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Original Article

The effects of bottom temperature and fishing on the structure and composition of an exploited demersal fish assemblage in West Greenland

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The distribution and abundance of marine fishes have been changing over the last decades due to climate change and overfishing. We evaluated the status of an important exploited marine ecosystem for one of the largest fisheries in Greenland, Greenland halibut *Reinhardtius hippoglossoides*, in the offshore slopes of West Greenland. We examined how five ecological indicators changed from 1997 to 2019 under the effect of climate and commercial fishery. The oscillatory tendency of the bottom temperature modified the structure and composition of the demersal fish community. In the shallower zone, the warming bottom temperature favoured high trophic level and warmer water species, and subsequently, an increase in halibut biomass, which reduced the biodiversity. In the middle depth zone, the high biomass of halibut masked increases of less common higher trophic level species. In the deep zone, the drastic reduction of halibut biomass coincided with an increase of high trophic level and colder-water species. Despite the increasing exploitation, especially the mid depth zone, the current fishery did not induce changes to community structure. With the present study, we demonstrate the value of using ecological indicators and estimating spatio-temporal trends to provide a further understanding of the ecosystem status.

Keywords: climate change, demersal fish, dominant species, ecological indicators, fishing effect

Introduction

Community response to environmental variation and exploitation can be complex (Hollowed *et al.*, 2013), and a more holistic, ecosystem-based approach for fisheries management can help us understand and more accurately predict changes in exploited fish communities (Pikitch *et al.*, 2004; Hilborn, 2011). Instead of considering only the direct mortality of commercial species, ecosystem-based measures incorporate indirect impacts of exploitation on ecological interactions among species and their environment (Essington, 2004). Ecological indicators are useful tools for evaluating the overall impact of environmental and anthropogenic drivers on communities (Coll *et al.*, 2016), but individual indicators cannot describe all aspects of ecosystem dynamics. Multiple, complementary indicators can give a more complete understanding of community response (Cury and Christensen, 2005).

Fluctuations in the abundance of important species (dominant species, keystone species, or ecological engineers) can strongly influence the pathways of energy and material flows (Hooper *et al.*, 2005). Competition, predation, and environmental variability all influence community dynamics resulting in species-specific effects on the distribution and vital rates, such as survival, growth, and reproduction (Hollowed *et al.*, 2000; Lorenzen, 2008). Mean trophic level (MTL) is a widely used ecological indicator that indexes the trophic structure of a community, generally with a specific focus on communities dominated by exploited species (Pauly *et al.*, 1998; Pauly and Watson, 2005). Ecosystem MTL may decline due to a loss of high-trophic level (TL) taxa or an increase in the abundance of low-TL species, but structural and compositional changes are not always reflected in the MTL index as changes may also manifest "horizontal" responses. The decline of competitors might be buffered in the system by a reorganization of biomass, preventing the system from exhibiting a strong trophic cascade (Tolimieri *et al.*, 2013).

Biodiversity loss has a strong potential to alter the function and the services of an ecosystem. Reduction in biodiversity may impact productivity and nutrient retention, susceptibility to invasion, and response to disturbances (Margalef, 1958; Hurlbert, 1971). High diversity ecosystems are expected to be more stable and resilient, decreasing potential risks in a rapidly changing marine environment (Worm *et al.*, 2006). In high latitudes, high biodiversity is usually related to the presence of boreal species, which can be highly responsive to temperature and other environmental variables. Because of warming ocean temperatures, marine species must adapt to the new environment or move to suitable habitats (Henson *et al.*, 2017). Hence, Cheung *et al.*, (2013) developed an ecological indicator, the mean temperature of the catch (MTC), to calculate the potential effects of climate change on global fish communities based on the temperature preference of each species.

The banks on the southern slope of the Davis Strait and the Disko Bay area (west of Greenland) are important spawning, nursery, and fishing grounds for many fishes (Buch *et al.*, 2004). With the decrease of the Atlantic cod (*Gadus morhua*) fishery after 1970, the Greenland halibut (*Reinhardtius hippoglossoides*, hereafter halibut) fishery emerged becoming one of the most important target species for trawlers, and occasionally longliners (Pedersen and Zeller, 2001; Buch *et al.*, 2004). Halibut is a high trophic-level flatfish (TL = 4.1) (Pauly *et al.*, 1998) distributed in the arctic and temperate waters in the northern hemisphere, inhabiting depths between 200 and 2000 m but mainly caught in depths below 800 m (Morgan *et al.*, 2013). It is vulnerable to fishing mortality (Froese and Pauly, 2019). In the Davis Strait, the stock biomass declined from the late 1980s to 1994 but increased from 1995 to 2000 and has remained stable until 2019 (Nogueira *et al.*, 2019; Nogueira and Estévez-Barcia, 2020).

The present research investigates long-term (1997–2019) trends in community metrics for an important halibut fishing ground in the offshore slopes of West Greenland. Since 1950, the climate in the West Greenland area has experienced large fluctuations, mixing extreme warm and cold periods, which have affected fish and shellfish recruitment and distribution (Pedersen and Rice, 2002; Buch *et al.*, 2004). We used fisheries-independent data from West Greenland offshore waters to evaluate how an exploited demersal fish community has changed through time for the last 23 years by examining temporal and spatial variability and trends in five indicators: total biomass, MTL, MTC, species evenness and species richness in relation to temporal changes in climate (here, bottom temperature), and fishing pressure. This suite of ecosystem indicators allowed us to evaluate and understand changes in community structure related to inter-annual and inter-decadal variability in climate.

Material and methods

Study area

The ocean currents around Greenland (Supplementary Figure S2.1) are part of the cyclonic sub-polar gyre circulation of the North Atlantic and the Arctic region, where the bottom topography has high relevance in their circulation and distribution (Ribergaard and Buch, 2008). The West Greenland Current (WGC) flows northward. It is the result of mixing the East Greenland Current and the Inminger Current (water with Atlantic origin), so it is warm and salty and flushes through the continental shelf. The complex topography and the strong tidal currents generate residual anticyclonic eddies around the banks in the Davis Strait area (Ribergaard *et al.*, 2004). The Baffin Island Current moves southward offshore of Greenland. It is cold and fresh due to the Arctic origin (Tang *et al.*, 2004). Consequently, there are two strong currents with different properties flowing in opposite directions, which provide a particular bottom temperature with relevant temperature differences in latitude, longitude, and depth (Hamilton and Wu, 2013).

The present research was carried out on the slopes of West Greenland from 3-miles of the coastal line to the border between Greenland and Canada, from 62°30'N to 66°15'N, in the Northwest Atlantic Fisheries Organization (NAFO) Divisions 1CD management areas and covering a depth range between 400 and 1500 m (Supplementary Figure S2.2).

Data source

We used data from the West Greenland halibut offshore (WGHL) survey, carried out by the Greenland Institute of Natural Resources in the NAFO divisions 1CD (Supplementary Figure S2.2). The survey has been carried out yearly since 1997 to estimate abundance and biomass of demersal resources. From 1997 to 2017, it was conducted on board R/V Paamiut. In 2018, no survey was conducted, and we decided not to use the data from 2013 since the number of samples was not enough to cover all the study area. The 2019 survey was carried out on a charter commercial vessel, C/V Helga Maria. All standard gear from the R/V Paamiut (such as cosmos trawl, doors, all equipment such as bridles, Marport sensors on doors, headlines, etc.) was used on the chartered commercial vessel to make the survey identical as possible (see Supplementary Material S1) and ensure the same selectivity (Nogueira and Treble, 2020). Both vessels used the "Alfredo III" bottom trawl with a mesh size of 140 mm and a 30-mm mesh-liner in the cod-end.

The WGHL surveys were planned as stratified random bottom trawl surveys until 2004, when they were replaced by buffered stratified random sampling design (Kingsley *et al.*, 2004). The sampling design divided the survey area (66º15'N–62º30'N) in NAFO divisions 1C and 1D, and further into depth strata (401–600 m, 601–800 m, 801–1000 m, 1201–1400 m, 1401–1500 m). The muddy and soft seabed in Division 1D within the stratum 601–800 m is generally not suitable for trawling; stations were fixed to trawlable areas in that stratum (Nogueira and Estévez-Barcia, 2020). Trawls were towed for 30 min at a speed of 3.0 knots. The bottom depth of each haul was obtained using the mean depth of the initial and final positions. The mean depth varied from 402 to 1495 m. A total of 1193 accepted stations were performed during the surveys from 1997 to 2019 (no data from 2013 and 2018) in the NAFO divisions 1CD (Supplementary Figure S2.2).

Environmental and anthropogenic drivers

To examine the potential effects of climate and human activities, we included three drivers in the statistical analyses: bottom temperature and two fisheries metrics. Bottom temperature was measured by a Starmon mini temperature logger attached to the nets. We included the Greenland halibut fishery's effort (hours of trawling) and the commercial catch of target species (catch in weight of halibut) as measures of anthropogenic impacts. We decided to include both drivers as the fishing efficiency had increased substantially in the last decade due to improvements in fishing technology and gears. Fisheries metrics were obtained from the logbooks provided by the Greenland Fishery License Control Authority and calculated for each depth stratum in the NAFO divisions 1CD area.

Biomass

To estimate the total biomass of all species, we used the swept-area method (Cochran, 1977) assuming that the scientific catchability was full ($C = 1$) for each species. We first calculated catch per unit effort (CPUE) based on the swept area of the haul (kg/km^2) and then expanded the biomass to the stratum area (depth zones: 400–800 m, 801–1200 m, and 1201–1500 m) (see Supplementary Material 3 for more detail). We also calculated the standardized biomass of most important species for each depth zone (see Supplementary Material 5), and the standardized total biomass with and without halibut into depth zones.

Mean trophic level

We calculated the MTL by converting all scientific catch data of taxa identified to species to CPUE (kg/km^2) and then calculating ecosystem MTL for each haul (Tolimieri *et al.*, 2013). The trophic level for each species was taken from FishBase (Supplementary Table S2.1; (Froese and Pauly, 2019)). We next calculated the MTL of each depth zone, T_d as the mean MTL of each haul within the depth zone (see Supplementary Material 3 and Supplementary Table S3.1 for more detail).

Mean temperature of the catch

We calculated the MTC by first calculating CPUE (kg/km^2) for each species and then calculating ecosystem MTC for each haul (Cheung *et al.*, 2013). Then, we calculated the MTC of each depth zone as the mean of MTC of each haul. See Supplementary Material 3 and Supplementary Table S3.1 for more detail.

Diversity measures

We examined two measures: species evenness and species richness. For species evenness, we used the Gini–Simpson index (D or $1 - \lambda$) such that higher values indicate a more even community. All taxa identified were included in the analysis; CPUE was used to calculate the evenness index per haul (thus, D is based on biomass not in numbers in our analyses). We averaged hauls within a depth zone to calculate the mean species evenness for each depth zone. For species richness, we applied sample-based rarefaction (Gotelli and Colwell, 2001; Colwell *et al.*, 2004; Tolimieri, 2007) to estimate the species richness to account for the effects of sampling effort on the number of species observed (See Supplementary Material 3 for more detail).

Statistical analysis

Following (Nogueira *et al.*, 2016), we conducted a two-step analysis to examine whether (i) the dependent continuous variable of interest (MTL, MTC, and species evenness) varied among independent variables, and (ii) if any variability was directional. For step one, we ran generalized linear mixed models to test whether the dependent variable differed among the fixed, categorical effects depth zone (depth) and year (year). We also considered the discrete variables bottom temperature (temperature), commercial fishing effort in hours of trawling (effort), and the commercial catch of halibut (catch) in each stratum as covariates. As logbook data did not have information from 1997 to 1999, the analyses in which we included commercial effort and catch were run from 1999 to 2019. In the second step, we used generalized additive models (GAMs) to summarize potentially non-linear relationships through time (year, continuous not fixed) for the response variables (total biomass, MTL, MTC, species evenness, and species richness). For each step, we ran the analyses twice: first, including all defined species, and second, without the dominant species, halibut, which might mask the changes in the rest of the demersal community.

For step one, we fitted four generalized linear models for the MTL and MTC data, including all independent variables, which allow to fit particular forms of nonlinear relationship between the response variable and explanatory variables. Model 1 was the base model (simple linear model, LM), which assumed homogeneity of variance and independence of hauls. Model 2 was a generalized linear mixed model (GLMM) allowing different variance among the categorical variables. Model 3 was a generalized least squares model (GLS) including an exponential spatial autocorrelation structure among hauls and homogeneous variance. Model 4 was a GLS assuming spatial autocorrelation and heterogeneous variance. First, we fitted the most complicated model for 1–4, then removed (backfit) non-significant terms and selected the best-fitted model based on AIC (Akaike information criterion). First step statistical output was included in the Supplementary Material S4. MTL and MTC data were fit in R v. 3.1.2 (Team R, 2013) using the package "nlme" (Pinheiro and Bates, 2006).

As evenness data are bounded between 0 and 1, we decided to use GLMMs with a β error distribution (package "betareg" in R, (Cribari-Neto and Zeileis, 2010)) for step one, instead of using the generalized linear models explained above. We tested 12 models including different combinations of the independent variables: year, depth zone, bottom temperature, commercial fishing effort, and commercial catch. We selected the model with the lowest AIC and highest pseudo r-squared values. For species richness, we could not conduct these analyses because the sample-based rarefaction produced an estimation for each depth zone and year combination, not per haul as with the other metrics. Thus, richness results will be computed as the number of species found in a determined number of analysed individuals (spp/ind). The estimated number of individuals correspond to the minimum number of individuals found in all the depth zone and year combination. Total biomass was added for complementing the ecological indicators (MTL, MTC, evenness, and richness) to understand why these indicators have changed, but biomass measurement by itself do not give any information about the structural and compositional changes, thus, we only analysed its temporal and spatial trends.

For step two, we used GAMs for all the indices to examine their temporal trends and to compare trends in different depth zones. We used non-linear models because preliminary plots suggested that

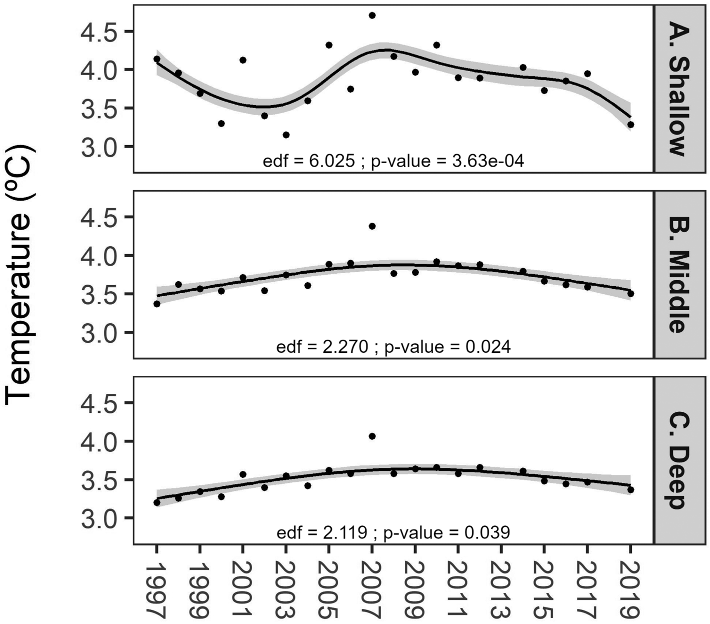

Figure 1. Temporal trend of the bottom temperature from 1997 to 2019 in the NAFO divisions 1CD (no data in 2013 and 2018). Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, $1 < \text{edf} \leq 2$: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Grey shadow: GAM model standard error interval. Points: Mean bottom temperature per depth zone. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

the index variations were not linear, and GAMs allow fitting models when the form of the function is unknown. For all the indices, GAM models outputs (standard error, edf, and *p*-value) were included in the figures. Data were fit in Rv. 3.1.2 (Team R, 2013) using the packages "ggplot2" and "mgcv" (Wood, 2018).

Results

From 1997 to 2019, the scientific trawl survey recorded a total of 156 species (Supplementary Table S3.1). Halibut was the most abundant species with 156933 kg making up 79% of the total catch by biomass.

Environmental and anthropogenic drivers

Bottom temperature followed a non-linear relationship across years (Figure 1) and showed a general decline with depth. Overall, there was a warming trend from the late 1990s to approximately 2009, after which water temperature cooled again. However, in the shallow zone, there was an initial short decline in temperature from 1997 to the early 2000s prior to warming. Inter-annual temperature fluctuation was higher in the shallow zone (between 400 and 800 m) than in the deeper regions. All three zones marked their warmest year in 2007 with the highest mean temperature in the shallow zone (4.71ºC).

Fishery effort and halibut commercial catch were consistently low in the shallow zone (Figures 2 and 3). In the middle zone, effort increased until it peaked in 2010 (6081.1 h in 2010) before decreasing somewhat from 2015 on. However, catch of halibut increased across the time series. In the deep zone, the commercial fishing effort and catch declined through the time-series reaching the minimum values in 2019.

Total biomass trends

The fisheries-independent surveys showed that total demersal fish biomass increased in the shallow zone from 1997 through 2019 (Figure 4). Biomass declined from approximately 2013 to 2019 when halibut was excluded showing that the increase in the latter years was due to increasing halibut biomass in the shallow zone. The middle zone showed no changes in biomass over time. However, we can see that much of the biomass was halibut. Total biomass declined in the deep zone but showed no trend when halibut was excluded indicating that the drop in total biomass resulted from a decrease in halibut abundance.

Trends in the biomass of individual species are explored in more detail in Supplementary Material S5.

Community metrics

The best-fit model (based on AIC comparison) showed that the MTL varied among years and depths (with homogeneous variance and normal error distribution) (Table 1). The effort of the halibut fishery and the bottom temperature had statistically significant influences in those variations with positive correlations (GLM, $b_{\text{temp}} = +0.018 \pm 0.004$, $P < 0.001$ and $b_{\text{effort}} = +4.610\text{e-}06 \pm 1.9\text{e-}06$, $p = 0.016$). When excluding halibut, commercial fishing effort was not significant, so it was excluded from the MTL best-fit model (GLM, $b_{\text{temp}} = +0.115 \pm 0.011$, $P < 0.001$).

The GAM models for MTL had different trends among depth zones (Figure 5). The changes were largest in the shallower zone, where MTL declined from 4.00 in 1997 to 3.84 in 2002 but then increased to 4.08 in 2012. When halibut was excluded, the changes were more evident, and it was possible to see MTL stabilize and potentially decrease in the last years of the time series. In the middle

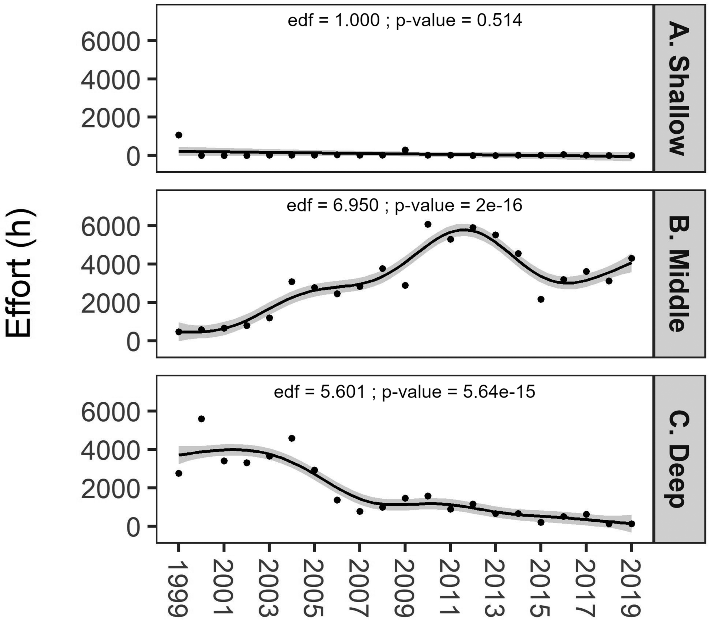

Figure 2. Halibut trawl effort (hours) from 1999 to 2019 (no data available in 1997 and 1998) in the NAFO divisions 1CD. Data provided by the Greenland Office of Fisheries Licenses (GFLK) logbooks. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, $1 < \text{edf} \leq 2$: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean effort values per depth zone. Grey shadow: GAM model standard error interval. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

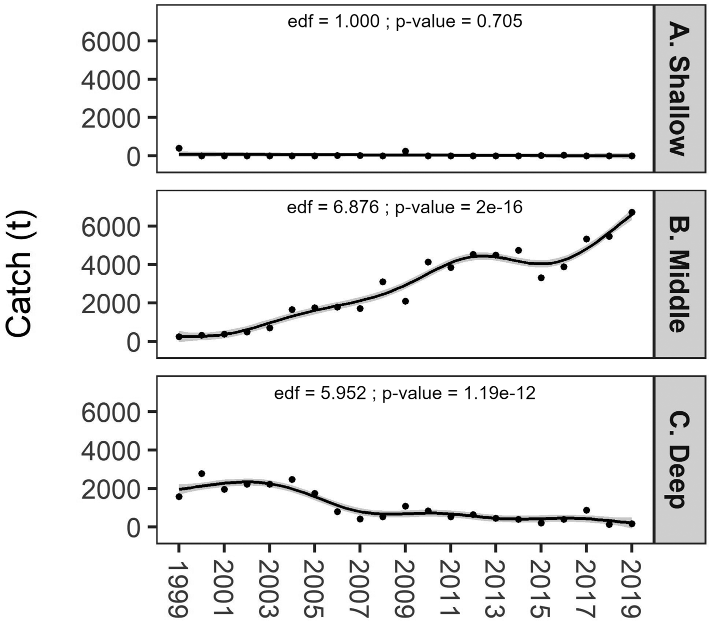

Figure 3. Halibut commercial catch in weight (tons) from 1999 to 2019 (no data available from 1997 and 1998) in the NAFO divisions 1CD. Data provided from the GFLK logbooks. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, $1 < \text{edf} \leq 2$: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean catch values per depth zone. Grey shadow: GAM model standard error interval. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

zone, MTL was stable through time (both GAMs $p > 0.05$) indicating that trophic structure remained stable in this zone regardless of other changes. In the deep zone, MTL also appeared stable (GAM $p > 0.05$) throughout time. However, when halibut was excluded, there was a long-term increase in MTL from 3.58 in 1997 to 3.68 in 2019 (GAM, edf = 1.0, $p < 0.05$).

The MTC was best explained by including spatial autocorrelation and different variances among years and depth zones in the

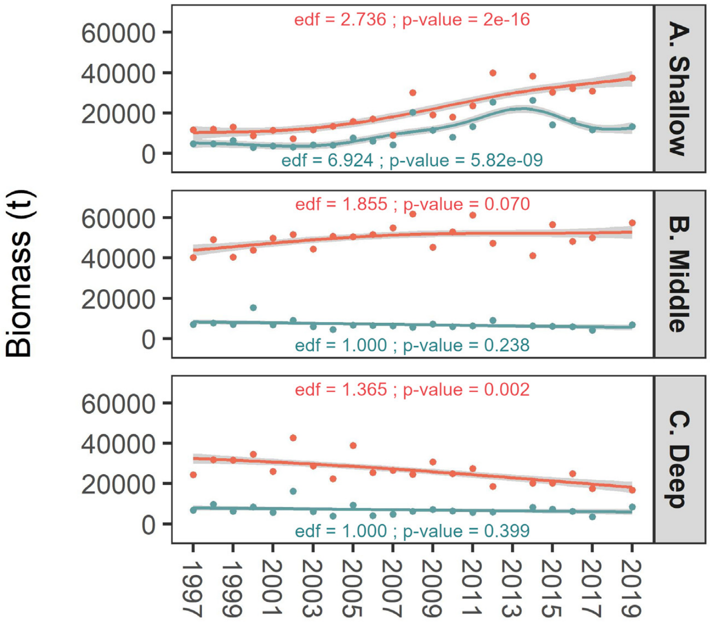

Figure 4. Temporal trend of the standardized total biomass from 1997 to 2019 (no data in 2013 and 2018) in the NAFO divisions 1CD. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, 1 < edf ≤ 2: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean biomass values per depth zone. Grey shadow: GAM model standard error interval. Red: Including all identified species. Blue: Excluding halibut. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

Table 1. Best-fit models.

			Best-fit model terms					
Response variable	**Model Type**	**Included species**	**Year**	**Depth**	**Temperature**	**Effort**	**Catch**	**Error and variance**
MTL	LM	All species	X	X	X	X		Normal distributed error + cte variances
		Without GHL	X	X	X			Normal distributed error + cte variances
MTC	GLS	All species	X	X	X	X		Spatial autocorrelation + different variances
		Without GHL	X	X	X			Spatial autocorrelation + different variances
Species evenness	GLMM	All species	X	X	X		X	With beta distributed error
		Without GHL	X	X	X		X	with beta distributed error

Significant terms are selected for each indicator (see Supplementary Material for full model fit comparisons). LM = linear model, GLS = generalized least square model, GLMM = generalized linear mixed model.

GLS (Table 1). The changes were different among depth zones and years and were influenced positively by the bottom temperature and negatively by the effort of the halibut fishery (GLS, $b_{temp} = +0.079 \pm 0.013$, $p < 0.001$ and $b_{effort} = -6.5e\text{-}06 \pm 2.3e\text{-}06$, $p = 0.0051$). When excluding halibut, commercial fishing effort was not significant, so it was excluded from the MTC best-fit model (GLS, $b_{temp} = 0.257 \pm 0.028$, $p < 0.001$).

The MTC showed different temporal trends in different depth zones and including or excluding halibut (Figure 6). In the shallow zone, the MTC increased near 2007 (from 3.24 in 2002 to 3.61 in 2007), and then returned to initial values (3.32 in 2019). When halibut was excluded, the MTC decreased drastically in 2002 (from 4.20 in 1997 to 3.44 in 2002), but then recovered to 4.11 in 2009, remaining stable for the rest of the time series. In the middle zone, MTC decreased slightly through time, although trends with and without halibut were non-significant. In the deep zone, there was no evident trend in MTC ($p > 0.05$), although when halibut was excluded MTC declined linearly from 4.07 in 1997 to 3.67 in 2002, after which it remained stable.

Species evenness varied over time and among depth zones (Table 1) and was negatively correlated with the bottom temperature and commercial catch of halibut (GLMM, $b_{temp} = -0.296 \pm 0.257$, $p = 0.25$ and $b_{GHL\_Catch} = -9.073e\text{-}04 \pm 1.196e\text{-}04$, $p = <0.001$). There were also interactions between depth and year and halibut commercial catch. So, the effect of these variables on species evenness varied among depths. Excluding halibut biomass for modelling, bottom temperature had positive correlation, while commercial catch continued negatively correlated (GLMM, $b_{temp} = +9.898e\text{-}03 \pm 0.233$, $p = 0.28$ and $b_{GHL\_Catch} = -5.359e\text{-}05 \pm 1.077e\text{–}04$, $p = 0.62$).

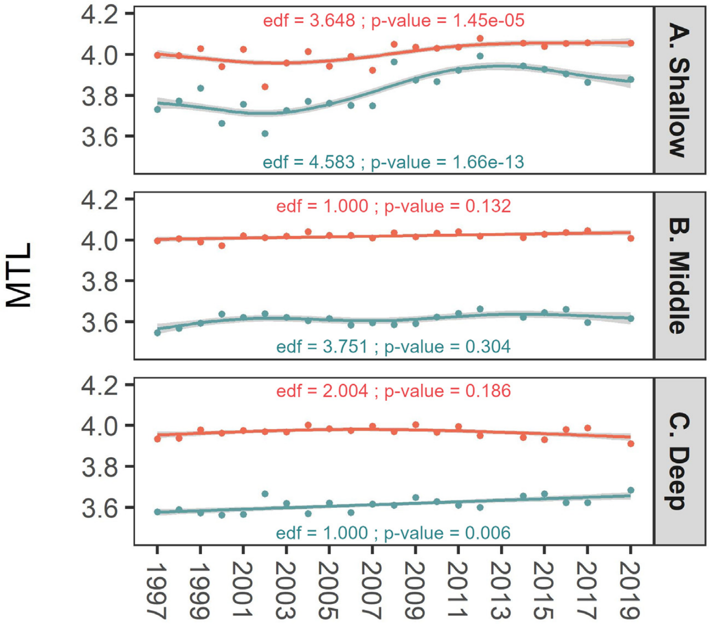

Figure 5. Temporal trend of the MTL from 1997 to 2019 (no data in 2013 and 2018) in the NAFO divisions 1CD. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, 1 < edf ≤ 2: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean MTL values per depth zone. Grey shadow: GAM model standard error interval. Red: Including all identified species. Blue: Excluding halibut. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

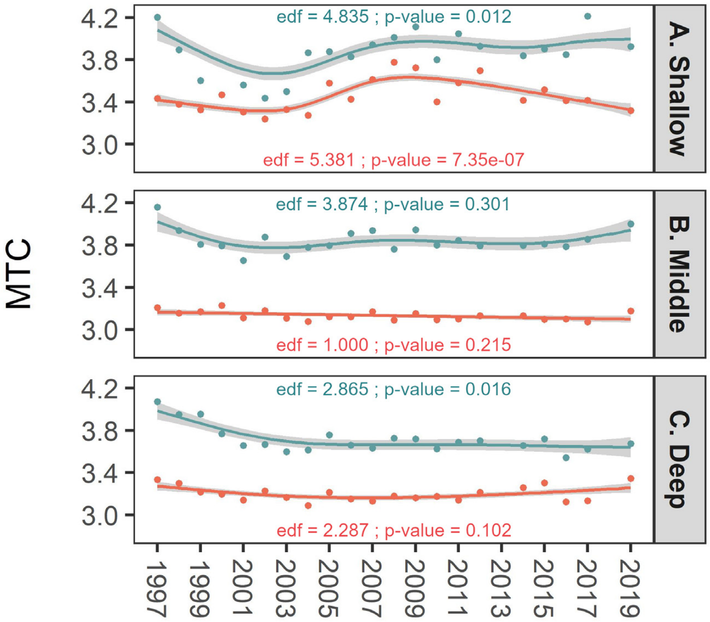

Figure 6. Temporal trend of the MTC from 1997 to 2019 (no data in 2013 and 2018) in the NAFO divisions 1CD. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, 1 < edf ≤ 2: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean MTC values per depth zone. Grey shadow: GAM model standard error interval. Red: Including all identified species. Blue: Excluding halibut. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

Species evenness had different temporal trends among the depth zones (Figure 7). Total species evenness (including halibut) was highest in the shallow zone, but after 2007 it dropped down from 0.63 in 2007 to 0.26 in 2017. When halibut was excluded, the species evenness fluctuated near to 0.55. In the middle zone, evenness showed a slight decline for all species and a slight increase when halibut was excluded, but neither trend was statistically significant. In the deep zone, the trend was a negative parabola, which declined

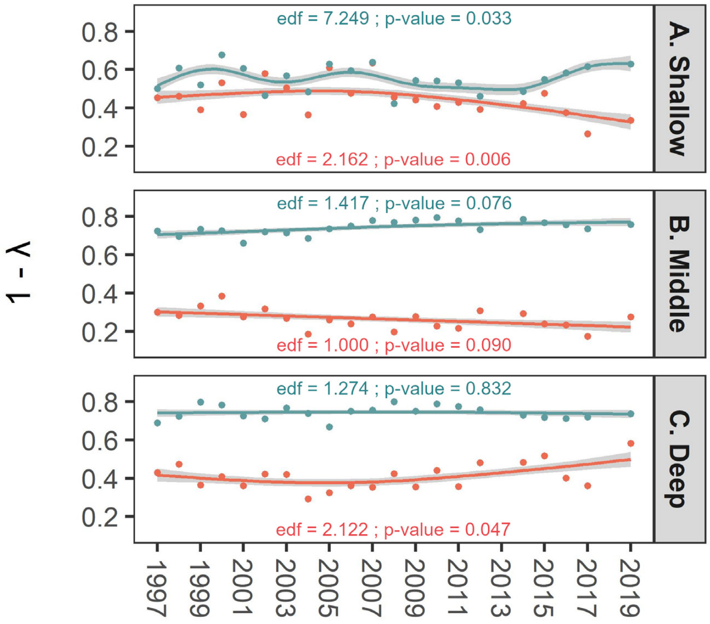

Figure 7. Temporal trend of the species evenness from 1997 to 2019 (no data in 2013 and 2018) in the NAFO divisions 1CD. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, $1 < \text{edf} \leq 2$: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($P < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean evenness value per depth zone. Grey shadow: GAM model standard error interval. Red: Including all identified species. Blue: Excluding halibut. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

from 0.47 in 1998 to the lowest value of 0.29 in 2004, and then increased until reaching the highest value in the time-series of 0.59 in 2019. When halibut was excluded from the analysis, evenness remained stable around 0.7.

The species richness (Figure 8) increased since 1997 in the study area, but trends were different among depth zones. There were no major differences in the trends when excluding halibut. In the shallow zone, species richness increased from the beginning of the time series until 2007, when it reached the maximum values (from 19spp/1489ind in 1997 to 44 spp/1489ind in 2007) but then decreased (31 spp/1489ind in 2019). In the middle and deep zones, the rise was less remarkable. In both zones, the species richness slightly increased until 2011 (from 21 and 24 spp/1489ind in 1997 to 34 and 32 spp/1489ind in 2019 in the middle and deep zones respectively). In the middle zone, after reaching the maximum in 2011, it dropped to lower values again (26 spp/1489ind in 2019) while in the deep zone, it remained stable.

Discussion

Ecological responses to environmental changes can be complex with exploitation amplifying responses (Hollowed *et al.*, 2013). While ecological indicators are useful tools for evaluating the overall impact of environmental and anthropogenic drivers on communities (Coll *et al.*, 2016), a single indicator may not describe all aspects of ecosystem dynamics. Therefore, it is necessary to use multiple, complementary indicators simultaneously for a better understanding of the mechanisms and processes that are acting (Cury and Christensen, 2005). The present study illustrates the applicability of combining five ecological indicators to study the changes of an exploited demersal fish assemblage.

Our results revealed that variability in bottom temperature was associated with changes in demersal fish community structure in West Greenland; all the community metrics showed a relationship with temperature. The community metrics also showed correlations with commercial halibut catch and fishery effort, which makes sense because halibut constitute ~80% of the biomass in this

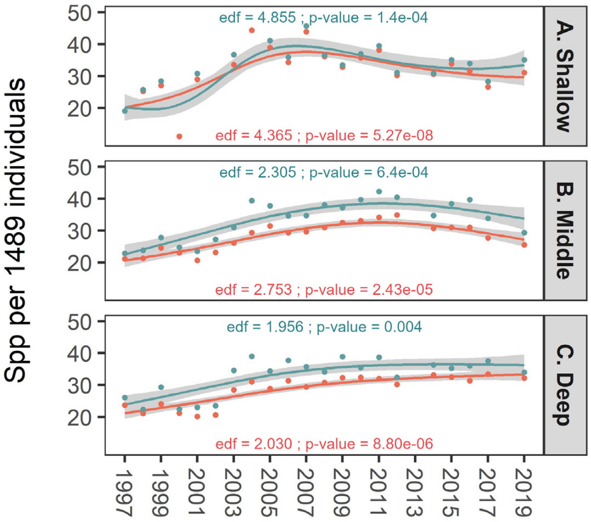

Figure 8. Temporal trend of the species richness from 1997 to 2019 (no data in 2013 and 2018) in the NAFO divisions 1CD. Edf: Degree of non-linearity of the curve of GAM model (edf = 1: linear relationship, $1 < \text{edf} \leq 2$: weakly non-linear relationship, and edf > 2: highly non-linear relationship). *P*-value: Changes in the line trend ($p < 0.05$ = trend has changed over time-series). Lines: GAM model prediction line. Points: mean richness values per depth zone. Grey shadow: GAM model standard error interval. Red: Including all identified species. Blue: Excluding halibut. A: shallow zone (400–800 m); B: middle zone (801–1200 m); C: deep zone (1201–1500 m).

community over our 20+ year time series. However, given that these two terms only appeared in models that included halibut, it is more likely that these two covariates were tracking changes in halibut biomass than driving changes in community structure. This result concurs with Fock (2008) who suggested that the main drivers for West Greenland demersal community variations are bottom-up (climate) and top-down forcing (community interactions), but effects of fisheries were not identified as important.

Calculating the indicators with and without halibut (the highest biomass species) helps us understanding changes in the rest of the community more clearly. For example, the increase in biomass in the shallow zone was initially community-wide, but from 2013 to 2019 halibut drove the increase in biomass, as evidenced by the decrease in the biomass of other species from approximately 2013. Similar differences can be seen in other metrics as well when halibut was excluded from the calculation.

The influence of bottom temperature and trawling in West Greenland demersal fish assemblage

Earlier studies (i.e. Zweng and Münchow, 2006; Muenchow *et al.*, 2011) have suggested that bottom temperatures in West Greenland were warming and that demersal fishes might shift their distribution in depth and latitude looking for more suitable habitats. However, the historical record in West Greenland also shows that bottom temperature has oscillated on a decadal scale and is related to variation in the North Atlantic Oscillation (NAO) and Atlantic Meridional Overturning Circulation (AMOC) (Curry and McCartney, 2001; Sarafanov, 2009; Smeed *et al.*, 2014). Likewise, our analysis of the trawl data shows that while bottom temperature initially increased, it started decreasing after 2007, reaching the lowest mean bottom temperatures recorded since 1997 in 2019. The start date for the WGHL survey carried out in 2019 was the earliest in the time-series, which may have contributed somewhat to the low temperature in 2019 due to seasonal variability, but the timing does not explain the overall cooling trend. A positive NAO index correlates a long-term strengthening of AMOC, which contributes to warming the WGC; the opposite happens after a long period with a negative NAO index (Curry and McCartney, 2001). The decrease in bottom temperature from approximately 2006 on coincides with a largely negative NAO and weakening of the AMOC (Smeed *et al.*, 2014). More recently the weakening of the AMOC has ceased (Smeed *et al.*, 2018), and we might expect warming if the NAO trends positive.

Stock dynamics in West Greenland have shown to be highly variable along time, with large fluctuations mainly in species sensitive to overexploitation and climate change since 1990s (Nogueira and Jørgensen, 2018; Nygaard and Nogueira, 2020). Understanding the effects of fishing on assemblage structure and composition is important because fishing pressure may accelerate and amplify the changes induced by environmental changes (Hsieh *et al.*, 2006). Fishing obviously has direct impacts on target species. Nevertheless, there may also be community-level effects of single species exploitation. The bycatch of the commercial fishery for halibut in NAFO division 1CD was estimated to be 13% of the total catch of halibut with blue hake being the most caught bycatch species (Jørgensen, 2016). However, it was indicated (Jørgensen *et al.*, 2014) that the halibut fishery has a relatively small influence on the abundance of the most common potential bycatch species due to the small size of the fishing area compared with the much wider distribution of these stocks. Most of the stock dynamics are outside the fishing area (Jørgensen *et al.*, 2014), and therefore, although overexploitation may affect the demersal fish community, the structural and compositional changes with the current fishing pressure are caused mainly by species-specific effects or migration out of the study area due to environmental changes. So, even though the extraction of mature individuals may have reduced the biomass of some bycatch species (Devine and Haedrich, 2008), most species' drastic changes are better explained by environmental changes and their corresponding community interactions.

Community structure

Decadal-scale borealization processes (movement of boreal species to more northern areas) have taken place around Greenland driven by the subpolar gyre (Post *et al.*, 2021). New southern (Atlantic) species have been continually described since 1992 in the shallow waters during warm periods (Møller *et al.*, 2018), increasing species richness. For example, there was an important input of boreal species (i.e. beaked redfish *Sebastes mantella*, Atlantic cod *Gadus morhua,* and American plaice *Hippoglossoides platessoides*) in West Greenland coinciding with the warm period around 2007 (Supplementary Figure S.5.1), but the effects of temperature variation on community structure varied with depth.

The shallow zone appears to be the most susceptible to variations in temperature. Temperature fluctuations were greatest there, and total biomass and the other four indicators all showed significant variation through time in this zone. Although the biomass of halibut continued to increase, the biomass of other species decreased from approximately 2013 to 2019, as can be seen by comparing the biomass index with and without halibut (Figure 4, as well as Supplementary Figure S.5.1). When halibut were excluded from the metric, species evenness increased over this same time period probably because increased bottom temperature resulted in appearance of high-TL and warm-water species (large biomass gain observed in beaked redfish, Atlantic cod, and American plaice) in the shallow zone. However, when halibut were included, species evenness decreased.

Community structure was relatively stable in the middle depth zone with species richness being the only metric to show any long-term trend. Thus, even though there were changes in temperature and species like halibut shifted their depth distributions, attributes of the assemblage like its trophic structure, and therefore the prevalence of processes like top-down forcing, remained stable. Richness did track bottom temperature and warming saw the increase of warm-water species, which later disappeared likely moving back to southern waters as the number of species decreased once the water cooled again.

In the deep zone, total biomass decreased with time as halibut biomass shifted to shallower waters; non-halibut biomass did not show a trend. At the same time, MTL increased slightly among the non-halibut portion of the assemblage, and evenness increased as halibut came to make up less of the total biomass. The increase in MTL suggests that top-down pressure in the deep zone has increased. However, this change must be interpreted in conjunction with the change in total biomass. Halibut is a high TL species (TL = 4.1). Lower overall predator biomass means that top-down forcing is less able to reduce a large influx of prey species from movement or recruitment pulses. The concurrent rise in species richness might be influenced by the improvement of the species identification over the time series, but it is unlikely to explain the overall community trend of tracking temperature.

Greenland halibut, a key species in the demersal fish community

The spatial distribution of adult halibut biomass changed over the time series increasing in shallow and middle waters (400–1200 m) but decreasing in the deep zone (Supplementary Figure S.5.1). Although it is possible that changes in biomass are independent at different depths, it is more likely that halibut shifted to shallower waters in West Greenland from 1997 to 2019. Tagging studies verify that adult halibut may change depth depending on abiotic and biotic factors (Hussey *et al.*, 2017). Halibut appear to have initially shifted depth to avoid cold temperatures (Morgan *et al.*, 2013). However, in West Greenland, halibut abundance continued rising even as the bottom temperature decreased in shallow waters later in the time series. Halibut are opportunistic feeders consuming the locally abundant prey (Giraldo *et al.*, 2018), including smaller halibut (cannibalism) when there is no alternate food available (Dwyer *et al.*, 2010), and demersal fishes are an important prey for individuals larger than 40 cm (Solmundsson, 2007). Thus, the increase of beaked redfish, an important diet item for halibut in West Greenland (Pedersen and Kanneworff, 1995), and other boreal species (i.e. Atlantic cod, American plaice, etc.), may have influenced the vertical migration of adult individuals shifting to or remaining in areas with higher prey availability despite the depth and temperature preferences.

Distributional shifts in the demersal fish fauna

A long-term increase in boreal fishes is expected in both shallow and deep regions (Post *et al.*, 2021), but our results show that in West Greenland boreal fish input during warm periods has been limited to the shallow zone. For example, the emergent boreal, high trophic-level species (beaked redfish, Atlantic cod, or American plaice) were limited to shallow waters (Froese and Pauly, 2019). The periodical warming scenario induced by climate change seems to have a positive effect on the recruitment success of these species in West Greenland due to the increase of spawning stock and the inflow of larvae from Icelandic spawning grounds (Buch *et al.*, 2004).

In the mid depth zone, the large biomass and high TL of halibut may result in enough top-down pressure to buffer that assemblage from large compositional and structural changes. The presence of generalist top predators able to prey-shift and target new, abundant taxa (Hollowed *et al.*, 2013), and the competitive interactions (Fock, 2008), may buffer against the invasion of boreal species. Note that, while the MTL in the mid zone did not increase over time with increasing halibut biomass, this result occurred because halibut TL (4.1) was approximately the same as the MTL in the mid zone (∼4). Thus, MTL remained the same, but predator biomass increased substantially through time.

In the deep zone, the decrease in halibut biomass and the proximity to the Atlantic Ocean may produce a refugee for deep, subarctic species in a global climate change scenario. As noted above, while the MTL increased, the absolute biomass of predators decreased as halibut shifted to shallower waters potentially reducing the ability of top-down pressure to limit immigration from normally non-resident species or increases in normally less common ones. Northern fish species might be expected to shift distribution to higher latitudes and deeper waters due to an increase of competition and predation by boreal species (Fossheim *et al.*, 2015; Friedland *et al.*, 2019). Subarctic species would expand into the Arctic Ocean shelves and slopes given appropriate temperature and feeding conditions (Hollowed *et al.*, 2013). However, the deep demersal species trying to reach colder waters in higher latitudes might encounter distributional limits. Westgaard *et al.*, (2017) suggested that the shallow Denmark Strait may act as an environmental and physical barrier between eastern and western Atlantic. So, if northward migration is inhibited, cold water species might shift distributions to reach an adequate habitat.

West Greenland has suitable conditions (i.e. bottom temperature, productivity, etc.) for cold water species. In East Greenland, halibut, blue hake, and northern wolfish *Anarhichas denticulatus* have become less abundant (Emblemsvåg *et al.*, 2020). However, their biomass has increased in West Greenland. For halibut, this increase in West Greenland may be due in part to better conditions for early life-history stages. Recruitment of halibut increased until 2017 in West Greenland, coinciding with the warm period, but declined drastically in 2018 and 2019 when the bottom temperature decreased (Nogueira and Treble, 2020; Nygaard and Nogueira, 2020). Assuming that surrounding waters will undergo warming while West Greenland will continue with decadal oscillatory processes (Smeed *et al.*, 2014), commercially attractive northern species, such as halibut, may be more prominent in the coming years. Nevertheless, while the current study enhances our understanding of the interaction between climate and community structure in West Greenland waters, our existing knowledge is in many respects incomplete and future work should seek to better understand and document the responses of subarctic demersal fish species in West Greenland in terms of population dynamics (e.g. somatic growth, recruitment, and rates of population growth) and movement (e.g. depth shifts and migration into the area).

Conclusion

The present research provides important insights for designing appropriate and effective measures for fisheries management in West Greenland. In the way of integrating the ecosystem into fisheries management, it has been evidenced the applicability of combining different ecological indicators to study the spatial and temporal changes of a demersal community exposed to climate variations and continuously increasing fishing pressure. The bottom temperature in West Greenland waters alternated between colder, warmer, and colder periods on a decadal scale from 1997 to 2019. Studying the community response in past warming and cooling processes lets us better understand ecosystem functioning and provide better advice for management. Nevertheless, it is expected that climate change will cause larger and more rapid interannual and decadal variability than previous natural changes and that the resilience of species and systems will be compromised by concurrent pressures, including fishing, loss of biodiversity, habitat destruction, pollution, and introduced and invasive species and pathogens (Brander, 2010). The periodical warming scenario induced by climate change has a positive effect on the recruitment success of high trophic level boreal species in the shallow zone of West Greenland. Prey availability influences the vertical migration of adult halibut individuals, shifting to or remaining in shallower areas, which reduces the biodiversity due to top-down forcing. On the other hand, the halibut is becoming less frequent at deeper depths potentially reducing the ability of top-down pressure and favouring the apparition of high trophic level subarctic species. Whereas, in the middle zone, despite increasing exploitation, halibut biomass increased substantially through time and buffered the demersal community from large compositional and structural changes.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article is subject to institutional and privacy policy limitations and may be shared on reasonable request to the corresponding authors.

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