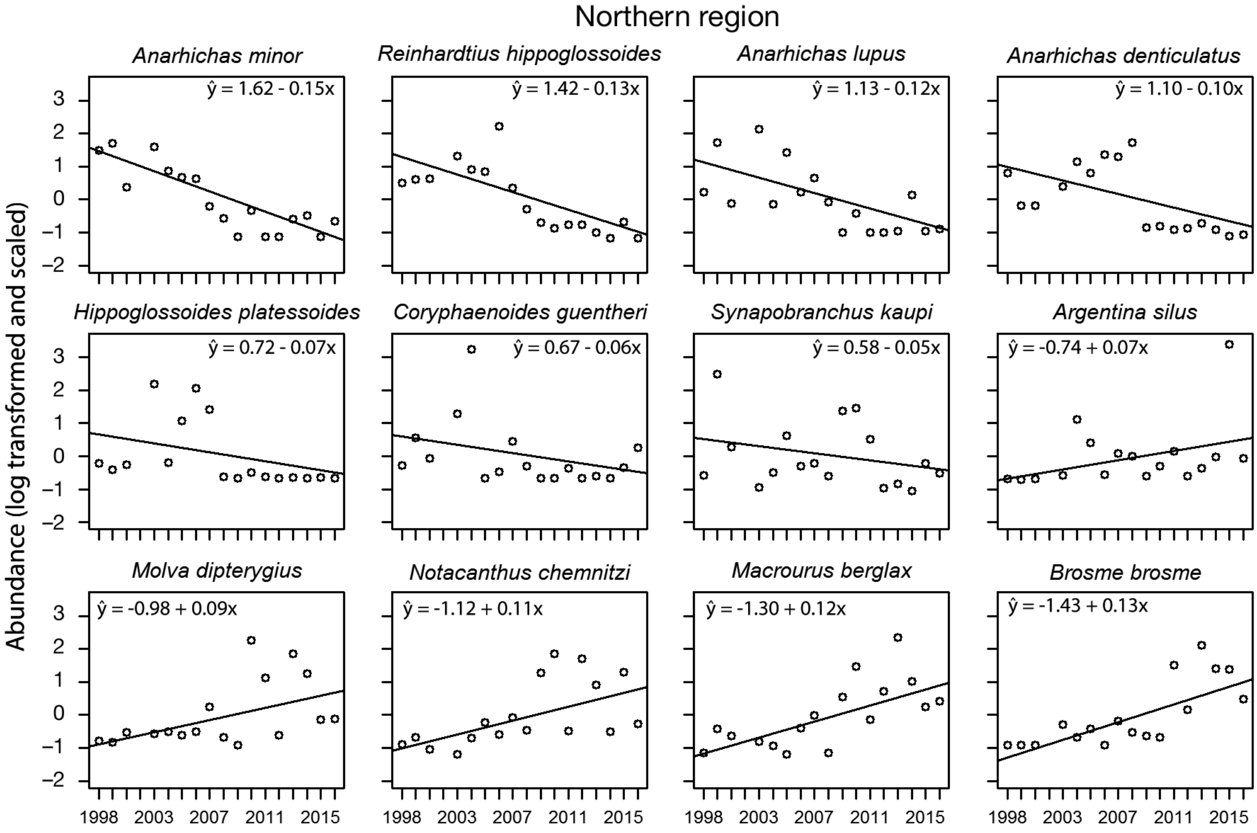

Fig. 5. Species displaying most rapid increase or decrease in abundance (log transformed and scaled) in the northern region

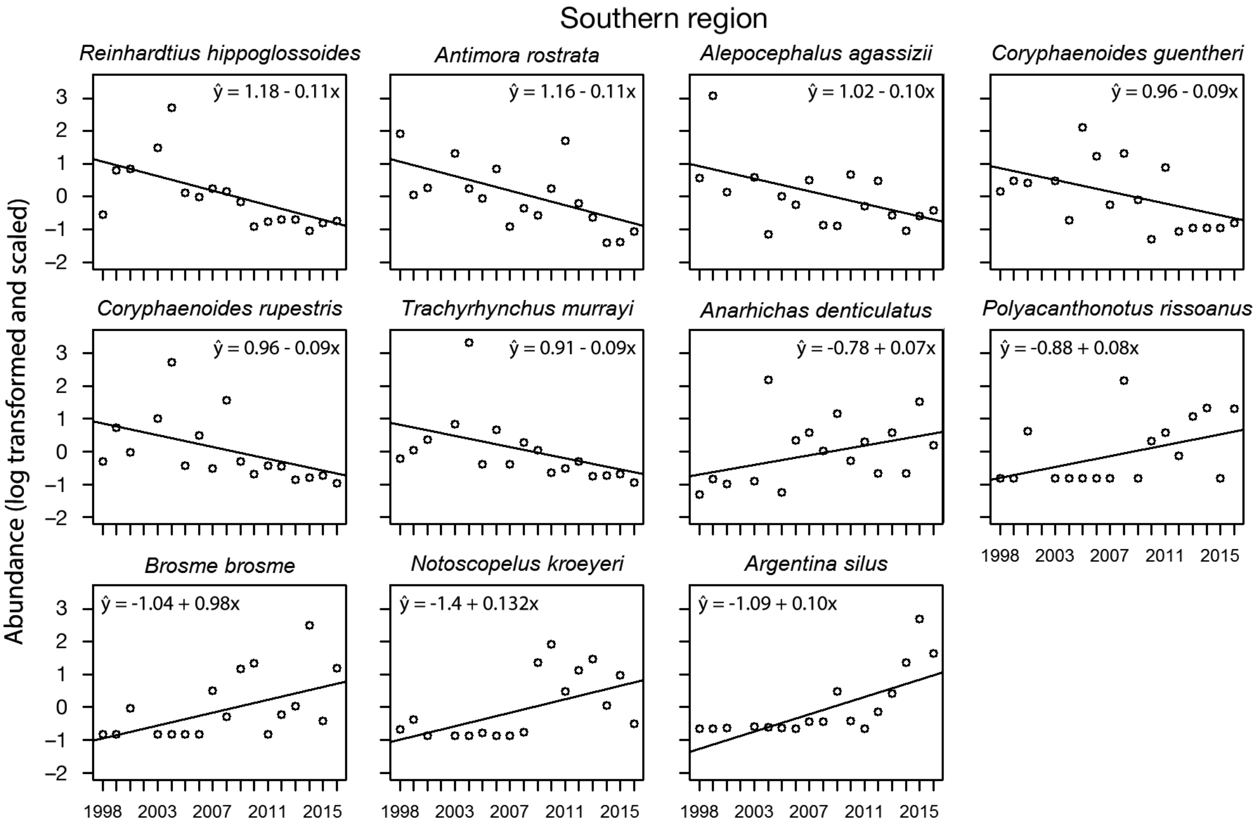

Fig. 6. Species displaying most rapid increase or decrease in abundance (log transformed and scaled) in the southern region

AHOI bottom temperatures, during a period (1998–2016) characterized by rapid warming of polar regions (Meredith et al. 2019). The trends were significant in both investigated slope areas, despite their oceanographic differences. The rates of change varied with depth, which, together with water temperature, was the main structuring environmental gradient for these fish assemblages. Abundances of individual species displayed different trends between investigated areas, with 3 species of wolffish, American plaice and Kaup's arrowtooth eel decreasing in the north, and blue antimora, Agassiz' slickhead and Günther's grenadier decreasing in the south. The regional differences may reflect different oceanographic characteristics, as the northern region is more influenced by colder Arctic water, whereas the southern region is primarily influenced by the SPG. Our results indicate extensive ecological change in the deep sea, likely influenced by the direct effect of temperature rise and indirect effects mediated by changes in habitat and species interactions. The observed changes in the deep-sea fish communities happened rapidly, emphasizing the urgent need for ecosystem-based approaches and climate adaptation in fisheries management.

4.1. Impact of climate and oceanography on diversity

The general prediction of macro-ecological trends of fish diversity in response to rising temperatures in subpolar regions is an increase in species richness due to poleward shifts of temperate species (Cheung et al. 2009). Our findings, on the other hand, showed an overall decline in species richness as water temperatures increased. The oceanographic characteristics of East Greenland help explain the decline in richness in the context of climate warming. Ecological responses have been linked to oceanographic interannual variability associated with the SPG (Hátún et al. 2005, Núñez-Riboni et al. 2013, Hátún & Chafik 2018), whereas multi-decadal variability is affected by the AMO (Kerr 2000, Nye et al. 2009, Alheit et al. 2014). In addition to these sources of variability, climate change drives long-term changes. Interannual fluctuations of the SPG cause shifts in temperatures and fronts, which ultimately affect population distributions and densities either directly or indirectly via e.g. changes in favourable spawning grounds and nursing areas, shifts in lower trophic levels, prey availability, predator abundances and year class success (Hátún et al. 2009a,b, Núñez-Riboni et al. 2013). In southeast Greenland, the SPG is correlated to redfish distribution (Pedchenko 2005, Núñez-Riboni et al. 2013) and is likely to influence the distribution of other species, possibly affecting the overall trend in species richness and abundance. However, the overall temperature trend through the study period does not correspond to changes in the SPG, which changed from a positive into a negative phase in 1996, and became positive again at the end of the study period. The steadily increasing temperatures along the continental shelf rather suggest warming of the IC due to reasons other than the SPG. The most probable cause seems to be an increase of temperature upstream along the IC, possibly caused by the AMO and/or by anthropogenic climate change. The long-term negative trend in richness is a likely response to the long-term, climate-driven oceanographic changes through environmental filtering of Arctic species and physical and topographic constraints on distributional shifts of boreal species, discussed further below.

In a nearby study area southwest of Iceland, covering similar depths, species richness is increasing as expected (Stefansdottir et al. 2010). The area is influenced by the warm-water IC, which is a likely conveyor of temperate fish species moving northward to both Iceland and our study region. A small branch of the IC splits to the north, west of Iceland, along the shelf, through the Denmark Strait. This branch of temperate water, in addition to local upwelling and high productivity, helps to explain the observed increase in species richness southwest of Iceland. Along East Greenland, however, the warm IC mixes with the Arctic EGC, which makes the study regions in East Greenland hydrographically different from the area southwest of Iceland. Fock (2008) investigated driving forces of groundfish assemblages on the shelf area (0–400 m) of West Greenland and East Greenland between 1981 and 2006 and found climate (using Nuuk annual air temperature as proxy for climate change) to be a stronger driver of community dynamics (community interactions and environmental relationship) in East Greenland compared to West Greenland. This might indicate that the East Greenland ecosystem is more vulnerable to climate change. Considering the rapid observed temporal changes in the deep ocean over the last 2 decades, one would expect temporal changes in fish communities also in the shallower shelf area. Regional differences based on topography and oceanographic conditions such as depth, different water masses, currents and fronts are important considerations in how fish communities respond to climate variability (Pinsky et al. 2013). Looking at large areas as a whole, one can easily overlook regional and local differences that are important in understanding responses in the ecosystem.

The depth- and area-specific responses in water temperature were accompanied by differences in trends of species richness, varying from no change to a rapid decline. The different local trends in species richness highlight the importance of local oceanographic and ecological conditions in mediating climate effects. The study regions experience southward currents, the IC and EGC, along which temperate and cold-water species may disperse, respectively. The climate-driven changes in hydrographic characteristics may affect fish communities in our study regions either directly, through environmental filtering where the environment selects against certain species, or indirectly, via changes in resource productivity and altered species interactions.

4.2. Temporal change in community structure

Although the northern and southern study regions covered the same depth ranges, the community dynamics differed. In marine environments, assemblage structure and diversity are strongly correlated with depth, but patterns of faunal change vary considerably from area to area (Gage & Tyler 1991). In our study, this was highlighted by different trends in species richness and total abundance between depth strata and between regions. The difference between regions might be associated with a more rapid temperature increase along the slope of the southern region. The latter could be explained by the stronger influence of the IC and the greater distance from the Denmark Strait and the cold-water flow from the north. The northern region is located where the IC and the EGC meet and thus the mixing of the two water masses might be less pronounced with a smaller influence of the warmer IC. Although there are several controlling factors of diversity such as harvesting (Smith et al. 2000, Worm et al. 2009, Nogueira et al. 2016), productivity, habitat characteristics and species interactions (Levin et al. 2001), water temperature is a strong candidate (Fossheim et al. 2015).

In the deep demersal communities, species richness may decline with warming due to characteristics of deep-water species. In contrast to shallow-water and pelagic species, poleward shifts of deep demersal species are expected to happen at a slower pace due to their relatively low mobility and slow life histories. Further, being more stationary, deep demersal species are more vulnerable to environmental filtering. As temperatures of the IC increase, conditions are worsening for the cold-water species, and may negatively affect their vital rates. In support of this hypothesis, we found that some of the 'slow' species, such as Greenland halibut and wolffishes, and species categorized as Arctic or arcto-boreal (Mecklenburg et al. 2018), were generally becoming less abundant. However, more research is needed to determine whether changes in community dynamics are demographically or behaviourally (migration) driven, or a combination of both.

We also saw an increase of certain species. Common for both regions are tusk and the greater argentine, which are both boreal species. These are also reported to be rapidly increasing in shallower depths on the shelf area (Post et al. 2020). Tusk, which was initially absent, displayed substantial increases in abundances in both regions. Previously, tusk was found at the southern tip of Greenland, with only stray appearances in East Greenland (Cohen et al. 1990). Elsewhere, in the Gulf of Maine, a distributional shift of tusk is projected as a result of spatial mismatch between suitable habitat and temperature (Hare et al. 2012). The increased abundance of tusk in East Greenland might therefore be driven by environmental change and redistribution. The greater argentine is a bathydemersal/-pelagic species with relatively high temperature preferences (Cohen et al. 1990). Although this is a schooling fish with patchy appearances, the increase of this species might be a result of rise in water temperatures and more favourable habitats. On the other hand, the greater argentine is a common bycatch in both the Greenland halibut and the redfish fishery (ICES Advisory Committee 2018), and the observed increase in abundance could also partly be a result of decreasing fishing effort, combined with the adoption of sorting grills by the shrimp fishery in 2002. The main species that are increasing in both regions are all categorized as boreal species, except northern wolffish, which is categorized as boreal-Arctic (Mecklenburg et al. 2018). This indicates that the so called 'borealization' of the demersal fish communities seen elsewhere in high-altitude regions (Fossheim et al. 2015) might also be happening in deeper waters of East Greenland.

The East Greenland deep water survey changed the sampling design in 2008 where time of the survey was shifted from June/July to August/September due to sea ice challenges. It is unlikely that this shift has affected the results. A sampling shift of 1 mo within the same season at these depths should not cause the magnitude of change that we observed. Further, the expected effect of a one-time shift in the timing of sampling would be a more abrupt change in 2008 rather than the gradual change over several years, observed in this study.

4.3. Distributional shifts

Demersal species are less mobile than pelagic species and are likely to migrate in the direction of currents following the ocean floor within their depth range. The northward migration of temperate species originating further south probably follows the path of the warm IC reaching the south of Iceland first, before further migration westward to East Greenland. These species would reach the northern region first and then disperse southwards following the mixed IC and EGC along the continental shelf. Importance of current properties and directions in creating a pathway for transport of species is also seen in other high-latitude systems such as the Barents Sea, where the warm north-running Gulf Stream supplies Atlantic species to the western Barents Sea, resulting in higher species richness than in the east (Johannesen et al. 2012).

New recordings of species in East Greenland that may have arrived due to temperature rise are mainly from waters with depth less than 400 m (Møller et al. 2010). In the present dataset, there are recordings of species in the later survey years that are absent in the early years. For example, the temperate species sea lamprey *Petromyzon marinus* was caught during the survey in 2013 in the southern region and in 2008 and between 2011 and 2014 in the northern region. The sea lamprey is described to occur south of Greenland and in sporadic occurrences with increasing frequency off Iceland (Astthorsson & Palsson 2006). This species has also been recorded as 'new' in Icelandic waters, where specimens have been assigned to the European stock, which supports the theory of large-scale migrations (Pereira et al. 2012).

Even though 'new' species are being recorded east of Greenland, species richness is declining. A possible explanation might be that the colder water off East Greenland inhibits the migration of some of the temperate species further from the Icelandic shelf into the Greenlandic waters where the temperate IC meets the cold EGC. The southward direction of flowing water masses and the shallow and narrow topography of the Denmark Strait might act, respectively, as an environmental and physical barrier for deep demersal species trying to reach colder waters further north. In support of this hypothesis, the shallow strait is suggested as a cause for the distinction of 2 populations of

Greenland halibut in the Atlantic (Albert & Vollen 2015, Westgaard et al. 2017). Topographic constraints are also reported as the reason for limited migration off the isolated Flemish Cap, an international fishing ground off Newfoundland, where shallow demersal species such as Atlantic cod are inhibited by the deep waters surrounding it (Konstantinov 1970). If northward migration is inhibited, species might shift depth distributions to reach colder waters. This is seen in the gulf of Mexico, where the topographic constraints of the coastline are causing assemblages to go deeper (Pinsky et al. 2013). Distributional shifts are most likely happening along the slope in East Greenland, depending on species location, preferences and available habitat. Due to regional and local differences in climate velocities, the large depth range and the complex oceanography of this area, species responses are likely heterogeneous, making it difficult to find specific patterns at assemblage levels or linking the assemblage changes to species characteristics or traits.

An 18 yr time series is relatively short to effectively isolate a climate signal from the multi-decadal variability. However, during this period, there was a significant increase in water temperature and a decrease in species richness. If, as we propose, this observed loss of species was related to the temperature increase and to limited possibilities of range shifts due to barriers like current directions and the Denmark Strait, East Greenland might be a so-called ‘dead end’ for deep-water demersal species. Such regions in the oceans, with barriers, are projected to limit range shifts under climate change, resulting in larger relative decreases in species richness (Cheung et al. 2013, Burrows et al. 2014, Jones & Cheung 2015, Rutterford et al. 2015). Identifying whether the East Greenland region represents such a barrier is of great importance for prediction and management decisions. A study on geographical redistribution of species in an extended study area is needed to determine whether this is the case.

4.4. Top down effect of a new predator and fishery

The abundance of Atlantic cod has rapidly increased in the last decade. Top predators such as cod can have a strong impact on prey abundances and behaviour (Pauly et al. 2005, Rochet et al. 2013). At the Flemish Cap, species diversity dropped when cod started to recover from the collapse in 1998 (Nogueira et al. 2016). Although the abundance of cod in the depth ranges of this study were relatively low, cod were present and increasing in abundance at depths from 400–700 m, especially in the northern region. In shallower waters above 400 m on the shelf area, cod, along with redfish, is highly dominant in the fish community. Recent analyses of cod stomach contents in the East Greenland area reveals a diet of crustaceans, krill and small fish likely to be mesopelagic species (Hedeholm et al. 2017). Although stomach analysis does not reveal predation on the species analysed in the present study, the presence of cod could cause avoidance behaviour in potential prey species, shifts in distribution (ICES Advisory Committee 2018) and change of habitat (Worm & Myers 2003, Frank et al. 2007). Cod predation has been described as the main source of small redfish mortality (Lilly 1987, Pérez-Rodríguez & Saborido-Rey 2012). Fock (2008) found fishing mortality of cod to be positively correlated to abundance of redfish juveniles in East Greenland, indicating the influence of cod as predator. Predation also depends on the densities of prey species as shown on the Flemish Cap, where small redfish are prey of cod in years with successful redfish recruitment events (NAFO 2015, Nogueira et al. 2018). The great cod collapse of the 1990s had a major impact on ecosystems elsewhere (Pace et al. 1999, Choi et al. 2004, Nogueira et al. 2018), but insufficient survey data exist prior to the cod collapse in Greenland, so it is not known how the disappearance of cod impacted trophic levels, or how the system will respond as the cod stock rebuilds. The relatively low abundance of cod in the southern region, where species richness decreased the most, suggests that the return of cod may not be a main driver of the observed diversity loss. However, if the northern region serves as a general source population for the southern region, the increase in cod could have affected diversity in East Greenland. To our knowledge, there are presently no studies or data in support of this hypothesis. More research on food webs and community dynamics is needed to determine how the presence of top predators may affect diversity and ecosystem structure.

East Greenland is an international fishing ground, and it is therefore plausible to assume that the fishery is affecting diversity. Fisheries can cause major disruptions to an ecosystem by affecting the energy flow in the natural food web and causing declines in fish population abundance. In East Greenland, fisheries have been present throughout the study period, but there has been a decrease in commercial fishing effort (Greenland halibut, northern shrimp and redfish), which indicates that fisheries are not the main driver of the observed changes. Bycatch of species may have provoked changes in community dynamics, especially until 2002, when mandatory sorting grids where introduced in the shrimp fishery. This measure reduced the bycatch of species considerably, and the fishery in East Greenland is now considered to be clean (ICES Advisory Committee 2018). Based on comparison of fishing effort and results of this study, a conclusive effect of the fishery on overall decreased species richness and abundance is not likely. However, additional effects of the fishery and possible interactions between climate and fishing on ecosystem sensitivity, cannot be disregarded (Perry et al. 2005). If species richness continues to decline, the ecosystem might become less resilient to fisheries as cold and species-poor communities are likely top-down controlled (Frank et al. 2007). Based on this assumption, removing predators might have a larger impact on the East Greenland ecosystem than expected and should therefore be considered in management.

5. CONCLUSION

We show that deep-water fish communities respond to long-term changes in climate and hydrographic conditions. Species richness and total abundance rapidly decreased concomitantly with an increase in bottom temperature. These observations contradict the general expectation of a delayed response to warming in deep-sea communities and an expected increase in diversity and abundance at high latitudes due to northward migration of temperate species. The results highlight the importance of regional and local oceanographic and topographic conditions in understanding how fish communities respond to a changing environment.

In East Greenland, warming of the IC upstream, due to an increasing phase of the AMO and/or possibly anthropogenic climate change, is a likely driver of the observed trends in deep-water demersal fish. Possible explanations for the loss of species richness and the decrease in abundance are that deep cold-water species might be struggling to follow climate velocities due to slow behavioural responses, and/or that regional topography and oceanography create a geographical and physical barrier for northward shifts. If the observed ecological trend continues in the future, as seems likely considering climate change projections, the overall vulnerability of the ecosystem will increase accordingly. Maintaining high taxonomic and functional diversity is important in buffering against climate variability, climate change and overexploitation, thereby reducing the risk of collapse of fish stocks and ecosystems.

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Paper II:

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 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

Fish communities, Arctic, Borealization, East Greenland, Fisheries, Atlantification, Deep sea, Ecosystem change

Introduction

A 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 et al., 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 et al., 2015; Van der Spoel, 1994; Yasuhara et al., 2014). However, rapid responses in abundance of deep-sea biota, 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 (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 et al., 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 (Fossheim 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 et al., 2008). Here, the East Greenland Current, which originates from Arctic regions, dominates the shelf regions and mixes with the Irminger Current, which flows along the deeper reaches of the slope. 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). At 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.

Materials and methods

Fish community data

The study area is in East Greenland waters expanding from 63° N to 66° N (Supplementary Fig. 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 (Supplementary Fig 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 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 (Supplementary Fig. S2). Moreover, similar, albeit more moderate, changes occurred in shallow waters, where the sampling timing was consistent over the whole time series (Supplementary Fig. S2).

Data processing

We used yearly data from 1998 to 2016 except for the year 2001, when there was no Greenland survey in deeper waters (Supplementary Fig. 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 et al., 2017; Haedrich et al., 1988) were likely caught during 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 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 six 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.

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 et al., 1998; Leibovici, 2010). Tensor decomposition analysis is a method to decompose a tensor (3D array), such as the one consisting of observations of abundances of multiple species (1st dimension), repeated across multiple depth layers (2nd dimension) and multiple years (3rd 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 et al., 1998; Leibovici, 2010). We selected the number of components, called principal tensors (PT), based on the scree 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 highest explanatory power (Supplementary Fig. S1). The original tensor was shuffled 1000 times and these four PTs explained more variance than was expected by chance (Supplementary Fig. S3). PTs represent the main spatio-temporal dynamics of species, providing scores for all species, depth strata and years (Supplementary Fig. S2). PTs 1-3 had high variability in depth scores, but low in temporal scores, while the opposite is true for PT4. This is visible in Supplementary Fig. 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 Jr, 1963). This cluster analysis was run on the four selected PTs. 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 (Supplementary Fig. 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 (Supplementary Fig. S2). We called this dominant temporal trend ‘tensor time series’, which is made of the temporal scores of PT4 and used this time series for further analysis, because it represents the dominant temporal dynamics of the dataset across all species and all depth layers. 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 strong positive PT4 score follows the increasing trend of the tensor time series, while 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 score close to zero.

Correlation maps

Monthly sea level air temperature with a resolution of 2.5º 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, while 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. Monthly temperature, salinity as well as longitudinal and meridional current velocities with a resolution of 0.25º 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 55-75ºN; 50-10ºW, 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 et al., 1985), i.e. (Becker et al., 1996; Núñez-Riboni et al., 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 et al., 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 et al. (1998); Pyper et al. (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 in Fig. 4. 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, while 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).

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 (Supplementary Fig. 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. 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.

Results

Fish community structure

The output of the tensor decomposition indicated four PTs accounting for most of the systematic variation in fish abundance (Supplementary Fig. 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 (Supplementary Fig. S2). Hierarchical clustering of the Euclidean distances between species scores on the four PTs revealed six clusters (Fig. 1 and Supplementary Fig. S4), each characterized by a unique subset of species (typical species in Fig. 1C, Supplementary Table S1). The six clusters summarized abundance patterns over depth and time (Fig. 1 and Supplementary 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 (Fig. 1). The main temporal developments took place in the intermediate layers, between 350 – 1000 m, covered by the four remaining clusters (Fig. 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 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.

Biogeographic affiliation within clusters

Clusters displaying increasing abundances were dominated by boreal and widely distributed fish (Fig. 3 and Supplementary Fig. S6). In contrast, 63% of species in clusters with decreasing abundance were found to be Arctic or Arctic-boreal (Fig. 3 and Supplementary Fig. S6). For example, abundance of Arctic rockling (*Gaidropsarus argentatus*) and threebeard rockling (*G. ensis*) and three Arctic species of eelpouts (*Lycodes paamiuti*, *L. pallidus*, *L. squamiventer*) decreased over time (Supplementary Fig. S6). Whereas abundance of boreal species, such as Atlantic argentine (*Argentina silus*), blue ling, witch flounder (*Glyptocephalus cynoglossus*) and round ray (*Rajella fyllae*) increased (Supplementary Fig. 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 (Supplementary Fig. S6).

Correlations between fish community responses and climate indices

While the main trend in temporal development in species abundances, captured by PT4 (see PT4 in Supplementary Fig. S2, Supplementary Fig. S6 and Supplementary 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 (Fig. 4). 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 (Fig. 5). Correlations between environmental variables aggregated over April to July and the tensor time series were strongest without lag, meaning that deep bottom fish communities responded within 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 (Fig. 5 and Supplementary Fig. 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 (Fig. 5 and Supplementary Fig. S7). The close association of the climate indicators with fish responses is exemplified by the extreme year of 2003, when warm waters expanded on to 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 (Supplementary Fig. S7). The correlations between fish responses and surface processes were highest in an area north of the Denmark Strait (Fig. 5)

Discussion

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 (Fig. 2) and highlights the importance of considering regional and local environmental conditions in analyses and predictions of ecosystem responses to climate change. A second hypothesis 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 abundance of other smaller species and mask community signals in our region.

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 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 (Supplementary Fig. S6 and 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 et al., 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).

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 et al., 2011) and caused a record-breaking heatwave with centre of action in central Europe (Feudale et al., 2011; Schär et al., 2004). This event may have caused a 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 low abundance of zooplankton in Southwest Greenland, indicating that a change in oceanographic conditions North of the Denmark Strait can affect food web processes in our study region (Pedersen et al., 2002).

While 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.

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 et al., 2019; Ruhl et al., 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 abundance of deep-sea fish (Bailey et al., 2006; Levin et al., 2020; Ruhl et al., 2004). In the Fram Strait, warming and changes in low trophic-levels led to an increase in phytodetritus 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 sea floor was recently documented in the South East Atlantic (Milligan et al., 2020). A possible change in transfer of 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 et al., 2017). Recently, unforeseen convection was observed upstream from the study region, along the ice edge, where the sea ice retreat is linked to 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 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 et al., 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. The abrupt changes we observed in deep demersal fish communities and the correlations with atmospheric events provide a new perspective on the dynamics and energetic connectivity across a large depth range.

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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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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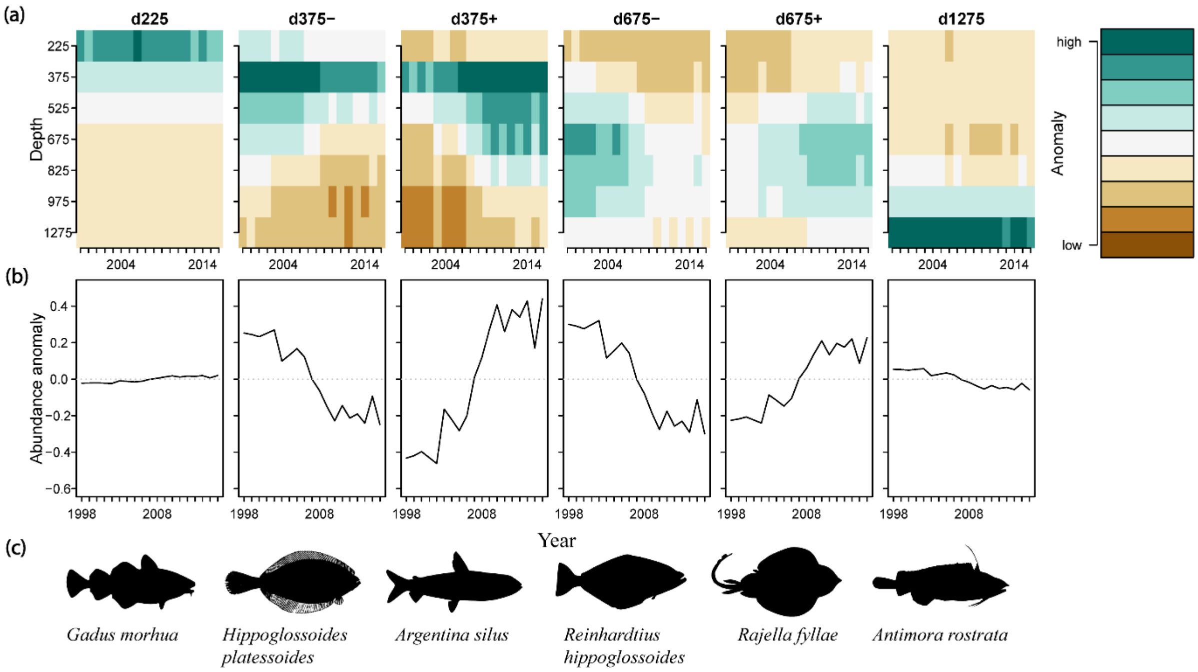

Fig. 1. Spatial-temporal dynamics in fish abundances. (a) Anomalies in fish community abundance in East Greenland represented in a heatmap showing the six clusters with time on the x-axis and depth on the y-axis. **(b)** Temporal average of the abundance of each cluster. **(c)** Indicator species reflecting 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 main occurrence ("-" for decreasing abundance, "+" for increasing abundance).

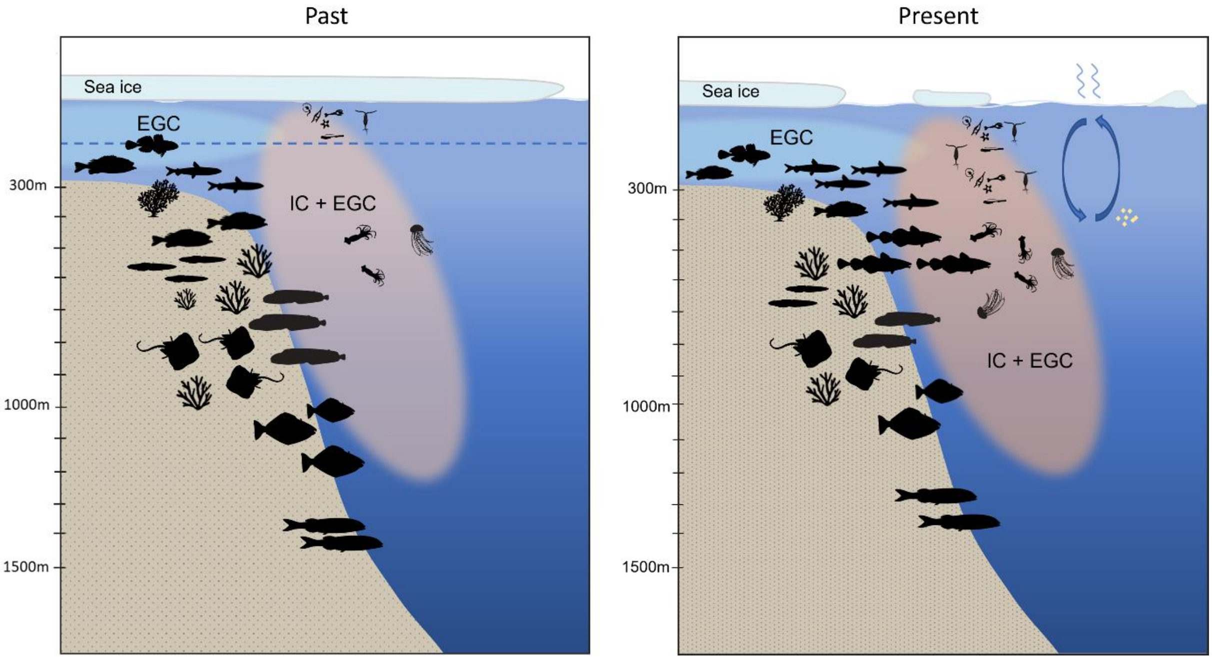

Fig. 2. Conceptual Illustration of past and present community structure in the East Greenland ecosystem along the continental margin. During the two last decades, sea surface temperatures increased whereas sea ice concentration decreased in the area. The changes in surface climate conditions likely led to 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).

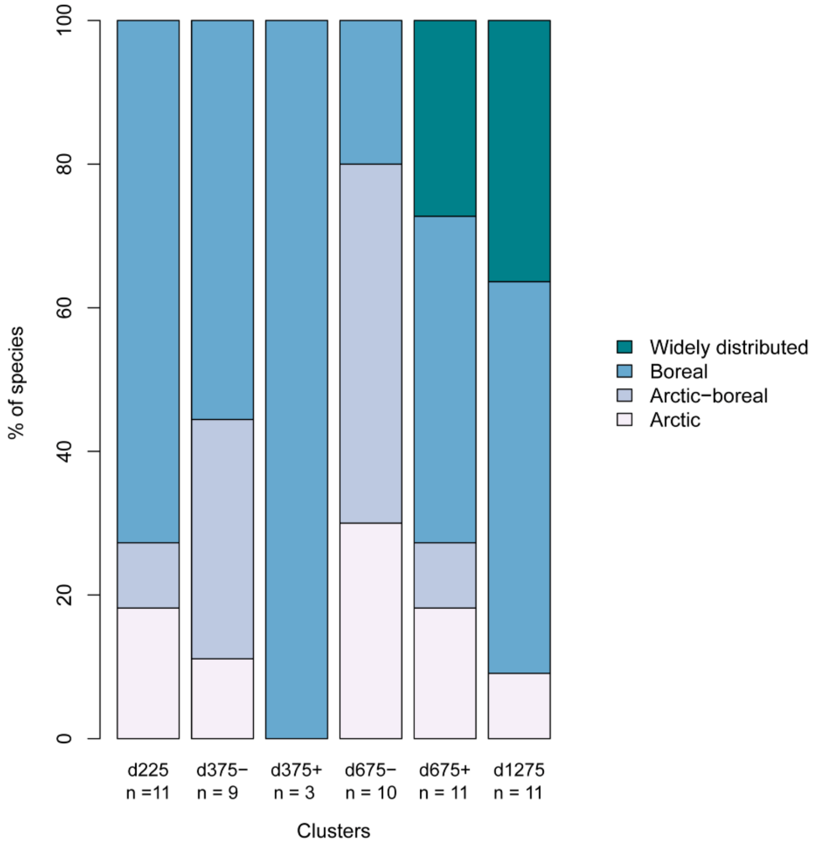

Fig. 3. Community-specific biogeographic affiliation of demersal fish species in East Greenland. The names of the communities are based on their spatio-temporal characterization (Fig. 1). The numbers below the names denote the number of species in each cluster.

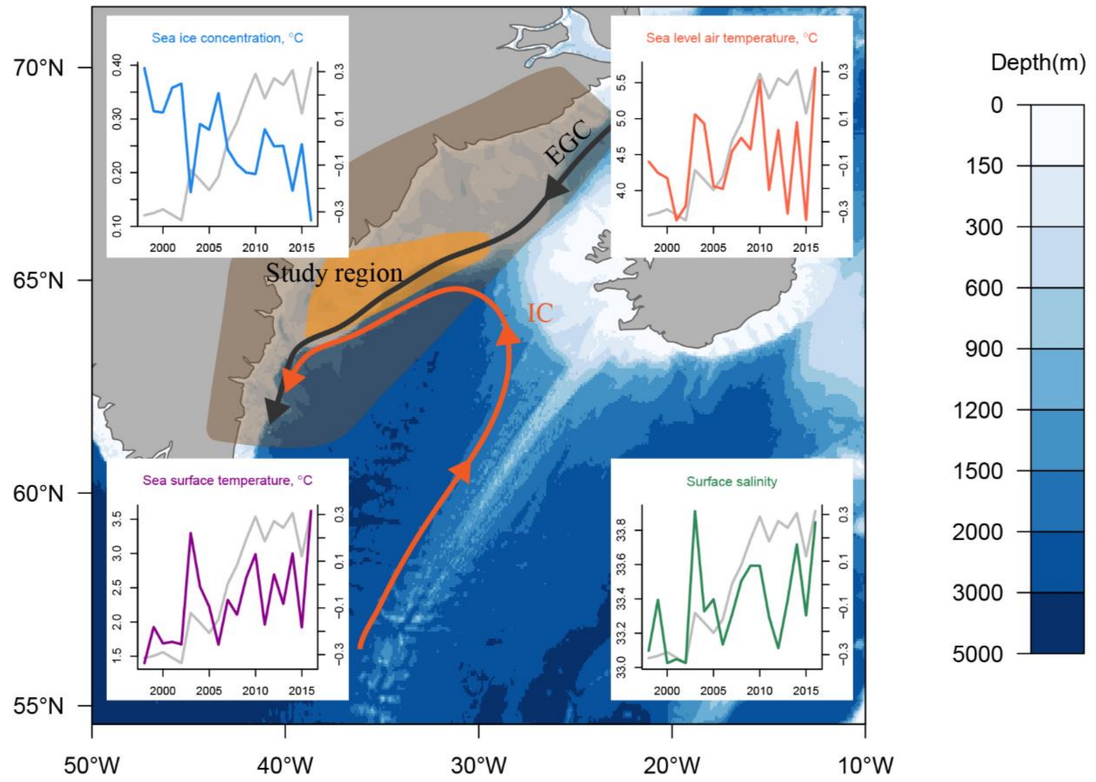

Fig. 4. Time series correlations between fish abundances and climate events. Time series of the four significantly correlated environmental parameters in relation to fish community abundance summarized by the tensor time series (grey line). Shaded orange area shows where fish samples were collected whereas the larger brown shaded polygon show the area from where the environmental time series where 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).

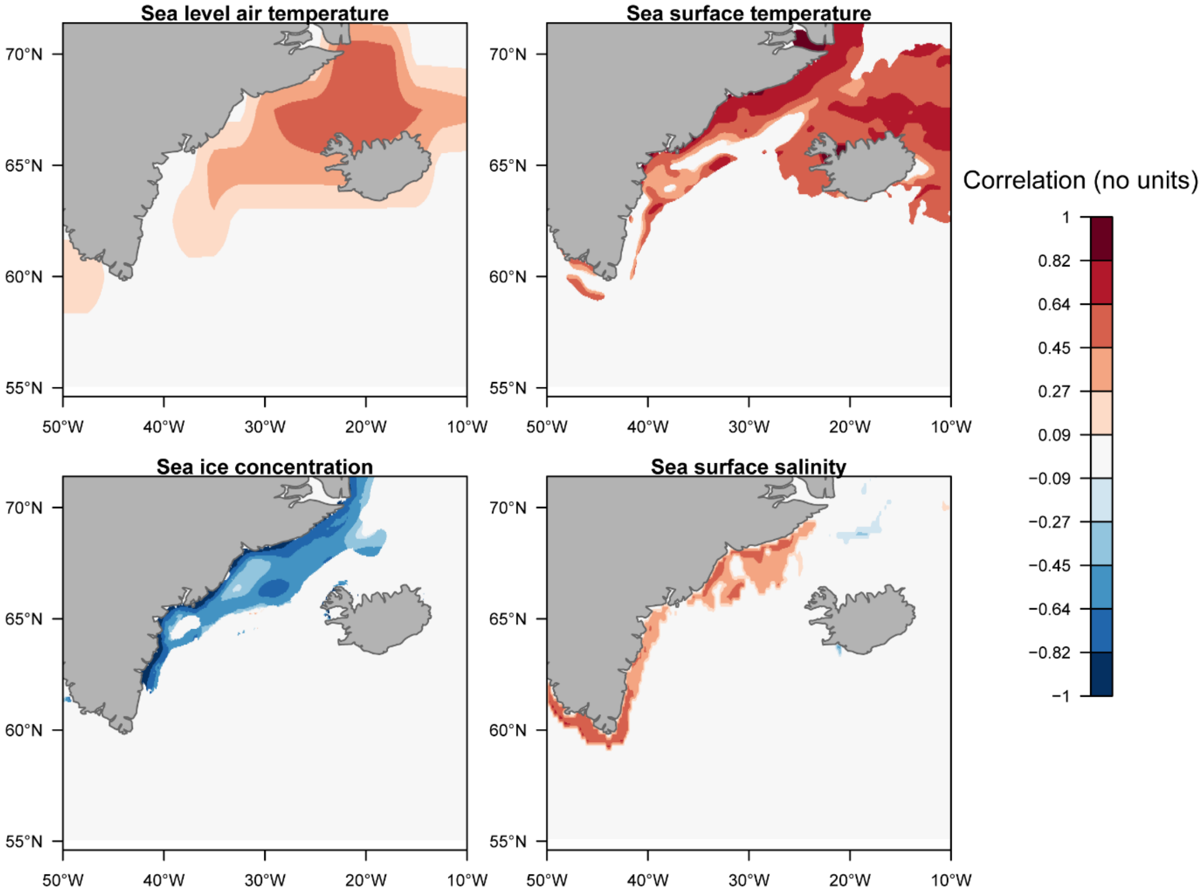

Fig. 5. Correlation maps. Maps of significant correlation coefficients between the tensor time series and the four environmental indices in the larger East Greenland-Iceland ecoregion.

Supplementary Materials for

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

Margrete Emblemsvåg, Karl M. Werner, Ismael Núñez-Riboni, Romain Frelat, Helle Torp Christensen, Heino O. Fock and Raul Primicerio

Table S1. List of species, their cluster affiliation and scores on the four principal tensors (PTs). Lines separate clusters.

Species	Cluster	Scores on PTs			
		PT1	**PT2**	**PT3**	**PT4**
Arctogadus glacialis	d225	-0,08496	-0,04827	-0,03475	0,01547
Cyclopterus lumpus	d225	-0,02629	-0,03788	0,05099	-0,01652
Gadus morhua	d225	-0,2344	-0,17198	0,1635	0,02807
Gymnelus retrodorsalis	d225	-0,1227	-0,08505	0,00545	0,08202
Hippoglossus hippoglossus	d225	-0,10364	-0,03324	0,13519	-0,09653
Melanogrammus aeglefinus	d225	-0,15597	-0,19341	0,35263	-0,02247
Microstomus kitt	d225	-0,08943	-0,13619	0,27303	-0,03548
Molva molva	d225	-0,10685	-0,0405	-0,0149	0,02614
Pollachius virens	d225	-0,12283	-0,0935	0,06141	-0,02164
Triglops murrayi	d225	-0,11818	-0,05156	-0,0606	0,08161
Trisopterus esmarki	d225	-0,06962	-0,07015	0,0996	0,07798
Anarhichas lupus	d375-	-0,24331	-0,07729	-0,15141	-0,11032
Anarhichas minor	d375-	-0,13256	0,14877	-0,17633	-0,32257
Artediellus atlanticus	d375-	-0,21728	-0,07459	-0,24634	-0,02771
Boreogadus saida	d375-	-0,0499	0,2035	-0,13074	-0,19051
Cottunculus microps	d375-	-0,10451	0,07526	-0,22316	-0,04455
Hippoglossoides platessoides	d375-	-0,2268	-0,02968	-0,0742	-0,24128
Lycodes vahlii	d375-	-0,11438	0,00337	-0,15783	-0,18357
Sebastes mentella	d375-	-0,18861	0,20933	-0,19019	-0,0452
Sebastes norvegicus	d375-	-0,25977	-0,09418	-0,0535	0,00801
Argentina silus	d375+	-0,15455	0,09135	-0,28216	0,2312
Brosme brosme	d375+	-0,18115	0,06264	-0,22681	0,28746
Molva dipterygia	d375+	-0,10779	0,17145	-0,20972	0,15444
Anarhichas denticulatus	d675-	0,08753	0,17696	0,04348	-0,14865
Gaidropsarus argentatus	d675-	0,19371	0,03834	-0,08995	-0,12246
Gaidropsarus ensis	d675-	-0,00373	0,04265	0,00085	-0,21635
Lycodes esmarkii	d675-	0,00047	0,12086	0,00535	-0,15721
Lycodes paamiuti	d675-	0,05638	0,03581	0,01897	-0,13258
Lycodes pallidus	d675-	0,02668	0,03377	-0,01041	-0,15889
Lycodes squamiventer	d675-	0,06124	-0,00473	-0,02788	-0,11701
Macrourus berglax	d675-	0,23541	0,16825	-0,12594	0,02945
Amblyraja radiata	d675-	0,0031	0,28598	0,03219	-0,2952
Reinhardtius hippoglossoides	d675-	0,1685	0,27943	0,07442	-0,22102
Aphanopus carbo	d675+	0,08395	-0,01472	0,00335	0,0941
Bathyraja spinicauda	d675+	0,13014	0,16939	0,10771	0,11959
Careproctus reinhardti	d675+	-0,02939	0,13797	-0,02187	-0,05868
Centroscyllium fabricii	d675+	0,14067	0,12719	0,13711	0,20761
Glyptocephalus cynoglossus	d675+	0,00782	0,17215	0,02784	0,24576
Lepidion eques	d675+	0,03274	0,18825	0,07723	0,05503
Lycodes eudipleurostictus	d675+	0,01947	0,07319	0,03109	0,09958
Myxine glutinosa	d675+	0,0146	0,11055	0,04612	0,21771

Notacanthus chemnitzii	d675+	0,21559	0,04177	0,0632	0,06463
Petromyzon marinus	d675+	0,00769	0,0127	-0,06048	0,09669
Rajella fyllae	d675+	-0,00459	0,25895	-0,05385	0,13721
Alepocephalus agassizii	d1275	0,16836	-0,15619	-0,10602	0,05438
Antimora rostrata	d1275	0,19626	-0,22731	-0,20733	0,01283
Borostomias antarcticus	d1275	0,13747	-0,15436	-0,18829	-0,04111
Coryphaenoides brevibarbis	d1275	0,06745	-0,09305	-0,10073	-0,07952
Coryphaenoides guentheri	d1275	0,11688	-0,16599	-0,1691	-0,06239
Coryphaenoides rupestris	d1275	0,18989	-0,1727	-0,15501	-0,11382
Dipterus linteus	d1275	0,09111	-0,10204	-0,10294	0,02492
Raja bathyphila	d1275	0,15762	-0,15718	-0,14641	-0,0146
Raja hyperborea	d1275	0,07845	-0,0869	-0,09622	-0,01134
Synaphobranchus kaupi	d1275	0,17218	-0,16344	-0,14796	-0,03009
Trachyrhynchus murrayi	d1275	0,14787	-0,13239	-0,08942	-0,05596

Table S2. Principal tensor time series.

Year	PT time series
1998	-0.314
1999	-0.305
2000	-0.289
2002	-0.336
2003	-0.121
2004	-0.162
2005	-0.206
2006	-0.148
2007	0.003
2008	0.083
2009	0.194
2010	0.291
2011	0.185
2012	0.271
2013	0.243
2014	0.306
2015	0.120
2016	0.315

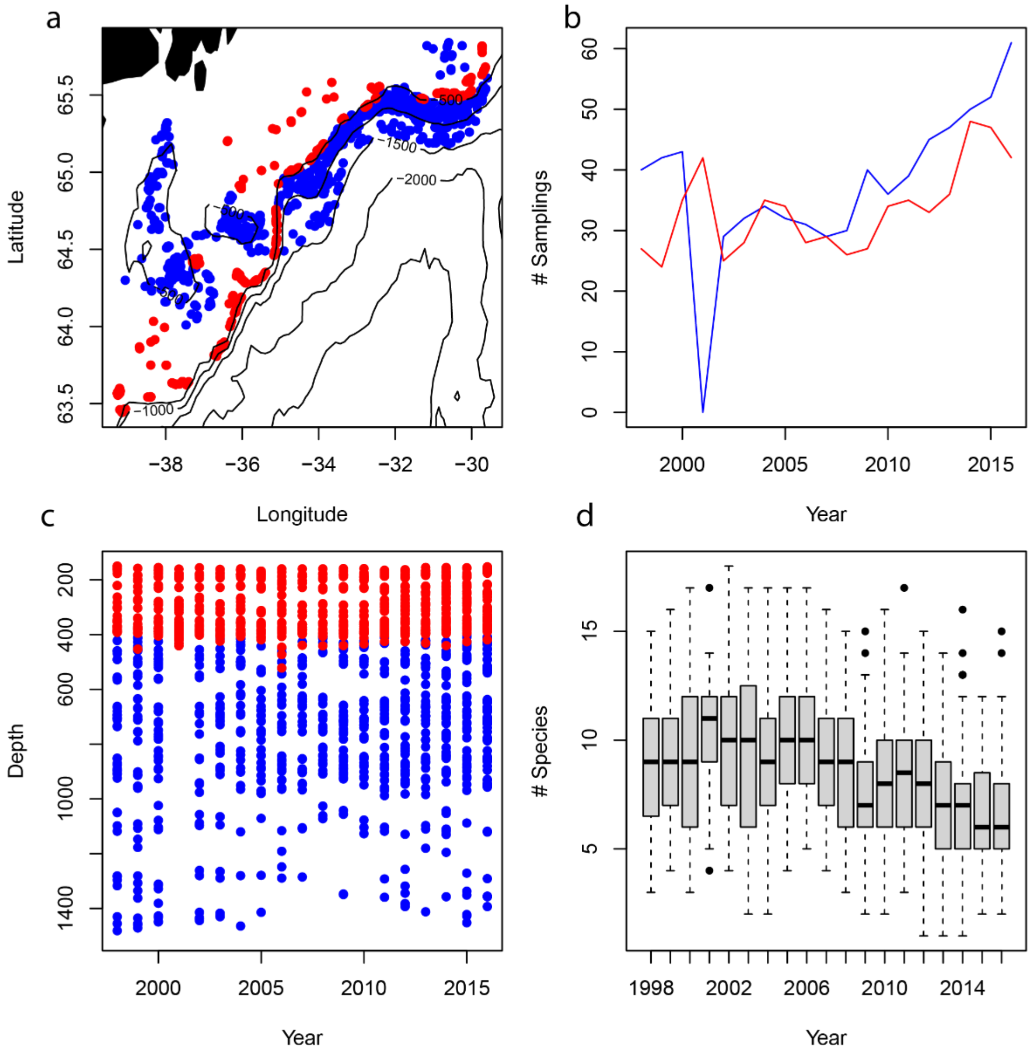

Figure S1. Summary of data collection and sampling design. Red colour represents sampling from the German, shallow survey (0 – 400m) and blue colour from the Greenlandic deep survey (400 – 1500m). a) All stations across years (1998-2016). b) Number of samples per year. c) Depth distribution of samples per year. d) Species richness.

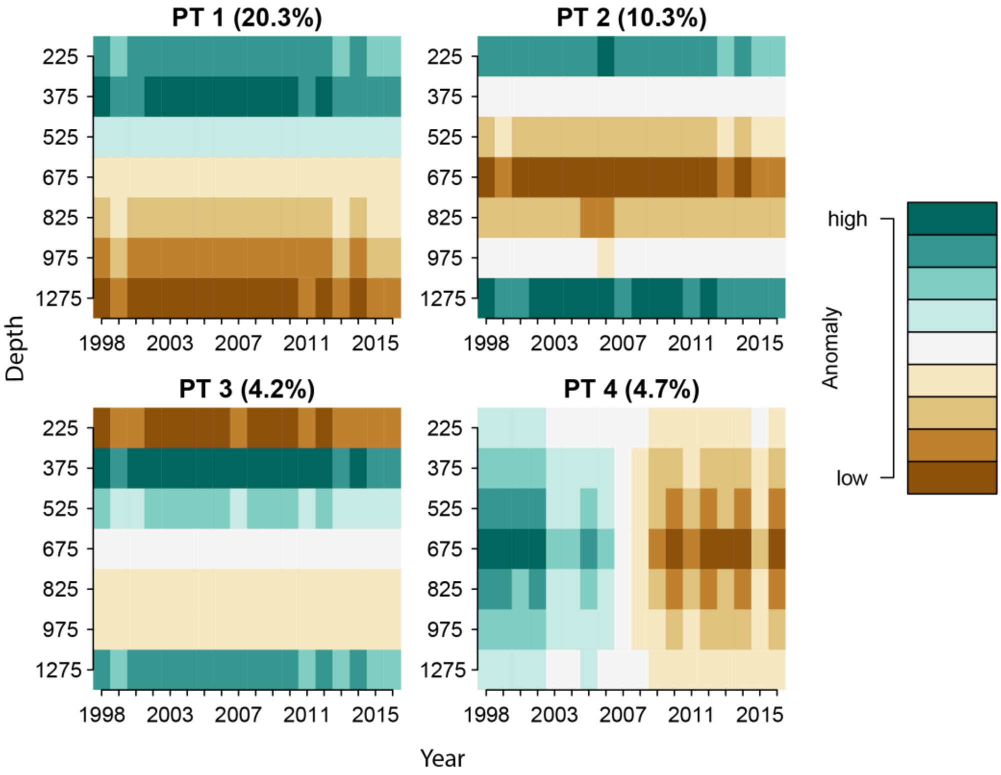

Figure S2. Principal tensors. Main patterns of spatial-temporal dynamics as described by the four principal tensors explaining most of the variability (39.5%). The heatmap visualizes the scores of depth layers (in rows) and years (in columns) on the principal tensors. The three first principal tensors describe variability between depth layers (strong differences among rows) and the fourth principal tensor describes variability mainly along the time series (strong differences among columns).

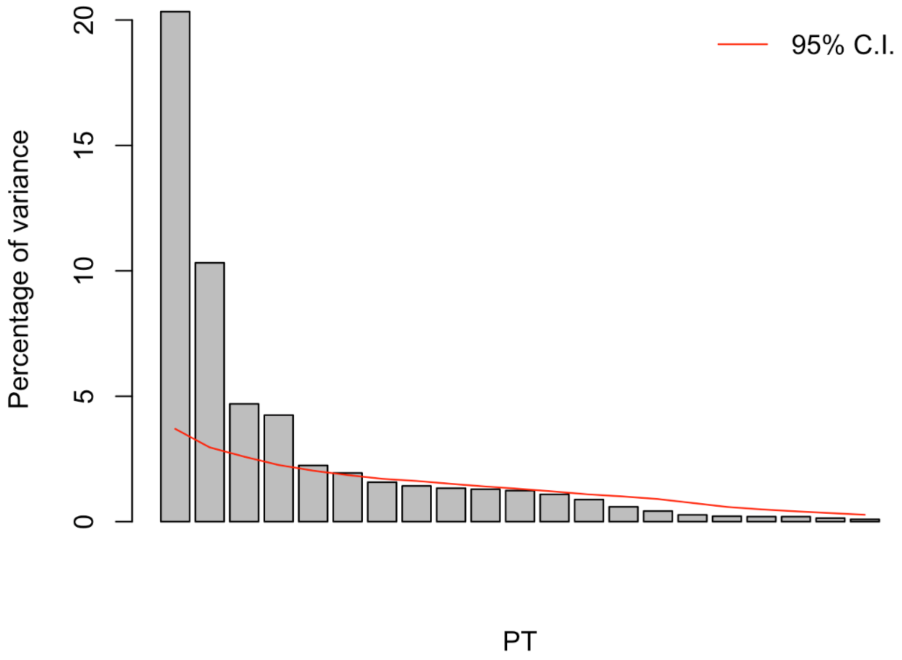

Fig. S3. Significance of the explanatory power of each of the principal tensors. The original tensor was randomly shuffled 1000 times, showing that the four selected principal tensors significantly explain more variance than expected by chance.

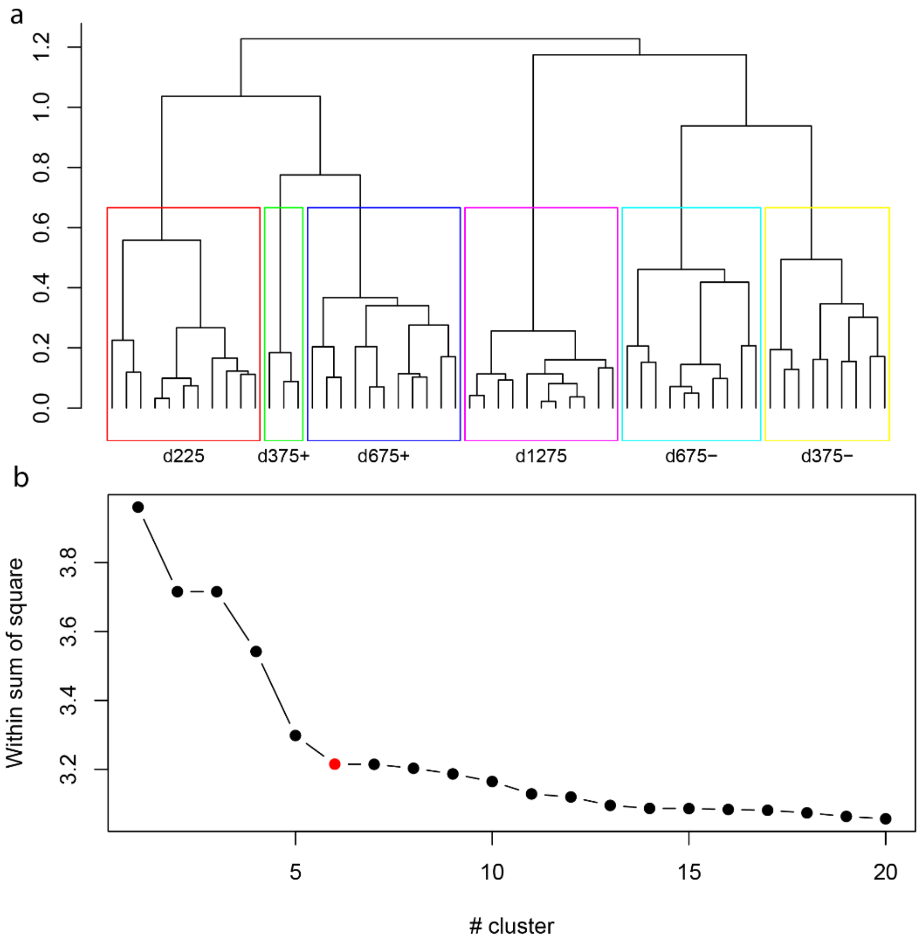

Figure S4. Dendrogram and selection of clusters. a) Dendrogram of the hierarchical clustering of species scores on the four principal tensors. Coloured framing shows the cut-off level and its resulting separation of six clusters. b) Scree plot of the within cluster sum of square with varying number of clusters. The elbow at cluster 6 (red dot) indicates the point of optimal balance between minimum number of clusters and minimum variance within each cluster.

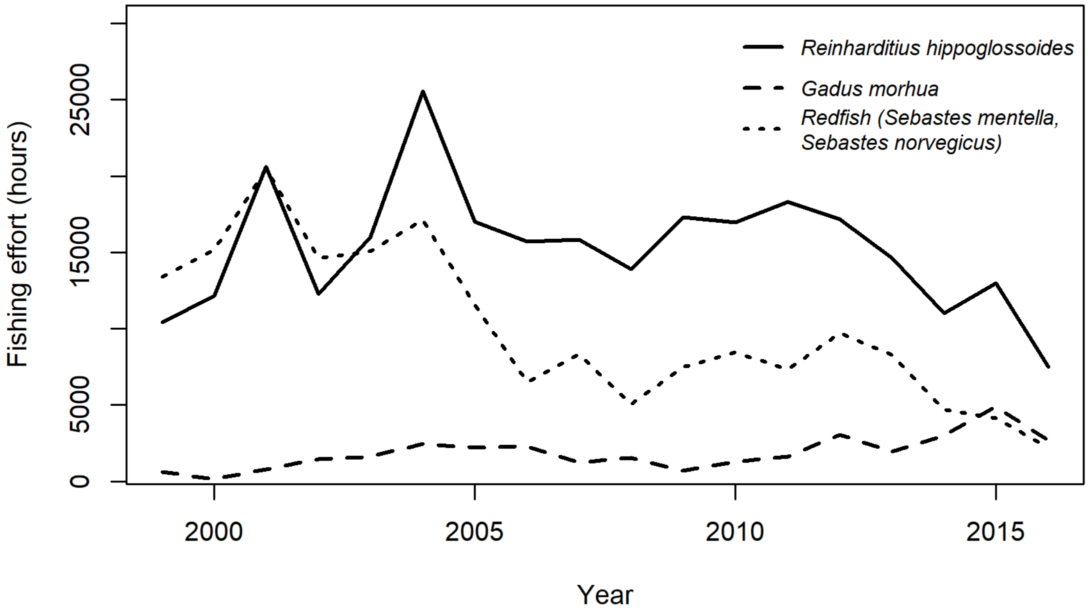

Figure S5. Fishing effort. Total hours of fishing targeting the main commercial species in East Greenland waters from 1999-2016. Calculations were based on haul duration in logbooks data obtained from the Greenland Fishery and Hunting License office for all fishing vessels operating in the exclusive economic zone in East Greenland. Fishing on these species takes place on the shelf, in slope and in deep-sea regions.

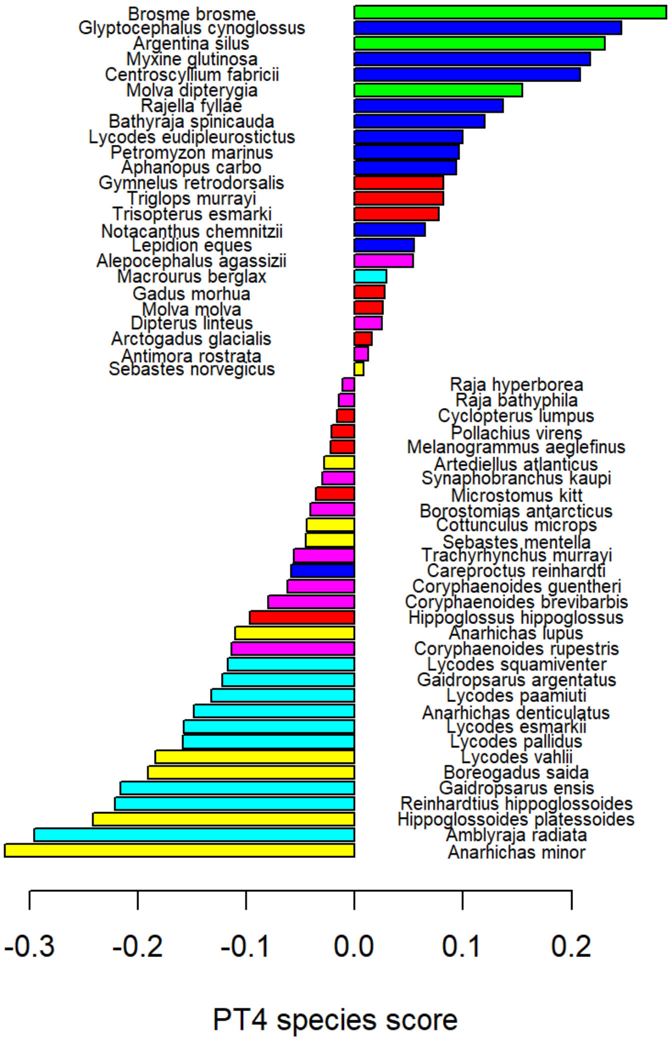

Figure S6. Species scores of principal tensor 4. The colours represent the clusters as displayed in Figure S2 (red = d225, green = d375+, yellow = d375-, blue = d675+, turquoise = d675-, pink = 1275).

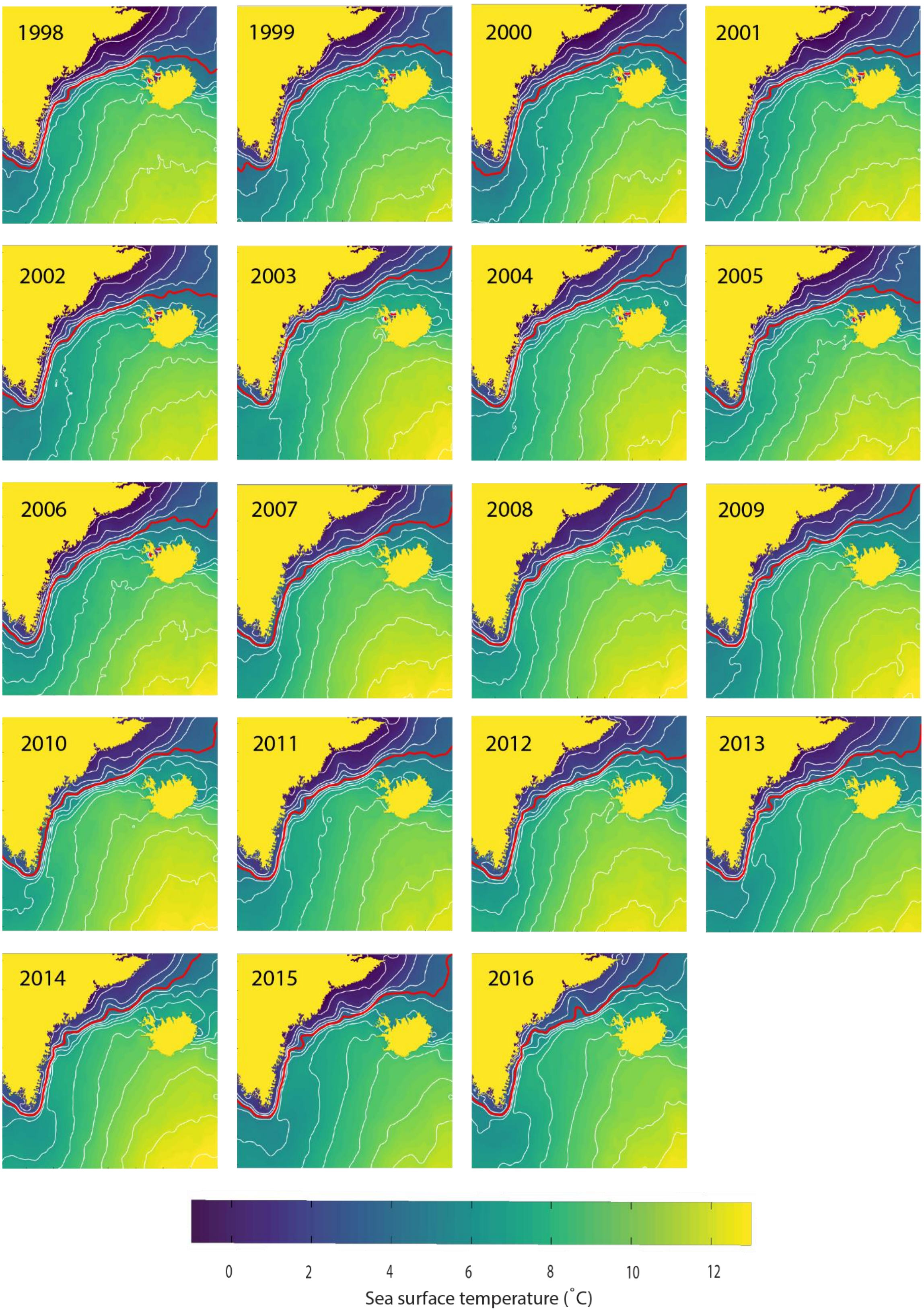

Figure S7. Maps of temporal sea surface temperature across the region. The 4 °C isoline is highlighted in red in order to visualize changes in temperature over time.

Paper III:

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

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Aim

We assessed temporal trends in functional diversity of the deep-sea (150 to 1500 m) demersal fish communities of east Greenland to characterize ecological responses to environmental change.

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 were combined with a fish trait dataset which included a mix of quantitative and categorial traits that characterised 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. The CWM traits matrix was further analysed by redundancy analysis (RDA) with depth-strata and year as explanatory variables.

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

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 et al., 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, leading to a borealization of Arctic communities (Alabia et al., 2020; Fossheim et al., 2015; Hiddink et al., 2008; Mueter et al., 2008; Pinsky et al., 2013; Stevenson et al., 2019; Sunday et al., 2012). 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 demonstrate an increasing trend in local diversity with warming (Frainer et al., 2021; Frainer et al., 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). 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).

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; Frainer et al., 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 would impact negatively 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). 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 et al., 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 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 and specialized life style (Drazen et al., 2012).

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 et al., 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 Through, in the East Atlantic, were shown to increase with depth down to 800m, 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 is found with increasing depth (Myers et al., 2021). Depth gradients have also been found in functional redundancy, the traits' overlap between species, which decreased with depth in the western 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 fish communities in East Greenland, south of the Denmark Strait, in a transition zone between the Arctic and the Atlantic Ocean (Emblemsvåg et al., 2020; Emblemsvåg et al., in press). This region has likely gone through a process of Atlantification, with warm water from the Atlantic ocean traveling to higher latitudes and 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. Surprisingly, contrary to the expected rise in species richness which is found elsewhere in the North Atlantic (Chaudhary et al., 2021; Frainer et al., 2017; Hiddink et al., 2008; Johannesen et al., 2012), there has been a decrease in species richness and total abundance in deep demersal fish communities (400 m-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 in 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 and ecological function. We also expected that trends in functional composition and diversity would differ between depths due to different oceanographic features and different rates of warming.

Methods

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 (Supplementary fig. 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*), which has shifted its distribution westward into Greenland waters (Jansen et al., 2016).

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 3nm 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 type rock hopper 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 during 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 that 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, 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., in press). The catch was sorted, identified to species level, weighted, and counted. A total of 1389 stations were used for further analyses (Supplementary fig. S1).

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 stations) were included in the analyses, which resulted in a final dataset of 55 species, out of the total 91 recorded species (Supplementary table 1). 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 of 150 m depth, between 150 and 1050 m, and a deepest stratum between 1050 m and 1500 m depth less intensively covered by the survey, as specified in (Emblemsvåg et al., in press).

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 et al., 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., 2014). Life history traits included offspring size, fecundity maximum length and longevity (as maximum registered age) (Supplementary table 1) (Wiedmann et al., 2014). Mean trophic level was calculated based on species prey items (Froese et al., 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 function such as mobility, feeding strategy and habitat use (Friedman et al., 2020; Martinez et al., 2021). Body shape is here 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)

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 was 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 triplot and the inferential statistics were performed by permutation.

To calculate functional diversity indices, traits sharing similar biological or functional information were grouped. Group weights were assigned in the modified Gower dissimilarity function 'gawdis' (R package *gawdis,* (de Bello et al., 2021) to avoid excessive influence on the outcomes by closely related traits and to provide each group of traits with the same weight . The four traits describing feeding habitat (benthopelagic, demersal, bathydemersal, bathypelagic) were therefore grouped together and given equal weight in the analysis. Same was done for traits describing feeding ecology (generalist, benthivorous, piscivorous and planktivorous), body shape (fusiform, eel-like, short and/or deep, flat and elongated), giving a total of three groups. 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 2021, which showed that most temporal change in fish community structure were observed in depths between 300 and 1000 m from 2005 until 2010, whereas little temporal change were 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 were used for GAMs (Wood, 2011). The results were plotted using the R package *vegan* (Oksanen et al., 2020) *and ggplot2* (Wickham et al., 2016)

Results

Functional characters of fish species

The East Greenland demersal fish traits displayed co-variation illustrated by the PCA results (fig. 1). The first axis of variation (PC1), accounting for 14.2 % of the fish traits variation, depicted a gradient from bathydemersal benthivores species with large offspring size and low fecundity to generalist species with high fecundity (fig 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 that are long livedwith a large body size, 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 are flatfishes (mainly rays) from whereas species with positive loadings on PC1 And PC2 are species with fusiform, elongated, and short/deep body shapes.

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) (fig. 2, supplementary table 2). Depth had significant effects on all four principal components. Depth dependent changes in time (interaction term) were significant for PC2-PC4, whereas time alone was significant for PC1, PC 2 and PC4. Based on visual inspection of the plots, the third and fourth principal components displayed temporal trends in the loading values, at depths between 300 and 750 m (fig. 2C). PC1 separates fish communities in the shallower strata (150 m - 450 m) with higher abundance of mobile generalist with fusiform body shape from fish communities in the deeper strata (450 m – 1500 m) with higher abundance of benthivores with 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 m – 750 m), there sems to be an increasing and decreasing trend of these traits respectively. PC3 distinguishes shallow (150 m – 300 m) and deep (750 m – 1500 m) communities with higher abundance of large flatfishes, feeding in the benthopelagic from mobile demersal with high fecundity, showing decreasing trends in intermediate depths (300 m – 750 m). 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, showing a decreasing trend in intermediate depths (450 m – 600 m).

The RDA results also showed significant spatio-temporal effects in CWM, summarized by a triplot (figure 3). The first and second axis of the RDA accounted for 24% and 10%, respectively, of the total variability. Communities within the three deepest strata (750 to 1500 m) accomplished an increase in the relative biomass of species with elongated body size and benthivorous feeding behaviour. Communities at intermediate depths between 450 and 750 m showed an increasing importance of species with large offspring size (egg size) high longevity and pelagic feeding habitat use. In depths between 300 and 450 m there was an increase in abundance of species of higher trophic level, good swimming capacities (high aspect ratio), fusiform body shape and generalist feeding behaviour.. Communities living in the shallowest depth strata (150 – 300 m) displayed the least temporal change in functional characterization with an increase in demersal species of large body size, high fecundity and pelagic feeding habitat use. In general, across all depths, there is a relative temporal increase in large demersal species with high fecundity.

Depth gradients of functional diversity

Functional dispersion was highest at depths between 800 and 1000 m across the three time periods (fig 4). In the first period, 1998 – 2004, functional dispersion was fairly stable until 500m then increase until 900 m and decrease again in the deepest stations. 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. 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 (fig. 4). Species richness displayed a peak 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 stations. It is to be noted that the deepest depth layer was less sampled compared to the shallower depth layers which may have caused the observed lower functional diversity at this depth. Model statistics are given in supplementary table 3.

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 (fig. 5). 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. In the deepest strata (1000-1500 m), there were no distinct temporal trends in any of the indices (fig. 5, Supplementary table 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, and functional dispersion increased with depth. The functional characterization of fish communities changed with warming, resulting in an increased prominence of boreal. At intermediate depths, numerical importance 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 loss of species with 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.

Functional characteristics of fish species

The distinction in functional characteristic 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. Arctic species live in a strongly seasonal and harsh environment, where specialization in benthic preys, relatively low fecundity and greater investment in individual offspring of larger size helps to increase their chance of survival (Marshall, 1953). A larger larva is generally a better swimmer with higher lipid storage capacity and therefore may better cope with low or heterogeneous food supplies (Allen et al., 2008; Bashey, 2008; Marshall et al., 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 larger size, and living longer, than Arctic species such as the eelpouts (*Lycodes* spp.).

Boreal species, like Atlantic cod or redfish, could also be distinguished in terms of foraging behaviour, being 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 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 an advantage in deeper waters, where food supply might be scattered and unstable, and sometimes limited (Drazen et al., 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).

Depth gradient in functional diversity

We found the highest species richness between 300-400 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 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., in press). 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 vertical redistribution in response to warming waters are 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).

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 et al., 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 an 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 m – 300 m), representing the shelf region, is in accordance with similar lack of response in fish community abundances (Emblemsvåg et al., in press). 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.

Increasing dominance of generalists

The decline in species richness in East Greenland (Emblemsvåg et al., 2020; Emblemsvåg et al., in press) 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 et al., 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; Frainer et al., 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 generalist species increase food-web connectivity and benthic-pelagic coupling, and 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 but also 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, of the eastern Greenland sea might lose adaptive capacity due to declining functional diversity and a reduced ecosystem robustness to perturbations due to increased food-web connectivity.

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.

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. This 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 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 redistributions. The loss of functional diversity threatens the maintenance of ecosystem function in an area undergoing rapid environmental change (Cadotte, 2017).

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 understanding the climate change impacts on deep-sea fish and their associated fisheries.

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Data accessibility statement

The species-traits matrix and community weighted means dataset used in this study is available at:

https://datadryad.org/stash/share/lr3yX-DmxIWECKKBfQb4-pN4desPG9qWLMG1mghU_M4

For usage of these data, a request must be made to the authors. Article DOI:

https://doi.org/10.5061/dryad.gxd2547nb.

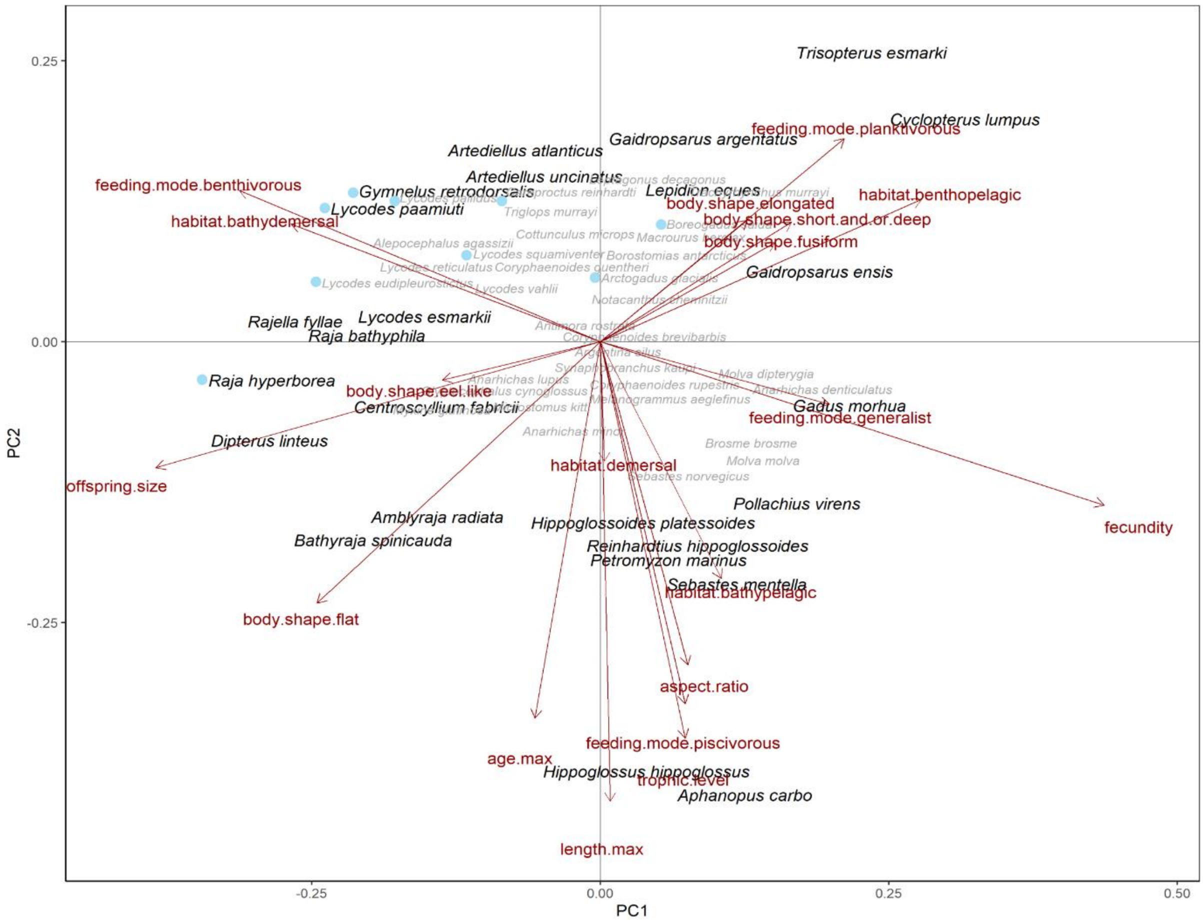

Figure 4: Principal component analysis (PCA) of East Greenland fish functional traits. Red arrows and labels represent traits whereas black and grey labels represent the species. Species in grey has scores between 0.15 and -0.15 on the axis. Blue dots marks the Arctic species characterized by Mecklenburg et al. (2018).

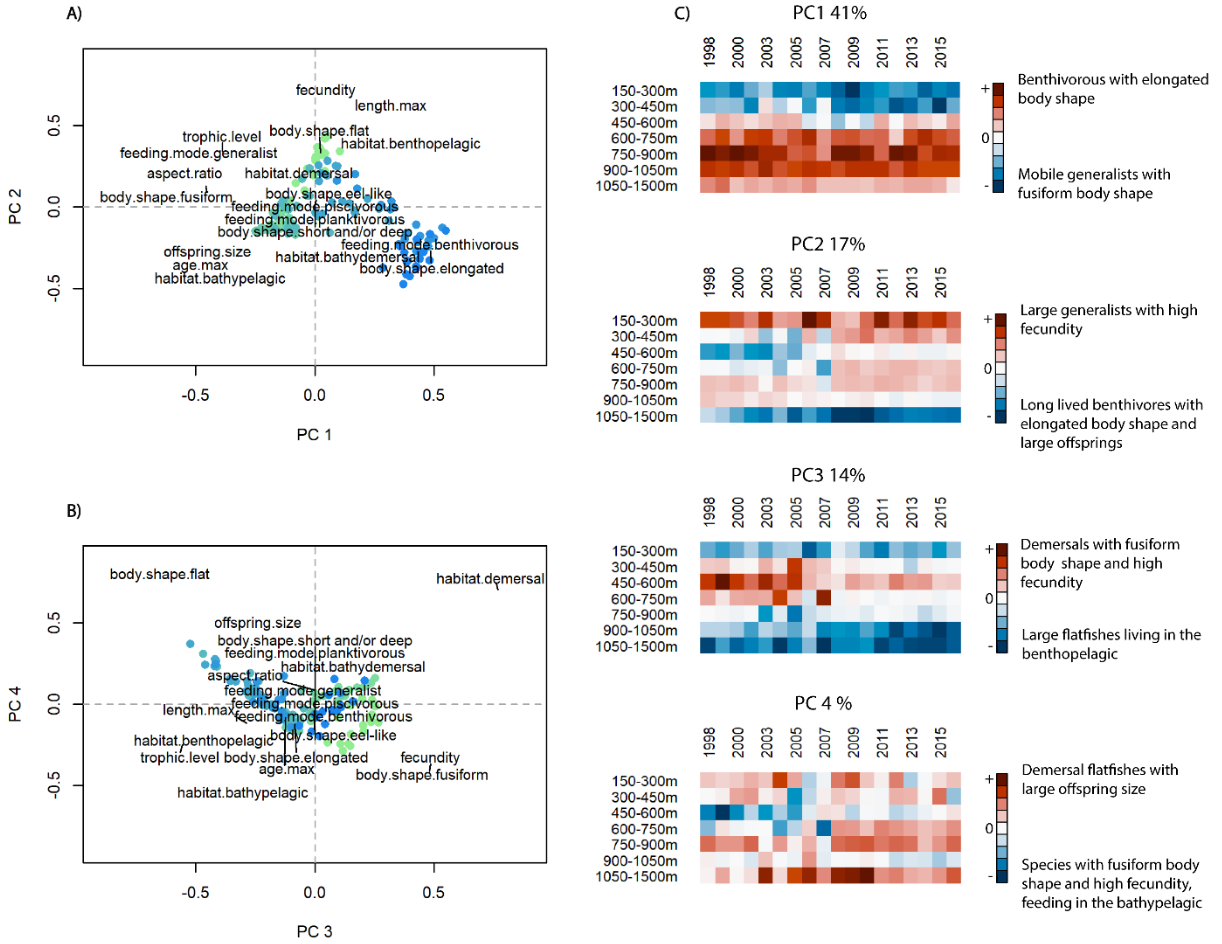

Figure 5. Principal Component Analysis (PCA) of Community Weighted Mean traits (CWM). A) PCA biplot of PC1 and PC2. B) Biplot of PC3 and PC4s. The dots represents centroids of depth stratum/year and colour coded accordingly, light green being the shallowest stratum and dark blue being the deepest stratum. C) Heatmaps of the four 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 that drive the gradient. Percentages represent proportion of variance explained.

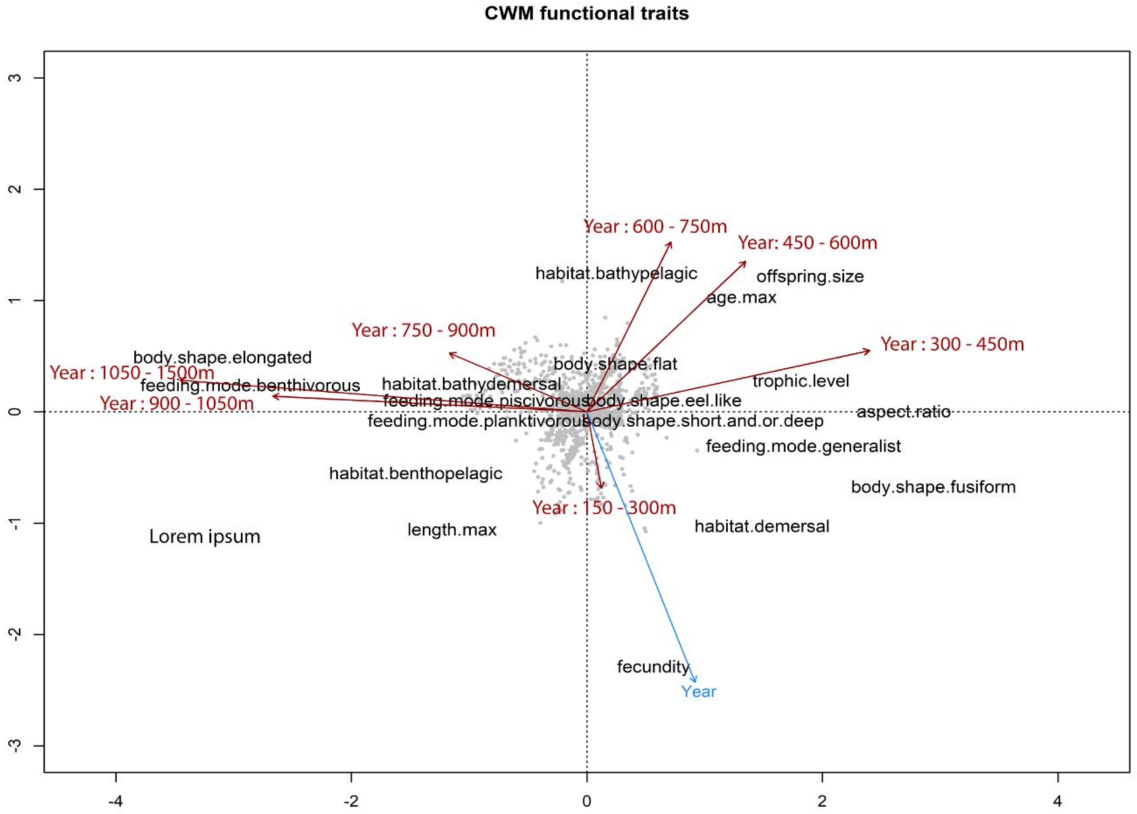

Figure 6: Redundancy analysis (RDA) triplot of the community-weighted mean trait values from 1998 to 2016. Red arrows indicate depth strata specific temporal trends, the blue arrow depicts the overall temporal trend. Length and direction of the arrows indicates the importance and magnitude, respectively. Grey dots show the 1389 stations.

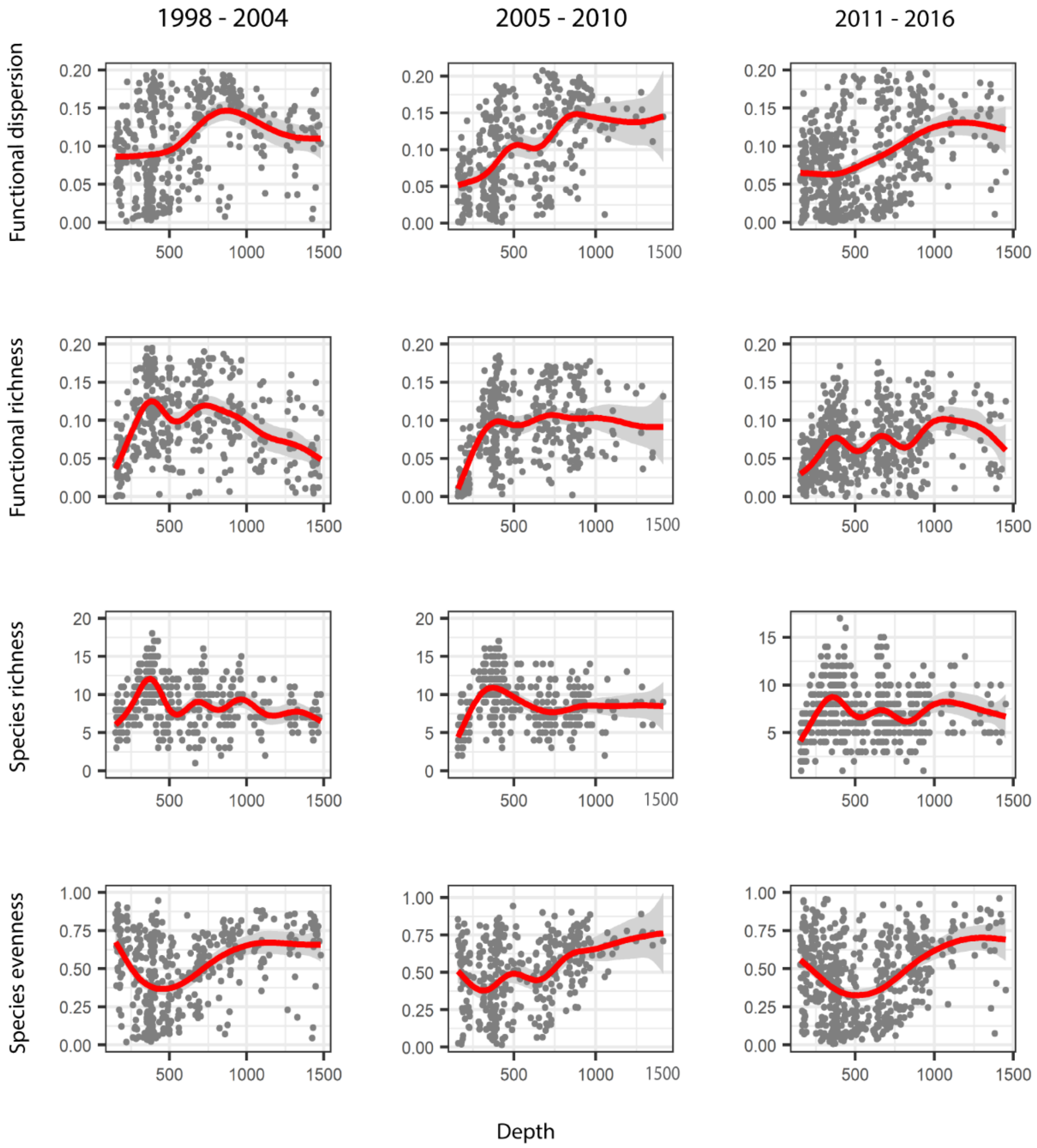

Figure 7: The depth profiles of diversity indices in three time periods. From top to bottom: functional dispersion, functional richness, species richness and species evenness. From left to right: 1998-2004, 2005-2010, 2011-2016. The red lines represent the smoother from a GAM model, grey dots represent each sample/site.

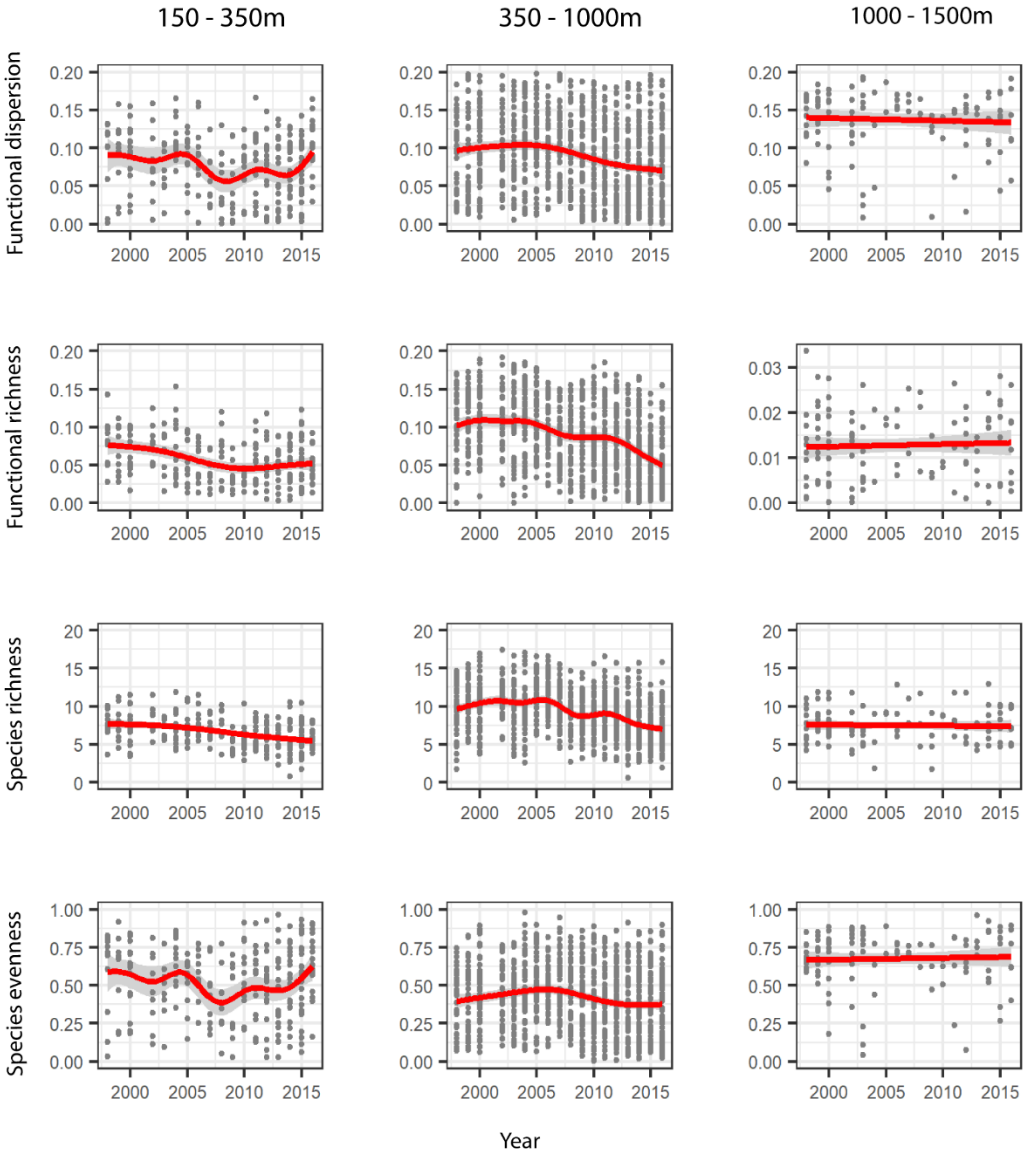

Figure 8: Temporal developments of diversity indices in three depth strata. From top to bottom: functional dispersion, functional richness, species richness, species evenness. From left to right: 150-350 m, 350-1000 m, 1000-1500 m. The red lines represent the smoother from a GAM model, grey dots represent each sample/site.

Supplementary material for: Recent warming causes functional borealization and diversity loss in deep fish communities east of Greenland

Margrete Emblemsvåg, Laurene Pecuchet, Liv Guri Velle, Adriana Nogueira and Raul Primicerio

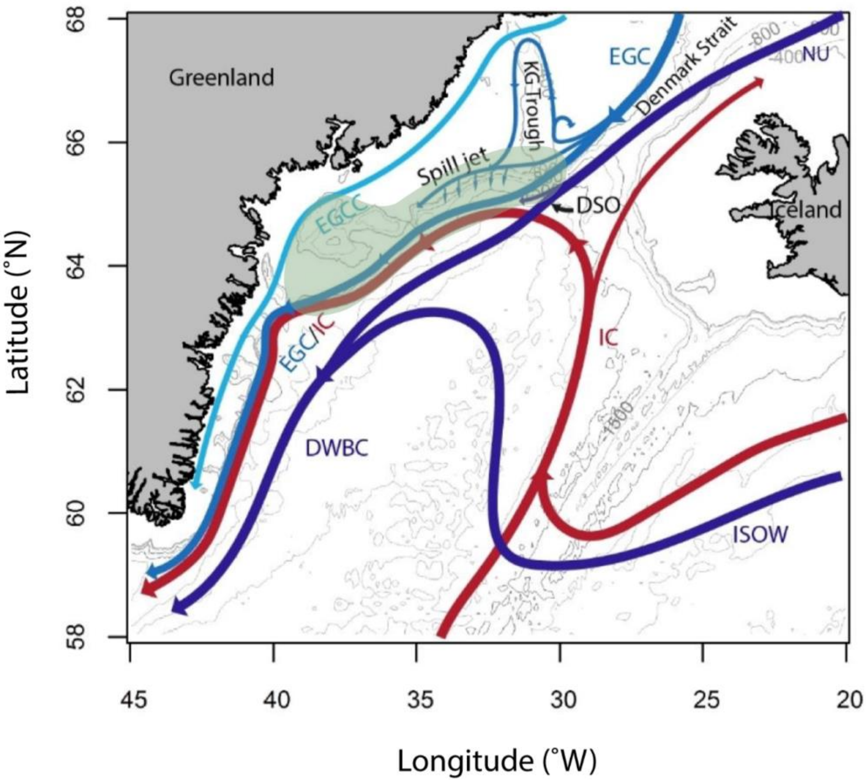

Figure S1: Map of study region. Shaded green area show the region from which survey samples were collected. Blue arrows represent cold water masses, whereas red arrows represent warmer waters. EGC = East Greenland Current, IC = Irminger Currrent, DSO = Denmark Strait Overflow, EGCC = East Greenland Costal Current, ISOW= Iceland Scotland Overflow Water, DWBC = Deep Western Boundary Current. The figure is obtained from Emblemsvåg et al. 2020 and modified.

Table S1: Species -traits dataset used in thTraits are retrieved from fishbase (Froese et al., 2017) online database of traits of marine fish species from the North Atlantic and Northeast Pacific (Beukhof et al., 2019).

S**pecies**	**Feeding habitat**	**Feeding mode**	**Body shape**	**Trophiv level**	**Aspect ratio**	**Offspring size**	**Fecundity**	**Length max**	**Age max**
Alepocephalus agassizii	bathydemersal	benthivorous	fusiform	0.64	0.30	0.57	3.57	1.46	1.59
Anarhichas denticulatus	benthopelagic	generalist	elongated	0.68	0.43	0.85	4.43	2.18	1.23
Anarhichas lupus	demersal	benthivorous	elongated	0.66	0.33	0.85	4.40	2.18	1.36
Anarhichas minor	demersal	benthivorous	elongated	0.66	0.37	0.64	4.29	2.28	1.61
Antimora rostrata	bathydemersal	benthivorous	elongated	0.66	0.41	0.30	5.78	1.91	1.41
Aphanopus carbo	bathypelagic	piscivorous	eel-like	0.74	0.59	0.44	5.70	2.08	1.52
Arctogadus glacialis	bathydemersal	generalist	fusiform	0.68	0.25	0.44	4.18	1.69	1.08
Argentina silus	bathydemersal	generalist	fusiform	0.64	0.39	0.63	4.00	1.85	1.56
Artediellus atlanticus	demersal	benthivorous	fusiform	0.65	0.19	0.51	1.80	1.26	1.04
Artediellus uncinatus	demersal	benthivorous	fusiform	0.65	0.29	0.51	2.29	1.04	1.04
Bathyraja spinicauda	bathydemersal	generalist	flat	0.73	0.33	1.99	1.08	2.24	1.45
Boreogadus saida	demersal	generalist	fusiform	0.61	0.37	0.44	4.52	1.38	0.90
Borostomias antarcticus	bathydemersal	generalist	elongated	0.66	0.41	0.44	4.65	1.56	0.81
Brosme brosme	demersal	generalist	elongated	0.69	0.36	0.37	6.40	2.08	1.32
Careproctus reinhardti	bathydemersal	generalist	fusiform	0.68	0.14	0.74	2.18	1.49	0.90
Centroscyllium fabricii	bathydemersal	generalist	elongated	0.68	0.26	2.25	1.04	1.93	1.76
Coryphaenoides brevibarbis	bathydemersal	generalist	elongated	0.72	0.08	0.40	4.48	1.66	1.71
Coryphaenoides guentheri	bathydemersal	generalist	elongated	0.63	0.08	0.40	4.49	1.71	1.74
Coryphaenoides rupestris	bathypelagic	generalist	elongated	0.66	0.08	0.40	4.48	1.49	1.79
Cottunculus microps	bathydemersal	generalist	elongated	0.71	0.25	0.74	2.58	1.20	1.11
Cyclopterus lumpus	benthopelagic	planktivorous	short and/or deep	0.69	0.24	0.53	5.35	1.76	1.15
Dipterus linteus	bathydemersal	benthivorous	flat	0.65	0.31	2.19	1.61	2.12	1.72

Gadus morhua	benthopelagic	generalist	fusiform	0.71	0.36	0.40	6.58	2.07	1.41
Gaidropsarus argentatus	bathydemersal	generalist	elongated	0.64	0.28	0.36	6.40	0.60	1.04
Gaidropsarus ensis	benthopelagic	generalist	elongated	0.64	0.47	0.25	5.85	1.63	0.95
Glyptocephalus cynoglossus	demersal	benthivorous	flat	0.62	0.32	0.33	5.00	1.90	1.41
Gymnelus retrodorsalis	demersal	benthivorous	eel-like	0.62	0.24	0.72	1.23	1.30	1.11
Hippoglossoides platessoides	demersal	generalist	flat	0.71	0.35	0.48	5.88	1.92	1.49
Hippoglossus hippoglossus	demersal	piscivorous	flat	0.70	0.49	0.64	6.38	2.67	1.49
Lepidion eques	benthopelagic	benthivorous	fusiform	0.63	0.24	0.30	5.78	1.63	1.15
Leptagonus decagonus	demersal	generalist	elongated	0.62	0.16	0.48	3.08	1.30	1.08
Lycodes esmarkii	bathydemersal	benthivorous	eel-like	0.69	0.29	0.85	3.08	1.81	1.18
Lycodes eudipleurostictus	demersal	benthivorous	eel-like	0.65	0.24	0.78	2.29	1.66	1.15
Lycodes pallidus	demersal	benthivorous	eel-like	0.62	0.25	0.81	1.61	1.48	1.00
Lycodes paamiuti	bathydemersal	benthivorous	eel-like	0.67	0.23	0.82	1.49	1.40	1.19
Lycodes reticulatus	bathydemersal	benthivorous	elongated	0.65	0.30	0.82	1.49	1.89	1.45
Lycodes squamiventer	bathydemersal	generalist	elongated	0.67	0.23	0.82	1.68	1.43	1.34
Lycodes vahlii	bathydemersal	generalist	eel-like	0.64	0.25	0.78	2.41	1.76	1.19
Macrourus berglax	benthopelagic	benthivorous	elongated	0.66	0.08	0.40	4.64	2.05	1.41
Melanogrammus aeglefinus	demersal	benthivorous	fusiform	0.70	0.39	0.38	5.94	1.89	1.32
Microstomus kitt	demersal	benthivorous	flat	0.62	0.42	0.36	4.98	1.83	1.38
Molva dipterygia	demersal	generalist	elongated	0.74	0.18	0.31	6.40	1.59	1.32
Molva molva	demersal	generalist	elongated	0.73	0.19	0.31	6.30	2.30	1.41
Myxine glutinosa	demersal	benthivorous	eel-like	0.74	0.21	0.78	1.41	1.90	1.43
Notacanthus chemnitzii	benthopelagic	benthivorous	elongated	0.65	0.29	0.36	4.30	2.09	1.40
Petromyzon marinus	demersal	piscivorous	eel-like	0.73	0.26	0.32	5.38	2.08	1.08
Pollachius virens	demersal	generalist	fusiform	0.73	0.45	0.32	6.66	2.12	1.41
Raja bathyphila	bathydemersal	benthivorous	flat	0.64	0.29	1.69	1.75	1.96	1.18
Rajella fyllae	bathydemersal	benthivorous	flat	0.64	0.28	1.69	1.68	1.79	1.18
Raja hyperborea	bathydemersal	benthivorous	flat	0.73	0.20	2.01	1.49	1.66	1.40

Amblyraja radiata	demersal	generalist	flat	0.72	0.27	2.05	1.26	2.04	1.46
Reinhardtius hippoglossoides	benthopelagic	generalist	flat	0.73	0.43	0.72	4.80	2.10	1.53
Sebastes norvegicus	demersal	generalist	fusiform	0.68	0.41	0.86	5.23	1.81	1.79
Sebastes mentella	bathypelagic	generalist	fusiform	0.71	0.45	0.85	4.41	1.77	1.88
Synaphobranchus kaupi	bathydemersal	generalist	eel-like	0.71	0.30	0.30	5.08	1.74	1.25
Trachyrhynchus murrayi	benthopelagic	generalist	elongated	0.65	0.08	0.40	4.15	1.69	1.08
Triglops murrayi	demersal	benthivorous	elongated	0.65	0.32	0.48	2.65	1.32	1.04
Trisopterus esmarki	benthopelagic	planktivorous	fusiform	0.63	0.29	0.33	5.31	1.34	0.78

Table S2: Model statistics of figure 2. Significance of environmental variables on Community Weighted Mean (CWM) on the first four principal components (PCs).

Scores on PC1 ~depth * Year

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Depths	6	0.5368	0.08947	251.452	< 0.001***
env$year	1	0.0019	0.00194	5.458	0.019*
Depths:env$year	6	0.0026	0.00043	1.196	0.318
Residuals	1289	0.4587	0.00036		

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Scores on PC2 ~depth * Year

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Depths	6	0.4861	0.08101	226.209	<0.001***
env$year	1	0.0001	0.00012	0.344	0.056
Depths:env$year	6	0.0522	0.00870	24.289	<0.001***
Residuals	1289	0.4616	0.00036		

Scores on PC3 ~depth * Year

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Depths	6	0.4616	0.07694	202.381	<0.001 ***
env$year	1	0.0328	0.03278	86.223	<0.001 ***
Depths:env$year	6	0.0156	0.00259	6.825	3.84e-07***
Residuals	1289	0.4900	0.00038		

Scores on PC4 ~depth * Year

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Depths	6	0.1052	0.017540	26.221	2,00e-16 ***
env$year	1	0.0041	0.004063	6.073	0.0139 *
Depths:env$year	6	0.0284	0.004736	7.080	1.96e-07***
Residuals	1289	0.8623	0.000669		

Signif. codes: 0: ‘***’ 0.001: ‘**’ 0.01: ‘*’

Table S3: Statistics from Generalized Additive Models (GAM) in figure 4. Diversity indices as function of “depth”. Depth is given as a smooth term. General function= $g(E(Y)) =\beta_0 + f_1(x_1)$

		1998 - 2004				**2005 - 2010**				**2011 - 2016**			
Functional Dispersion		**Estimate**	**Std, Error**	**t value**	**P value**	**Estimate**	**Std, Error**	**t value**	**P value**	**Estimate**	**Std, Error**	**t value**	**P value**
	Intercept	0.010	0.003	39.055	<0.001	0.100	0.003	38.173	<0.001	0.085	0.002	36.166	<0.001
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(depth)	4.951	6.016	10.000	<0.001	6.603	70.717	71.518	<0.001	3.487	4.296	25.977	<0.001
Functional Richness		**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**
	Intercept	0.083	0.002	42.236	<0.001	0.081	0.0018	42.863	<0.001	0.072	0.002	46.698	<0.001
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(depth)	8.382	8.888	14.717	<0.001	6.392	7.572	18.270	<0.001	8.237	8.841	8.740	<0.001
Species Richness		**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**
	Intercept	9.189	0.136	67.468	<0.001	8.877	0.133	66.950	<0.001	7.217	0.108	66.840	<0.001
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(depth)	8.731	8.977	20.894	<0.001	6.449	7.574	22.012	<0.001	8.060	8.764	12.733	<0.001
Species Evenness		**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**
	Intercept	0.497	0.011	45.367	<0.001	0.492	0.011	44.984	<0.001	0.444	0.010	44.496	<0.001
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(depth)	5.056	6.133	18.691	<0.001	6.765	7.861	9.788	<0.001	4.339	5.304	20.893	<0.001

Table S4. Statistics from Generalized Additive Models (GAM) in figure 5. Diversity indices as function of “Year”, with “depth” as covariate. Year is given as a smooth term. General function= $g(E(Y)) = \beta_0 + f_1(x_1) + x_2$

		150 – 300 m				**300 – 1000 m**				**1000 – 1500 m**			
Functional Dispersion		**Estimate**	**Std, Error**	**t value**	**P value**	**Estimate**	**Std, Error**	**t value**	**P value**	**Estimate**	**Std, Error**	**t value**	**P value**
	Intercept	0.077	0.0126	6.129	<0.001	0.025	5.194e-03	4.918	<0.001	0.0167	0.034	4.889	<0.001
	Depth	0.000	0.000	-0.085	0.09	0.000	0.000	13.521	<0.001	0.000	0.000	-1.622	0.534
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(Year)	6.753	7.870	3.196	0.002	2.948	3.648	10.550	<0.001	1.000	1.000	0.058	0.810
Functional Richness		**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**
	Intercept	-0.051	0.009	-5.196	<0.001	0.087	0.004	23.580	<0.001	0.0878	0.007	3.396	<0.001
	Depth	0.000	0.000	11.399	<0.001	0.000	0.000	0.447	0.065	0.000	0.000	-1.469	0.145
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(Year)	3.274	4.052	7.440	<0.001	6.641	7.768	28.631	<0.001	1.638	2.033	0.576	0.570
Species Richness		**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**
	Intercept	-0.540	0.597	-0.904	0.367	11.397	0.271	42.127	<0.001	9.259	1.947	4.756	<0.001
	Depth	0.033	0.003	12.341	<0.001	-0.004	0.000	-10.102	<0.001	-0.001	0.002	-0.900	0.370
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(Year)	2.377	2.950	14.347	<0.001	7.854	8.655	23.406	<0.001	1.000	1.000	0.095	0.758
Species Evenness		**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**	**Estimate**	**Std. Error**	**t value**	**P value**
	Intercept	0.773	0.073	10.555	<0.001	0.218	0.022	10.026	<0.001	0.661	0.156	4.234	<0.001
	Depth	-0.001	0.000	-3.660	<0.001	0.000	0.000	10.817	<0.001	0.000	0.000	0.095	0.924
		edf	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**	**edf**	**Ref.df**	**F**	**p-value**
	s(Year)	6.859	7.960	2.664	0.009	3.862	4.764	6.030	<0.001	1.000	1.000	0.153	0.696

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