

Subpolar gyre and temperature drive boreal fish abundance in Greenland waters

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Abstract

As result of ocean warming, marine boreal species have shifted their distribution poleward, with increases in abundance at higher latitudes, and declines in abundance at lower latitudes. A key to predict future changes in fish communities is to understand how fish stocks respond to climate variability. Scattered field observations in the first half of the 20th century suggested that boreal fish may coherently invade Greenland waters when temperatures rise, but this hypothesis has remained untested. Therefore, we studied how local temperature variability and the dynamics of the subpolar gyre, a large-scale driver of oceanic conditions in the North Atlantic, affect abundance of boreal fishes in a region that sharply defines their lower thermal boundary. We analysed information from demersal trawl surveys from 1981 to 2017, for species distributed from shallow shelf to depths of 1,500 m, collected at over 10,000 stations along ~3,000 km of Greenland. Our results show that local temperature and variability of Labrador and Irminger Sea water in the subpolar gyre region drive interdecadal variability of boreal fish abundance in Greenland waters. Although temperature fluctuations were higher in shallow than deep regions, fish abundance changed as quickly in great depths as in shallow depths. This link between physics and biology provides an opportunity for prediction of future trends, which is of utility in Greenland, where fisheries constitute more than 90% of the national export value.

KEYWORDS

environmental drivers, GAM, Irminger–Labrador Seas, lagged response, trawl survey, water density

1 | INTRODUCTION

The distribution and abundance of marine fish species have changed in response to rising temperatures (Hastings et al., 2020; Perry et al., 2005; Simpson et al., 2011). In Arctic and subarctic regions, global warming is estimated to happen faster than the global average and ecosystems are predicted to change faster than anywhere else (Fossheim et al., 2015; IPCC, 2019). Here, where boreal fishes face their lower thermal threshold, abundance is particularly sensitive to changes in temperature (Fossheim et al., 2015; Fredston-Hermann et al., 2020; Kortsch et al., 2015). While boreal

species are predicted to invade arctic and arcto-boreal ecosystems, cold-water-adapted specialists might face declining habitat suitability, increasing competition and potentially extinctions (Cheung et al., 2009; Christiansen et al., 2014; Dahlke et al., 2018; Fossheim et al., 2015). Greenland waters encompass several climatic zones and border the Irminger Sea and the Labrador Sea (Figure 1). Off the east coast, in the central Irminger Sea, warm and salty Atlantic water dominates the surface waters (Figure 1). These surface waters protrude onto the East Greenland shelf, where they face the cold and fresh southward-flowing East Greenland current (Våge et al., 2011). As consequence, suitable conditions for boreal

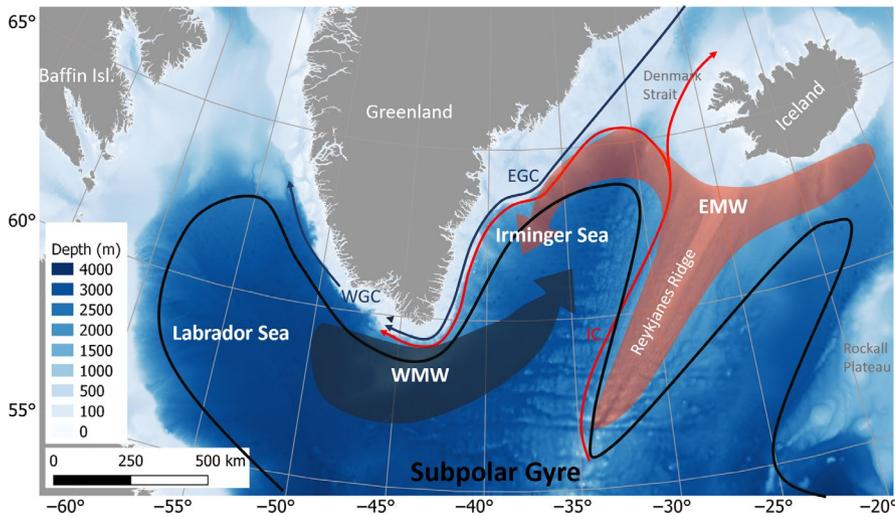


FIGURE 1 Map of the central and North-west Atlantic. The Subpolar gyre is roughly outlined in black, and the principal mode water classes, EMW (Eastern Mode Water) and WMW (Western Mode Water), are illustrated with red and blue colours, respectively. Arrows indicate directions of the currents: IC (Irminger current), EGC (East Greenland current) and WGC (West Greenland current)

species can mainly be found in eastern and southern Greenland, where Atlantic water masses dominate the environmental regime (Jørgensen et al., 2015; Riget et al., 2000).

In the subpolar North Atlantic, water characteristics such as temperature, salinity and density are intrinsically linked to volume and distribution of mode waters (Figure 1). Mode waters are water masses with identifiable relatively uniform properties of large volumes (Speer & Forget, 2013). Boundaries between these mode waters are associated with large density gradients and thus the main current systems.

Variable air-sea forcing over the North Atlantic (e.g., North Atlantic Oscillations (NAO)) drives water formation (convection) (Häkkinen & Rhines, 2004), modifies the properties and distribution of mode waters. The associated deep-reaching density anomalies are reflected as changes in the sea surface height through the steric relation (Gill & Niller, 1973). The subpolar gyre (SPG) index, which is calculated from the sea surface height field (Hátún & Chafik, 2018), thus represents the principal changes in the mode waters and reflects fundamental aspects of the marine climate in the North Atlantic. The variability represented by the gyre index has its centre of action in the western Irminger Sea and along a swath around the southern tip of Greenland and into the Labrador Sea (Figure 1). The concept of the SPG index as a single time series can, however, not adequately represent the conditions in the Irminger and Labrador Seas. A recent analysis shows that the gyre dynamics are split in two so-called principal components, which reflect water density properties in the subpolar North Atlantic (Hátún & Chafik, 2018). The first principal component reflects the slow variability in the deep waters in the Labrador Sea, extending into the western Irminger Sea—the Western Mode Water (WMW) (Figure 1), while the second principal component represents the stronger interannual variability of the lighter mode water classes between the Rockall plateau and the eastern Irminger Sea—the Eastern Mode Water (EMW) (Hátún & Chafik, 2018) (Figure 1).

The strength of the SPG affects concentration of nutrients (Hátún et al., 2017; Johnson et al., 2013) and abundance and distribution of zooplankton, fish and marine mammals (Hátún et al., 2009,

2016; Núñez-Riboni et al., 2013; Pedchenko, 2005). Yet, these biological links related to the SPG have been described almost solely in the eastern and central part of the gyre (the Rockall plateau, the Faroese and Icelandic waters), and information about how the SPG affects ecosystems around Greenland is still scarce.

Anecdotal and scattered information from the early 20th century suggests that abundance of pelagic and demersal boreal fish increases in Greenland waters, when temperatures rise (Hansen, 1949; Jensen & Hansen, 1931; Tåning, 1948). However, this is limited to qualitative (e.g. “high” or “low” abundance) descriptions. For the majority of non-target species in Greenland waters and in contrast with other arctic-boreal ecosystems, such as the Barents Sea, sensitivity to temperature has not been quantitatively tested and recent reviews must still rely on information based on observations from the early 20th century (Drinkwater, 2006; Drinkwater & Kristiansen, 2018). Yet, information about how fish abundance responds to environmental change is necessary to lay the foundation to predict fish distribution in the future and draw conclusions on socio-ecological implications of rising temperatures.

Over recent years, increasing amounts of evidence have shown that marine biota in the subpolar North Atlantic are regulated by the SPG (Fluhr et al., 2017; Hátún et al., 2016, 2017). This suggests that water densities in the Irminger and Labrador Seas, local temperature and fish abundance could covary in shelf and slope regions in offshore Greenland waters. To test this hypothesis, we use observational data from 35 years of scientific fishery surveys covering shelf and slope regions from 40 to 1,500 m depth to include often neglected slope and deep-sea species. We focus on boreal fish with low commercial exploitation rates to ensure that the population signals are only related to the environment. We firstly test if fish abundances correlate with physical properties (i.e. temperature, salinity and current speed) in Greenland shelf and slope areas and secondly investigate if water densities in the Labrador and Irminger Seas, which cover fundamental aspects of the oceanography in the study region, are a driving force of boreal fish abundance. Moreover, we investigate if high (e.g., interannual) or low-frequency (e.g., inter-decadal) variability dominates correlations between fish abundance

and environmental drivers. Lastly, we investigate if changes in the oceanic conditions precede the changes in fish abundance.

2 | MATERIALS AND METHODS

2.1 | Fish data collection

More than 260 fish species have been documented in the Exclusive Economic Zone of Greenland (Møller et al., 2010), of which the majority is classified as boreal species (Mecklenburg et al., 2018). Data on fish abundance for 1981–2017 were collected during three annual bottom trawl surveys covering different regions, depths and periods: the German groundfish survey in Greenland waters conducted by the Thünen Institute of Sea Fisheries (1981–2017) and two Greenlandic surveys, the shrimp and fish survey (2005–2017) and the Greenland halibut survey (1997–2017), both carried out by the Greenland Institute of Natural Resources (Figure 2, Supporting information Table S1) (Fock, 2016; Jørgensen, 2017; Retzel, 2017, 2019). Each survey is designed to monitor groundfish stocks and to serve the assumption that catches representatively cover groundfish composition and abundance. However, most species are not caught frequently, and some are targeted by large fisheries, which can mask signals from the environment. Prior to analysis, we therefore scanned the survey data to identify the species suitable for including in the study. This selection was conducted using a set of criteria: Firstly, a species should be present in at least 1% of the total number of stations. Secondly, using plots of their distributions, species were selected by visual inspection when they showed higher presence in East than in West Greenland and if classified as boreal in Mecklenburg et al. (2018). To focus on non-target species, we examined commercial fishery logbooks, which became available in 1997 as well as catch records for the whole time series. The

commercially important species, Atlantic cod and redfish (*Sebastes* spp., Sebastidae), were excluded to avoid biases due to effect of fisheries. Following these criteria, ten fish species were chosen for analysis: Atlantic wolffish (*Anarhichas lupus*, Anarhichadidae), blue ling (*Molva dipterygia*, Lotidae), blue whiting (*Micromesistius poutassou*, Gadidae), greater argentine (*Argentina silus*, Argentinidae), haddock (*Melanogrammus aeglefinus*, Gadidae), ling (*Molva molva*, Lotidae), roughhead grenadier (*Macrourus berglax*, Macrouridae), round ray (*Raja fyllae*, Rajidae), saithe (*Pollachius virens*, Gadidae) and tusk (*Brosme brosme*, Lotidae). Particular species, for example blue whiting and greater argentine, often occur pelagically and are not ideally sampled with bottom trawls, which can result in non-representative sampling. However, bottom trawl surveys are accepted as valuable information in their stock assessments and also used for studying abundance trends of these species in other regions (Heino et al., 2008; ICES, 2018b, 2018a) and we therefore decided to include them in the analysis. 1992 and 1994 were omitted due to poor survey coverage. A description of the three surveys spatial overlap is given in Post et al. (2019). In total, observations from 10,373 trawl stations covering a shore distance of ~3,000 km went into the analysis.

2.2 | Fish abundance model

We used data from trawl surveys to model annual abundance indices, which we afterwards linked to environmental parameters. Prior to modelling catch data, they were explored for outliers, heterogeneity of variance, normality, collinearity and independence following the protocol from Zuur et al. (2010). In order to standardize abundance and eliminate bias from uneven sampling effort, we applied generalized additive models (GAMs) (Hastie & Tibshirani, 1986). GAMs have been broadly accepted for analysing ecological data including fish distribution and

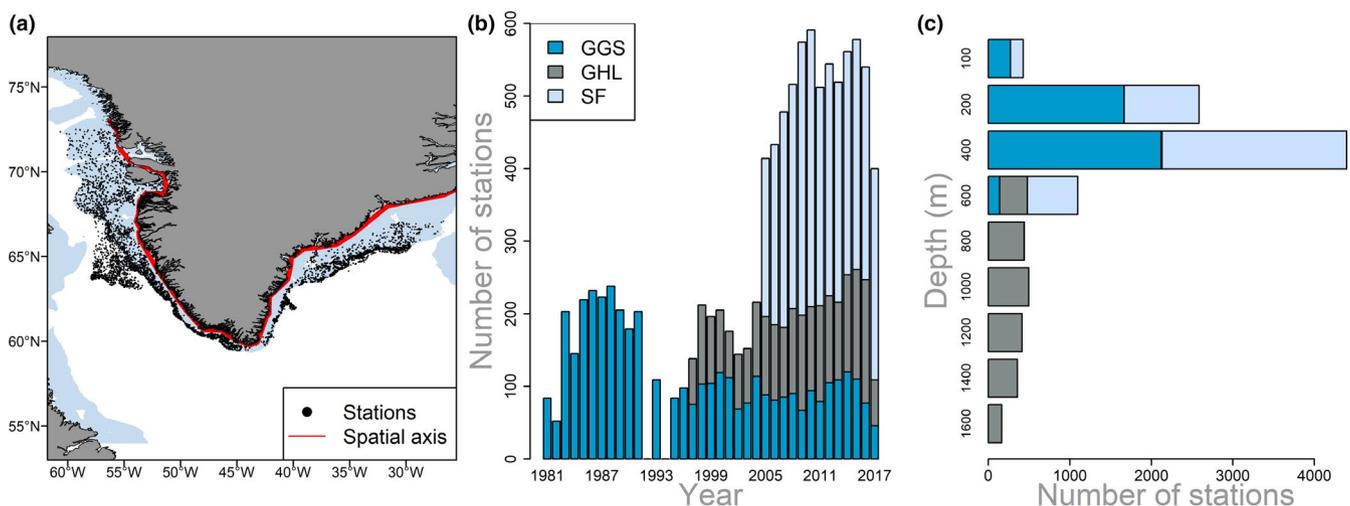


FIGURE 2 Sample distributions of bottom trawl surveys used for modelling abundance (German groundfish survey GGS, Greenland halibut survey GHG and Greenland fish and shrimp survey SF). (a) Map of Greenland and trawl positions. Light grey area displays depth contours from 0 to 500 metres. Red line shows the axis following the coast used for modelling fish abundance (Section 2.2). (b) Number of samples by year. (c) Number of samples by depth

abundance (Berg et al., 2014; Maunder & Punt, 2004; Wood, 2017) and suited our case with various non-linear relationships between the observed numbers and the covariates. To develop the models, we used an information theoretical approach (Burnham & Anderson, 2002), defining candidate models (based on biological knowledge) and fitting them to the observations. Observations were highly zero inflated (absence ranged from 47.8% to 98.7% across species) and overdispersed (with few outstandingly large catches). To overcome these challenges, we chose a negative binomial distribution for the observations, which has been applied successfully in other studies for modelling spatiotemporal fish distribution from zero inflated data (Irwin et al., 2013; Stenberg et al., 2015). Initially, we also inspected a Tweedie distribution (Tweedie, 1984), which can also deal with some of the same issues but decided to use negative binomial distribution because of better model performance. To deal with the large heteroscedasticity typical of fish abundance data, a logarithmic link function between the predictors and response variable was chosen. Model fitting was done in R (R Core Team, 2018) using the *mgcv* package (Wood, 2017). In the full model prior model selection for every individual species, we assumed the following relationship between numbers of caught fish (μ) at station i and the external factors:

$$\log(\mu_i) = \log(\text{Sweptarea}_i) + f(\text{Axis}_i) + f(\text{Depth}_i) + f(\text{Time}_i) + f(\text{Dayofyear}_i) + \text{Survey}_i + \text{Year}_i$$

where *Swept area* was an offset variable accounting for uneven sampling effort (Maunder & Punt, 2004). *Axis* (red line in Figure 2a) represented locations on a line following the coast on which fishing stations were assigned to by shortest distance and was used for describing the spatial distribution. *Depth*, *Time*, *Day of Year* and *Year* were their respective values, while *Survey* was one of the three surveys used (Supporting information Table S2). For modelling the non-linear effects, smoothing functions $f()$ were used, and for constructing these, we largely followed Wood (2017). Thin plate regression splines were applied for $f(\text{Axis})$ and $f(\text{Depth})$ and a cyclic cubic regression spline for $f(\text{Time})$ and $f(\text{Day of year})$. Whenever interactions occurred, tensor product smoothers were used. A small value ($k = 5$) was chosen for the basis dimension k (related to the number of knots) for $f(\text{Depth})$, $f(\text{Time})$ and $f(\text{Day of year})$. This allowed for only few optima, which is a realistic representation of the dependence of fish abundance with these variables. For the case of $f(\text{Axis})$, there were no theoretical reasons to constrain k , and following suggestions from Wood (2017), it was chosen as large as the computation capabilities permitted ($k = 100$ in our case). This allowed for many hotspots along the coast. The final models for every species were selected by means of Akaike information criteria (AIC) (Akaike, 1974), using a backward selection procedure beginning with all covariates included and stepwise reduction (Table S3).

2.3 | Hydrography

The full-depth temperature, salinity and current velocity data are based on the global ocean reanalysis ORAS5 (ORAS5, 2019; Zuo

et al., 2019). The spatial resolution is 0.25° in latitude and longitude while the vertical resolution varies with depth, increasing from bottom towards surface (~1 m near surface and ~100 m at 1,000 m depth). To inspect the correlations of fish abundance with temperature, salinity and current speed, we used the hydrography data from five areas along the coast (characterized by high fish densities) with 6 positions in each (bottom right inset in Figure 3), of which different bottom depths (200 m, 300 m, 400 m, 1,000 m, 1,500 m and > 1,500 m outside the shelf) were represented. To achieve data from positions as close as possible to these depths, we found positions that could be verified by trawl survey data. As a result, the positions were located in irregular patterns, i.e. not in straight transects. For the chosen positions, we calculated the average July–September value of each ORAS5 depth level for every year between 1981 and 2017. We then used the temperature from the depths having the highest (modelled) abundance for each species to correlate with the abundance index.

2.4 | Subpolar gyre and water densities

Traditionally, the SPG index, which reflects variations of the gyre strength, has been calculated using altimetry data that are available since 1993 (Häkkinen & Rhines, 2004; Hátún & Chafik, 2018). However, as demonstrated in Hátún and Chafik (2018), the SPG strength can be successfully reconstructed from potential density anomaly referenced to 1,000 dbar and averaged over the top 1000-m layer in the vicinity of the Reykjanes Ridge as calculated from the EN4 data set (1950–2018). This reconstruction is important since our aim is to examine the environmental conditions back to 1981, which would not have been possible using satellite altimetry only. Furthermore, we also use a second index reflecting predominantly the variability of deep convection in the Labrador Sea, an important indicator of the marine climate in the Subpolar North Atlantic. This index is reconstructed using potential density anomaly referenced to 2000 dbar and averaged between 1,000 and 2,500 m in the Labrador Sea. Thus, to capture the water mass variability in the SPG, we have constructed two different time series of the density anomalies at two separate regions, the Irminger Sea (Reykjanes Ridge, 0–1000m depth, 40–15°W, 55–65°N) and Labrador Sea (1000–2500m depth, 60–45°W, 55–65°N) using the EN4 data set (Good et al., 2013) with a bias correction method described in Gouretski and Reseghetti (2010). From now on these two indices, which largely reflect the density and volume of Labrador and Irminger Sea Water, are referred to as the Labrador Sea density (LD) and Reykjanes Ridge density (RD), respectively. The relationship between the two indices and temperatures of the central North Atlantic, including Greenland waters, is investigated through spatial correlations. Varying oceanic conditions during different SPG regimes were inspected through an analysis of the temperature field during anomalous periods of the density anomaly at four transects crossing some of the high fish abundance areas and central Seas.

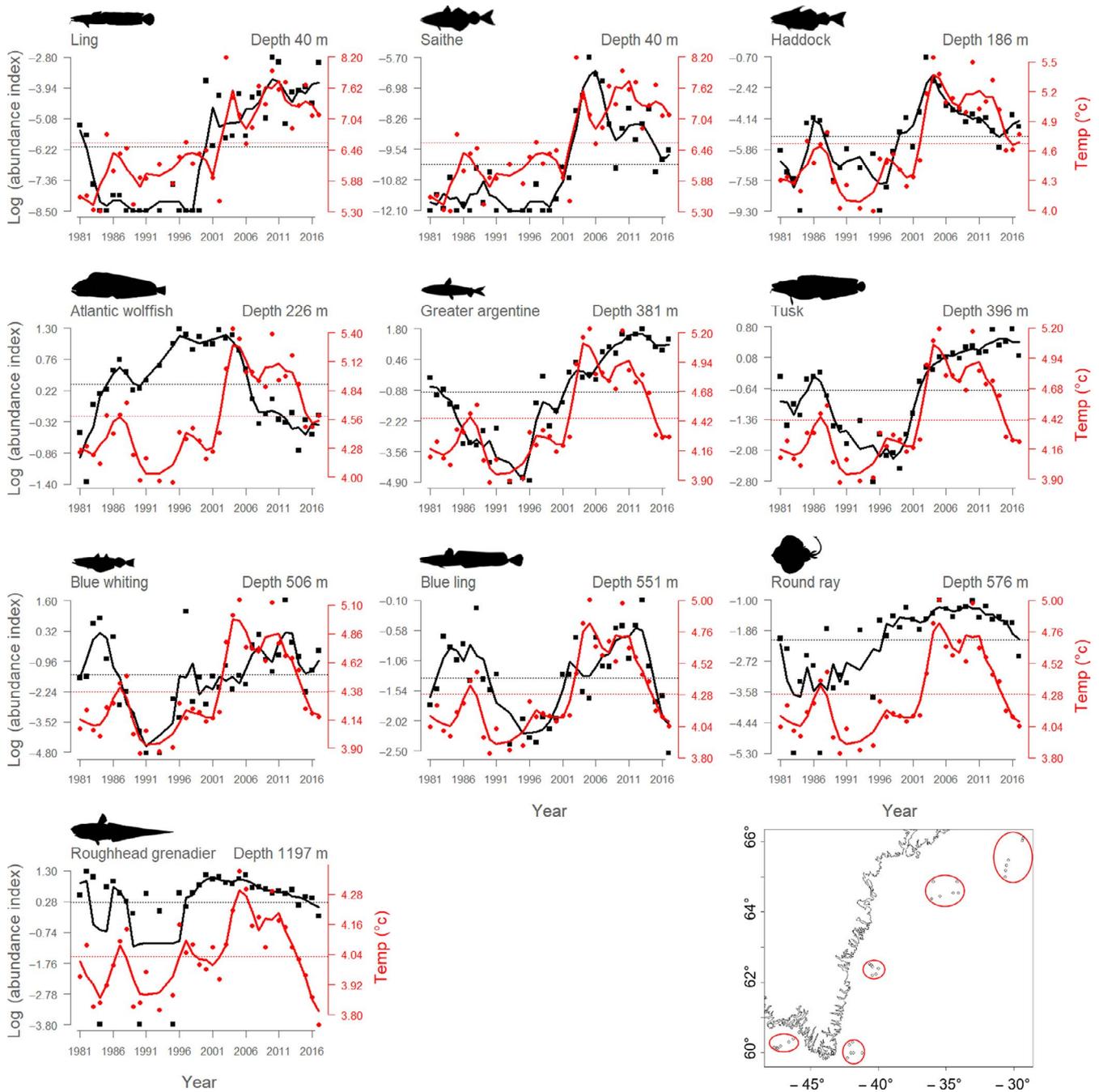


FIGURE 3 Log abundance indices of the ten fish species (black dots) and summer temperature (avg. Jul–Sep values at 30 positions) along the coast at depth where fish densities are highest (red dots). Curves are three-year running means and horizontal dashed lines the average values. Species are sorted after depth, using the depth with highest densities. Abundance indices are catch numbers at an average survey station. Log abundance is only used for display purpose. The bottom right insert maps the locations of the 30 positions

2.5 | Statistical tests

We used Spearman’s rank correlation, a measure of the monotonic relationship between the variables, which does not require a linear relationship between covariates and observations to be normal distributed (Hauke & Kossowski, 2011; Spearman, 1904). Modelled trawl catch data were used as proxy

for fish abundance. Inspections of the catches showed that not all species were caught in all years, despite consistent survey coverage. When testing correlations among abundance and other covariates, abundance index values for zero catch years were replaced with values equal to the lowest observed in the time series. We then tested the sensitivity of our results against this choice, by examining the difference between using with and

TABLE 1 Metrics of Spearman's correlations between abundance indices and temperature, salinity, current speed, Labrador Sea density (LD) and Reykjanes Ridge density (RD). Species sorted after modelled depth distribution with shallowest occurring in the top and deepest in the bottom. Shaded cells show correlations significant at 90%, 95% and 98% confidence levels, with higher confidence represented as darker colours

Species	Temperature		Salinity		Current speed		LD		RD	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Ling	0.57	0.052	0.45	0.068	-0.01	0.976	-0.70	0.011	-0.34	0.246
Saithe	0.65	0.003	0.58	0.013	-0.10	0.680	-0.77	0.001	-0.59	0.013
Haddock	0.72	0.000	0.31	0.138	-0.30	0.161	-0.58	0.005	-0.60	0.002
Atlantic wolffish	-0.15	0.731	-0.16	0.610	-0.33	0.305	0.55	0.197	-0.26	0.506
Greater argentine	0.61	0.153	0.43	0.155	0.00	0.998	-0.83	0.033	-0.50	0.222
Tusk	0.64	0.125	0.45	0.136	0.27	0.421	-0.86	0.021	-0.30	0.489
Blue whiting	0.33	0.031	0.17	0.338	0.20	0.253	-0.44	0.003	-0.27	0.084
Blue ling	0.47	0.050	0.15	0.518	0.28	0.228	-0.55	0.025	-0.16	0.523
Round ray	0.74	0.033	0.54	0.031	-0.12	0.693	-0.58	0.167	-0.69	0.050
Roughhead grenadier	0.46	0.041	0.16	0.522	-0.07	0.781	-0.18	0.550	-0.48	0.053

without replacement of zeros. A significance threshold of 0.05 was set for the *p*-value. Autocorrelation in time series inflates the chance of getting type I errors (detecting significant relationships where none exist) (Pyper & Peterman, 1998). In order to account for this, the test procedure for significance of correlations was adjusted following Pyper and Peterman (1998, 2011) by reducing the effective number of degrees of freedom (increasing the *p*-values) according to the degree of autocorrelation. The degrees of freedom were calculated following Garret and Petrie (1981), i.e., Equation 1 of Pyper and Peterman (1998) including the normalization. While the Pyper and Peterman (1998) method was originally designed for Pearson correlation, it is also commonly applied to Spearman (see Kane, 2011; Wieland et al., 2007). Running multiple correlation tests also inflate the change of getting type I errors. Hence, to examine whether significant correlations could be an artefact of this, we calculated the amount of expected type I errors and the probability of achieving n^+ positive correlations out of a total of *N* correlations analysis without any of these being true. The number of falsely significant correlations was assumed to be binomial distributed with the probability of success $p = .05/2$. In order to gain insight if fish abundance and environmental drivers correlate stronger on high (e.g., interannual) or low-frequency (e.g., interdecadal) time scales, we compared correlation results from the default settings (explained above) with first-differenced and 3-year running mean abundance values (Pyper & Peterman, 1998). A first-differenced time series of abundance depicted as $\Delta\text{abundance}_{\text{year}} = \text{abundance}_{\text{year}} - \text{abundance}_{\text{year}-1}$ were used to investigate interannual changes, while the 3-year running mean for assessing low-frequency variations (Pyper & Peterman, 1998). Delayed relationships between environmental parameters and abundance were investigated by lagging environmental parameters compared to the abundance.

3 | RESULTS

3.1 | Fish abundance in relation to temperature, salinity and current speed

Fish abundance models without interactions were selected for further analyses because these were the only models that fitted the observations adequately concerning residual patterns and did not show problematic edge effects. Minor differences in explanatory variables occurred between the individual species models (Supporting information Table S3). The final models explained 46%–88% of the deviance in the data, with a mean of 69%.

For all species, abundance was low in the late 1980s and early 1990s and increased in the mid and late 1990s, which coincided with an increase in temperature (Figure 3). The only exception to this common pattern was Atlantic wolffish, which showed highest abundance in the late 1980s to the early 2000s. The amplitude of fluctuations in temperature differed across depths (Figure 3). Fish abundance followed variations in temperature from shallow parts of the shelf (40 m) where temperature fluctuated with $\sim 3^\circ\text{C}$ over time, to deep regions of the slope (1,200 m) where temperature did not fluctuate with more than $\sim 0.5^\circ\text{C}$ (Figure 3). Temperature showed similar temporal trends across depths but decreased considerably stronger and quicker in deep regions than in shallow regions after 2010. Out of the ten species, five were significantly positively correlated with temperature. This is more than expected by random ($p < .001$, $N = 10$, $n^+ = 5$) (Table 1, Figure 3, and Supporting information Figure S1 and S2 for results on normal scale and with model uncertainties). The choice of using zero or the lowest observed value in years where the given species were not present in any samples did not qualitatively change the results. Salinity showed positive correlations with abundance for two species and current speed with none (Table 1).

TABLE 2 Correlation metrics between abundance indices and temperature, Labrador Sea density (LD) and Reykjanes Ridge density (RD) using three different correlation analysis: direct abundance indices, 3-year running mean of abundance and first-differenced abundance. Shaded cells show correlations significant at 90%, 95% and 98% confidence levels, with higher confidence represented as darker colours

Species	Temperature																	
	LD						RD											
	3-year running mean ab		First-differenced ab		Default ab		3-year running mean ab		First-differenced ab		Default ab							
	r	p	r	p	r	p	r	p	r	p	r	p						
Ling	0.57	0.052	0.64	0.101	0.12	0.494	-0.70	0.011	-0.75	0.052	-0.08	0.664	-0.34	0.246	-0.37	0.361	-0.12	0.508
Saithe	0.65	0.003	0.67	0.009	0.18	0.296	-0.77	0.001	-0.79	0.005	-0.10	0.571	-0.59	0.013	-0.59	0.035	-0.18	0.300
Haddock	0.72	0.000	0.73	0.004	-0.27	0.124	-0.58	0.005	-0.63	0.032	0.23	0.193	-0.60	0.002	-0.65	0.010	0.27	0.127
Atlantic wolffish	-0.15	0.731	-0.11	0.808	-0.38	0.028	0.55	0.197	0.53	0.242	0.30	0.091	-0.26	0.506	-0.32	0.433	0.40	0.019
Greater argentine	0.61	0.153	0.64	0.154	0.13	0.459	-0.83	0.033	-0.85	0.037	-0.03	0.882	-0.50	0.222	-0.53	0.221	-0.39	0.023
Tusk	0.64	0.125	0.60	0.193	0.20	0.253	-0.86	0.021	-0.84	0.043	-0.09	0.593	-0.30	0.489	-0.25	0.588	-0.12	0.507
Blue whiting	0.33	0.031	0.37	0.114	-0.11	0.531	-0.44	0.003	-0.29	0.240	0.05	0.785	-0.27	0.084	-0.23	0.302	0.02	0.904
Blue ling	0.47	0.050	0.50	0.118	0.12	0.491	-0.55	0.025	-0.65	0.046	-0.02	0.912	-0.16	0.523	-0.12	0.715	-0.13	0.463
Round ray	0.74	0.033	0.71	0.090	0.25	0.146	-0.58	0.167	-0.67	0.170	0.09	0.595	-0.69	0.050	-0.71	0.081	-0.08	0.663
Roughhead grenadier	0.46	0.041	0.46	0.115	0.26	0.141	-0.18	0.550	-0.27	0.511	0.05	0.767	-0.48	0.053	-0.55	0.090	-0.11	0.525

When testing low-frequency correlations (3-year running mean abundance) between abundance and temperature, significant correlations dropped to two species (Table 2). For the high-frequency changes (first-differenced data), only Atlantic wolffish correlated significantly with temperature (Table 2). The correlation coefficients between lagged abundances and temperature were highest at lag zero and decreased with increasing lag years (Supporting information Table S4).

3.2 | Fish abundance and the subpolar gyre

Both LD and RD increased in the 1980s and peaked in the early-mid 1990s coinciding with decreasing temperatures (Figures 3 and 4). They decreased again in the late 1990s until RD increased around 2006 and LD around 2013. Eight out of ten species were either significantly correlated with LD or RD (Table 1). LD and RD were significantly negative correlated with the abundance of seven and three species, respectively (Table 1). The probability of getting three type I errors was very low ($p < .001$, $N = 10$, $n^+ = 3$). Low-frequency correlations (3 year running mean abundance) between abundance and LD and RD decreased compared to the default method (Table 2), but was still above what could be expected by random coincidences (LD, $p < .001$, $N = 10$, $n^+ = 5$; RD, $p = 1.64e^{-3}$, $N = 10$, $n^+ = 2$). For the high-frequency changes (first-differenced data), two species correlated with RD and none with LD (Table 2). The correlation coefficients between abundance and LD were highest without lag for most species and significant correlations peaked at lags between two and six years between abundance and RD (Supporting information Table S5 and Figure S3).

3.3 | Subpolar gyre and temperature

Temperature conditions were examined during high (1995), low (2007) and medium (2017) LD and RD (Figure 5). During high water densities (1995), less warm Atlantic water occurred in the Labrador and Irminger Seas and along the Greenland coast compared to low densities (2007). More cold water of Arctic origin was found close to the East Greenland coast in the early 1990s, where it both extended further off the coast and reached deeper. Along the Labrador Sea transect, water below 3°C was considerably more present when LD and RD were higher. These observations illustrate that cold waters showed stronger presence in East and South Greenland, when water densities were high in the early 1990s. Maps of correlation coefficients between the two SPG indices (LD and RD) and summer temperatures at different depths in the wider North Atlantic confirm this negative correlation, especially along and on the Greenland shelf (Supporting information Figure S4). In the most recent period of the time series (2017), where RD was positive and LD negative, temperature in surface waters was slightly below the mid-2000s, but warmer than the 1990s. In the Ikermit transect, reflecting the Irminger Sea conditions, the deeper waters are seen to be colder than in the 1990s and 2000s.

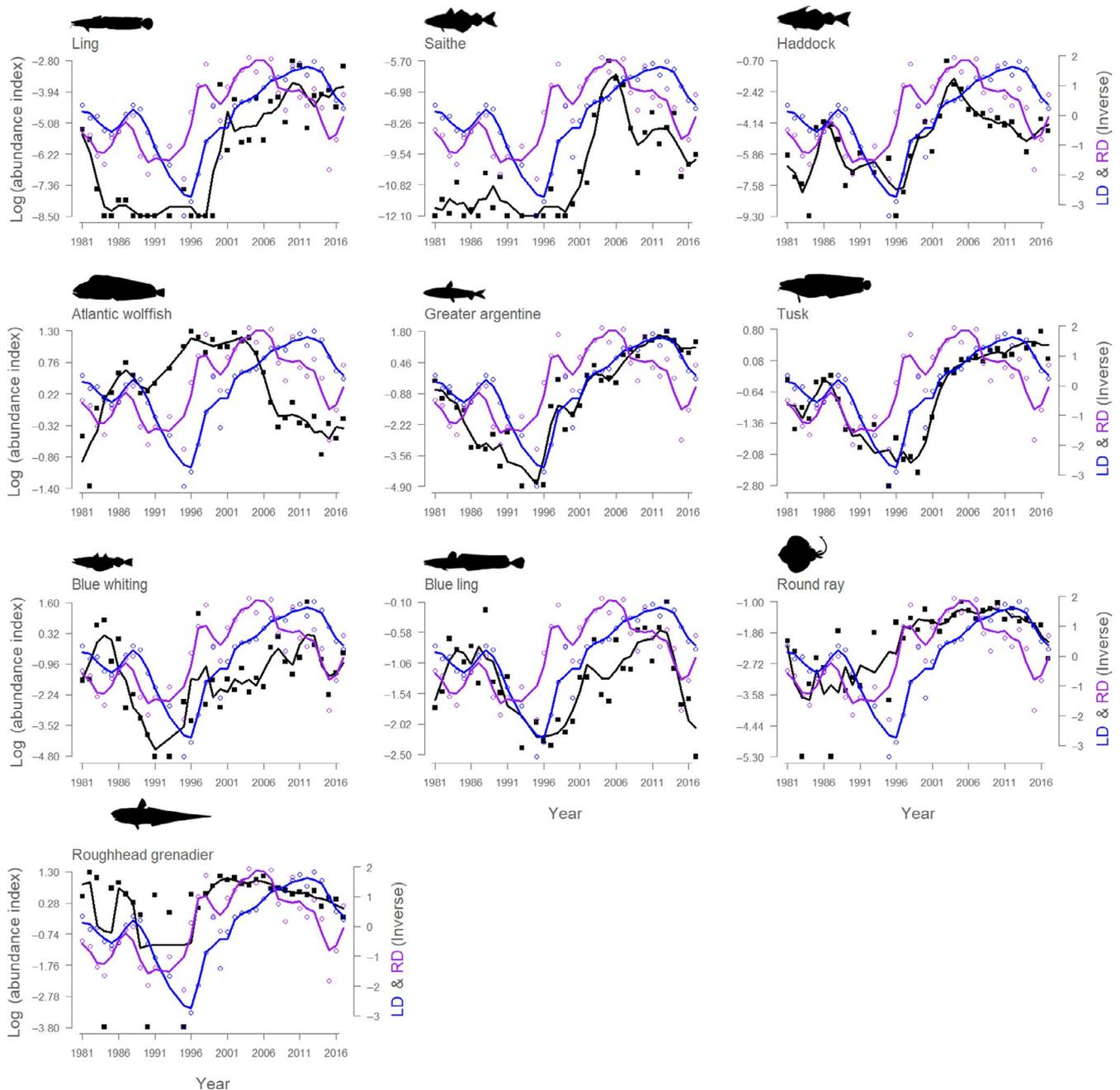


FIGURE 4 Log abundance indices of the ten fish species (black) and inverse Labrador Sea density (LD, blue) and Reykjanes Ridge density (RD, purple) from 1981 to 2017. Curves are three-year running means of the values. Species sorted after depth distribution with the shallowest occurring in the top

4 | DISCUSSION

Results of this study show that abundance of boreal fish covaries with local temperature and water density anomalies in offshore regions in the Labrador and Irminger Seas. These results are in line with previous findings that distribution and abundance of boreal species follow increasing temperatures in regions, where they encounter their lower thermal threshold (Fosshem et al., 2015; Fredston-Hermann et al., 2020). However, our results furthermore indicate that variation in Labrador and Irminger Sea water formation is a better indicator than only temperature, salinity or current

speed, for describing the variation of fish abundance in this region. This leads to the conclusion that yet not all biogeographic implications of variability in the SPG are understood. The fast response of deeper living species to temperature fluctuations indicates that abundance of fish species can change as quick in great depths as in shallow depths, which sheds new light on fish dynamics in deep slope regions. Abundance of fish in Greenland waters can be influenced by local and external physical and biological processes. Local processes may consist of changes affecting fish growth, reproduction and survival, while changes in conditions in adjacent areas could as well affect migration or drift patterns of early

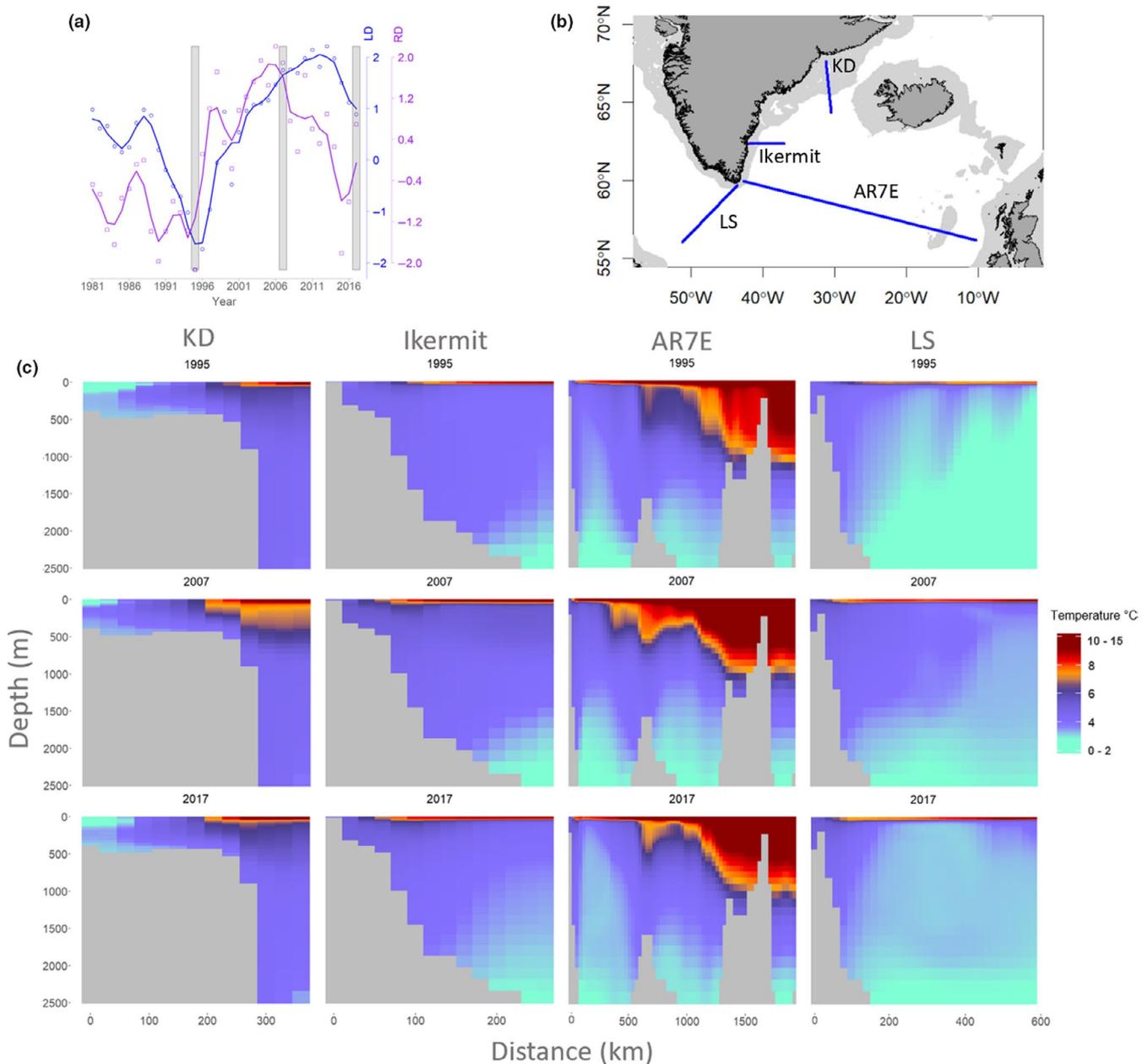


FIGURE 5 (a) Plot of inverse mean annual Labrador Sea density (LD) and Reykjanes Ridge density (RD) from 1981 to 2017. Curves are 3-year running mean values, and grey bars indicate periods plotted in c). (b) Map with the location of the four transects (blue lines) plotted in c). (c) Average summer temperature (Jul–Sep) in three different periods at the four transects. All transect starts near the coast of Greenland and ends off shelf

life stages and thereby affect local abundance (Biro et al., 2010; Dahlke et al., 2018; Kuczynski et al., 2017; Souza et al., 2018). As local temperature is not the only mechanistic driver of these processes, we discuss the role of temperature and other pathways linked to the distribution of mode waters in the North Atlantic as guidance for future research.

4.1 | The mechanistic role of temperature

All boreal species are expected to encounter the lower edge of their thermal affinity at a particular point in our study region (Mecklenburg

et al., 2018), which thereby limits their distribution. Because distribution and abundance for many species are positively correlated through fish density dependent processes (Blanchard et al., 2005; Ralston et al., 2017; Zimmermann et al., 2018), it is expected that abundance of boreal fish in Greenland waters increases with increasing thermal habitat. Temperature can affect fish, and in turn their abundance through direct physiological responses as well as indirect through predation and food availability (Bakun, 1996; Lloret et al., 2013; Pörtner & Peck, 2010).

Unlike the unequivocal effect of expansion/contraction of the thermal habitat, indirect effects through the food web are more complex and less well understood in East Greenland waters. No

comprehensive information exists on the functional relationship between temperature and productivity of low-trophic level prey species in East Greenland. In Southwest and West Greenland waters zooplankton abundance is higher during warm periods (Pedersen & Smidt, 2000). Because these areas act as nursery grounds for several boreal fish species, such as Atlantic cod, blue whiting, redfish (*Sebastes mentella* and *S. norvegicus*, Sebastidae) and wolffish (*Anarhichas* spp., Anarhichadidae) (Pedersen & Kannevorff, 1995; Pedersen & Rice, 2002; Post et al., 2019), it appears that survival of the early life stages could benefit from increased abundance of zooplankton species, such as the copepod *Calanus finmarchicus*, during periods of higher temperatures (Pedersen & Smidt, 2000). Higher zooplankton availability could lead to improved feeding conditions for fish species higher in the food chain. This might cause intensified feeding migrations of, for example, saithe, which was recaptured in Greenland waters in the early 2000s after being tagged in Iceland, indicating that such mobile species migrate to Greenland waters (ICES, 2019). On the other hand, during periods of strong SPG, when temperatures decrease, vertical mixing increases and thereby brings limiting minerals essential for phytoplankton communities, such as silicate, to the surface waters in the Irminger and Labrador Seas (Hátún et al., 2017). This can contribute to higher food availability in off-shelf regions, such as south of Iceland, where zooplankton biomass is positively correlated with the SPG (Hátún et al., 2016). As studies thereby show contradicting relationships between zooplankton, temperature and SPG regimes, it is difficult to draw conclusions about how food availability changes with temperature. Nevertheless, observations of zooplankton (including fish larvae) numbers in South and West Greenland suggest a positive correlation with temperature, which suggests that in shelf and slope regions zooplankton production is locally decoupled from the ocean basins of the Labrador and Irminger Seas. The cold and fresh East Greenland current (Figure 1) could play an important role in this context, and warmer temperatures might be observed when less arctic waters enter regions on and along the Greenland shelf.

4.2 | The possible impact of mode waters on fish abundance

Our results suggest that temperature is the most important environmental parameter regulating abundance of boreal fish in Greenland, which are not targeted by the commercial fishery. Furthermore, because LD and RD, which are mainly affected by variability in mode waters, correlated with abundance for more species than temperature (Table 1), it appears that additional confounding parameters intrinsically related to variability in the SPG, can affect abundance. Water density correlates with temperature, salinity, current strength and oxygen content (Rhein et al., 2017), which affect fish behaviour and physiology (Kisten et al., 2019; Pörtner et al., 2001). Salinity and current speed, however, showed weaker correlations with abundance and hence seem to be of minor importance than temperature (Table 1). Sound information on oxygen content along the shelf was

not available, but as oxygen content in the Labrador and Irminger Sea is positively linked with the SPG (Rhein et al., 2017) (the opposite direction of abundance), changes in oxygen content are unlikely a driver of abundance. The additional effect from the mode water variability seems therefore to be taking place outside the study area. This may be through bottom up processed as explained above and/or by affecting migration patterns of the fish species.

Because the Irminger current passes the western coast of Iceland, before it enters Greenland waters, eggs and larvae of haddock, Atlantic cod and capelin (*Mallotus villosus*, Osmeridae) occasionally drift from Icelandic spawning grounds to Southwest Greenland waters, which positively affects local abundance of these species (Buch et al., 1994; Vilhjálmsson & Fridgeirsson, 1976; Wieland & Hovgård, 2002). Due to the fact that especially non-commercial and deep slope species investigated in this study are notoriously under-researched and their spawning grounds are unknown, it cannot be excluded that their abundance in Greenland waters is affected by influx events from Iceland, which might be linked to processes regulated by the SPG. Abundance estimates for blue ling, greater argentine, haddock, ling, saithe and tusk in Iceland waters seem to follow similar temporal trends (ICES, 2018a, 2018b). This indicates that abundance of several boreal species, which we investigated in our study, is subject to similar environmental forcing in Iceland waters and as well linked to the overarching role of the subpolar gyre.

Low-frequent correlation results between abundance and LD and RD were considerably more similar to the default approach, than to the high-frequent correlations (and showed more significant correlations). This suggests that most of the variability in fish abundance is explained by decadal rather than annual fluctuations driven by the subpolar gyre (Table 2). The correlation coefficients between abundance and LD were highest without lag for most species and significant correlations peaked at lags between two and six years between abundance and RD (Supporting information Table S5 and Figure S3). The results thereby indicate that fish abundance shows a lagged relation to RD, and thereby properties of Eastern Mode Waters.

4.3 | Projections under climate change

The results of this study suggest that borealization processes take place around Greenland, when ocean temperatures increase. Similar patterns are observed in the Barents Sea and the Bering Sea, which have experienced transformations of Arctic fish communities towards a dominance of subarctic and boreal species during recent warm-water anomalies (Fosheim et al., 2015; Huntington et al., 2020; Kortsch et al., 2015). In the Barents Sea and the Fram Strait, these changes occur as well on low-trophic levels, indicating that increasing temperatures transform the entire food web (Frainer et al., 2017; Soltwedel et al., 2016). In the Barents sea, warmer waters favour large generalists, such as Atlantic cod and haddock, which alters energy pathways towards stronger benthic–pelagic coupling and pushes arctic specialists to the remaining cold refuges

(Frainer et al., 2017). Several species investigated in our study, e.g., haddock, saithe or ling, belong to the group of such large-bodied omnivorous species and have been associated with a decline of small-bodied benthivorous arctic species through increasing predation and competition in the Barents Sea (Frainer et al., 2017). Although we did not investigate, if arctic species retreat during warm periods, it seems likely that the arctic bottom fish communities in South and East Greenland will alter, when temperatures increase.

Prediction of fish abundance is recognized as a challenging task, as both physical and biological processes must be incorporated, and especially the latter is difficult (Payne et al., 2019; Payne et al., 2017). The impacts of climate change will vary across regions in Greenland waters. Strongest temperature changes are expected to happen in high Arctic areas, while changes in the subpolar gyre region and the southern Labrador Sea are predicted to be smaller (IPCC, 2013, 2019; Peck & Pinnegar, 2018). The Atlantic Meridional Overturning Circulation (AMOC) is predicted to decline due to atmospheric warming and additional inflow of fresh water from ice melting, which both tend to intensify stratification and thus weaken convection (Collins et al., 2013; IPCC, 2019; Weaver et al., 2012). However, convection depth in the Labrador Sea in recent years has been some of the deepest ever observed (back to the 1930s) (Yashayaev & Loder, 2017). Thus, long-term climate projections related to the main processes in the SPG region are uncertain (IPCC, 2019). This may both be due to the relatively coarse spatial resolution in such models, and due to the complexity of the multiple oceanographic and atmospheric processes governing these waters. In the long term, the northern regions are predicted to become more suitable for boreal species as a result of increases in temperature (Fossheim et al., 2015; Kortsch et al., 2015). Hence, it can be expected that boreal fishes will increase in numbers in the future, both in shallow and deep regions. In addition, the predicted weakening of the SPG will further enhance this process. Increasing habitat suitability for boreal fish might further enhance survival of larvae drifting with ocean currents and thereby experience higher colonization from surrounding regions as recently seen in northern East Greenland (Andrews et al., 2019; Christiansen et al., 2016; Strand et al., 2017). Our results improve the foundation for prediction of boreal fish abundance in Greenland in a warming future, while accounting for the natural variability of the SPG.

5 | CONCLUSION

We demonstrate that during warm periods, boreal fish species with varying life-history characteristics, habitats and depth preferences, increase in abundance in shelf regions around Greenland. Both shallow and deeper living species reacted to temperature on a multiannual time scale. Abundance and local shelf temperatures correlated negatively with water densities of mode waters in the Labrador and Irminger Seas, which represents properties of the subpolar gyre. Our findings that abundance has a lagged response to Eastern Mode Waters, suggest that trends in abundance for boreal fish species around Greenland can be predicted several years in advance.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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