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Long-term variability in spawning stock age structure influences climate–recruitment link for Barents Sea cod

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Abstract

Fish populations may spawn a vast number of offspring, while only a small and highly variable fraction of a new cohort survives long enough to enter into the fisheries as recruits. It is intuitive that the size and state of the spawning stock, the adult part of the fish population, is important for recruitment. Additionally, environmental conditions can greatly influence survival through vulnerable early life stages until recruitment. To understand what regulates recruitment, an essential part of fish population dynamics, it is thus necessary to explain the impact of fluctuations in both spawning stock and environment, including interactions. Here, we examine if the connection between the environment and recruitment is affected by the state of the spawning stock, including biomass, mean age and age diversity. Specifically, we re-evaluate the hypothesis stating that recruitment from a spawning stock dominated by young fish and few age classes is more vulnerable to environmental fluctuations. We expand upon earlier work on the Barents Sea stock of Atlantic cod, now with data series extended in time both backwards and forwards to cover the period 1922–2019. While our findings are correlative and cannot prove a specific cause and effect mechanism, they support earlier work and strengthen the evidence for the hypothesis above. Furthermore, this study supports that advice to fisheries management should include considerations of environmental status.

KEYWORDS
age structure, Barents Sea, cod, environment, recruitment, sea temperature, spawning stock biomass

1 | INTRODUCTION

1.1 | Environment–fish stock recruitment relations

Weak stock–recruitment relations and an understanding that environmental variability may play a role led to a scientific quest for finding that oceanographic and biological phenomena influence variability in early life stages of commercially exploited fish populations already in the days of Spencer Fullerton Baird in the United States (late 1800s; Kendall & Duker, 1998) and Johan Hjort (Hjort, 1914) in Norway. Since then, the pursuit towards understanding environmental impact on recruitment dynamics has been a key issue in quantitative fisheries science and especially the field of fisheries oceanography, and it is still ongoing (Sguotti et al., 2020; Szuwalski et al., 2015).

Sea temperature is for many fish species and stocks a natural starting point when examining environment-recruitment links, and over the years, numerous connections have been found through more and more advanced statistical or dynamic modelling approaches.

However, scepticism to the general validity of these connections appeared quite early, and Myers (1998) found that most previously established environment–recruitment correlations broke down when he re-calculated them with extended time series. Correlations only represent linear links, but it would seem that many environment–recruitment relations seem to be only transient (e.g., Bogstad et al., 2013; Ottersen et al., 2013; Stige et al., 2013; Zwolinski & Demer, 2019).

Myers (1998), however, highlighted the interesting pattern of correlations for populations close to the limit of a species' geographical range often remaining statistically significant when re-tested. Here, recruitment increased when environmental conditions were moderated (Myers, 1998), for example, higher recruitment in the least cold years for a species' northernmost populations. This validity of the 'species range hypothesis' (Huffaker & Messenger, 1964) to northeast Atlantic fish populations was confirmed by Brunel and Boucher (2006) based upon 62 stocks. For Atlantic cod (*Gadus morhua*) specifically, recruitment to populations towards the colder, northern end of the species overall distribution range tended to be higher in warmer years, while the more southern stocks had enhanced recruitment in colder years (Ottersen, 1996; Planque & Fredou, 1999).

1.2 | Spawning stock–recruitment relations

Many fish populations that initially produce enormous numbers of offspring still have only a small and very variable fraction of a new cohort that survive long enough to enter into the fisheries as recruits. Within a single stock, a management unit where the exchange of individuals with other stocks generally is assumed to be negligible, the only source of new individuals is through recruitment. Therefore, recruitment places a firm constraint on the number of individuals that can potentially grow to maturity (Payne et al., 2009) and contribute to the fishable stock.

Intuitively, there should be a quantitative relationship between the mature population and the recruits, that is, a stock–recruitment relationship (this becomes particularly obvious when moving towards a really low spawner population). Typically, the mature population is represented by spawning stock biomass, SSB—the aggregated weight of the mature fish in a stock.

Myers and Barrowman (1996), based upon analyses of 364 spawner-recruitment time series, and other authors since have concluded that strong recruitment does tend to co-occur with high spawner abundance. Still, the stock–recruitment relationship in marine fish is frequently weak (Hilborn & Walters, 1992; Koslow, 1992), often non-stationary over time (Ottersen et al., 2013) and/or non-linear (Pierre et al., 2018). Especially, the forecasting of recruitment remains a formidable challenge (Houde, 2008), although progress has been made more recently (e.g., Pierre et al., 2018). However, a general denial of the existence of meaningful stock–recruitment relationships would have rather alarming consequences for the science of fish population dynamics (Iles, 1994), and there are several good reasons why links may remain undetected even if present. Ottersen et al. (2013) gave several possible reasons for this seemingly weak link: (1) Not all stocks may have exhibited variation in stock size large enough to see a significant influence on recruitment, (2) there is uncertainty in the recruitment estimates, (3) the data are insufficient (e.g., short time series) and (4) the influence of environmental variability (interannual and long-term) on recruitment may complicate identification of stock–recruitment connections.

1.3 | Stock maternal effects and recruitment

While SSB is a keystone in stock–recruitment relations, it may not contain all relevant stock information available and virtual population analysis (VPA)-based SSB may be an inadequate measure of the reproductive potential of a fish stock (Marshall et al., 1998, 2003; Trippel, 1999). In particular maternal effects, non-genetic contributions from a female to the phenotype of her offspring (Green, 2008) may affect population productivity through several mechanisms.

Substantial evidence suggests that one such maternal effect may be important at the population level, and the size composition of the mature female fish population may be important for reproductive potential (Lambert, 1990; Shelton et al., 2015). Larger (and thus older) females tend to produce a relatively greater number of bigger, more high-quality and viable eggs (Kjesbu et al., 1992; Marshall et al., 2003; Marteinsdottir & Begg, 2002; Meekan & Fortier, 1996; Ohlberger et al., 2020; Trippel, 1999). Underlying this lies the fact that in many marine fish species, female reproductive investment scales hyperallometrically with body mass. This means that the total energy invested in reproduction per unit biomass increases with spawner body size (Barneche et al., 2018; Hixon et al., 2014; Ohlberger et al., 2022).

Further, a diverse age structure in the spawning stock may be favourable for recruitment as a heterogeneous stock is expected to display broader variety in timing, duration or location of spawning. This 'bet hedging strategy' works towards ensuring that a sufficient number of eggs or larvae encounter favourable environmental conditions, reducing risk of recruitment failure (Marteinsdottir & Thorarinsson, 1998; Ottersen, 2008; Secor, 2000).

For the Barents Sea cod stock, which we study here, Ohlberger et al. (2022) provide a good summary of various acting maternal effects, so that a spawning stock composed of older (larger) females should tend to produce higher recruitment. Firstly, older females spawn over longer periods of time and partly in different locations than younger age classes (Kjesbu et al., 1996; Opdal & Jørgensen, 2015; Wright & Trippel, 2009). Secondly, they are less likely to skip spawning (Jørgensen et al., 2006), and thirdly, an older spawning stock may have a larger fraction of females due to sex-specific growth, maturation thresholds or survival rates (Jørgensen, 1990; Marshall et al., 2006; Ohlberger et al., 2022).

Many mechanisms in reality relate more directly to the individual fish's size (length, weight, condition) than age. However, we, like many other authors, use data on fish age because that is what's available. Age may in the following be considered a proxy for several aspects of 'size'.

1.4 | Stock and environment both influence recruitment

From the above, it seems reasonable that both size and properties of the spawning population and the environmental conditions should be considered in recruitment studies. This thought goes back at least to Hjort (1914), who phrased it as: 'Easy to understand that even the richest spawning might yield but a poor amount of fish, while poorer spawning, taking place at a time more favourable in respect of the future nourishment of the young larvae, might often produce the richest classes'. Numerous studies have followed up on this by including both spawning stock size, maternal effects and environmental variables in explanatory models for recruitment. Brosset et al. (2020), while studying the northern contingent of the Northwest Atlantic stock of mackerel (*Scomber scombrus*), provide a good general conceptual framework and tabulated overview of the hypotheses put forward to link spawners to recruitment through intermediate steps. The many studies exploring such hypotheses include work on Atlantic cod, like central Baltic cod (Cardinale & Arrhenius, 2000; Køster et al., 2005), Icelandic cod (Shelton et al., 2012), North Sea cod (Kuhn et al., 2021; Olsen et al., 2011) and also Barents Sea cod (Ohlberger et al., 2022). Some studies covered several or many stocks and species, including by Hidalgo et al. (2012), Ottersen et al. (2013) and Shelton et al. (2015).

While the studies just mentioned focus on, roughly speaking, how environmental variability affects stock–recruitment relationships, we will here turn things somewhat around and consider how properties of the spawning stock may affect the vulnerability of recruitment to environmental fluctuations. We build upon our earlier work including Stige et al. (2017), but especially on Ottersen et al. (2006), which recently was included in Fisheries Oceanography's 30th Anniversary virtual collection and is suitable to return to for this 30th Anniversary Special Issue.

The main idea put forth in Ottersen et al. (2006) is that year-to-year variability in recruitment is more closely linked to fluctuations in sea temperature in periods when the spawning stock mainly consists of younger, smaller fish; that is, both have a lower mean age and are dominated by fewer age classes than otherwise. Ottersen et al. (2006) studied the Barents Sea cod stock based upon data for 1946–2002 and concluded that the sea temperature–cod recruitment correlation increases with decreasing mean age in the spawning stock. By fisheries biology standards these were long time series, but there may still have been special circumstances behind the connections found. Further analyses are particularly warranted since major changes have taken place in the Barents Sea cod stock over the most recent two decades. Thanks to good management and favourable environmental conditions (Kjesbu et al., 2014), the SSB has increased again, and the age structure moved more towards 'normality', although not returned to the semi-pristine state of the first post WW II years. We now are fortunate enough to have available the same time series extended not only forward in time but also backwards, allowing us to re-evaluate the results of Ottersen et al. (2006) for the period 1922–2019.

1.5 | Our study system

The Barents Sea is an open arcto-boreal shelf sea situated off the Northeast Atlantic, north of Norway and north-western Russia between 70 and 80°N (Figure 1). Interannual variation in sea temperatures is strongly influenced by the relatively warm Atlantic water masses flowing in from the south-west (Ingvaldsen et al., 2021; Loeng, 1991). This year-to-year variability is, to a large extent, determined by conditions during winter, the season when the differences in temperature both between inflowing and local water masses and between atmospheric temperatures and SST are at their highest (Loeng, 1991; Ottersen & Stenseth, 2001). Since the early 2000s, there has been a trend towards warming of the Barents Sea, related to changes in inflow of Atlantic water masses (Ingvaldsen et al., 2021). This has significant impact on the ecosystem, including the distribution of cod (Fossheim et al., 2015; Frainer et al., 2021; Kjesbu et al., 2014).

The Barents Sea cod spawn in March–May in patchy areas off mid and northern Norway, from Møre at 63°N to Finnmark at 71°N (Ellertsen et al., 1989; Endo et al., 2021; Figure 1). During the following ca 5-month pelagic eggs, larvae and early juveniles follow the currents towards the north and east and are spread all over the southern Barents Sea and south-west of Spitsbergen, 600–1200 km from their spawning ground, when they settle towards the bottom as 0-group. At this stage, year-class strength is to a large degree determined (Sundby et al., 1989), although demersal 0-group cod may in some years be subject to considerable cannibalism by older conspecifics (Yaragina et al., 2009).

The impact of interannual and decadal shifts in regional climate, sea temperature in particular, on recruitment of Barents Sea cod has been well documented by among others Hjort (1914), Ottersen and Sundby (1995) and Ottersen et al. (2014). A positive impact on fish of above-normal sea temperatures is reasonable, given that 'warm' years are good years for production in the Barents Sea for three principal reasons: (1) a larger ice-free area allows for higher primary productivity; (2) warm years imply large influxes of zooplankton from the south into the Barents Sea; and (3) higher temperatures lead to higher biological activity at all trophic levels (Sakshaug, 1997).

2 | MATERIALS AND METHODS

2.1 | Barents Sea cod population data and characteristic

Estimates of overall SSB, and spawner biomass per age class for Barents Sea cod from age 3 to 13 and older (13+), derived from VPA from 1913 to 2020 were used. Values on year-class strength, estimated as the number of recruits to the stock at age 3, are based on VPA (VPA_3). Age 3 is the earliest life stage where long-term data are available. For the first part of our study period, 1913–1945, values were taken from Hylen (2002) and K. Nedreaas (Institute of Marine Research, Norway; pers comm.). Data from 1946 to 2020 are from the publically available most recent report from ICES Arctic Fisheries

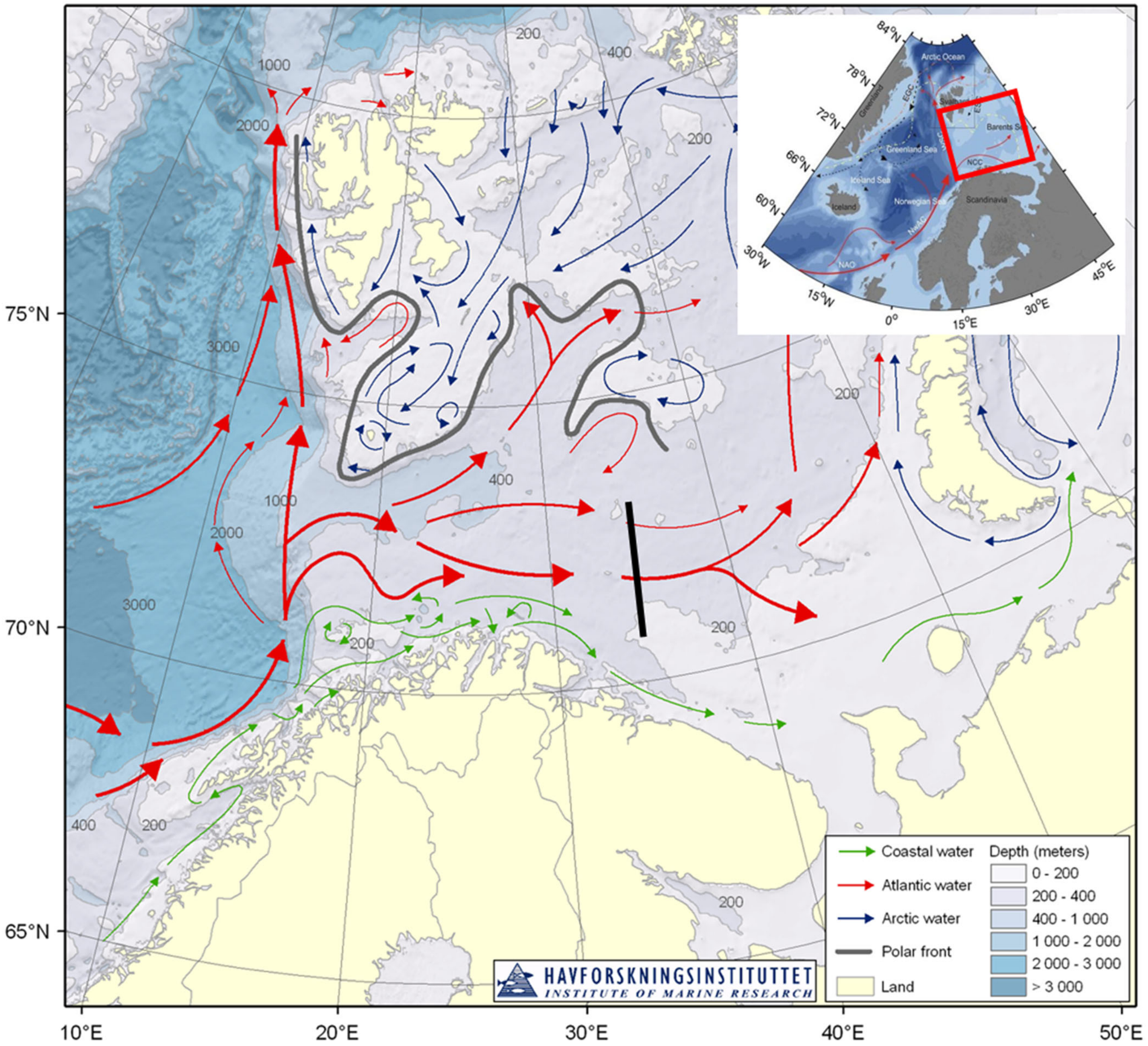

FIGURE 1 The panel in the upper right (from Daase, 2007) shows the Nordic seas with its main currents and the location of the Barents Sea given by the red box. The main panel indicates the three principal current systems in the Barents Sea and the bottom topography (in different shades of blue). The thick black line indicates the Kola meridian section

Working Group (ICES, 2020). Both sources give spawner biomass values at the time of spawning, so no temporal adjustment was necessary. VPA is mainly based upon commercial catch statistics, while recent years are tuned by scientific surveys. Extended survivors analysis (XSA; Shepherd, 1999) was used by ICES for the VPA tuning.

$$\text{Total SSB was calculated as } SSB = \sum_{i=3}^{13+} N_i \cdot \overline{W_i} \cdot M_i \tag{1}$$

where N_i is numbers-at-age i, $\overline{W_i}$ is the mean weight-at-age i and M_i the proportion of mature females at age i (see ICES, 2020 for more information). It follows that the biomass of spawners of age i is as follows.

$$BIOMASS_i = N_i \cdot \overline{W_i} \cdot M_i \tag{2}$$

Temporal development of VPA_3 and SSB is shown in Figure 2.

The 'mean age' of the spawning population (mature fraction of the total population), determined for each year separately, was estimated by calculating a mean value weighted on $BIOMASS_i$ added over all age groups potentially contributing to the spawning stock (age classes 3–13+).

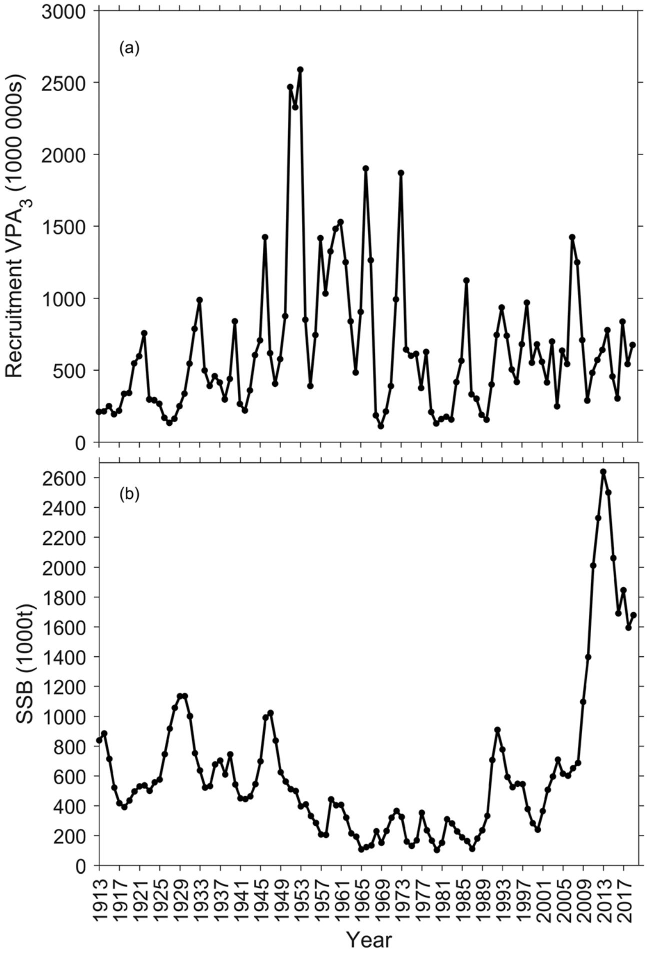

FIGURE 2 Temporal development of (a) recruitment at age 3 (VPA$_3$, numbers in millions) and (b) spawning stock biomass (SSB, in 1000 metric tonnes) 1913–2020.

$$AGE = \sum_{i=3}^{13+} (BIOMASS_i \cdot AGE_i) / \sum_{i=3}^{13+} BIOMASS_i \tag{3}$$

The Shannon diversity index (H; Shannon, 1948) is a well-known measure of species diversity in the field of ecology; see, for example, Magurran (1988). Here, we use H to make annual estimates of the degree of diversity in age of cod contributing to the SSB (mature individuals). Such an application of H is not novel. Marteinsdottir and Thorarinsson (1998) and Ajiad and Jakobsen (2002) used H to estimate yearly diversity of the age structure of cod spawning stock *abundance*, while others, like us, calculated yearly diversity of the age structure of cod SSB (O'Brien et al., 2003; Ottersen et al., 2006; Stige et al., 2017). H is independent of stock size and describes both the number of cohorts in the stock and the diversity of the distribution of fish among cohorts (Marteinsdottir & Thorarinsson, 1998).

$$H = -\sum_{i=1}^{k} (p_i \cdot (\log p_i)) \tag{4}$$

where k is the number of age groups present and p_i the proportion in age group i of the total SSB. A large value of H thus denotes many year groups contributing equally to the SSB, while small values describe cases with large differences between age groups regarding contribution to the total SSB.

2.2 | Sea temperature data

To represent sea temperature fluctuations we use the time series from the Kola meridian transect (33° 30′E, 70° 30′N to 72° 30′N, stations no. 3–7; location shown in Figure 1, time series in Figure 3), intersecting the Murman Current in the south central Barents Sea. This time series has earlier been demonstrated to effectively capture variability in the whole Atlantic domain in the Barents Sea, particularly the Atlantic Water flowing east towards Novaja Zemlya (Ingvaldsen et al., 2003; Ottersen et al., 2006). Monthly values have been calculated at each station averaging vertically from 0 to 200 m water depth, between stations along the transect and in time. The historical data have been taken from Bochkov (1982) and Tereshchenko (1996), while the most recent values have been provided by VNIRO Arctic, Murmansk. We use winter (December–March) means, Kola$_T$, for 1922–2019. Specifically, the value for December year n-1 is averaged with January, February and March for year n to ensure it is representative for year n; for example, December 1921 is averaged with January, February and March 1922 to provide a representative estimate for winter 1922.

2.3 | Moving window correlations

Ordinary (Pearson product–moment) correlations were used to describe the degree of linear relation between two variables.

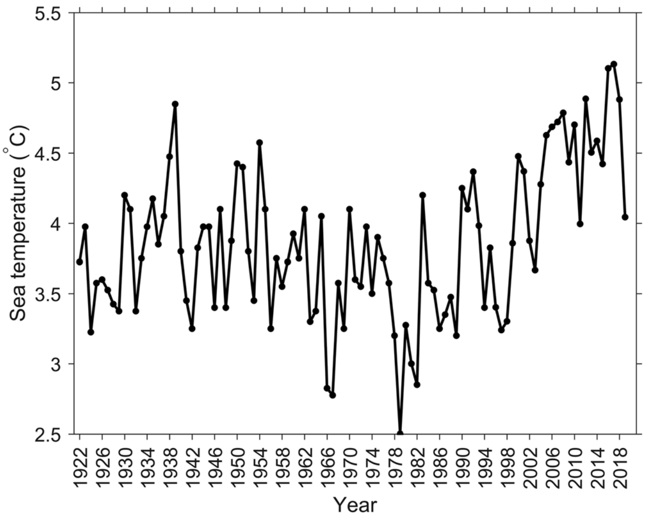

FIGURE 3 Temporal development of winter (December–March) means of 0- to 200-m depth sea temperature along the Kola meridian in the south-central Barents Sea 1922–2019.

Moving Pearson correlations were used to characterize the temporal development of sea temperature–cod links. We are not aware of any objective mathematical method for detecting the optimal length of a moving correlation window. Like Ottersen et al. (2006), we are interested in the long-term development and therefore choose a moving correlation window of 21 years; this also to maintain consistency. The moving correlations were calculated through the R platform, using the package 'RolWinMulCor' (Polanco-Martinez, 2020). Since we expect the main temperature effect on BS cod recruitment to be during the first half year of the fishes' life (e.g., Sundby et al., 1989) and VPA$_3$ represents the abundance of the year class at age 3, we correlate Kola$_T$ with VPA$_3$ 3 years later (VPA$_3$ [n + 3] represents a 3 year lag, VPA$_3$ year n + 3 represents the strength of the year class spawned year n). Note that, as a consequence of the width of the time window, 10 years are lost at each end of the time series of correlated values. This time series of correlations is later correlated with time series representing stock age structure.

3 | RESULTS

The 21-year moving time window correlations between Kola$_T$ and VPA$_3$ (n + 3) are negative during the first part of the study period, with a minimum value of −.36 in 1938. Subsequently, an increasing trend is found to around 1980 with a maximum correlation of .59, followed by a decrease until the most recent years with correlations close to 0 (Figure 4). On top of this dominating long term trend, there is marked interannual to decadal variability. If moving 15-year correlations were used instead of 21, the main pattern remains, except for positive correlations the first years of study.

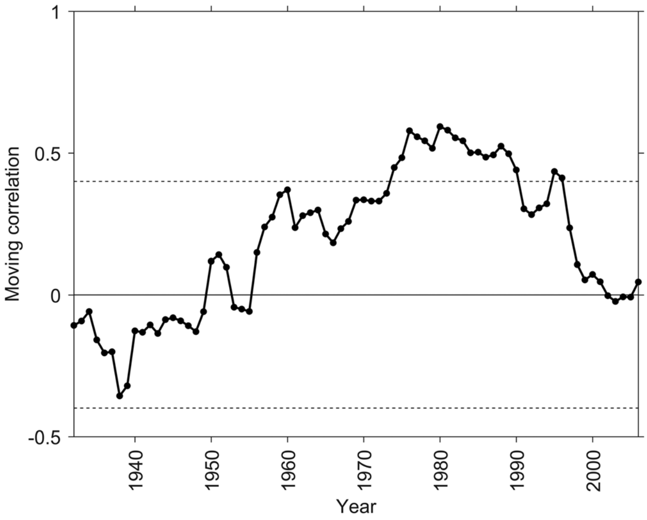

FIGURE 4 Moving 21-year time window correlations between temperature in the Kola section and Barents Sea cod recruitment at age 3, 3 years later. A 21-year correlation outside the stippled bands is statistically significantly different from 0 (p < 0.05, two-sided test).

The mean age in the spawning fraction of the BS cod population was around 11 years from 1913 until the end of WW II but with a clear peak in the 1930s with a maximum value of 12.6 years in 1933 (Figure 5). This was followed by a pronounced long-term reduction until the late 1980s with a minimum age of 6.8 years in 1988. From then until around 2010, the mean age fluctuated between 7 and 8 1/2 years. This was followed by 5 years of rapid increase until the present period with mean ages around 10 years. There is far less of an obvious trend in age diversity of the spawning stock, as represented by Shannon's H, although there is a decline from around 1950 to the late 1990s (Figure 5b). A strong year-to-year variability is more pronounced.

The running correlations between climate and cod recruitment are compared to spawning stock age structure (Figures 6 and 7). There is a pattern of high mean age in the spawning stock corresponding to low correlations; that is, the link between sea temperature and cod recruitment is weaker when the mean age is higher. However, also

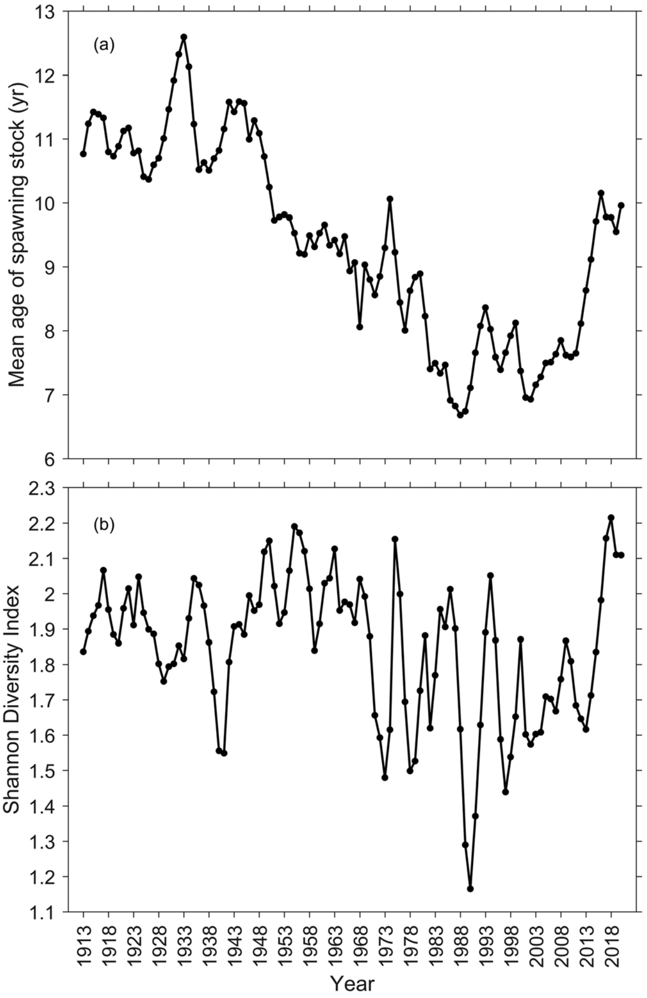

FIGURE 5 Temporal development of spawning stock age characteristics for Barents Sea cod 1913–2020. Biomass weighted (a) mean age in the spawning stock (b) age diversity represented by the Shannon diversity index, H.

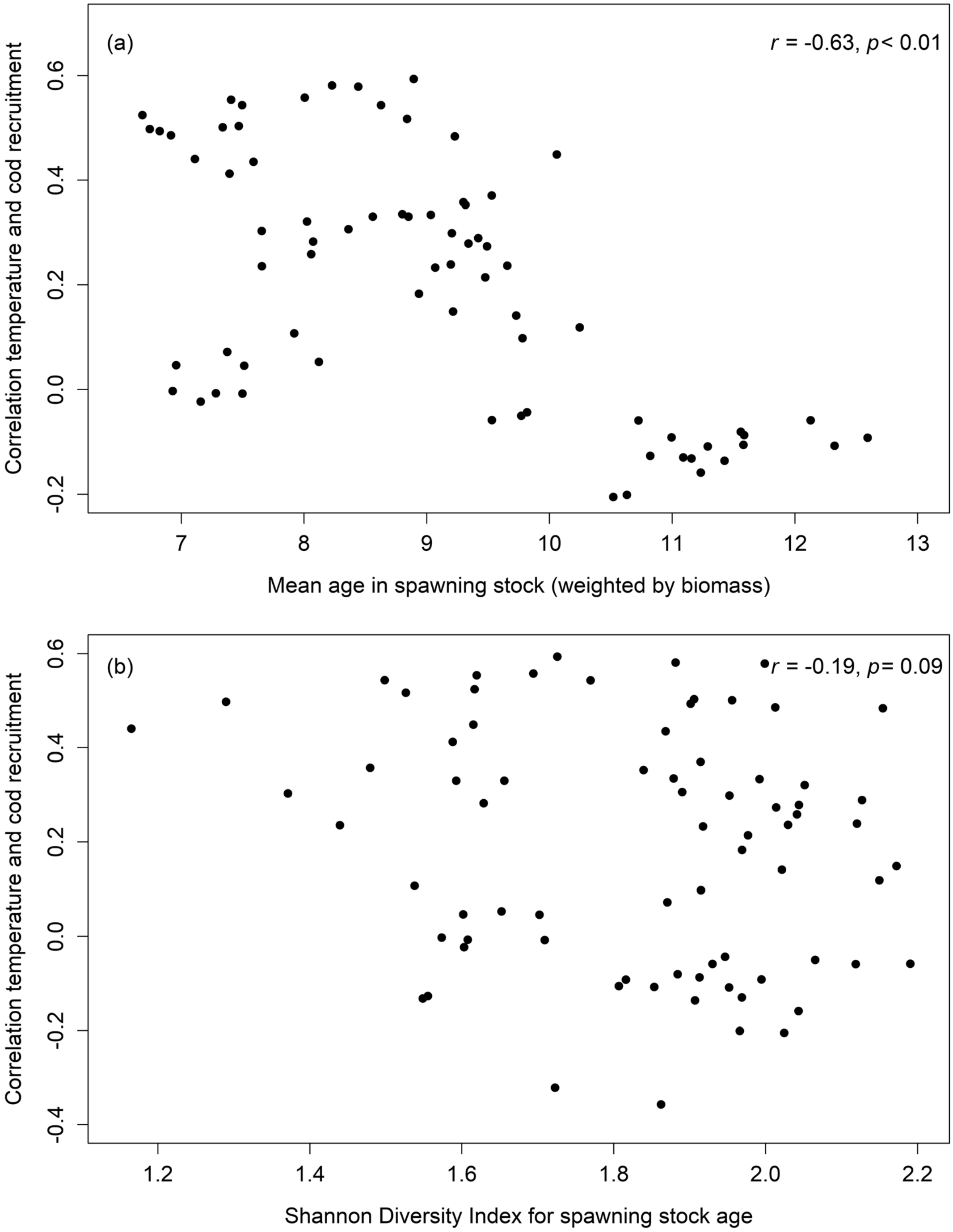

FIGURE 6 Scatter plots of variables characterizing spawning stock biomass structure versus moving, 21-year time window, correlations between temperature in the Kola section and Barents Sea cod recruitment at age 3, 3 years later: (a) mean age in the spawning stock weighted by biomass per age group and (b) Shannon diversity index of spawning stock biomass by age. Pearson product correlations with corresponding statistical significance levels are shown in the top right hand of panels.

some years with low mean age (7–8 years) have correlations around 0 (Figure 6a). The connection between biomass weighted age diversity (H) and temperature–recruitment correlations is weakly negative, as indicated by this 'second-order correlation' being −.19 and not statistical significant at the 5% level. Furthermore, visual inspection of the development of the two variables shows no obvious connection (Figure 7b).

4 | DISCUSSION

4.1 | Temperature and recruitment

We present a pattern of temperature-BS cod recruitment correlations developing slowly through time, since around 1950 being positive (Figure 4). The positive correlation fits in with the understanding that

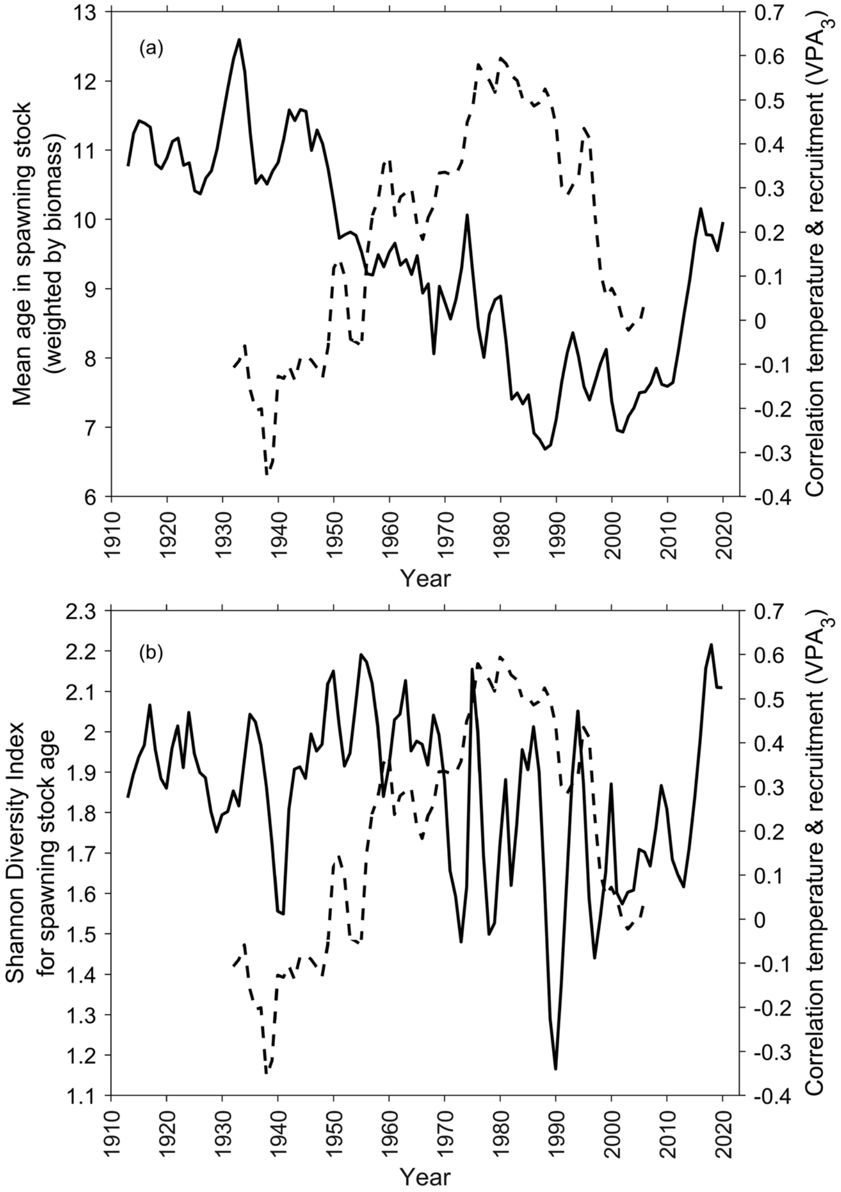

FIGURE 7 Time series of moving, 21-year time window, correlations between temperature in the Kola section and Barents Sea cod recruitment at age 3, 3 years later (stippled line; 1932–2006) and (a) mean biomass-weighted age in the spawning stock (in years), (b) Shannon diversity index H of contribution to spawning stock biomass by age, both 1913–2020 with solid line.

recruitment to the Barents Sea cod stock is influenced by sea temperature, in the direction that recruitment generally is higher when early life stages go through ontogeny during warmer than average conditions. The conception of this idea originates at least as early as Helland-Hansen and Nansen (1909) and Hjort (1914) and was supported by analyses by, for example, Sætersdal and Loeng (1987) and Ottersen and Stenseth (2001) and more recently Kjesbu et al. (2014). It also fits in to a more general pattern of higher recruitment in warmer years for a (northern hemisphere) species' northernmost populations (Brunel & Boucher, 2006; Ottersen, 1996; Planque & Fredou, 1999).

However, Kjesbu et al. (2014) also stated, for BS cod, 'No convincing evidence indicated a direct temperature influence on survival of early year classes, that is, R/SSB', and the results of Bogstad et al. (2013) indicate that this relationship may be only transient, perhaps shifting through time because of other changes in the ecosystem or fisheries. Maybe the question in the title of Myers (1998) 'When do environment - recruitment correlations work?' is best answered by the subtitle of Myers et al. (1995) 'Now you see it – now you don't' also for BS cod?

Ottersen et al. (2006, their fig. 4) graphed the same 21-year moving time window correlations as in our Figure 4, but for the shorter time period 1943–1999, in practice showing 1953–1989 as half the time window of 21 years is 'lost' at each end. Based upon this, Ottersen et al. (2006) concluded that one of their main findings is that this correlation increased (more or less linearly) over their study period and linked it to a coinciding pronounced reduction in the mean age in the spawning stock. By significantly expanding the study period, also backwards in time (Figure 4), we obviously get more information but also more complexity. For the most recent decades, the correlation has decreased steadily to near zero. We will soon examine how this connects with the recent development in spawning stock age and age diversity.

4.2 | Mean age in the spawning stock

The development of the mean age in the spawning stock of BS cod through our 108-year-long study period is quite remarkable (Figure 5a). This is the case for the reduction in the age of the 'typical' spawner from about 11 years until 1945 to 7 years around 1990. Even more interesting, and definitely more unusual, is the rebound to the recent mean age of 10 years.

The age decrease in the spawning stock until ca 1990 should, in hindsight at least, not be surprising. As discussed by Ottersen et al. (2006), such a development was of concern already for Sætersdal and Hylen (1964), who observed that the catch of old and large cod was decreasing relative to that of the younger and smaller fish. Furthermore, they noted already at this early date that the mean age of the spawners had decreased and attributed this to increased exploitation (Nakken, 1994; Sætersdal & Hylen, 1964) starting with the onset of industrial fishery in the 1920s. Not only did the fishing pressure increase from then on, but the fishing pattern shifted from fisheries with passive gear towards trawling. Also, this led to expansion from predominantly coastal winter fisheries to year round fisheries covering most of the southern (and more recently also northern) Barents Sea (Godø, 2003). Consequently, the fishing mortality of immature age groups 5–8 increased, and mean age at 50% maturity decreased from around 10 years to 7 from the late 1940s until present (Rørvik et al., 2022). Nilssen et al. (1994) described the abundance of cod older than 10 years at the time to be at less than 1% of that in the late 1940s, and Law (1991) estimated that prior to the industrial trawl fisheries, an immature BS cod had an approximately 40% change of surviving from age 3 to 8, as compared to only 2% around the time of his analysis.

The high mean age and large SSB in the late 1940s are a direct consequence of greatly reduced fishing during WWII (Hylen, 2002; Ottersen, 2008). There was a peak in SSB of around 1 million tons then (Figure 2) but lower than in the late 1920s and less than half of the above 2 million tons during 2011–2015. The latter and the related recovery of the mean age and age diversity (Figure 5) are quite extraordinary. The period was also one of high temperature (Figure 3) and preceded by a few years with high, but not exceptionally high, recruitment (Figure 2). However, a thorough evaluation by Kjesbu et al. (2014) concluded that unprecedented high spawning stock level was due to successful management actions reinforced by the favourable warm conditions. A key new management action was that of harvest control rules, more long-term criteria than the annual quotas total allowable catch, coming into effect in 2007. The introduction of harvest control rules was essential for the reduction in fishing mortality that followed, which again was a main reason for the increase in total stock size, SSB and spawner mean age (Kjesbu et al., 2014). The role of sea temperature should not be underestimated though, as a main driver for the events above was that warmer waters and decreased ice-coverage allowed for an unparalleled expansion of the BS cod feeding range (Fossheim et al., 2015; Kjesbu et al., 2014; Meredith et al., 2019).

The 'rebound' of the BS cod stock from small and juvenated in the 1980s to record high SSB values is highly unusual, not only for this stock, but in general. The state of the other once-large Atlantic cod stocks is less favourable, although the Icelandic stock now is in healthy shape again. This relatively fast rebound would seem to question the generality of fisheries induced evolution having significant impact on large stocks in the wild. Much theoretical, modelling and experimental work has shown the potential for not only phenotypic but also genetic changes in response to fisheries (Law, 2000; Pinsky et al., 2021). Following this, a genetically depleted stock would take a very long time to return to its natural state, as the evolutionary driving forces in that direction would be weak. Atlantic cod has been much studied in this context, both for stocks in the wild (e.g., Olsen et al., 2005; Swain, 2011) and in an aquaculture context (Bangera et al., 2015; Gjerde et al., 2004). The break-through in whole-genome sequencing of Atlantic cod (Star et al., 2011) and well-preserved archives of Atlantic cod scales and otoliths allowed Pinsky et al. (2021) to compare genetic diversity and effective population sizes of BS cod before and after a period of high fishing mortality and pronounced changes in stock properties (Figures 2 and 5). They concluded, supported by a commentary from Hutchings and Kuparinen (2021), that 'phenotypic change in these populations is not constrained by irreversible loss of genomic variation and thus imply that former traits could be reestablished with demographic recovery' (Pinsky et al., 2021). Instead of the purely genetic *fishing induced evolution*, implying irreversible loss in genetic variation, Rørvik et al. (2022) explored for BS cod the more general concept of *fisheries-induced adaptive change* (FIAC, e.g., Rijnsdorp & Witthames, 2005), also including epigenetic transgenerational modifications; Heckwolf et al., 2020). Rørvik et al. (2022) concluded that FIAC was necessary for explaining the strong changes in age at 50% maturity that they observed.

Several other authors have over the recent decade or so examined connections between spawner mean age and recruitment for different cod stocks. Brunel (2010) studied no less than 39 Northeast Atlantic fish stocks, including several stocks of Atlantic cod. He found the effects of higher mean age in the spawning stock on cod recruitment to be generally weakly positive, so also for BS cod. Shelton et al. (2015) examined the effect of age-structure on recruitment dynamics of 10 stocks of Atlantic cod. They compared the performance of standard Ricker stock–recruit models with models that included maternal age-structure effects on recruitment. In all 10 stocks, a recruitment model that included a maternal age-dependent effect was preferred over the standard Ricker model, and in 7 of the 10 stocks, the preferred model included a positive effect on recruitment of either maternal age or biomass. This suggests a positive impact of high mean cod spawner age on population productivity, but the effect varied between stocks and was relatively weak for BS cod (Shelton et al., 2015).

For BS cod, Ohlberger et al. (2022) found that the mean age of spawners had a positive effect on population productivity, measured as recruits per SSB. Further, their results suggest a threefold difference in population productivity between the lowest and highest mean ages of spawners observed over their 75 years study period 1946–2020.

4.3 | Age diversity in the spawning stock

The long-term development in age diversity in the spawning stock (H) is far less pronounced than that in mean age (Figure 5). The two are not independent, though, and similarities can be seen. During the first part of our study period, also H varied around the same level. This was followed by a decline from around 1950 to the late 1990s and a clear increase over the recent 2–3 decades, more or less in synchrony with the increase in mean age. The pronounced troughs in H in some years (Figure 5b; e.g., 1940/1941 and 1990) indicates single or two strong year classes and thus age groups, dominating the SSB, while in the years of peaks in H (e.g., 1975 and 1994), the SSB is more evenly distributed between groups. While our results show no long-term negative effects of strongly reduced age diversity, both theory and earlier empirical results indicate potentially serious issues. Diversity in age (as well as in geographic and/or genetic structure, neither of which we study here) is expected to enhance a population's reproductive potential through size- or age-dependent differences in timing, duration or location of spawning, ensuring that a sufficient number of eggs and larvae encounter environmentally favourable conditions (Ottersen et al., 2006). Earlier literature has many examples in support of this for species including cod (Marteinsdottir & Thorarinsson, 1998; O'Brien et al., 2003), herring (*Clupea harengus*; Lambert, 1987) and striped bass (*Morone saxatilis*; Secor, 2000).

As forementioned, mean age and age diversity in the spawning stock are not independent properties, periods with a relatively large proportion of older fish are typically also periods with many age classes contributing to the spawning stock. As a consequence, both Brunel (2010) and Ohlberger et al. (2022) found similar results if mean age of spawners (see Section 4.2 above) was replaced by age diversity in their expanded stock–recruitment models.

4.4 | Connection between spawning stock age structure and climate–recruitment link

Our results confirm those of Ottersen et al. (2006) in that the link between sea temperature and cod recruitment is stronger in periods when the mean spawning stock age is low (Figures 6 and 7). Thus, this pattern remains also for the much longer period we now have examined. Even though we find the link to be statistically significant ($r = -.63$, $p < .01$), we (similarly to Ottersen et al., 2006) do not claim we have proved any causal relationship. However, our new results strengthen the foundation for the hypothesis that the stock is more susceptible to environmental fluctuations in periods when it is young, in that it is less robust towards harsh conditions. The ‘storage effect’ theory gives a good, reasonable explanation. Long-lived fish stocks living in areas with pronounced year-to-year and decadal differences in environmental conditions experience periods that are favourable or less favourable to them. In particular, populations located near the extremes of the geographical range of the species may depend on irregular recruitment occurring mainly during periods of favourable climatic conditions (Berkeley et al., 2004; MacCall, 1996). Consequently, a population with a large fraction of ‘BOFFFs’ (big, old, fat, fertile, females; Hixon et al., 2014) constitute a ‘storage effect’ if occasional strong recruitment produces cohorts of adults that survive over a number of potential reproductive periods. When environmental conditions favourable for recruitment occur, a stock with a high reproductive potential is more likely to be able to generate new strong year classes that drive population growth. The loss during the years when recruitment is weak is compensated by the high adult survival (Chesson, 1994; Longhurst, 2002; Warner & Chesson, 1985). To the contrary, in a juvenated spawning stock (Figure 5, 1980s–1990s), the potential for storage is strongly reduced. It is quite obvious that there aren't many repeat spawners around when the mean age in the spawning stock is 7–8 years and the female age at maturation was around 7, as for the BS cod in the late 1990s (Ajiad et al., 1999).

Ottersen et al. (2006) found some indication for a link between age diversity in the BS spawning stock and climate–cod recruitment correlations. They point to plausible mechanisms for why a stock consisting of few age classes is more vulnerable to environmental fluctuations, beyond those relating to benefits of large/old fish. This includes the match–mismatch hypothesis (Brosset et al., 2020; Cushing, 1990; Durant et al., 2007; Ferreira et al., 2020; Laurel et al., 2021). Still, Ottersen et al. (2006) described the age diversity–recruitment link as relatively weak for BS cod. Based upon our analyses of extended time series, the ‘relatively weak’ link is quite close to non-existent (Figures 6b and 7b).

4.5 | Data and methods

The virtual population-based stock data we use have some underlying properties that should be mentioned. A main point is that the underlying data are not uniform in time. Hylen (2002) did a formidable job in establishing the time series from 1913 to 1945 but was met with several challenges. Firstly, the age determination was based upon fish scales prior to 1932, otholits from that year onwards. Further, the proportion and mean weight of mature fish was set to be constant for 1913–1931; thus, year-to-year differences in spawner biomass-at-age are for this period determined by changes in numbers at age alone (Hylen, 2002; Ottersen, 2008). There are many sources of uncertainty also in the more modern data from 1946 onwards. Importantly, the ICES Arctic Fisheries Working Group rerun their VPAs as new data from the fisheries come in and if significant new information back in time becomes available revisions may be made. Here, this has the consequence that the VPA output we use from the most recent AFWG report (ICES, 2020) is not identical to that used by Ottersen et al. (2006), and there are observable differences throughout the overlapping period of 1946–2002.

We have chosen to use the same rather simple straight forward methods as in Ottersen et al. (2006). This is partly due to the importance of consistency when the aim is to prolong the analysis forward and backwards in time. Some argumentation for choice of method is however warranted. The choice of 21 years as length of the moving correlation window is indeed a choice and not based on any objective mathematical method for optimal length detection; we are not aware of any such algorithm. Like Ottersen et al. (2006), we are interested in the long-term development and found 21 years to give a good balance between showing long-term changes and numbers of years lost at each end of the time series.

It may be argued that a completely different approach would be more appropriate. A statistical time series analysis (following Box et al., 2015) or regression model, for example, general additive model (GAM, Hastie & Tibshirani, 1990), could indeed provide further interesting results. However, we consider that including this would make our work a completely different paper and not as intended an expansion of Ottersen et al. (2006). Further, a recent paper by colleagues (Ohlberger et al., 2022) ensures that the GAM approach has been applied to the same stock and a similar question. They apply GAM to explore effects of age structure in the BS cod spawning stock on population productivity.

5 | CONCLUSIONS

Theory and earlier analyses point to juvenated fish stocks having reduced reproductive capacity and increased vulnerability to unfavourable environmental conditions. Our data support this for the Barents Sea cod stock; concretely, the changing degree of linkage between temperature and cod recruitment is affected by the age (size) structure of the spawning stock. In periods with a juvenated spawning stock, BS cod recruitment is more vulnerable to temperature variation.

The age composition of the spawning stock of Barents Sea cod has undergone pronounced changes over the studied 1913–2020 period. The age of the average spawner was around 11 years until ca 1945, decreased to 7 years in the early 1990s and increased again to the recent ca 10 years. Throughout the same period, the age diversity in the spawning stock has also fluctuated strongly, with stability followed by decrease and then increase again. The strong increase in spawning stock mean age and age diversity from ca 2000 was linked to a marked simultaneous increase in SSB, from ca 400,000 tonnes around year 2000 to a staggering all-time record of 2.6 million tonnes in 2013. The sea temperature–cod recruitment correlation increased clearly from the late 1940s to the late 1970s, lay stable at approximately 0.6 until around 1990 and has since dropped to near 0. Our results confirm earlier findings in that the link between sea temperature and Barents Sea cod recruitment is stronger in periods when the mean spawning stock age is low. This strengthens the foundation for the hypothesis that the stock is more susceptible to environmental fluctuations and less robust towards harsh conditions in periods when it is young. We do not find evidence for the sea temperature–cod recruitment relationship being affected by the level of age diversity per se in the spawning stock.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

GO wrote the manuscript with input from REH. REH performed all analyses and produced paper figures, Both authors provided input and edited the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Several sources of data were used for analyses. Some of the data were derived from public domain resources with a doi, while other data are available only on request:

VPA from 1946 to 2020. Values on spawning stock size and properties and year-class strength for Barents Sea cod are publically available in the ICES Arctic Fisheries Working Group annual report for 2020 (ICES, 2020). https://doi.org/10.17895/ices.pub.6050.

VPA from 1913 to 1945. Values on spawning stock size and properties and year-class strength for Barents Sea cod for this time period are to our knowledge not available as a public domain resource. These data were a result of reconstruction work described in Hylen (2002), but this paper gives no indication of data availability. We received the data from our colleague at IMR, Kjell Nedreaas (pers comm.).

Sea temperature data from the Kola meridian section. Older data are publicly available, not the recent values. Historical data have been taken from Bochkov (1982) and Tereshchenko (1996), where they are tabulated. More recent values, 1996–2019, were made available to us (more than a year ago) through institutional collaboration between Institute of Marine Research, Norway and VNIRO Arctic, Murmansk, Russia.

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