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Effects of sea ice cover, temperature and predation on the stock dynamics of the key Arctic fish species polar cod *Boreogadus saida*

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ABSTRACT: Climate change has large effects on population dynamics of fish species in high latitude ecosystems. Arctic fish stocks experience multiple pressures with changing abiotic living conditions and increased competition and predation from boreal species. However, there are many unknowns regarding how environmental change influences the dynamics of those populations. Here, we focused on the Barents Sea polar cod, a pan-Arctic zooplanktivorous key fish species physiologically and ecologically adapted to the presence of sea ice. We developed an age-resolved Bayesian state-space model of the dynamics of polar cod based on 30 yr of survey data (1986–2015). Using this model, we quantified how inter-annual changes in abundance were associated with abiotic variables (temperature and sea ice cover) and biotic variables (prey biomasses and a predation index). Using the model output, we used a hindcast scenario approach to investigate to which degree the observed variations in total population size were related to the abiotic or biotic variables. Our results showed that variation in abundance of young polar cod (ages 0 and 1) was best explained by abiotic variables while variation in the older age groups (ages 3 and 4) was best explained by predation. Hindcast scenarios showed that the abiotic variables had a more evident effect than predation on population dynamics, but none of the variables we considered could explain the drastic population decline observed in recent years. Our work shows the advantages of studying age-specific responses as a stepping stone to understand changes at the population level.

KEY WORDS: *Boreogadus saida* · Sea ice · Temperature · Predation · Barents Sea · Arctic · Population dynamics · State-space model

1. INTRODUCTION

Climate change is a global phenomenon impacting marine ecosystems on both regional and global scales (Link et al. 2009, Beaugrand et al. 2015, Kröncke et al. 2019). In the Northern Hemisphere, the greatest increase in sea temperature has occurred in the Arctic regions, together with a large decrease in sea ice cover (Laidre et al. 2015, Lind et al. 2018, Post et al. 2019). Sea ice and sea temperature are major factors affecting Arctic marine species through direct effects as well as indirect effects through other species in the food web (Moline et al. 2008, Post et al. 2013). Climate change has been associated with a 'borealization' of Arctic ecosystems, i.e. fish communities with historically more southern distribution have moved into the Arctic (Fossheim et al. 2015). These immigrant species,

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characterized by high reproduction, growth and consumption rates, increase predation pressure, which may pose a challenge to endemic species with lower potential for population growth (Frainer et al. 2017). However, there is a general lack of quantitative knowledge about how the population dynamics of Arctic species respond to the multiple pressures from changing biotic and abiotic conditions.

Changes in sea ice cover may directly affect species and communities dependent on ice for critical phases of their life cycle (Daase et al. 2013, Leu et al. 2015). For example, eggs of polar cod *Boreogadus saida* develop protected under sea ice (Hop & Gjøsæter 2013), and a reduction in sea ice has been associated with decreased survival of polar cod larvae in the Barents Sea (Huserbråten et al. 2019). Moreover, an increase in sea temperature may affect abundance, growth and life strategies of species adapted to cold waters (Wassmann et al. 2011, Carstensen et al. 2012, Marsh & Mueter 2020).

Change in prey availability may affect predator species through bottom-up effects. For example, in Arctic waters in the Barents Sea, the biomass of lipid-rich zooplankton groups has declined in recent warm years, providing impaired feeding conditions for key Arctic forage fishes (Dalpadado et al. 2012, Stige et al. 2019, Dalpadado et al. 2020). In general, the survival of young-of the-year marine fishes depends on adequate food levels to avoid starvation and predation (Anderson 1988, Beaugrand 2003, Divoky et al. 2015). Food levels may also influence survival of older individuals (Buren et al. 2014, Stige et al. 2018).

Change in predator abundance may affect the survival of prey through top-down effects (Frank et al. 2007), notably between top predators and forage fishes (Baum & Worm 2009). Forage fishes have also been reported to have top-down effects on zooplankton in Arctic water masses (Stige et al. 2014). The current 'borealization' of Arctic communities by northward shifts of boreal species and the increase in boreal predator abundances (Fossheim et al. 2015, Frainer et al. 2017) may be expected to have repercussions on Arctic prey population dynamics, as well as on food web structure and dynamics (Mueter & Litzow 2008, Frainer et al. 2017).

Knowledge about the relationships between species and their environment is still sparse for Arctic areas (Mueter et al. 2016), and it remains unclear what roles abiotic factors, prey and predation play in shaping population dynamics and biomass of Arctic marine species under global warming. Shedding light on this topic is essential to the understanding of ecosystem functioning (Casini et al. 2010, Renaud et al. 2012). In this study, we focused on the polar cod population in the Barents Sea (see Fig. 1). This species is a pan-Arctic forage fish (Chernova 2011) and a key species in Arctic ecosystems, as it is the dominating forage fish in large parts of its distribution area and sustains a large diversity of predators (Welch et al. 1992, Bluhm & Gradinger 2008). The Barents Sea stock, currently at an historic low level (Gjøsæter et al. 2020, ICES 2020), is under pressure from a changing Arctic environment signified by reduction in sea ice and increase in sea temperature (Lind et al. 2018, Asbjørnsen et al. 2020), decrease of the biomass of its main Arctic zooplankton prey (Dalpadado et al. 2012, Stige et al. 2019) and an increase in the presence of boreal predator and competitor species (Fossheim et al. 2015).

With this study, we aimed to (1) simultaneously quantify the effects of abiotic factors (i.e. sea temperature and sea ice cover) as well as biotic factors (i.e. prey and predators) on the polar cod population in the Barents Sea and (2) assess the effects of current environmental changes (i.e. decreased sea ice cover, increased temperature and increased predation pressure) on the population dynamics of this Arctic species. For this purpose, we developed an age-resolved statistical state-space model of the population dynamics of polar cod in the Barents Sea. This model jointly estimated the effects of sea ice, sea temperature and biomass of prey and predators on age-specific survival (ages 0–4). The model also estimated the strength of intraspecific interactions through the density-dependent relationship between the polar cod spawning stock biomass (SSB) and abundance of the youngest age class (age 0) as well as density-dependent effects between older age classes (ages 1–4). We then synthesized the effects of abiotic variables and predation pressure on the stock dynamics of polar cod using hindcast simulations of scenarios with different climate or predation levels.

2. MATERIALS AND METHODS

2.1. Polar cod data

The age-specific abundance, biomass, weight-at-age and length-at-age data for polar cod in the Barents Sea were extracted from the reports of the Russian/Norwegian EcoSystem Survey of the Barents Sea and adjacent waters (BESS) for the period 1986–2015. The values are reported yearly and represent the state of the stock by age group (ages 0–4) for the months of August–September when the Institute of

Marine Research (IMR) and the current Polar Branch of the Russian Federal Institute of Fisheries and Oceanography (VNIRO, formerly PINRO) conduct their joint surveys. The abundance data for ages 1–4 are based on annual stock estimates using acoustics measurements, whereas stock abundance estimates for age 0 are based on pelagic trawl sampling (see Fig. 2; for more details on acoustics measurement and sampling see the Supplement at www.int-res.com/articles/suppl/m677p141_supp.pdf). The reported abundance for age 0 is divided between 2 spatial components (eastern and western) based on the potential polar cod spawning grounds (Novaya Zemlya and Svalbard; Fig. 1) in the Barents Sea (Huserbråten et al. 2019). We used the summed abundance of the age 0 fish as input to our model (Fig. 2a). Average weights-at-age for ages 1–4 were used to compute age-specific annual biomass from age-specific annual abundance. Weight-at-age is not provided for age 0. Instead, we used the average of yearly biomass-at-age divided by the corresponding abundance-at-age for age 0 for the years of available data (1993–2015). Finally, we calculated the proportion of fish that are mature at a given age (Mat_a) from the yearly reported individual length distribution for ages 1–4 and the maturing fraction at length (Nahrgang et al. 2014) for estimation of yearly SSB.

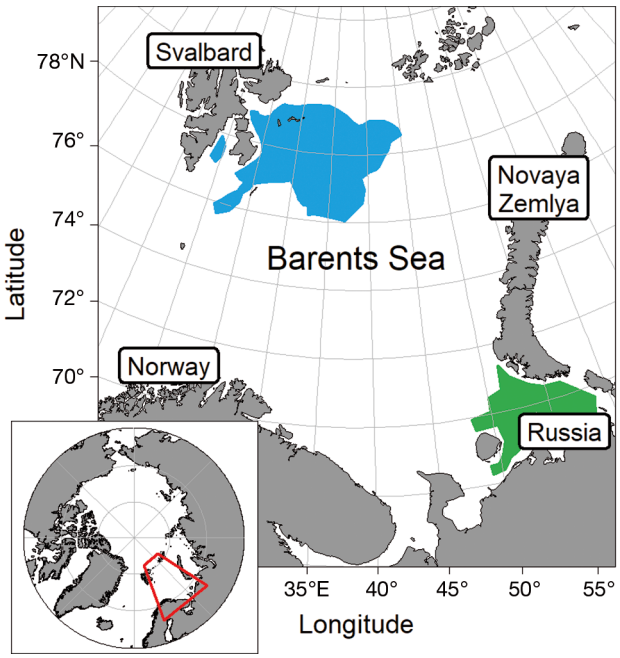

Fig. 1. Barents Sea and western (blue) and eastern (green) spawning grounds for polar cod (redrawn from Huserbråten et al. 2019). Map was generated using the R 'ggOceanMap' package (Vihtakari 2021)

The geographical coverage of the surveys varied between years. This variation may have led to an underestimation of age-specific stock abundances in years with reduced survey coverage of the Barents Sea. We included this effect in the model by using a binary index based on qualitative assessment of coverage based on the maps and survey description in the survey reports, dividing the years between 'limited' (16 yr for age 0 and 11 yr for ages 1–4) and 'extended' (14 yr for age 0 and 19 yr for ages 1–4) coverage (Fig. 3a). We considered the surveys with limited northeastern extent to result in a reduced coverage of the polar cod geographical distribution, i.e. 'limited' coverage.

2.2. Sea ice cover

Sea ice concentrations were extracted from satellite-derived data (Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, NSIDC-0051) provided by the National Snow and Ice Data Center website (Cavalieri et al. 1996; https://nsidc.org/data/NSIDC-0051/versions/1 [updated yearly], accessed 17 Feb 2020). These data represent the spatial average over a geographical grid (grid cell resolution 25 × 25 km) of monthly mean sea ice cover for the months from November–May for the whole Barents Sea, defined as the area between 69–80° N and 16–55° E, which covers both the western and eastern spawning grounds (Fig. 1). For each grid cell, sea ice cover was converted to percentage based on a threshold of 15%. All cells with sea ice cover below that threshold were considered ice-free (0% covered). We then computed the average sea ice cover across all cells to obtain a yearly sea ice cover index for the Barents Sea (Fig. 3b). The November–May period was chosen because it covers both the spawning and hatching periods (Rass 1968, Hop & Gjøsæter 2013), when sea ice may protect the fragile eggs from mechanical tear in open water and provides a critical refuge for larvae and juveniles as well as a foraging habitat for all age groups (Hop & Gjøsæter 2013, Eriksen et al. 2020, Aune et al. 2021). Moreover, the period includes the 6 mo period of the year with the highest average sea ice cover inside the Barents Sea.

2.3. Bottom sea temperature

Bottom sea temperature was computed as the mean annual summer temperature below 150 m from conductivity temperature depth (CTD) water column

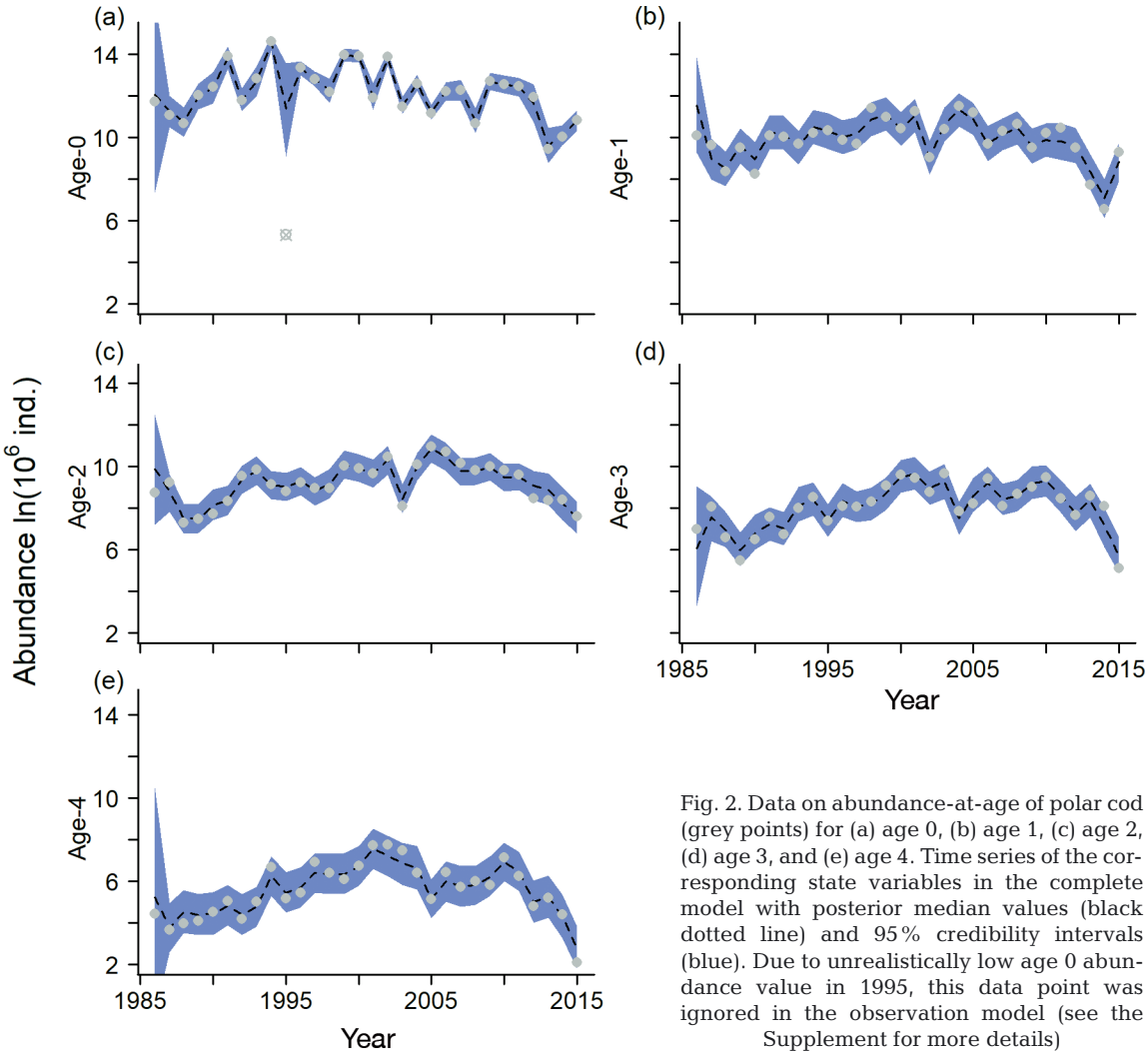

Fig. 2. Data on abundance-at-age of polar cod (grey points) for (a) age 0, (b) age 1, (c) age 2, (d) age 3, and (e) age 4. Time series of the corresponding state variables in the complete model with posterior median values (black dotted line) and 95% credibility intervals (blue). Due to unrealistically low age 0 abundance value in 1995, this data point was ignored in the observation model (see the Supplement for more details)

profiles extracted from the ICES marine database (ICES Data Portal 2020). The summer season was used to represent the primary and secondary production periods in the Central and Northern Barents Sea (Wassmann et al. 2006). We selected temperatures recorded in the Arctic part of the Barents Sea (74–80° N, 20–50° E), as the area is characterized by the presence of Arctic pelagic amphipods, one of the main prey for polar cod aged 1–4 years in the Barents Sea (Stige et al. 2019). We focused our selection on the summer months of August and September, when temperature profiles were the most regularly sampled both in space and time for the period 1986–2015. We further constrained the bottom temperature index by selecting only profiles with a maximum depth below 150 m and computing the average temperature below that depth. Sub-150 m temperatures were used to match the assumed depth range of adult polar cod. Since little is known about the polar cod depth distribution in the central and northern Barents Sea, we assumed it is similar to observations in the fjords of Svalbard (Falk-Petersen et al. 1986), north of Novaya Zemlya (Wathne et al. 2000) and in the Canadian Arctic (Geoffroy et al. 2016). In those areas, the depth distribution of polar cod changes ontogenically with young-of-the-year in surface layers and older age classes at deeper depths. The Arctic part of the Barents Sea is a shallow area with bottom depths under 200 m (Central and Great Banks; Klungsøyr et al. 1995). By selecting 150 m as the depth threshold, we selected a large number of stations while excluding shallow stations and depths that should mainly contain young-of-the-year polar cod. To account for differences in station locations and sampling date among years, we fitted a spatio-temporal generalized additive model to the average temperatures below 150 m and extracted the year-specific intercepts as an index of the mean annual

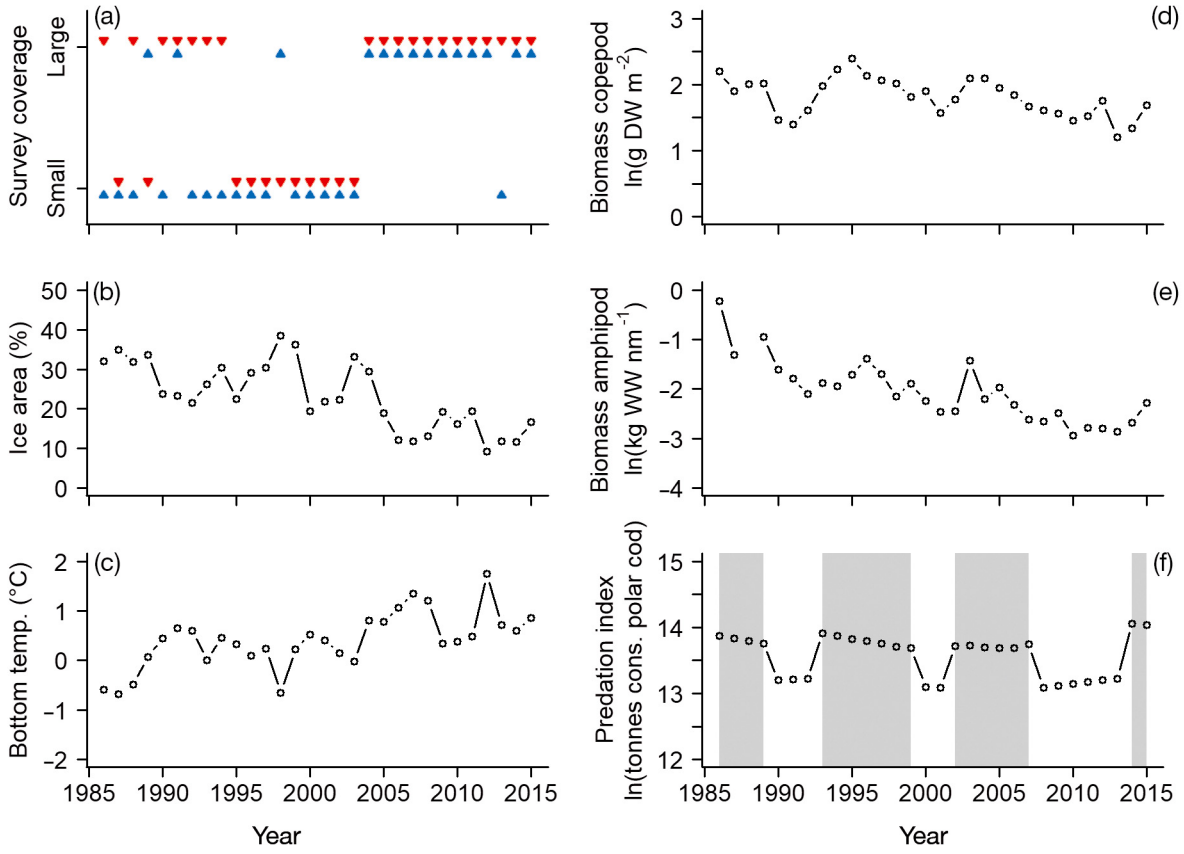

Fig. 3. Environmental data used in the complete model. (a) Survey coverage represents the quality of coverage for ages 1–4 (red) and age 0 (blue) polar cod; (b) sea ice cover; (c) mean bottom temperature index; (d) copepod biomass index; (e) amphipod biomass index (amphipod data for 1988 was missing and was replaced by the overall mean of the time series: $Amp_{1988} = -2.06$) and (f) predation pressure index—the index depends on amounts of cod, harp seals and capelin, assuming higher predation rates by cod and harp seals on polar cod in low-capelin years (grey background) than high-capelin years (white background)

temperature below 150 m (Fig. 3c; see the Supplement for details).

2.4. Prey indices

Prey were divided into 2 indices based on the main diet items of polar cod: large pelagic amphipods and copepods (Orlova et al. 2009, Hop & Gjøsæter 2013). Smaller and younger polar cod prefer copepod prey, whereas larger and older polar cod prefer amphipods. The dominant taxon represented by the amphipod index is *Themisto libellula*, a large amphipod endemic to Arctic waters (Stige et al. 2019). Dominant taxa for copepod biomass are *Calanus glacialis*, *C. finmarchicus* and *C. hyperboreus* (Aarflot et al. 2018). Data for those 2 zooplankton groups originate from the BESS surveys and constitute the only available long-term time series of mesozooplankton data for regions described as the northern and central Barents Sea (Stige et al. 2014). In the Barents Sea, August–September mesozooplankton data have been related to population dynamics of different fish species in the Barents Sea, including polar cod (Stige et al. 2010, Dupont et al. 2020). Both prey biomass time series (kg wet weight nm^{-1} from horizontal trawls for amphipods and g dry weight m^{-2} from vertical net sampling for copepods) were transformed into logarithmic annual indices by extracting the yearly component of statistical models predicting biomass of zooplankton accounting for the difference in sampling (see Stige et al. 2019 for details) (Fig. 3d,e).

2.5. Predation index

Main predators of polar cod in the Barents Sea include Northeast Arctic (NEA) cod *Gadus morhua* and harp seals *Pagophilus groenlandicus* (Ajiad et al. 2011). Predation pressure by both predators was

summarized into a single index to limit the number of parameters to be estimated in the model. Both predators may not exert the same predation pressure on polar cod; hence, the index was constructed to scale with the total biomass of polar cod consumed by cod and harp seals combined, on a logarithmic scale, and was considered a proxy for the total predation pressure from both predators.

The annual predation index included the consumption rates of both predators in addition to the biomass of NEA cod and abundance of harp seals, with the following equation:

$$Pred_t = \ln(m_{NEAcod,t}\, NEAcod_t + m_{seal,t}\, Seal_t) \quad (1)$$

where $Pred_t$ is the predation index on the logarithmic scale for year t, $NEAcod_t$ is the NEA cod biomass and $Seal_t$ is the harp seal abundance. For NEA cod biomass (1000s of tonnes), we used the estimated Barents Sea biomass of NEA cod older than 3 yr of age (ICES 2018), as NEA cod have been shown to start eating polar cod when reaching 20–30 cm in size (Holt et al. 2019), indicative of fish of 2–3 yr old (ICES 2018). For harp sea abundance, we used the number of individuals older than 1 yr of age, as younger seals mainly eat crustacean prey (Nilssen et al. 2001, ICES 2016). The terms $m_{NEAcod,t}$ and $m_{seal,t}$ are the estimated consumption rates of polar cod by NEA cod and harp seals, respectively. The consumption of polar cod by harp seals and NEA cod appeared to increase with a decrease in the stock abundance of capelin *Mallotus villosus* (Nilssen et al. 2000, Orlova et al. 2009). Therefore, we used different consumption rates for low and high capelin stock periods. These rates represent the mean yearly consumption rates based on an estimation of consumed polar cod biomass in the 1990–1996 period by each predator species and depending on year t having a lower or higher capelin stock (Fig. 3f) compared to the estimated average capelin stock biomass for the 1990–1996 period during the BESS (Prozorkevich et al. 2018).

2.6. State-space model

The time series of abundance of polar cod age groups were analyzed simultaneously in one statistical model that estimated the strength of abiotic and biotic effects. The population dynamics of polar cod was modeled using a state-space model in a Bayesian framework using the program STAN and the R package 'rstan' (Stan Development Team 2018, R Core Team 2020). The dynamics of each age group from age 1–4 were modeled according to the following general equation:

$$N_{a,t} = N_{a-1,t-1} e^{-M_a + \Sigma n_i E_{i,t} + \varepsilon^p_{a,t}} \quad (2)$$

where $N_{a,t}$ represents the true abundance of age a in year t, $N_{a-1,t-1}$ is the abundance of the same year class the previous year, M_a is a scaling factor that depends on the mean natural mortality as well as emigration and immigration rates of age a, n_i is the coefficient for effect of the environmental variable E_i and $\varepsilon^p_{a,t}$ is an error term, i.e. process error, normally distributed with a mean of zero. The process error represents all non-observed environmental effects influencing the state variables that are not explicitly accounted for by the model. The term $e^{-M_a + \Sigma n_i E_{i,t} + \varepsilon^p_{a,t}}$ represents the survival of the year class from year $t-1$ to t (if we assume that emigration and immigration rates are negligible). The dynamics of age 0 were modeled as in Eq. (1) but replacing $N_{a-1,t-1}$ with SSB_{t-1}, the SSB at year $t-1$. The model is described in more detail in Sections 2.6.1–2.6.3. On the natural logarithmic scale, Eq. (1) becomes a linear combination of population variables and environmental factors in addition to the process error term:

$$\ln(N_{a,t}) = -M_a + \ln(N_{a-1,t-1}) + \Sigma n_i E_{i,t} + \varepsilon^p_{a,t} \quad (3)$$

where $\ln(N_{a,t})$ is the true natural logarithmic abundance of age a in year t. By using this formulation, the model, which we refer to as the process model, effectively predicts the survival of age a based on a multiplicative effect of abundance the previous year and additive effects of environmental variables on the mortality rate (Stige et al. 2018). The process model is linked to abundance data by an observation model which describes the relationship between the modeled abundances and the reported abundances, using the following general equation:

$$\ln(Nobs_{a,t}) = \ln(N_{a,t}) + \varepsilon^{obs}_{a,t} \quad (4)$$

where $Nobs_{a,t}$ is the reported abundance at age a in year t and the $\varepsilon^{obs}_{a,t}$ are random observation errors for age a in year t, which are assumed to be normally distributed with a mean of zero. Observation errors are errors representing observation noise and possible bias in the sampling methods. This formulation allows the state-space model to explicitly account for uncertainties in all influential processes (biological or not) inside the process model ($\varepsilon^p_{a,t}$ in Eq. 3) as well as observation errors inside the observation model ($\varepsilon^{obs}_{a,t}$ in Eq. 4). The state-space model hence aims to provide an unbiased estimation of process model parameters and their credibility intervals. In this way, the results show the magnitude and uncertainty of the

different environmental and population effects, estimated simultaneously in one model.

2.6.1. The process model

The dynamics of each age group followed a Gompertz model (Gompertz 1825), schematically represented in Fig. 4 and referred to as the 'process model'. The Gompertz model has been successfully used to analyze population dynamics of fish stocks while simultaneously accounting for environmental factors (Langangen et al. 2017, Stige et al. 2019, Durant et al. 2020) and is described by the 2 following equations based on Eq. (3):

$$\ln(N_{0,t}) = Int_0 + (1-b)\ln(\mathrm{SSB}_{t-1}) + c_{0,ice}Ice_t + c_{0,cop}Cop_{t-1} + c_{0,pred}Pred_t + \varepsilon^p_{0,t} \quad (5a)$$

$$\ln(N_{a,t}) = Int_a + (1-c_{a,N_{a-1}})\ln(N_{a-1,t-1}) + c_{a,ice}Ice_t + c_{a,Bot}BotT_t + c_{a,cop}Cop_{t-1} + c_{a,amp}Amp_{t-1} + c_{a,pred}Pred_t + \varepsilon^p_{a,t} \quad \text{for } 1 \le a \le 4 \quad (5b)$$

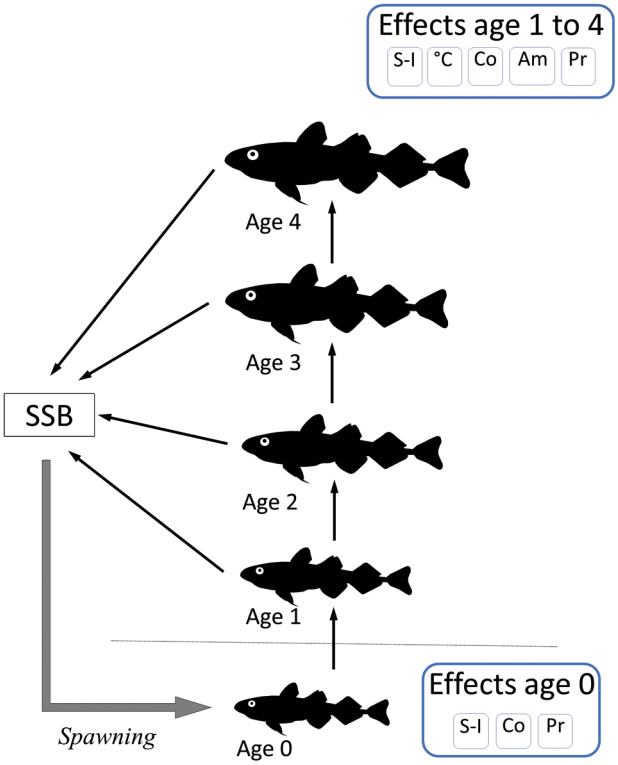

Fig. 4. State-space model concept. Environmental variables S-I: sea ice; °C: bottom temperature; Co: copepod biomass; Am: amphipod biomass; Pr: predation index. SSB: polar cod spawning stock biomass

where Int_0 and Int_a are the age-specific intercepts for ages 0 and a and $\ln(\mathrm{SSB}_{t-1})$ represents the natural logarithm of polar cod SSB at year $t-1$. SSB is calculated in the process model from:

$$\mathrm{SSB}_t = \Sigma^4_{a=1} Mat_a \overline{W_a} N_{a,t} \quad (6)$$

Here, $N_{a,t}$ is the modeled abundance at age a and year t, $\overline{W_a}$ is the observed long-term mean weight at age a and Mat_a is the long-term mean maturity at age a fraction. The Gompertz model includes a density-dependence parameter, b, that accounts for the effects of a changing SSB on the number of young-of-the-year ($N_{0,t}$) per SSB. The parameter b was restricted to values between 0 and 1 to avoid predicting that an increase in SSB led to decreasing abundance of young-of-the-year (overcompensation, $b > 1$) or to a proportionally larger increase in young-of-the-year (depensation, $b < 0$). A similar density-dependence parameter ($c_{a,N_{a-1}}$) was used for abundance of ages a ($N_{a,t}$) but allowing an overcompensation effect defined by an upper limit of 2. Parameters used in the process model equations account for environmental factors that, *a priori*, are thought to influence the abundance of polar cod: effect of sea ice cover (Ice_t) on age 0 ($c_{0,ice}$) and ages a ($c_{a,ice}$), effect of bottom temperature ($BotT_t$) at ages a ($c_{a,BotT}$), effect of copepod biomass the preceding year (Cop_{t-1}) on age 0 ($c_{0,ice}$) and ages a ($c_{a,cop}$), effect of amphipod biomass the preceding year (Amp_{t-1}) on ages a ($c_{a,amp}$) and effect of predator pressure the same year ($Pred_t$) on age 0 ($c_{0,ice}$) and ages a ($c_{a,pred}$). The bottom temperature effect was only included for ages 1–4, as age 0 mainly occupies the upper layer of the water column while older ages have been observed to live in deeper layers (Geoffroy et al. 2016). Effect of sea surface temperature was not included in the equation for age 0 because surface temperature is strongly correlated with sea ice cover (Huserbråten et al. 2019). The process error for age 0 ($\varepsilon^p_{0,t}$) and ages a ($\varepsilon^p_{a,t}$) were jointly drawn from a multivariate normal distribution to account for correlated process errors between the different ages.

2.6.2. The observation model

We accounted for survey coverage in the observation model with the following equation based on Eq. (4):

$$\ln(Nobs_{a,t}) = \ln(N_{a,t}) + \ln(1 - Cover_a I_{a,t}) + \varepsilon^{obs}_{a,t} \quad (7)$$

Here, $Cover_a$ is a scaling coefficient for the effect of reduced survey coverage, ranging between 0 and 1,

with 0 for no effect and 1 for a strong effect of reduced coverage, and $I_{0,t}$ and $I_{a,t}$ are Boolean values of 0 for 'extended' coverage (i.e. no applied correction) and 1 for 'limited' coverage. $\varepsilon_{a,t}^{obs}$ are the normally distributed observational errors for age a. Variance for the distribution of observational errors, $\varepsilon_{a,t}^{obs}$, was set to a fixed value based on the reported confidence interval around the abundance estimate for age $a = 0$. Confidence intervals are reported for the 0-group data, with specific data for the eastern and western components. We used the R package 'lognorm' (Wutzler 2019, R Core Team 2020) to estimate an uncertainty interval for the sum of the 2 lognormal components assuming no correlation between the 2 time series of abundance for age 0. Then we approximated the standard error of abundance at age 0 by dividing the logarithmic difference between the upper confidence interval and the estimated abundance at age 0 by 1.96, i.e. the z-score for the 95% confidence interval. Since the confidence interval of abundance estimates are not given for ages 1–4 in the BESS report (Prozorkevich et al. 2018), we assumed that the variance of the observational errors was equal to the variance of the process errors for each of these age groups.

2.6.3. Posterior distributions, convergence diagnostics and model fitting

The model parameters and state variables were estimated using 4 chains and a total of 40 000 iterations per chain to ensure convergence. Chains were visually inspected using the diagnostic tool 'shinystan' (Gabry 2018) to ensure good mixing and low autocorrelation. Convergence of chains was also confirmed using the Gelman and Rubin convergence index $\hat{R}$ (Gelman & Rubin 1992), checking that all parameters had values below 1.01. The parameter values were sampled in each chain after a 20 000 iteration initial sequence (i.e. burn-in), and for every 10th iteration in the remaining 20 000 values to avoid autocorrelation in the sampled values, leading to a total of 8000 independent values. Those values constitute the estimated statistical distribution of the parameter, i.e. the posterior distribution. In Section 3.1 we presented the median of the posterior distributions as the most likely value for the parameter as well as the 95% sampled value interval, i.e. the credibility interval. The width of the credibility interval represents the uncertainty of the estimated effect. We interpreted a credibility interval that did not include zero as strong evidence for the existence of an environmental effect. If the credibility interval included zero, we interpreted the effect as weak if the associated median value was close to zero and/or as uncertain if the associated credibility interval was broad.

In addition, we used the same 8000 sampled parameter values and associated process errors to reproduce 8000 time series of abundances for all age groups from observed environmental variables values. Yearly medians and 95% credibility intervals for the estimated times series were used to visually assess the fit of the model to the observed times series of abundance.

2.7. Hindcast scenarios

To explore the effect of environmental conditions on the polar cod population, we used hindcast scenarios that simulated the dynamics under different climate states (as represented by sea ice and sea temperature) or different predation regimes. First, we extracted the process errors for each estimated time series of abundance-at-age for the modeled years 1986–2015, representing the null scenario with observed environmental conditions. Second, using the associated posterior values for each parameter of the model, we simulated new time series of abundances-at-age of polar cod in hindcast-scenario approach. Here, the specific abiotic (i.e. sea ice and bottom temperature) or biotic (i.e. predation) environmental variables that defined each hindcast scenario were kept constant and the observed values were used for the remaining environmental variables. We evaluated 4 different hindcast scenarios: (1) low ice cover and high bottom temperature (since both variables are highly negatively correlated), hereafter referred to as the warm condition scenario, (2) high sea ice cover and low bottom temperature, referred to as the cold condition scenario, (3) low predation pressure and (4) high predation pressure. Sea ice and bottom temperatures were kept constant at either low or high values representing the 15th and 85th percentiles of their observed distributions. These percentiles were chosen to represent extreme values of the combination of ice and temperature within the range of observations. Low and high predation pressure values were set at the lowest or highest observed predation index values in 2008 and 2014, respectively. In order to make biologically meaningful hindcast scenarios, we used a restricted version of the model where we only kept parameters that showed a posterior distribution with a median value that was consis-

tent with a biologically interpretable effect. We chose 3 biological metrics to describe the results for hindcasting (1) total stock biomass (TSB), which was obtained by summing the different age groups abundance times their respective mean weight-at-age, (2) SSB, which was extracted from the model, and (3) recruitment to the adult stock at age 1, which was represented by the total biomass at age 1, obtained by multiplying predicted abundance and mean weight for age 1.

3. RESULTS

3.1. Posterior distribution of parameters: complete and restricted models

The survey coverage parameters ($Cover_a$) posterior distributions had medians from 0.22 to 0.40 depending on age (highest for age 2), implying that abundances in years with poor survey coverage were underestimated by 22–40% (Fig. 5).

The parameter b posterior distribution at age 0 suggested a weak but uncertain stock-recruitment relationship with a large 95% credibility interval and a high median (b = 0.73) (Fig. 5). Density-dependence posterior distribution in the complete model for age 1 was also characterized by a high median (c_{1,N_0} = 0.69), albeit a smaller 95% credibility interval (i.e. more certain) than density-dependence for age 0. This suggests compensatory density-dependence in survival between age 0 and age 1. In contrast, density dependence in survival for ages 2–4 was estimated to be much lower (Fig. 5).

The posterior distributions for the parameters for ice effects on abundance of ages 0 and 1 ($c_{0,ice}$ and $c_{1,ice}$) had positive medians with the 95% credibility intervals including strictly positive values, indicating strong sea-ice effects (Fig. 5). For these ages, the ice parameter was around 0.1, implying that a reduction in sea ice cover from 30 to 10%, as observed in the study period, was associated with a 7-fold reduction in survival. Posterior distributions for the effects of ice on abundance at ages 2 to 4 ($c_{2,ice}$, $c_{3,ice}$ and $c_{4,ice}$) also showed positive medians but were closer to 0 with associated 95% credibility intervals including zero, suggesting weak effects of ice for these ages.

The posterior distributions for the parameters for the effects of bottom temperature on abundance at ages 1 and 2 ($c_{1,BotT}$ and $c_{2,BotT}$) were mostly positive

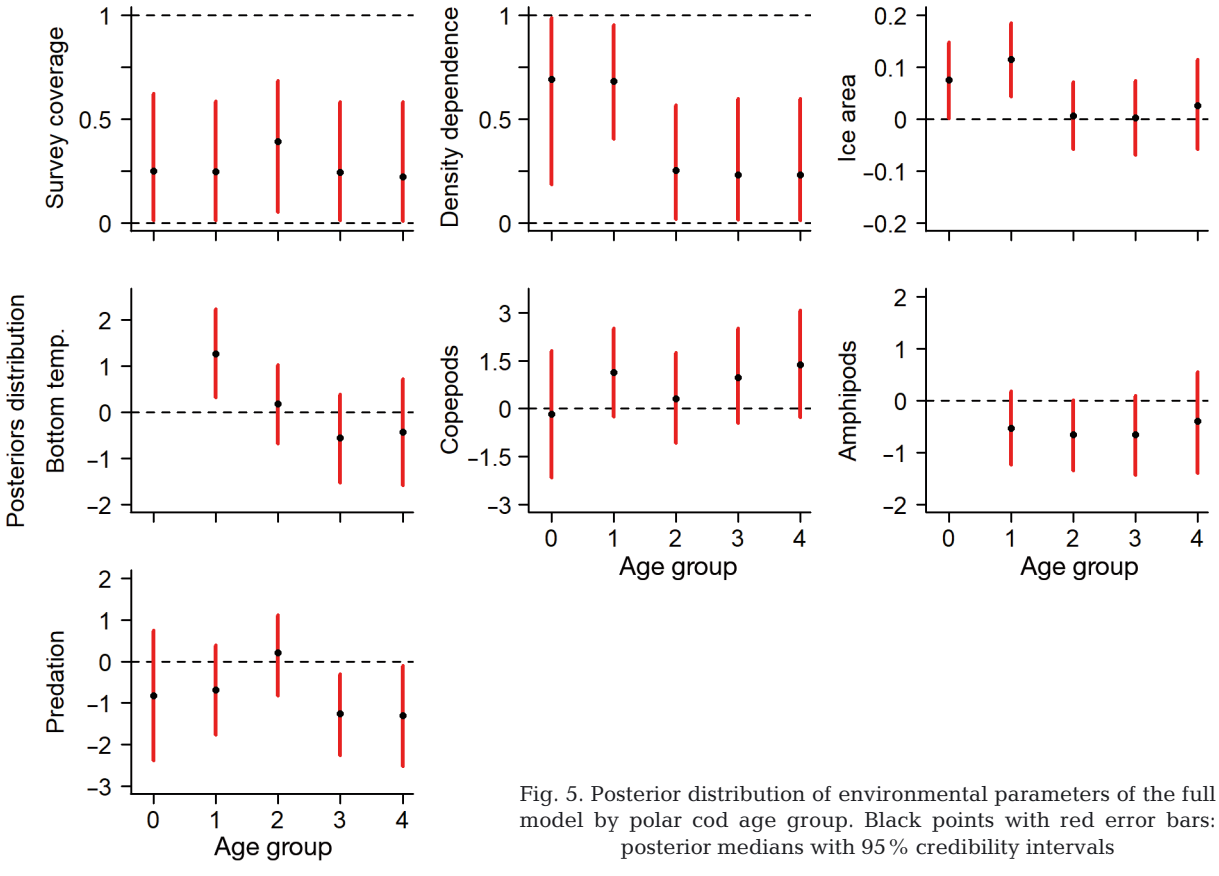

Fig. 5. Posterior distribution of environmental parameters of the full model by polar cod age group. Black points with red error bars: posterior medians with 95% credibility intervals

with median values higher than zero (Fig. 5). However, only the 95% credibility interval for age 1 included strictly positive values, indicating a strong temperature effect. The parameter value was around 1, implying that a 1°C increase in temperature was associated with approximately a 3-fold increase in survival to age 1. Posterior distributions for effects of bottom temperature on abundance at ages 3 and 4 ($c_{3,BotT}$ and $c_{4,BotT}$) showed negative median values. However, effects were weak as indicated by the median values being around −0.5 and the 95% credibility intervals including zero.

Positive median values of the posterior distributions for the copepod biomass parameter ($c_{a,cop}$) indicated predominantly positive effects for ages 1 to 4 (Fig. 5). Parameter values were around 1, implying that a doubling in copepod biomass (+0.69 on the logarithmic-scale prey index) was associated with approximately a doubling in survival. However, all posterior distributions included zero in the 95% credibility interval, suggesting high uncertainty in the effect of copepod biomass on the abundance of the different age groups.

Amphipod biomass had negative effects on abundance at ages 1 to 4 ($c_{a,amp}$), with posterior distributions showing only negative medians (Fig. 5). Parameter values were around −0.5, implying that a doubling in amphipod biomass was associated with approximately a 30% reduction in survival. None of these posterior distributions excluded zero from their 95% credibility interval, implying high uncertainty in the effects of amphipod biomass on the polar cod stock.

The posterior distributions for the predation parameters ($c_{0,pred}$ and $c_{a,pred}$) had negative median values for all ages except age 2 (Fig. 5). Only ages 3 and 4 had 95% credibility intervals that excluded zero, indicating a strong negative effect of predation for these age groups. The parameter values for these ages were around −1, implying that a doubling in predation pressure (+0.69 in the logarithmic-scale predation pressure index) was associated with approximately a 50% reduction in survival of these ages. Note that increased predation pressure in the model could be caused by increased abundances of harp seals and NEA cod as well as by reduced capelin abundance.

A restricted version of the complete model was used to simulate hindcast scenarios. We removed the amphipod variable from the model since all posterior distributions suggested a negative effect of amphipods on abundance of polar cod, which is biologically difficult to explain as a prey effect on its predator. In the restricted version of the model, the retained parameters were all distributed similarly to the posterior distributions shown for the complete model (see Fig. S1 in the Supplement).

3.2. Trends in population variables

Both the complete and restricted models reproduced well the observed time series in abundance for all ages of polar cod (Figs. 2 & S2). There were no obvious deviations from the estimated trends compared to the observed time series, which would indicate a misspecification of the model (Fig. 4). For the restricted model, this showed that the variability in abundance explained by the removed parameters was well integrated in the process errors as non-specified environmental effects. Yearly medians of TSB and SSB calculated from the state variables in the restricted model showed a general increase from the late 1980s to the early 2000s, followed by a decrease from 2005 (Fig. 6a,b). Recruitment at age 1 showed a similar trend, with high interannual variability (Fig. 6c).

3.3. Scenario results

Across the time series, TSB increased on average by 87% in the 'cold' scenario with high ice cover and low temperature and decreased by 34% in the 'warm' scenario with low ice and high temperature compared to the 'null' scenario with observed ice and temperature values (Fig. 6a), i.e. the modeled state variables representing the observed time series (see above). SSB and recruitment at age 1 increased by 58 and 155%, respectively, in the cold scenario and decreased by 26 and 43% in the warm scenario (Fig. 6b,c). The differences between cold and warm scenarios increased over the first 5 yr of the simulated time series (1986–1990) as environmental effects on TSB and SSB accumulated (Fig. 7a,b). After this transient period, i.e. in years 1991–2015, the yearly difference in simulated biomass time series between cold and warm scenarios remained stable and resulted in higher biomass values in the cold scenario than the warm scenario. On average for the latter period, TSB for the warm and cold scenarios differed by 1.1 on the logarithmic scale (logarithmic average median difference; Fig. 7a), corresponding to a change by a factor of 3. SSB and recruitment at age 1 differed by 0.8 and 1.46, respectively, on the logarithmic scale, corresponding to changes by a factor of 2.2 and 4.3 (Fig. 7b,c). Effects

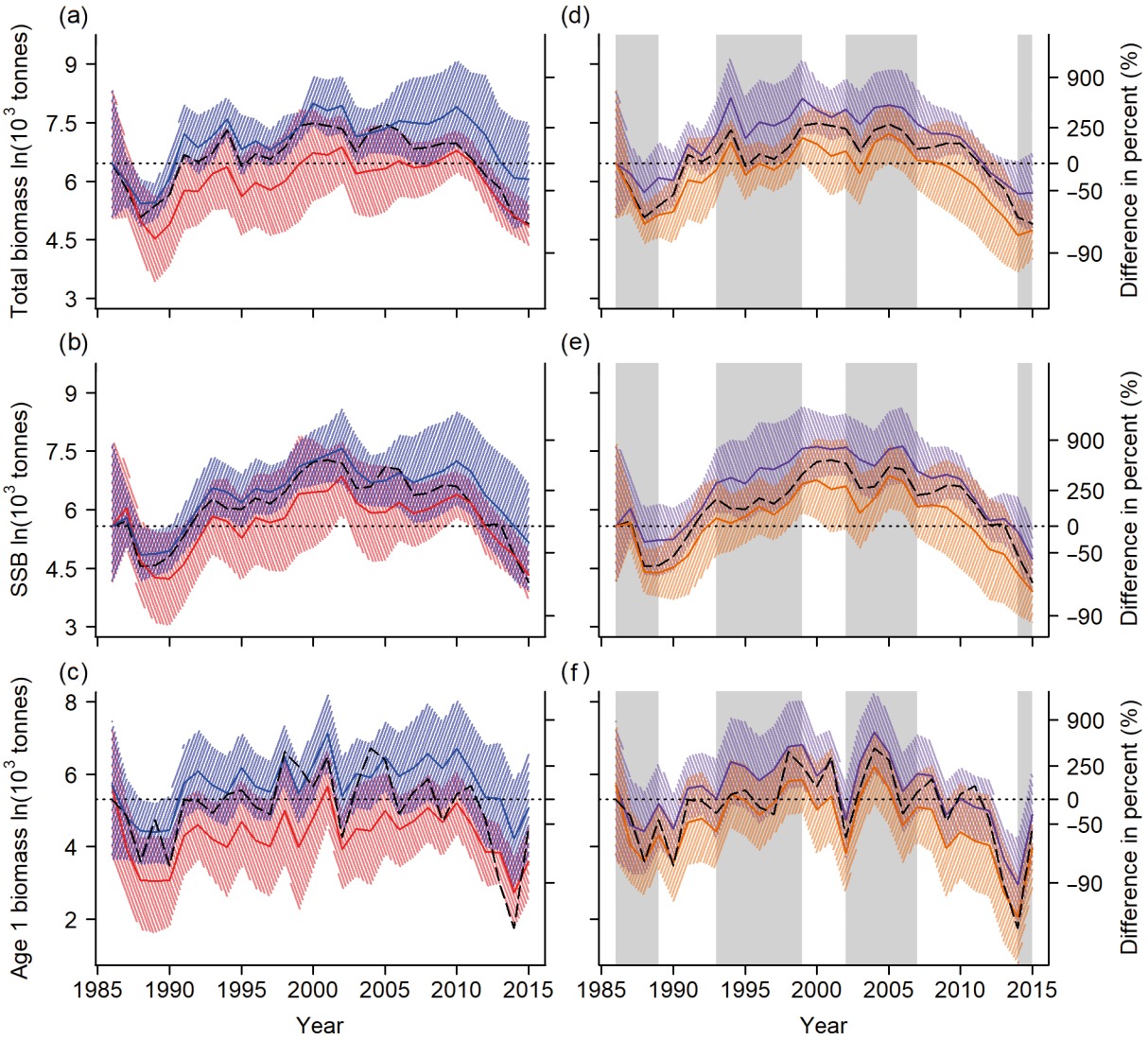

Fig. 6. Polar cod (a) total stock biomass, (b) spawning stock biomass (SSB), and (c) recruitment at age 1 simulated using observed environmental values (dashed black line: posterior median values), in hindcast warm scenario with low ice/high temperature (red line: median; hatched red area: 95% credibility interval) and cold scenario with high ice/low temperature (blue: median; hatched blue area: 95% credibility interval). (d) Total stock biomass, (e) SSB and (f) recruitment at age 1 simulated using observed environmental values (dashed black line: median values) in hindcast scenario with low predation (solid purple line: median; hatched purple area: 95% credibility interval) and scenario with high predation (solid orange line: median; hatched orange area: 95% credibility interval). Left axes show values in tonnes; right axes show values as differences from the first year of the time series (1986)

on TSB, SSB and recruitment at age 1 were all uncertain, as shown by broad credibility intervals (Fig. 7a,b,c). The effect on recruitment at age 1 appeared stronger than the effects on TSB and SSB and had a credibility interval excluding zero. The effect on TSB appeared stronger than the effect on SSB and the credibility interval of TSB excluded zero in some years.

The general high levels in TSB and SSB from 1990 to the early 2000s were reproduced in the cold scenario (Fig. 6a,b). This finding suggests that strong year classes of polar cod in the Barents Sea were associated with high ice cover and low temperature in the 1990s to early 2000s. Through the 2000s, TSB, SSB and recruitment at age 1 gradually declined as temperature increased and sea ice cover retreated (Fig. 6a,b,c). Our results suggest that this decline would not have occurred if the ice and temperature conditions had remained constant as simulated in the hindcast scenarios. There were, however, 2 major declines that were not explainable through temperature and sea ice, as similar declines occurred in both

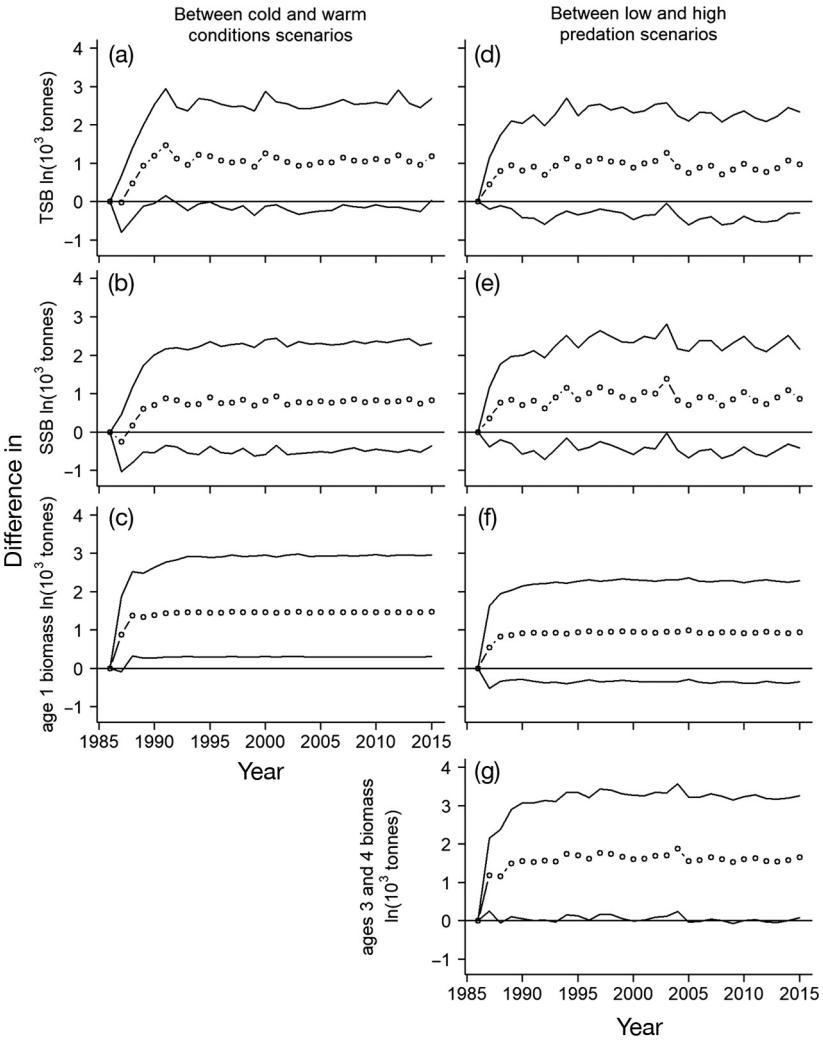

Fig. 7. Logarithmic difference between time series of polar cod (a) total stock biomass (TSB), (b) spawning stock biomass (SSB) and (c) recruitment at age 1 in cold and warm scenarios. Logarithmic difference between time series of (d) TSB, (e) SSB, (f) age 1 biomass and (g) ages 3 and 4 biomass in low and high predation scenarios. Points and full lines show the annual median value and the upper and lower limit of the 95% credibility interval for the logarithmic difference

cold and warm scenarios. The first major decline occurred in the late 1980s and the second in the 2010s, both with large impacts on both TSB and SSB (Fig. 6a,b).

The TSB, SSB and recruitment at age 1 were on average 78, 76 and 70% higher, respectively, in the low predation scenario compared to the null scenario with observed predation index values (Fig. 6d,e,f). In contrast, TSB, SSB and recruitment at age 1 were on average 28, 26 and 31% lower in the high predation scenario than in the null scenario (Figs. 6d,e,f). As for cold and warm scenarios, the distributions of yearly differences between low and high predation scenarios increased through the first 5 simulated years and was stable in the 1991–2015 period (Fig. 7e,f). The average median difference between high and low predation scenarios in the latter period was ~0.9 on the logarithmic scale, corresponding to a change by a factor of 2.5 for TSB, SSB and recruitment at age 1 (Fig. 7d,e,f). Focusing on the ages with the strongest estimated predation effects, the average logarithmic median difference was 1.6 for the summed biomass of ages 3 and 4, corresponding to a change by a factor of 5.1 (Fig. 7g). The changes in TSB, SSB and recruitment at age 1 were all uncertain, characterized by large credibility intervals that clearly included zero. Only the 95% credibility interval for the predation effect on biomass of ages 3 and 4 excluded zero (Fig. 7g). These findings suggest an overall weaker effect of predation on TSB and recruitment at age 1 compared to the effects of the abiotic factors. This weak effect was reflected in the trends in TSB and SSB in low and high predation scenarios, which conserved to a large extent the temporal trend of the null scenario throughout the studied period (Fig. 6d,e).

4. DISCUSSION

In this study, we developed a statistical model that jointly estimated the age-specific effects of abiotic and biotic factors on the population dynamics of polar cod in the Barents Sea. Our results showed positive effects of sea ice and bottom temperature on young ages of polar cod, and negative effects of predation pressure on older ages. However, the model parameter estimates did not indicate significant age-specific effects of prey biomass. In addition, our results suggested a weak stock-recruitment relationship as well as compensatory dependence between ages 0 and 1. Upscaling the effects of significant abiotic and biotic effects from age-specific to the population level using hindcast scenarios showed a negative effect of decreased sea ice and increased bottom temperature as well as a negative effect of increased

predation pressure. However, the impact of a predation change at the population level was weaker than the effect of a change in abiotic conditions.

4.1. Effects of abiotic factors on the survival of polar cod

Our results showed positive significant effects of the 2 included abiotic factors, i.e. winter sea ice on the abundance of ages 0 and 1 and summer sea bottom temperature on the abundance of age 1 polar cod. Decreases in sea ice extent have been related to a variety of observed changes in the food web at different trophic levels. For example, decreasing sea ice is associated with increasing primary production (Dalpadado et al. 2020), decreasing biomass of Arctic zooplankton (Stige et al. 2019, Møller & Nielsen 2020) and decreasing survival of sea ice-associated species (Wassmann et al. 2011), as we showed for polar cod in this study.

In the Barents Sea, a decrease in winter sea ice cover or increase in summer sea surface temperature may cause a reduction in the spawning grounds of polar cod and decreased survival of larvae, resulting in decreased age 0 abundance (Eriksen et al. 2015, Huserbråten et al. 2019). Our results are in accordance with those results by showing a positive effect of winter sea ice cover on age 0 abundance. Our results also showed a positive association between winter sea ice cover and age 1 abundance. Age 1 fish have been observed to actively hide in crevices and sandwich ice floes southeast of Svalbard (Lønne & Gulliksen 1989), and predators of age 1 polar cod have been observed avoiding areas of high ice cover (LeBlanc et al. 2019). Those observations suggest that sea ice may be used as a refuge from predation during winter and support a positive association between winter sea ice and survival to age 1. In addition, young polar cod may feed on sea ice-associated species (Renaud et al. 2012, Kohlbach et al. 2017) and a decrease in winter sea ice is likely to be associated with reduced access to sympagic prey during winter. Polar cod may sustain good body condition and find sufficient food resources by feeding on sympagic prey below the sea ice (Kohlbach et al. 2017). However, Renaud et al. (2012) suggested that ice fauna does not contribute to a large portion of the diet of polar cod based on analyzing diet data from both open water and sea ice-covered areas around Svalbard. In the seasonally ice-covered Barents Sea, polar cod may have access to both sympagic and pelagic prey over the course of a year. It remains poorly understood how much the survival of polar cod in these areas depends on access to sympagic prey in the ice-covered period compared to pelagic prey during the open water season. Finally, reduction of the sea ice import to the Barents Sea linked to the decrease of sea ice area in the northern Barents Sea (Lind et al. 2018) may be associated with a reduction in the recruitment of polar cod from nearby seas (David et al. 2016). However, the proportion of polar cod recruits that originate from spawning outside of the Barents Sea is unknown.

Our results showed a decrease in age 0 survival associated with a decrease in winter sea ice cover. However, concurrent with the decrease in survival, an increase in length-at-age of age 0 polar cod is associated with the reduction of winter sea ice in the Barents Sea (Dupont et al. 2020). These associations contrast with the situation in the Canadian Arctic where both survival and length-at-age of age 0 polar cod increased in years with an earlier sea ice breakup and decreased winter sea ice cover (Laidre et al. 2015, Bouchard et al. 2017, Mudryk et al. 2018, LeBlanc et al. 2020). The positive association between length-at-age and survival of age 0 polar cod is related to the increase of summer zooplankton biomass in years of early sea ice break-up during the summer months (LeBlanc et al. 2020) and increased survival of early hatchers (Bouchard et al. 2017). A positive association between length-at-age and survival is generally expected if variation in growth is large, as increased size may lead to improved resilience to starvation and decreased size-dependent mortality (Miller et al. 1988, Sogard 1997). A negative association between length-at-age and survival can, however, occur if the variation in such size-dependent mortality is large, driven by, e.g. variations in predation levels or if an increase in length comes at the expense of increased lipid reserves needed for overwintering. Population dynamics of polar cod appear to react differently to sea ice changes in the Barents Sea compared to the Canadian Arctic. In the Barents Sea, sea ice breakup starts in spring (Dong et al. 2020) and an early breakup may lead to a 'match/mismatch' effect (Cushing 1990), decreasing the survival of age 0 polar cod in years of reduced ice cover (Huserbråten et al. 2019) even as the extended feeding season may lead to increased length in the surviving individuals (Dupont et al. 2020). In the Barents Sea, the contrasting associations of sea ice with different population dynamics parameters such as growth and survival are likely to contribute to the uncertain population-level effects of sea ice on polar cod.

Our study found a positive relationship between summer bottom sea temperature and survival of age 1 polar cod in the −1 to 2°C range. Our temperature index is representative of the area where polar cod undertakes its feeding migration, as well as the time of the year corresponding to the highest stomach fullness indicative of strong feeding activity (Aune et al. 2021). Our result is consistent with observed increases in growth and activity rates with increasing temperature up to 10°C (Laurel et al. 2016, Kunz et al. 2018), which may offer a physiological benefit against starvation and predation pressure (e.g. through increased swimming speed). At a population level, the positive association between survival at age 1 and temperature in the −1 to 2°C range is similar to the positive association between abundance and summer temperature reported for the Beaufort Sea (Forster et al. 2020) but opposite to the negative association found in the Bering Sea (Marsh & Mueter 2020). The difference in the sign of association with temperature may be due to temperature influencing different ecological aspects in the different geographic areas. In the Barents Sea, the summer bottom sea temperature is representative of the warm North Atlantic water masses located under colder Arctic water masses (Lind et al. 2018). Increased bottom temperatures, therefore, reflect the increase in heat content and inflow of North Atlantic water masses into the Barents Sea observed in the last decades (Lind et al. 2018). Age 1 fish located in these water masses in summer could benefit from increased availability of prey species advected from productive areas farther south, such as Atlantic zooplankton (Loeng & Gjøsæter 1990), and better temperature conditions for growth (Laurel et al. 2016) during their feeding season in the Arctic (Aune et al. 2021). Winter sea ice and summer bottom temperature are negatively correlated (Dupont et al. 2020). This suggests that, potentially, the positive effect of increased bottom sea temperature on survival of age 1 may counteract the simultaneous negative effect of decreased sea ice on survival of ages 0 and 1, until temperature values reach physiological optimums (Laurel et al. 2016, Kunz et al. 2018).

4.2. Effects of biotic factors on the survival of polar cod

Our results showed a significant negative relationship between the predation index and abundances for ages 3 and 4. This result is consistent with NEA cod and harp seals being important predators for polar cod (Ajiad et al. 2011). The strong age-dependent association may be explained by those predators' abilities to prey on older polar cod located in deeper waters (Wathne et al. 2000, Geoffroy et al. 2016, LeBlanc et al. 2019). In the Barents Sea, deep located older polar cod could overlap with the depth distribution of Atlantic cod (Fall et al. 2018) as well as be captured by harp seals capable of deep diving (Folkow et al. 2004). The weak association between the predation index and the abundance of age 0 to 2 does not rule out that a stronger effect on the younger stages could be exerted by other predators not included in our model such as other seal species, e.g. ringed seal *Pusa hispida*, or seabirds, e.g. Brünnich's guillemot *Uria lomvi*a (Erikstad 1990, Wathne et al. 2000, Benoit et al. 2010, Wold et al. 2011).

Our predation index did not explicitly consider the increasing overlap between NEA cod and polar cod related to the northward expansion of the NEA cod population in association with increased temperature in the Barents Sea and NEA cod population size (Fossheim et al. 2015, Fall et al. 2018). An increased geographical overlap between prey and predators may affect consumption by NEA cod and may lead to an underestimation of predation pressure by our model in periods with high overlap. The increase in overlap was only studied for the period 2004–2015 that represents only the second half of our time series (Fossheim et al. 2015, Fall et al. 2018). In addition, the effective degree of overlap between prey and predators is difficult to assess due to the seasonal migrations of NEA cod in the Barents Sea and the difficulty of disentangling a long-term trend from inter-annual variations in spatial overlap (Howell & Filin 2014, Fall et al. 2018). Hence, it remains unclear if predation by NEA cod was underestimated for recent years and may have led to a weaker predation effect in our results.

Our results showed a weak effect of prey biomass in late summer on the survival of polar cod at any age group. No significant association between biomass of polar cod and biomass of copepods and amphipods in late summer was found either at the population level in the Barents Sea (Stige et al. 2019). However, our study and Stige et al. (2019) differ by using different time lags for the effects of the zooplankton prey on polar cod. We used previous-year data while Stige et al. (2019) used same-year data. Our study considered the amount of prey before the productive season, while Stige et al. (2019) considered the amount of prey left after the productive season. In practice, either previous- or same-year prey biomass can be an index of yearly production of prey in the Barents

Sea during the productive season (Gjøsæter et al. 2002). In addition, in seasonally ice-covered areas, the production at all trophic levels is likely to depend on the length of the ice-free period. Because both studies found similar results, we suggest that the survival of polar cod in the Barents Sea is generally weakly dependent on the biomass levels of pelagic copepods and amphipods; although both prey are a fixed feature of the diet of polar cod (Aune et al. 2021). Similarly, the length-at-age of polar cod showed mostly weak associations with prey biomass levels, but consistently negative associations with winter sea ice concentration (Dupont et al. 2020). That finding suggests that growth is more strongly associated with the length of the productive season than with prey biomass levels, which could also explain why prey biomass levels in this study were not correlated with survival. Furthermore, polar cod diet mirrors prey availability in both space and time (Renaud et al. 2012, Aune et al. 2021). Other prey items that were not included in our analysis may thus be of importance for survival of polar cod. For example, euphausiids *Thysanoessa raschii* are also a regular item in the diet of polar cod and appear to dominate stomach content in the southern part of the distribution of polar cod in the Barents Sea (Bogstad et al. 2011, Aune et al. 2021).

4.3. Effects of a changing environment on an Arctic marine species

Not all Arctic species react in a similar way to environmental changes (reviewed in Wassmann et al. 2011). Our results synthesized the effects of both abiotic and biotic environmental factors on polar cod, a fish species with a close relationship to sea ice cover, in addition to being a common prey for a large variety of Arctic top predators (Welch et al. 1992). State-space models have already been used in the Barents Sea ecosystem to study ecological dynamics, including studies of predator–prey interactions (Stige et al. 2018, Durant et al. 2020), effects of mass mortality events (Langangen et al. 2017) and the effects of density-dependence and stochastic ecosystem processes on a fish population (Ohlberger et al. 2014). Our approach illustrates the use of the state-space framework to separate and estimate the effects of multiple environmental factors on a population at an age-resolved level and simulate consequences of change in environmental conditions on the population, while taking into account uncertainties linked to environmental effects. It represents a development of previous state-space model work on the polar cod population (Stige et al. 2019) by extending the model resolution to an age-specific level, which appears essential to assess the ecological processes and mechanisms at work for observed associations at the population level. Our results showed strong associations between polar cod age-specific survival and environmental factors that are sensitive to global warming and underlined that environmental factors may affect age groups differently, as hypothesized in Stige et al. (2019).

Effects at different ages have distinct consequences for the dynamics at the population level. Our results showed strong evidence that recruitment at age 1 was higher under the cold scenario than the warm scenario. This difference suggests that changes in abiotic conditions affected the recruitment of polar cod into the adult stages. However, the strong effect of the abiotic factors on recruitment at age 1 did not translate into similarly strong effects on TSB and SSB of polar cod. The change from a strong effect on recruitment at age 1 to a weaker effect on TSB and SSB suggests that changes in recruitment at age 1 caused by abiotic factors are dampened during later stages and are unlikely to be responsible for major changes in TSB and SSB as suggested previously (Huserbråten et al. 2019). Reduction of the environmental effects may be a result of density dependence between age groups (Ohlberger et al. 2014, Langangen et al. 2017) as evidenced by the slight but nonetheless compensatory density-dependent effects on survival at ages 2 to 4.

According to our predation scenarios, variation in predation pressure had a weak effect on the TSB, SSB and recruitment at age 1 of polar cod, although the predation effect on ages 3 and 4 biomasses was similarly strong as the effects of the abiotic factors on age 1 biomass in the abiotic factors scenarios. This differs from other high latitude fish species like capelin and NEA cod, with top-down effects on pre-recruit stages that may have a significant effect on the species' population dynamics (Hjermann et al. 2010, Stige et al. 2010). Top-down effects of predators on older age groups may affect population dynamics of polar cod through different mechanisms: firstly, by directly removing individuals that contribute to SSB and by indirectly affecting the recruitment of young age groups (0 and 1) through the stock-recruitment relationship, e.g. in Norwegian spring spawning herring *Clupea harrengus* (Fiksen & Slotte 2002), and secondly, by removing the oldest and largest spawners that potentially have the highest reproductive output per weight of spawners as

observed for e.g. Atlantic cod (Marteinsdottir & Begg 2002). However, the importance of the first mechanism was reduced by ages 3 and 4 having a lower contribution to SSB than other age groups (Fig. S3) and by high compensatory density-dependence between SSB and age 0 as well as between age 0 and age 1 dampening the stock-recruitment relationship. The importance of the second mechanism is questioned by the finding that reproductive output per weight of spawners is similar for different age groups of polar cod in the Barents Sea (Aune et al. 2021). In summary, the top-down effects mainly impacted age groups with a limited contribution to SSB, and strong density dependence between SSB and recruitment may result in resilience of the polar cod population to changes in predation in the Barents Sea.

Using state-space models, we quantified the effects of multiple environmental factors on the population dynamics of an Arctic fish species. Our results showed that in association with the warming of the Barents Sea, decreased winter sea ice and increased summer bottom temperature were associated with a strong decrease in survival of young age groups, resulting in a decrease, albeit not similarly strong, of the TSB of polar cod. Considering the central role of polar cod within the Arctic food web, reduced population size of polar cod in a warmer climate may eventually affect the transfer of energy along the food chain toward Arctic top predators. Top-down predation effects, which are changing under the pressure of global change as well, were weaker than effects of abiotic factors at the population level. We propose that top-down effects mainly affecting old age groups combined with strong compensatory density dependence in recruitment may so far have made the polar cod population in the Barents Sea relatively resilient to changes in predation.

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