






## Original Article

# Sea ice, temperature, and prey effects on annual variations in mean lengths of a key Arctic fish, *Boreogadus saida*, in the Barents Sea

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Oceanographic conditions in the Arctic are changing, with sea ice cover decreasing and sea temperatures increasing. Our understanding of the effects on marine populations in the area is, however, limited. Here, we focus on the Barents Sea stock of polar cod (*Boreogadus saida*). Polar cod is a key fish species for the transfer of energy from zooplankton to higher trophic levels in the Arctic food web. We analyse the relationships between 30-year data series on the length-at-age of polar cod cohorts (ages 0–4) and sea surface temperature, sea ice concentration, prey biomasses, predator indices, and length-at-age the previous year using multiple linear regression. Results for several ages showed that high length-at-age is significantly associated with low sea ice concentration and high length-at-age the previous year. Only length-at-age for age 1 shows a positive significant relationship with prey biomass. Our results suggest that retreating sea ice has positive effects on the growth of polar cod in the Barents Sea despite previous observations of a stagnating stock biomass and decreasing stock abundance. Our results contribute to identifying mechanisms by which climate variability affects the polar cod population, with implications for our understanding of how future climate change may affect Arctic ecosystems.

**Keywords:** amphipod, Barents Sea, global warming, length-at-age, polar cod, sea ice

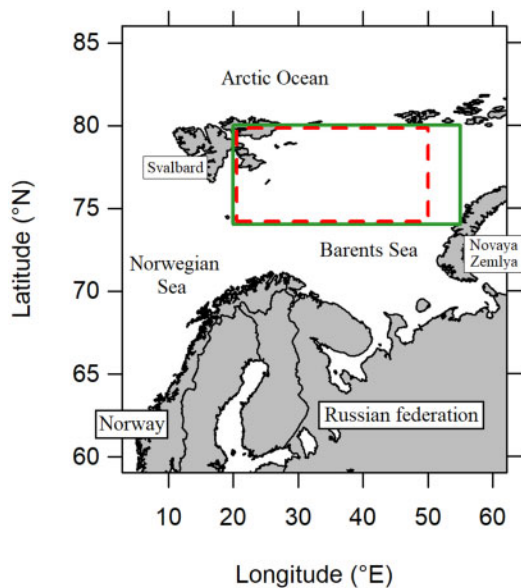
## Introduction

The largest changes in temperature are recorded in the Arctic areas at the northernmost part of the northern hemisphere (Hansen *et al.*, 2006). The Arctic sea surface temperature (SST) in August has increased by an average of 1°C per decade (over the 1982–2019 period; Timmermans and Ladd, 2019). Simultaneously (1978–2010), the observed sea ice cover and sea ice period, as well as the modelled sea ice thickness, have decreased in the Arctic marginal seas often associated with increased net primary production (Stroeve *et al.*, 2012; Arrigo and van Dijken, 2015; Laidre *et al.*, 2015). The Barents Sea, an Arctic

marginal sea located north of Norway and Russia, is a transition zone between the warmer and deeper Norwegian Sea in the west and the Arctic Ocean. In the Barents Sea (Figure 1), increased sea temperature together with increased extent of warm Atlantic waters and retreat of cold Arctic waters may also allow boreal to sub-Arctic fish populations like piscivorous Atlantic cod (*Gadus morhua*) and planktivorous capelin (*Mallotus villosus*) to expand northeastward into areas previously occupied by Arctic fish species such as polar cod (*Boreogadus saida*) (Fossheim *et al.*, 2015; Fall *et al.*, 2018). In the near future, sea ice cover is projected to continue shrinking and thinning, leading to changes in the

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**Figure 1.** Map of the Barents Sea. Relevant sampling area for copepod, amphipod, krill (solid green box), and relevant sampling area for sea ice and sea surface temperature (dashed red box).

frequency and extent of sub-ice blooms, amount and spatio-temporal distribution of secondary production, and increased visual predation (Slagstad *et al.*, 2011; Horvat *et al.*, 2017; Langbehn and Varpe, 2017). Climate change is expected to affect Arctic species directly, e.g. through effect of temperature on growth rates, or indirectly by affecting the prey, predators, or competitors of the focal species (Stenseth *et al.*, 2002; Drinkwater *et al.*, 2010). For example, reduced ice cover in the Barents Sea may potentially influence survival and/or growth of young polar cod through loss of predation refuge, as well as indirectly by acting on the biomass or phenology of prey populations (Hop and Gjøsaeter, 2013). Identification of potential pathways of climate effects and quantification of the strength of these effects on Arctic marine species are current research topics that are being investigated to predict the possible ecological consequences of climate change in the region (see, for example Johannesen *et al.*, 2012; Stige *et al.*, 2019a).

Length-at-age of a fish stock can be used to investigate the consequences of climate change as a measure of the effect of direct or indirect effects of ecosystem variables on the condition of the individuals composing the stock (Dutil *et al.*, 1999). Variation in length-at-age of a stock depends on (i) the growth rates experienced by the individuals, e.g. following variations in temperature, food quantity, or food quality, and (ii) size-dependent mortality, e.g. predation on the smaller individuals, size-selective fishing, or removal of the largest individuals through mortality associated with spawning in the case of semelparous species. In addition, especially for the youngest age class of a population with a protracted spawning season, mean size may vary depending on spawning dates and experienced mortality rates during the first year of life. For example, individuals spawned early in the season may benefit from a longer growing period than individuals born late in the season. The mean size at a given time of year is, therefore, higher if a high fraction of the year class is born early in the year, and the mortality rate is lower than in a situation where the fraction is low and/or the mortality rate is high. Increase in

length-at-age may indicate a positive development for a population, with favourable growth conditions, i.e. high food intake and suitable temperatures (Sogard, 1997). Large size in early life implies that the individuals may be more resilient to periods of reduced food intake (Miller *et al.*, 1988). Individuals may also be less susceptible to predation, as predation rates generally decrease with size early in life (Sogard, 1997, but with noticeable exceptions, see Pepin, 2016). In contrast, smaller length-at-age can reveal suboptimal growth conditions with potential starvation and has been related to deteriorating conditions of fish stocks (Dutil *et al.*, 1999).

Polar cod is a semi-pelagic fish species from the Gadidae family and a key species in the Arctic waters of the Barents Sea. It is an important component in the Arctic trophic chain by virtue of its large biomass and by channelling energy from the sympagic and marginal ice zones as well as from open-water copepods and amphipods to the higher trophic levels (reviewed in Hop and Gjøsaeter, 2013). Eggs can be found under the ice in the first months of winter (Rass, 1968; David *et al.*, 2016) and hatch into larvae from May to September (Baranenkova *et al.*, 1966). Young-of-the-year are usually found in open water (Baranenkova *et al.*, 1966), with some exceptions for late hatchers that may be found under the ice (Lønne and Gulliksen, 1989; David *et al.*, 2016). Older individuals (ages 1 and 2) may also be found under the ice where they use cracks or crevices as refuges from predation (Lønne and Gulliksen, 1989; David *et al.*, 2016). Alternatively, young individuals may migrate to deeper water and join older individuals of the stock (Falk-Petersen *et al.*, 1986). Key prey items in the diet of polar cod are calanoid copepods (particularly *Calanus glacialis*), large pelagic amphipods (e.g. *Themisto libellula*), sympagic amphipods (e.g. *Apherusa glacialis*), and krill (e.g. *Thysanoessa inermis*) (Orlova *et al.*, 2009; Hop and Gjøsaeter, 2013). The biomass of these copepods as well as pelagic amphipods in the northern Barents Sea decreases following winters with low sea ice cover (Stige *et al.*, 2019a). Juvenile polar cod are also potentially directly influenced by changing temperature conditions in the Barents Sea as growth and survival have been associated with temperature both in field observations and in rearing experiments (Bouchard and Fortier, 2011; Laurel *et al.*, 2016). The stock of polar cod in the Barents Sea can also be influenced directly by the main predators Atlantic cod and harp seals (*Phoca groenlandica*) (Ajjad *et al.*, 2011).

There are still major gaps in knowledge associated with the interaction between the different Arctic species and their environment (Mueter *et al.*, 2016). For Arctic fishes in general, growth is often *a priori* expected to decrease in a warming Arctic (Wassmann *et al.*, 2011). In the case of polar cod, the relationship between body size and environmental factors has been analysed for the young-of-the-year (Eriksen *et al.*, 2015; Bouchard *et al.*, 2017). However, less is known about how length-at-age of older stages is associated with environmental factors. Here, we analyse statistically the associations between abiotic (sea ice extent, sea temperature) and biotic (prey and predator biomasses) environmental factors and length-at-age of polar cod to improve our understanding of the effects of climate change on this Arctic species.

## Material and methods

### Datasets

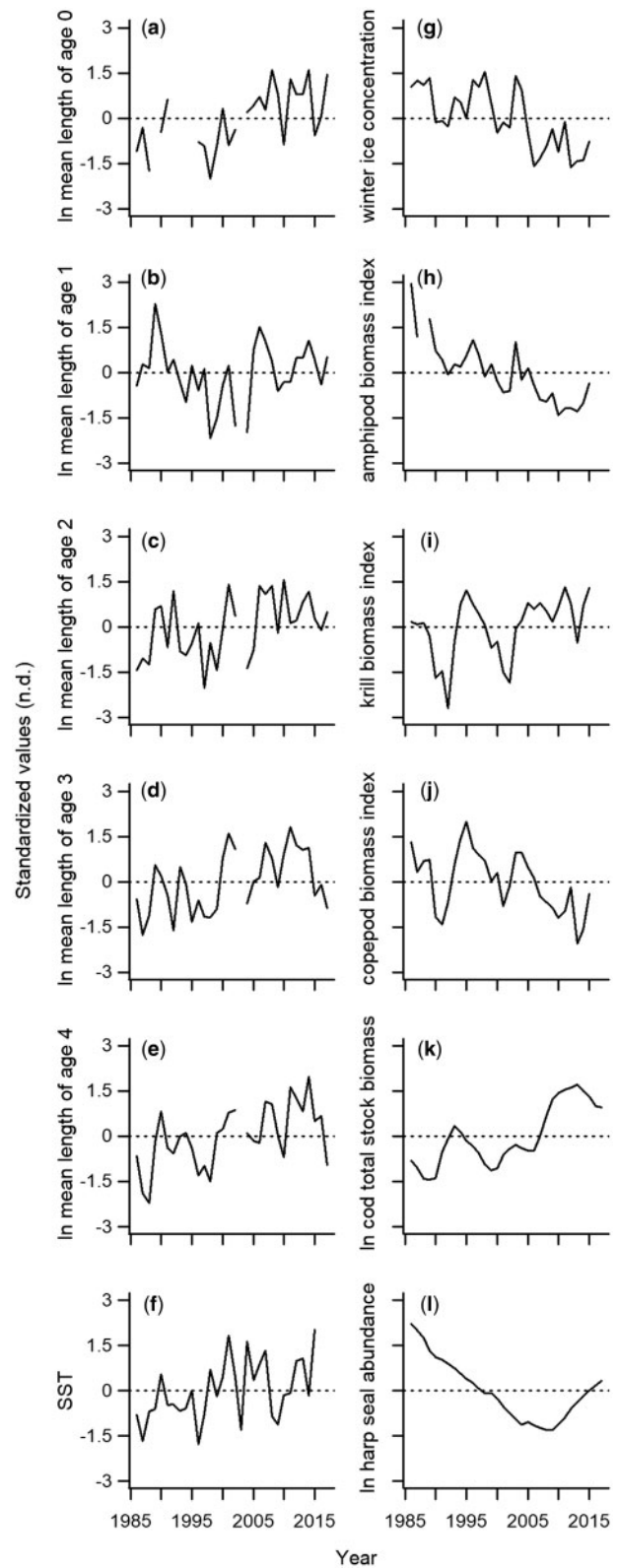
In this study, we used 30 years of length-at-age data of polar cod originating from the joint Norwegian/Russian ecosystem survey

in the Barents Sea and adjacent waters (BESS) carried out annually in August–October by the Institute of Marine Research in Norway (IMR) and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), the current Polar Branch of the Russian Federal Institute of Fisheries and Oceanography (VNIRO). We chose to use length-at-age values over weight-at-age in our study as weight is more sensitive to short-term variation in food and is less conservative than length in reflecting the growth history of an individual. We here used data for the years 1986–2015 obtained through the annual survey reports (Figure 2a–e). In this study, we analysed data on young-of-the-year (age 0) and older (ages 1+) polar cod. The data for fish of age 1 and older are based on annual stock size estimates, which are acoustic estimates distributed by age and length groups. The estimates were made using standard methods for acoustic surveys (e.g. Simmonds and MacLennan, 2005), where nautical area scattering coefficients (NASC) output from echosounders are transformed into number of fish per areal unit based on trawl samples where lengths are measured (total length to the nearest half centimetre below) and age (in years) estimated from otoliths. In this way, abundance-weighted length distributions (based on the midpoint in each length bin of 0.5 cm size class) are constructed. The NASCs are obtained from 38-kHz echosounders, which are normally calibrated by standard spheres at the start of the survey. The trawl used for obtaining biological samples of pelagic fish is a standard sampling trawl (“Harstad”; Godø *et al.*, 1993) with small meshed (8 mm) net in the codend. For polar cod, otoliths from 96 specimens from each sample were extracted and the otoliths were read by experienced age readers according to species-specific protocols. Age readers at the two participating institutes undergo tests for inter-reader bias to check that ages estimated at the various participating vessels are comparable over years.

The data for age 0 (0-group) polar cod originate from the same survey, but abundance is estimated based on a grid of special trawl hauls covering the upper 60 m of the water column and where the abundance index is based on the catches (Eriksen *et al.*, 2009). The trawl used for these 0-group hauls is the same as used for targeted sampling of older polar cod as described above. For some years, data on age 0 are spatially differentiated between a western component (Svalbard region, Figure 1) and an eastern component (Novaya Zemlya region, Figure 1). In this case, an age 0 total mean length-at-age was computed by averaging western and eastern mean lengths-at-age weighted by the stock abundance estimates for each spatial component.

As an index of SST (Figure 2f), we considered annual mean summer SST (taken as the months May–September) in the area 74–80°N, 20–50°E (Figure 1). This period covers the main primary and secondary production seasons in the central and northern Barents Sea (Wassmann *et al.*, 2006). The index was calculated from monthly SST data on a 2° × 2° grid provided by the National Oceanic and Atmospheric Administration (NOAA\_ERSST\_V3 data set <http://www.esrl.noaa.gov/psd/>).

An index of winter sea ice concentration was calculated from monthly satellite-derived sea ice concentrations (Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, NSIDC-0051) provided by the National Snow and Ice Data Center (Cavalieri *et al.*, 1996; updated yearly <https://nsidc.org/data/NSIDC-0051/versions/1>). The index was calculated for the same representative area as for SST. Ice index for year  $t$  referred to the average ice cover between December of year  $t-1$  and May



**Figure 2.** Time-series of standardized data for the different variables considered in the analysis. (a) Natural logarithm of polar cod length-at-age for age 0, (b) age 1, (c) age 2, (d) age 3, and (e) age 4, (f) sea surface temperature, (g) winter sea ice concentration, (h) amphipod biomass index, (i) krill biomass index, (j) copepod biomass index, (k) natural logarithm of total stock biomass of cod (age 3+), and (l) natural logarithm of modelled abundance of harp seals (age 1+).

of year  $t$ , which were the 6 months that had the highest sea ice concentrations for the analysed years, on average (Figure 2g).

To shed light on the possible mechanisms behind the correlations between the climate variables and polar cod length-at-age, we calculated correlations with the following three additional indices: (i) August–September bottom temperature in the central and northern Barents Sea, (ii) April sea ice cover in the same area, and (iii) net primary production in the Barents Sea (Supplementary Table S1). We chose to focus on winter sea ice and summer SST in the main analysis to restrict the number of predictor variables and hence the risk of type I errors. In addition, winter and April sea ice are strongly correlated but the former shows a stronger correlation with the response variables (Supplementary Table S1). Finally SST has a better spatial data coverage compared to bottom temperature.

Prey was divided into three categories based on the known diet of polar cod: pelagic amphipods, copepods and krill (Orlova *et al.*, 2009). Pelagic amphipod and krill biomass were sampled from 0- to 60-m depth using a pelagic trawl with seven panels of decreasing mesh size from 100 to 30 mm ending in a codend of mesh size 8 mm. Sampling took place in August–September in the Barents Sea north of 74°N, and biomass was reported as kg wet weight per nautical mile towed for amphipods and g wet weight  $m^{-3}$  for krill (Dalpadado *et al.*, 2012; Eriksen *et al.*, 2016; ICES, 2018a). Note that because data for amphipod and krill were only available from the upper water layer (0–60 m), these indices do not necessarily represent all amphipods and krill present in the area. The dominant amphipod taxon was the large pelagic species *T. libellula*, while smaller species such as *Themisto abyssorum* were not sampled representatively (ICES, 2018a). We here used an annual log-scale amphipod biomass index (Figure 2h) that was constructed from spatio-temporal observations using a statistical regression approach to account for interannual differences in sampling protocol (as described in Dalpadado *et al.*, 2012; Stige *et al.*, 2019a).

Dominant krill taxa sampled were large stages of *Thysanoessa* spp. and *Meganycitiphanes norvegica*. Smaller *Thysanoessa* spp. and juvenile euphausiids were not sampled representatively due to escapement through the mesh (Eriksen *et al.*, 2016; ICES, 2018a). We used an annual log-scale krill index (Figure 2i) that was calculated from day and night catches, as described in Stige *et al.* (2019a).

Copepods were represented by biomass (g dry weight  $m^{-2}$ ) of mesozooplankton, for brevity referred to as “copepods” due to their dominance in the mesozooplankton biomass (Orlova *et al.*, 2011; Aarflot *et al.*, 2017). Copepods were sampled during annual surveys by IMR from August to early October using 180- $\mu$ m mesh plankton nets throughout the water column (ICES, 2018a). We here used an annual log-scale index of copepod biomass (Figure 2j) calculated from the spatio-temporal observation data from the central and northern parts of the Barents Sea (characterized by long-term average surface temperatures  $<3^{\circ}C$  at the time of the survey) using a statistical regression approach to account for interannual differences in sampling protocol (as described in Stige *et al.*, 2014, 2019a). Dominant taxa represented by the biomass index were *C. glacialis*, *Calanus finmarchicus*, and *Calanus hyperboreus* (Aarflot *et al.*, 2017).

As the main consumers of polar cod in the Barents Sea, we included indices for both Atlantic cod and harp seals. Annual biomass [ $\ln(1000 t)$ ] of age 3+ of the Northeast Arctic stock of Atlantic cod (hereafter referred to as cod) was obtained from

ICES (2018b). Cod population biomass (Figure 2k) estimates were from virtual population analyses, mostly relying on fisheries catch data, and referred to as biomass at the beginning of the year.

Annual abundance of harp seal individuals was extracted from ICES (2016). The data represent harp seals at age 1+ (Figure 2l) and were predicted from a deterministic age-structured population dynamics model (Øigård *et al.*, 2014). The model uses historical data, reproductive data, and estimates of pup population to predict yearly total population divided into age classes (from 0 to 20+ years). Abundance of seals aged 1+ is predicted from mortality rates of pups and older individuals, and age class annual seal catch. Yearly pup abundance is predicted using observed fecundity and maturation norm for female seals and annual pup catch.

### Statistical analysis

Yearly means of fish length were regressed against a combination of environmental factors that could influence growth: SST, sea ice concentration, biomass of prey items, biomass of predators, and length-at-age of the cohort the preceding year. We investigated the relationship between the response variables [log-transformed mean length-at-age,  $\ln(L_{i,t})$  for the  $i$ th age class of polar cod in year  $t$ ] and the independent variables using a multilinear regression with a Gaussian error distribution. Annual means of log-transformed length-at-age for each age class (0, 1, 2, 3, and 4 years) were analysed separately. The independent variables considered were (i) length-at-age of the year class the previous year ( $L_{i-1,t-1}$ ; for ages  $i > 0$ ); (ii) abiotic variables: winter sea ice concentration (Ice) and summer SST (SST); (iii) food sources: copepods (Cop), amphipods (Amp), and krill (Krill); and (iv) potential fish and mammal predators: cod (Cod) and harp seal (HSeal). The regression equation for the full model was:

$$\ln(L_{i,t}) = a_i + b_i \ln(L_{i-1,t-1}) + c_i \text{Ice}_t + d_i \text{SST}_t + e_i \ln(\text{Amp}_t) + f_i \ln(\text{Cop}_t) + g_i \ln(\text{Krill}_t) + h_i \ln(\text{Cod}_t) + i_i \ln(\text{HSeal}_t) + \varepsilon_{i,t},$$

$$\varepsilon \sim N(0, \sigma_i).$$

Here,  $a_i$ ,  $b_i$ ,  $c_i$ ,  $d_i$ ,  $e_i$ ,  $f_i$ ,  $g_i$ ,  $h_i$ , and  $i_i$  are model coefficients for age class  $i$  and  $\varepsilon_{i,t}$  is an independent and normal distributed noise term with standard deviation  $\sigma_i$ . All biotic variables including length-at-age were on natural logarithmic scale, and all independent variables were centred on their median. The log-transformation was applied to achieve homoscedasticity and normality in the residuals of the regressions and to facilitate comparison across ages as all predictor effects could be interpreted as linear effects on the instantaneous rate of change in length. Due to the lack of information on length-at-age for age 0 in the reports for 1989 and 1992–1995, missing amphipod index for 1988, and failure of the BESS in 2003, the numbers of data points in the age 0 and age 1 regressions were reduced to, respectively, 22 and 21, compared to 26 for ages 2–4.

Some of the explanatory variables used in the model are significantly correlated with one another, e.g. amphipod and sea ice concentration (Supplementary Table S1). To avoid variance inflation in our model due to collinearity in our datasets, we reduced the number of covariates by using the forward selection of environmental predictor variables. This procedure permitted us to find the reduced model with the best compromise between model

**Table 1.** Model selection results for the multilinear regression for the different ages of polar cod.

Age	Model	Intercept	Length-at-age <sub>year-1</sub>	Ice	SST	ln(Amp)	ln(HSeal)	$\Delta$ AICc	R <sup>2</sup>	n
0	1	1.43 ± 0.02****	not available	-0.006 ± 0.001****	-0.06 ± 0.03*	-	-	0	0.47	22
	2	1.42 ± 0.02****	not available	-0.005 ± 0.001****	-	-	-	1.79	0.39	
1	1	2.37 ± 0.01****	0.10 ± 0.09	-0.003 ± 0.001****	-	0.11 ± 0.02****	-	0	0.49	21
	2	2.85 ± 0.01****	0.34 ± 0.16**	-0.002 ± 0.001****	-	-	-	0	0.45	26
3	1	2.85 ± 0.02****	0.34 ± 0.23	-	-	-0.07 ± 0.02***	-	0	0.4	26
	2	2.85 ± 0.01****	0.46 ± 0.22*	-	-	-	-0.41 ± 0.16**	1.66	0.36	
	3	2.85 ± 0.01****	0.42 ± 0.23	-0.002 ± 0.001**	-	-	-	2.18	0.35	
4	1	2.98 ± 0.01****	0.53 ± 0.20**	-0.002 ± 0.001*	-	-	-	0	0.53	26
	2	2.98 ± 0.01****	0.79 ± 0.16***	-	-	-	-	1.28	0.48	
	3	2.98 ± 0.01****	0.59 ± 0.21***	-	-	-0.04 ± 0.03	-	1.51	0.5	
	4	2.98 ± 0.01****	0.68 ± 0.17***	-	-	-	-	1.58	0.5	

Estimates for the different regression parameters that were retained by the selection procedure are presented ± their standard error and *p*-value levels:

\*0.05 < *p* < 0.1, \*\*0.01 < *p* < 0.05, \*\*\*0.001 < *p* < 0.01, \*\*\*\**p* < 0.001.

parsimony and goodness-of-fit. First, the previous year's mean length of a year class was *a priori* retained in all models (except for age 0, where no previous year length was available). We then processed forward by adding one of the predictor variables to the current model and assessed the Akaike information criterion (AICc) corrected for low sample size (Hurvich and Tsai, 1989) of the new model. We then selected the predictor variable providing the highest decrease in AICc to add to the current model. We repeated the selection procedure on the updated model until no further addition of remaining predictor variables led to a decrease in the AICc value. Note that a small difference ( $\Delta$ AICc) between different models does not provide strong statistical support for one model over the other. Therefore, in addition to the model with the lowest AICc, we presented the models with a  $\Delta$ AICc of <2 compared to the model with lowest AICc.

To assess collinearity among the explanatory variables and to help with the interpretation of the regression parameters for the different models, the Pearson's correlation coefficient *R* was computed between each of the explanatory variables (Supplementary Table S1).

## Results

The multilinear regression model with the lowest AICc showed that length at age 0 was negatively related to winter sea ice concentration (age 0 model 1, Table 1, Figure 3a). The same model also showed a non-significant negative association between length at age 0 and SST (*p* > 0.05, Figure 3b). A model without SST (age 0 model 2, Table 1) had similar statistical support ( $\Delta$ AICc < 2).

The multilinear regression for age 1 showed that length at age 1 was not significantly associated with the mean length of the same year class the previous year (i.e. as age 0, age 1 model 1, Table 1, Figure 3c) and that length was negatively associated with winter sea ice concentration and positively associated with the amphipod index (age 1 model 1, Table 1, Figure 3d and e).

The multilinear regression for age 2 showed that length-at-age was positively associated with the length-at-age of the cohort the previous year (age 2 model 1, Table 1, Figure 3f). This suggests that a year class composed of large individuals as 1-year olds also tends to have large mean size as 2-year olds. In addition, length-at-age was negatively associated with winter sea ice concentration, but with no significant relationship with amphipods or other prey indices (Figure 3g).

The model with lowest AICc for length at age 3 indicated a non-significant relationship with length-at-age the previous year

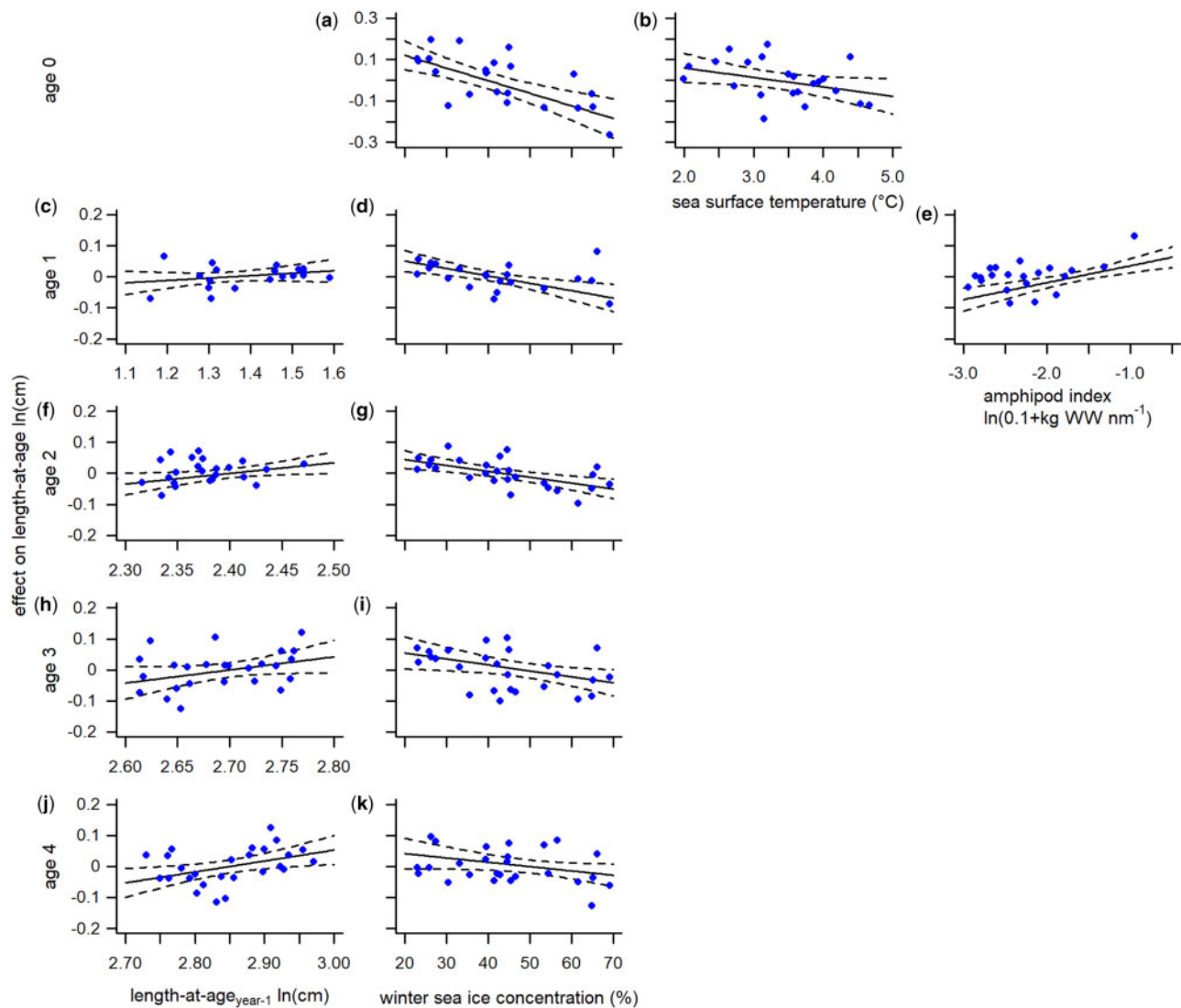
and a negative relationship with the amphipod index (age 3 model 1, Table 1). A model with harp seal abundance as predictor (age 3 model 2, Table 1) had similar statistical support ( $\Delta$ AICc < 2). One competitive model considered during the forward selection process (Supplementary Table S2) suggested a significant negative relationship with winter sea ice concentration. However, this model had a  $\Delta$ AICc of slightly >2 ( $\Delta$ AICc = 2.18) compared to the model with the lowest AICc. From a statistical point of view, the model including the amphipod index or harp seal abundance provided a better prediction of the observed variation in the response variable. We nevertheless chose to consider and to present the results for the model including length-at-age the previous year and winter sea ice concentration (age 3 model 3, Table 1, Figure 3h and i) because (i) the negative association with winter sea ice concentration is consistent with the models for other ages and (ii) the lowest  $\Delta$ AICc model implied a negative prey effect that is difficult to interpret biologically. We note that the positive correlations among the amphipod index, harp seal abundance, and sea ice concentration (Supplementary Table S1) may cause statistical confounding between the effects of these factors. In a sensitivity analysis excluding the amphipod biomass index from the tested covariates for all age classes, the selection process resulted in no statistically significant covariates being selected for the age 1 model and the model with length-at-age the previous year and winter sea ice to become competitive for the age 3 model ( $\Delta$ AICc = 0.52).

The model with lowest AICc for age 4+ length showed a positive association with length-at-age of the previous year and a non-significant negative relationship with winter sea ice concentration (age 4 model 1, Table 1, Figure 3j and k). A model without sea ice concentration as covariate had similar statistical support (age 4 model 2, Table 1).

Competitive models to the model 1 for age 4+ excluded sea ice as a predictor (age 4 model 2, Table 1) or selected either amphipod prey index (age 4 model 3, Table 1) or SST (age 4 model 4, Table 1). In all competitive models for age 4+, only length-at-age of the previous year showed a significant positive relationship.

## Discussion

Our results show the associations between environmental variables and length-at-age of polar cod in the Barents Sea. Contrary to expectation for Arctic animals (see Introduction section and Wassmann *et al.*, 2011), we found that the most rapid increases in mean body length of the Barents Sea polar cod occurred in



**Figure 3.** Partial regression plots of length-at-age for the different age groups depending on the selected predictors by AICc forward selection. Effect on age 0 length-at-age by (a) winter sea ice concentration and (b) sea surface temperature. Effect on age 1 length-at-age by (c) previous year length-at-age, (d) winter sea ice concentration, and (e) amphipod prey biomass index. Effect on age 2 length-at-age by (f) previous year length-at-age and (g) winter sea ice concentration. Effect on age 3 length-at-age by (h) previous year length-at-age and (i) winter sea ice concentration. Effect on age 4 length-at-age by (j) previous year length-at-age and (k) winter sea ice concentration.

years with little sea ice. Specifically, low winter sea ice concentration was associated with high mean length of polar cod at ages 0, 1, 2, and 3. High biomass of amphipod prey was only associated with high mean length at age 1 of polar cod. SST in summer and biomasses of fish predators and other prey groups than amphipods were not significantly related with length-at-age of polar cod.

### Effect of sea ice on length-at-age of polar cod

Our results are in accordance with findings from the Canadian Arctic (Bouchard and Fortier, 2011; Bouchard *et al.*, 2017) by suggesting a negative relationship between sea ice extent in winter and mean length of polar cod at age 0. One possible explanation for this negative association is that in years with an early sea ice retreat, the early hatched larvae comprise a larger proportion of

the cohort by the first winter, compared to years with later sea ice retreat (Bouchard and Fortier, 2011; Bouchard *et al.*, 2017).

As the hatching of polar cod larvae takes place from May to September in the Barents Sea (Baranenkov *et al.*, 1966), age 0 fish are from 0 to ca. 4 months post-hatching at the time of the survey in autumn. With such large variation in monthly age within the year class, it is expected that an increased early season survival in low-ice years would lead to an increase in mean age and length, as well as abundance of age 0. This is in apparent contrast with observations of a positive association between sea ice and age 0 abundance in the Barents Sea (Eriksen *et al.*, 2015). However, this positive association is hypothesized to be a result of effects of sea ice on spawning areas for polar cod (Eriksen *et al.*, 2015) and not larval survival. In summary, these findings suggest that the observed trend towards a decrease in winter sea ice cover (Stroeve *et al.*, 2012) and an early sea ice spring retreat

in the Barents Sea (Laidre *et al.*, 2015) may lead to higher survival of early hatchlings and possibly faster growth of polar cod through the first summer, resulting in an increased mean length in autumn when sampled, while abundance is decreasing probably due to a reduction in spawning areas for mature polar cod (Eriksen *et al.*, 2015).

In addition, our results suggest negative associations between winter sea ice concentration and mean lengths-at-age 1 to 3 (and non-significantly at age 4+), which cannot be explained by early hatching and effect of previous year size, as we included previous year mean length of the year class as predictor variable in the statistical analysis. This finding suggests that sea ice condition has an additional effect on the change in mean length for each age interval. We hypothesize that these associations are caused by low winter sea ice concentration extending the duration of the period with suitable conditions for the growth of polar cod.

Both copepods and amphipods, which are main components of the diet of polar cod (Hop and Gjøsaeter, 2013), decrease in biomass in years with low winter sea ice cover (Stige *et al.*, 2019a), resulting in positive correlations between copepod and amphipod biomasses and sea ice concentration (Supplementary Table S1). Large size of polar cod in low-ice years, therefore, occurs despite reduced prey biomass in these years. However, low sea ice cover is associated with earlier phytoplankton blooms, increased primary production, and longer phytoplankton growing season (Arrigo *et al.*, 2008; Dalpadado *et al.*, 2014; ICES, 2018a). An early start of the spring primary production period in low-ice years is, therefore, potentially associated with increased secondary production in the Barents Sea, as shown in the Canadian Arctic seas (LeBlanc *et al.*, 2019). However, in the Barents Sea, zooplankton loss rates, particularly from capelin predation, may also be higher in these years (Stige *et al.*, 2019a). Despite the lack of high zooplankton biomass concentrations in years with low ice coverage in our data, an increase in length-at-age related to an increase in primary production may be suspected from satellite-derived data of primary production in the Barents Sea. Time-series of primary production in Arctic waters do not cover the period before 1998 and were, therefore, not included in our models. Nevertheless, the correlation coefficient between length-at-age and annual net primary production in the Barents Sea for the period 1998–2012 (Arrigo and van Dijken, 2015; see Supplementary Table S1) suggests a significant positive association in accordance with the hypothesis of increased length-at-age due to a potential increase in secondary production in years with increased primary production. Additional analyses also showed that length-at-age is similarly strongly positively correlated with sea ice cover in April (Supplementary Table S1), pointing to a possible role of the timing of the onset of production in spring. We hypothesize that in low-ice years, zooplankton concentrations start increasing earlier in the season, as do light levels and prey detection rate for visual feeding. The feeding season for polar cod is then extended, allowing individuals to grow to a larger size by the end of summer, assuming that prey availability is not limiting.

### Influence of zooplankton biomass on the length-at-age of polar cod

Considering that copepods, together with amphipods, constitute an important fraction in the diet of polar cod (Lønne and Gulliksen, 1989; Hop and Gjøsaeter, 2013; Kohlbach *et al.*, 2017), it is surprising that our results only suggest a relationship between

pelagic amphipod biomass and polar cod length at age 1. In comparison, significant associations between growth in length of different age groups and prey biomass have been reported for the other key zooplanktivorous fish in the Barents Sea, i.e. capelin (Gjøsaeter *et al.*, 2002; Stige *et al.*, 2018).

As a prey, *Calanus* spp. copepods have high fat content and provide higher energy content per prey biomass than amphipods, the latter appearing less beneficial for faster growth (Hop *et al.*, 1997). However, amphipod species provide a higher percentage of protein per dry weight than copepods. This could help the development of the somatic body of polar cod, i.e. lean and fat tissues in addition to skeleton, but excluding liver and intestines, which are the body parts richest in protein in an individual polar cod (Hop *et al.*, 1997). Amphipods in the diet may hence hypothetically enhance growth in length, whereas lipid-rich copepods support the storage of energy.

It was unexpected that prey biomass indices were not associated with polar cod length at other ages than age 1. We note that the species may use different reproductive strategies, with part of the stock being semelparous, i.e. dying off after the first reproductive event (Nahrgang *et al.*, 2014). This may confound our results between prey availability and growth because of a length-dependent spawning mortality for the larger mature individuals, i.e. ages 2+. We do not think that the lack of significant association is caused by the copepod index failing to represent the preferred copepod prey of polar cod, i.e. the largest size fractions of the copepods (mainly *C. glacialis* and *C. hyperboreus*, Hop and Gjøsaeter, 2013), as the interannual trends in large (>2 mm) copepods correlate strongly with the trends in total copepod biomass (Stige *et al.*, 2014).

Nevertheless, our results suggest that growth in length is more dependent on length of the feeding season, as captured by the winter sea ice index, than the biomass levels of prey. We note, however, that prey biomasses were measured at the end of the feeding season and do not necessarily reflect biomass levels earlier in the season (as discussed in Gjøsaeter *et al.*, 2002). The multianual life cycles of the main zooplankton species represented by our prey indices tend, on the other hand, to reduce the short-term fluctuations in biomass levels. We also note that 0-group individuals may be too small to exploit amphipods as prey, as the proportion of amphipods in the polar cod diet drops with decreased fish length (Hop *et al.*, 2002).

### Effect of temperature on length-at-age of polar cod

We used summer SST extracted from satellite observations in the northern Barents Sea as a proxy for temperature conditions during the primary and secondary production periods in the Barents Sea, expecting high SST to potentially lead to fast growth in summer and high mean length in autumn. Such association has been suggested with the length of age 0 juvenile polar cod in the Barents Sea (Eriksen *et al.*, 2015) and Canadian Arctic waters (Bouchard *et al.*, 2017). The findings of Eriksen *et al.* (2015) were based on *in situ* 0–50-m water column temperatures and size differences among individual polar cod in different water masses and, therefore, do not necessarily reflect effects of interannual temperature variations. The findings of Bouchard *et al.* (2017), however, were based on SST averages for May–July, which is comparable to our study, and the comparison of mean length between years. The absence of a temperature–length association in our results may be explained by a suggestion from Bouchard and

Fortier (2011). In their circum-Arctic comparison of hatching season of polar cod, it was suggested that juveniles, i.e. age 0 polar cod, relied more on length of the growing season (negatively correlated with hatching date) to achieve a large pre-winter size, rather than on fast growth (positively correlated with SST during hatching month).

The absence of associations between SST and mean lengths of polar cod at ages 1 and older in our results may also be explained by the ontogenetic depth distribution of the species. Specifically, during the spring–summer period (February–September), these age groups of polar cod are found in deep waters (Falk-Petersen *et al.*, 1986; Ajiad *et al.*, 2011), making summer SST in the northern Barents Sea a poor proxy for the ambient temperature experienced by the polar cod. Additional analyses showed that summer bottom temperature correlated significantly positively with mean lengths at age 0 and ages 2–4, with the correlations at ages 0 and 4 being similarly strong as with winter sea ice (Supplementary Table S1). Physiological effects of temperature on growth rates may hence potentially contribute to explain the associations we found between sea ice cover and length-at-age of polar cod.

### Consistency in length anomalies with age

Polar cod length-at-age was a significant predictor of the next year's mean length from age 1 to age 2 and from age 3 to age 4. This implies that positive or negative anomalies in mean length of a cohort tended to be retained across these ages. We found, however, no consistency in length anomalies from age 0 to age 1 and from age 2 to age 3. Low consistency of length anomalies across early life stages has also been reported for other marine fishes and may reflect compensatory mechanisms (Stige *et al.*, 2019b). From age 0 to age 1, we hypothesize that the length distribution may be strongly modified by size-dependent survival, which has been reported to occur during the first winter of life (Fortier *et al.*, 2006). From age 2 to age 3, variable investment of resources towards maturation and gonad development rather than growth in length may hypothetically play a role. High measurement errors may also have contributed to reduce the strengths of associations in our analysis, although the significant and consistent associations with sea ice concentration suggest that the length-at-age time-series do contain biologically meaningful signals.

### Implications for Arctic ecosystem

Our results show positive associations between sea ice concentration in winter and length-at-age of polar cod at age 0 as well as at the older ages. We interpret these results in terms of the length of the period with suitable conditions for growth, which we propose is longer in low-ice years, and larval survival. The findings suggest that in this Arctic environment, variation in yearly winter ice condition is a main driver of polar cod length-at-age, rather than variation in food concentrations or temperature *per se*.

In summary, our study suggests that polar cod in the Barents Sea are increasing in body length under global warming and retreating sea ice. While increase in mean body length may have positive effects on the population and potentially benefit higher trophic levels, with a possible reduction in size-dependent predation and increased reproduction potential, the total biomass of polar cod in the Barents Sea does not appear to change in response to changes in winter sea ice or sea temperatures (Stige *et al.*, 2019a). We hypothesize that positive growth effects of low

sea ice for the population of polar cod are offset by reduced survival, possibly through increased overall predation rates with the increased dominance of boreal species in the Arctic, such as the Northeast Atlantic cod (Fossheim *et al.*, 2015; Frainer *et al.*, 2017) or reduced spawning areas (Eriksen *et al.*, 2015). Such positive effects may, however, be transient, as nonlinear effects may set in when the Arctic warms beyond the current range. Until now, the relationships between winter sea ice and length-at-age of polar cod appear to be linear (Figure 3a, d, g, i, and k). However, a continuation of the decrease in sea ice concentration may become disadvantageous, e.g. by desynchronizing the primary and secondary production periods and then affecting the food conditions of young polar cod (as proposed by Bouchard *et al.*, 2017) or by causing shifts in zooplankton species composition, and increased competition or predation with boreal planktivores and fish predators.

### Supplementary data

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

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