

1 **Running head:** Age structure affects productivity

2 **Age structure affects population productivity in an exploited fish species**

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## 12 **ABSTRACT**

13 Long-term changes in the age and size structure of animal populations are well-documented, yet  
14 their impacts on population productivity are poorly understood. Fishery exploitation can be a  
15 major driver of changes in population age-size structure, because fisheries significantly increase  
16 mortality and often selectively remove larger and older fish. Climate change is another potential  
17 driver of shifts in the demographic structure of fish populations. Northeast Arctic (NEA) cod is  
18 the largest population of Atlantic cod (*Gadus morhua*) and one of the world's most important  
19 commercial fish stocks. This population has experienced considerable changes in population age-  
20 size structure over the past century, largely in response to fishing. In this study, we investigate  
21 whether changes in spawner age structure have affected population productivity in NEA cod,  
22 measured as recruits per spawning stock biomass, over the past 75 years. We find evidence that  
23 shifts in age structure toward younger spawners negatively affect population productivity,  
24 implying higher recruitment success when the spawning stock is composed of older individuals.  
25 The positive effect of an older spawning stock is likely linked to maternal effects and higher  
26 reproductive output of larger females. Our results indicate a three-fold difference in productivity  
27 between the youngest and oldest spawning stock that has been observed since the 1950s. Further,  
28 our results suggest a positive effect of environmental temperature and a negative effect of  
29 intraspecific cannibalism by older juveniles on population productivity, which partly masked the  
30 effect of spawner age structure unless accounted for in the model. Collectively, these findings  
31 emphasize the importance of population age structure for the productivity of fish populations,  
32 and suggest that harvest-induced demographic changes can have negative feedbacks for fisheries  
33 that lead to a younger spawning stock. Incorporating demographic data into harvest strategies  
34 could thus facilitate sustainable fishery management.

35 ***Keywords:*** age structure, demography, exploitation, population productivity, reproductive output

## 36 INTRODUCTION

37 Animal populations are inherently structured with respect to age, size, and life-history stage.  
38 The age structure of the adult population is determined by a species' life-history, in particular the  
39 maturation schedule and longevity, as well as potential sources of mortality that alter the age  
40 composition of the population. In fish populations, harvesting can be a major driver of changes  
41 in age and size structure, because fisheries increase mortality such that fewer individuals survive  
42 to old age, and because fisheries often selectively remove larger and older fish (Law 2000;  
43 Berkeley et al. 2004; Beamish et al. 2006; Barnett et al. 2017). These changes may persist after  
44 fishing pressure is reduced if fishing has resulted in evolutionary changes in traits related to  
45 growth and maturation (Jørgensen et al. 2007; Swain et al. 2007; Wright and Trippel 2009;  
46 Heino et al. 2015). Fisheries-induced demographic change of a population can have negative  
47 repercussions for a fishery via increased variability in abundance (Anderson et al. 2008; Shelton  
48 and Mangel 2011; Botsford et al. 2014). While the impact of large individuals on population  
49 health and replenishment remains controversial (Brunel and Piet 2011; Andersen et al. 2019), the  
50 importance of conserving diverse age-size structures of populations has been emphasized in the  
51 context of fisheries sustainability (Birkeland and Dayton 2005; Hsieh et al. 2010; Stige et al.  
52 2017; Ahrens et al. 2020; Marshall et al. 2021).

53 In addition to exploitation, environmental changes contribute to shifting age structures through  
54 altered rates of growth and survival as well as the selection they impose on maturation schedules.  
55 One potential cause of contemporary changes in population age and size structure is climate  
56 warming (Daufresne et al. 2009; Gardner et al. 2011; Forster et al. 2012). Warming is expected  
57 to result in a faster life-history with higher growth rates and earlier maturation, as long as  
58 thermal conditions rarely exceed optimal temperatures for growth and survival (Ohlberger 2013;

59 Baudron et al. 2014; Huss et al. 2019). The effects of warming depend on currently experienced  
60 temperatures relative to organism thermal constraints, and may vary by population within  
61 species, for instance along latitudinal gradients (Ohlberger 2013). While the impacts of climate  
62 warming on fish body size also vary between species and may depend on local ecological  
63 conditions and life-history traits (van Rijn et al. 2017; Audzijonyte et al. 2020; Denderen et al.  
64 2020), changes in thermal regimes commonly result in altered population age-size structures.  
65 Shifts in demographic structure can affect population productivity through various mechanisms.  
66 First, shifts toward younger and smaller female spawners are expected to cause a reduction in  
67 average per capita reproductive output, because smaller females carry fewer and often smaller or  
68 lower quality eggs (Kjesbu et al. 1996; Murawski 2001; Scott et al. 2006; Ohlberger et al. 2020).  
69 In many marine fish species, female reproductive investment scales hyperallometrically with  
70 body mass, such that the total energy invested into reproduction per unit biomass increases with  
71 spawner body size (Hixon et al. 2014; Barneche et al. 2018). Second, a spawning stock that is  
72 composed of older females may also result in higher population recruitment due to a variety of  
73 maternal effects. In the Northeast Arctic (NEA) stock of Atlantic cod (*Gadus morhua*), for  
74 instance, older females spawn in different locations and over longer periods of time (Kjesbu et  
75 al. 1996; Wright and Trippel 2009; Opdal and Jørgensen 2015), are less likely to skip spawning  
76 (Jørgensen et al. 2006), and produce eggs and larvae that have higher survival rates (Solemdal  
77 1997). Third, an older spawning stock may exhibit a higher proportion of female spawners due to  
78 sex-specific growth, maturation thresholds, and/or survival rates (Jørgensen 1990; Marshall et al.  
79 2006). These studies suggest that spawner age structure may affect recruitment success and  
80 population productivity.

81 A diverse set of metrics has been used to describe changes in population age structure over time.  
82 The most commonly used metrics include the biomass-weighted mean age or mean weight of  
83 spawners, spawner age diversity, the proportion of old individuals in the population, and the  
84 proportion of repeat spawners (Marteinsdottir and Thorarinsson 1998; Ottersen et al. 2006;  
85 Ottersen 2008; Brunel 2010; Barnett et al. 2017). While shifts in demographic structure cannot  
86 be fully captured by any single age structure metric, such metrics are useful for illustrative and  
87 predictive purposes. Furthermore, which metric best reflects observed changes in age structure  
88 over time may depend on the processes involved and the major drivers of demographic change.  
89 For example, the proportion of old individuals in the population may best reflect shifting age  
90 structures due to the removal of large fish in size-selective fisheries, whereas mean age of the  
91 spawning stock may best reflect shifts in age structure in populations that have experienced long-  
92 term changes in age at first maturation, including evolutionary change.

93 While evidence exists that shifts towards a younger and less age diverse spawning stock can  
94 have negative effects on population recruitment and productivity, meta-analyses of marine fishes  
95 have found that these effects vary by population, for instance in Atlantic cod (Brunel 2010;  
96 Shelton et al. 2015). Populations differ in life-history characteristics such as growth, age at  
97 maturation, maximum age, and intrinsic density regulation due to size-based intraspecific  
98 competition and cannibalism (Anderson and Gregory 2000). Specifically, cannibalism mortality  
99 of pre-recruits may increase with the abundance of older juveniles that have recruited to the  
100 fishery but have not matured and are therefore not part of the spawning stock, as is the case for  
101 NEA cod (Bogstad et al. 1994; Yaragina et al. 2009). Accounting for other factors beyond  
102 spawner biomass might thus be critical to fully understand how the age structure of a population  
103 affects its productivity.

104 The NEA cod stock is currently the world's largest population of Atlantic cod and sustains a  
105 large and profitable fishery. The stock mainly feeds in the Barents Sea and spawns along the  
106 west and north coasts of Norway (Fig. 1). Changes in the population age structure of NEA cod  
107 have occurred for almost a century, largely in response to intense exploitation (Ottersen 2008;  
108 Eikeset et al. 2016). The typical age at maturation and the mean age of the spawning stock have  
109 both declined considerably during the 2<sup>nd</sup> half of the 20<sup>th</sup> century, although spawner age structure  
110 has partly recovered over the past two decades (Fig. 2), coinciding with a reduction in fishing  
111 mortality (Kjesbu et al. 2014). Here, we ask whether population productivity in NEA cod  
112 (measured as the natural logarithm of recruits per spawning stock biomass) is affected by  
113 changes in the age structure of the spawning stock. We test for effects of intraspecific predation  
114 of pre-recruits by older juveniles, and assess potential effects of other ecological conditions on  
115 population productivity, including changes in temperature and species interactions.

## 116 **METHODS**

### 117 *Study species and region*

118 NEA cod are mainly distributed throughout the Barents Sea off the northern coasts of Norway  
119 and Russia. Adults perform annual migrations to the spawning grounds along the west coast of  
120 Norway, where they spawn primarily in March-April (Fig. 1; Ottersen et al. 2014). Spawning  
121 eggs drift northeastward in the Norwegian Coastal Current and develop into pelagic larvae and  
122 juveniles that reach the main feeding grounds in the Barents Sea after about five months of drift.  
123 The fish remain in the Barents Sea until they reach maturity, typically at the age of 6-8 years  
124 (Olsen et al. 2010). Compared to other populations of Atlantic cod, NEA cod are relatively slow  
125 growing and late maturing (Köster et al. 2013). NEA cod can grow to over 1 m in length and live

126 over 20 years (Holt and Jørgensen 2014). The stock has been harvested for centuries along the  
127 Norwegian coast, and more recently (since the 1930s) in the Barents Sea.

### 128 ***Data sources***

129 We used annual estimates of numbers at age, weight at age, and proportion mature at age as  
130 reported in the NEA cod stock assessment (ICES 2020). NEA cod are assumed to recruit to the  
131 fishery at age-3, and recruitment is measured as the abundance of 3-year-old fish (ICES 2020).  
132 Numbers at age include cod ages 1-13 and a plus group combining all fish ages 14 and older.

133 Temperature data were obtained from the Kola transect (Tereschenko 1996), an indicator of the  
134 thermal conditions in the Barents Sea (Ottersen and Stenseth 2001). We used a mean temperature  
135 value averaged over six months (July-December), across Kola stations 3-7 (Fig. 1), and vertically  
136 from 0-200m depth (available online at: [www.pinro.ru](http://www.pinro.ru)). Temperature records were available for  
137 the years 1946-2017, except during August-December 2016. These data were added using  
138 bivariate interpolation of temperature data (using function *interp* in R) across years and months.

139 Data on biomass and abundances of interacting species were obtained from various sources.  
140 These include estimates of total abundance of capelin (*Mallotus villosus*) in the Barents Sea for  
141 the years 1972-2015 (ICES 2020), estimates of Norwegian spring spawning herring (*Clupea*  
142 *harengus*) biomass (ages 1-2) for the years 1950-2015 (ICES 2020), an index of krill abundance  
143 for the years 1950-2005 based on Russian bottom surveys in winter (Zhukova et al. 2009), and a  
144 zooplankton abundance index (copepod nauplii) based on Russian surveys in April-May and  
145 June-July for the years 1959-1990 (Stige et al. 2010). We also included a more recent index of  
146 zooplankton biomass in the southwestern and central Barents Sea in summer (August-  
147 September) for the years 1981-2015 (Stige et al. 2018). Previous studies suggested that  
148 recruitment success in NEA cod depends on the abundance of mesozooplankton, a critical food



149 source for early life-stages of cod, the abundance of capelin, another important prey species, via  
 150 increased growth and reduced inter-cohort cannibalism, as well as the biomass of herring, which  
 151 feed on capelin larvae and thus affect capelin recruitment (Hamre 1994; Hjermann et al. 2007;  
 152 Langangen et al. 2017).

### 153 *Calculating stock metrics*

154 Spawner biomass of cod at age  $a$  in year  $y$  ( $S_{a,y}$ ) was calculated from annual numbers at age (  
 155  $N_{a,y}$ ), weight at age ( $W_{a,y}$ ), and proportion mature at age ( $M_{a,y}$ ):

$$156 \quad S_{a,y} = N_{a,y}W_{a,y}M_{a,y}, \quad (1)$$

157 Total spawning stock biomass in a given year was then calculated as the sum across ages:

$$158 \quad S_y = \sum_a S_{a,y}. \quad (2)$$

159 The biomass of 3-6 year-old cod was used as a proxy for potential cannibalism on pre-recruits:

$$160 \quad C_y = \sum_{a=3}^{a=6} N_{a,y}W_{a,y}. \quad (3)$$

161 This index of cannibal biomass is only weakly correlated with spawning stock biomass because  
 162 NEA cod typically do not mature before age-6 (Olsen et al. 2010).

163 We used biomass-weighted mean age of spawners ( $\bar{A}_y$ ) as a metric of spawner age structure, as  
 164 done previously for this and other stocks (Ottersen et al. 2006; Ottersen 2008):

$$165 \quad \bar{A}_y = \frac{\sum_a S_{a,y} a}{\sum_a S_{a,y}}. \quad (4)$$

166 We also used the biomass-weighted mean weight ( $\bar{W}_y$ ) of spawners (Langangen et al. 2019):

$$167 \quad \bar{W}_y = \frac{\sum_a S_{a,y} W_{a,y}}{\sum_a S_{a,y}}. \quad (5)$$

168 Previous work that explored various metrics of spawner age and size structure as predictors of  
 169 changes in the abundance and distribution of NEA cod eggs found that biomass-weighted mean  
 170 age and weight were better predictors than other metrics (Stige et al. 2017), and spawner mean  
 171 age appears to reflect the major shift in spawner age structure in this population (Appendix S1:  
 172 Fig. S1). However, we considered other commonly used metrics of spawner age structure in our  
 173 model selection, specifically the proportion of individuals in the oldest age class (+group), the  
 174 Shannon index of age diversity, and the proportion of repeat spawners, (Marteinsdottir and  
 175 Thorarinsson 1998; Brunel 2010; Barnett et al. 2017).

176 We calculated an index of the proportion of the oldest fish in the population as the log ratio of  
 177 the proportion of individuals in the plus group in any given year relative to the proportion of  
 178 individuals in the plus group at the beginning of the time series ( $PG_y$ ) (Barnett et al. 2017):

$$179 \quad PG_y = \log \left( \frac{pPG_y}{pPG_{y=1946}} \right), \text{ with } pPG_y = \frac{N_{a \geq 15,y}}{\sum_{a=1}^{14} N_{a,y}}, \quad (6)$$

180 where  $pPG_y$  is the proportion of the plus group individuals (ages 15+) in the population.

181 The Shannon diversity index ( $DIV_y$ ) was calculated based on the frequency of mature biomass at  
 182 age ( $f_{a,y}$ ):

$$183 \quad DIV_y = - \sum_a (f_{a,y} \ln(f_{a,y})), \text{ for } f_{a,y} > 0. \quad (7)$$

184 The proportion repeat spawners ( $PRS_y$ ) was calculated based on the proportions mature in each  
 185 age and year:

$$186 \quad PRS_y = \frac{\sum_a (M_{a-1,y-1}/M_{a,y}) S_{a,y}}{\sum_a S_{a,y}}. \quad (8)$$

187 ***Statistical analyses***

188 Our analysis is based on a Ricker stock-recruitment model (Ricker 1954) to describe the  
 189 relationship between spawning stock biomass in year  $y$  ( $S_y$ ) and subsequent recruitment ( $R_{y+3}$ )  
 190 three years later. The linearized version is:

$$191 \ln\left(\frac{R_{y+3}}{S_y}\right) = \alpha + \beta S_y + \epsilon_y, \quad (9)$$

192 where  $\alpha$  is the intercept,  $\beta$  is the rate at which productivity declines with spawner biomass (  
 193  $\beta \leq 0$ ), and  $\epsilon_y$  is an error term that was modeled to account for autocorrelation in the residuals:

$$194 \epsilon_y = \epsilon_{y-1}\varphi + \omega_y, \quad (10)$$

195 where  $\varphi$  is the autocorrelation coefficient and  $\omega_y \sim N(0, \sigma^2)$  are normal random errors.

196 The natural logarithm of recruits per spawner biomass was thus used as a metric of population  
 197 productivity. To explain variation in population productivity over time beyond the effect of  
 198 spawner biomass, we extended this model to incorporate other predictor variables:

$$199 \ln\left(\frac{R_{y+3}}{S_y}\right) = \alpha + \beta_0 S_y + \beta_1 X_1 + \dots + \beta_n X_n + \epsilon_y, \quad (11)$$

200 where  $\beta_1, \dots, \beta_n$  are the regression coefficients and  $X_1, \dots, X_n$  are the covariate time series lagged  
 201 relative to spawn year when the covariate is hypothesized to affect population productivity via  
 202 effects on spawners, eggs, larvae, or pre-recruit juveniles. By using a linearized Ricker model,  
 203 we implicitly assume that potential covariate effects are additive on log scale (multiplicative on  
 204 arithmetic scale), and we test whether covariates affect population productivity, not whether they  
 205 modulate the density dependence between recruitment and spawner biomass.

206 We considered the following continuous predictor variables in addition to total spawner biomass,  
 207 which was set as a fixed term in the regression analysis: biomass of age 3-6 cannibals in the year  
 208 after spawning (as a proxy of intraspecific predation by preceding cohorts during the pre-recruit

209 life-stages), average temperature of the Kola section in the Barents Sea from July through  
210 December, i.e. during the larval and 0-group stages, and one of the age structure metrics:  
211 biomass-weighted mean age or mean weight of spawners, the Shannon index of age diversity, the  
212 proportion of individuals in the plus group, and the proportion of repeat spawners. We did not  
213 include more than one age structure metric in the same model due to high pairwise correlations  
214 among these metrics. We considered other seasonal temperature averages during our preliminary  
215 analysis that were less strongly associated with our response variable. All of the above covariate  
216 time series were available for all years with data on spawner biomass and recruitment (1946-  
217 2017), with the exception that the proportion repeat spawners could not be computed for the first  
218 year. A lag of one year post spawning was used for the cannibal biomass covariate because  
219 cannibalism mortality is highest among 1-year old cod (Yaragina et al. 2009). We also tested for  
220 effects of food web interactions, using indices of capelin abundance, biomass of young herring  
221 (ages 1-2), krill abundance, and mesozooplankton abundance, which were not available for all  
222 years. The model selection was run using years with observations for each predictor, and was  
223 extended to include more years as predictors with shorter time series were dropped from the  
224 model. Information on covariates included in the model selection, available data, lags  
225 considered, and potential mechanisms are presented in the Supplementary Material (Appendix  
226 S1: Table S1). We considered non-linear temperature effects by including a quadratic term in  
227 addition to the linear effect, and tested for an interaction effect between temperature and age  
228 structure (Ottersen et al. 2006), by constructing a dummy variable representing ‘high’ and ‘low’  
229 values. The optimal threshold for splitting the age structure metric into two categories was  
230 determined by testing a range of quantiles (0.2-0.8).

231 Model selection was performed using the *dredge* function of the package *MuMIn* (v. 1.43.15,  
232 Burnham and Anderson 2002) in R (R Core Team 2020) and was based on Akaike's Information  
233 Criterion corrected for small sample size (AICc). All variables were centered and standardized to  
234 a mean of zero and a standard deviation of one for the analysis to ensure that main effects are  
235 biologically interpretable in the presence of interactions and that slopes are comparable within  
236 and between models (Schielzeth 2010). We tested for the inclusion of model weights for  
237 explaining the variance structure of the residuals using fixed and exponential functions of the  
238 selected covariates (Zuur et al. 2010). Because we tested a variable threshold effect for the  
239 interaction between temperature and mean age, we penalized the interaction model when  
240 calculating the AICc value by counting the threshold as one additional parameter (Ottersen et al.  
241 2013). We assessed multicollinearity between selected explanatory variables using variance  
242 inflation factors (VIF) (Zuur et al. 2010).

243 To assess the ability of the models of varying complexity to make out-of-sample predictions, we  
244 performed a model cross validation. The data were randomly split into a training dataset (75% of  
245 data) and a test dataset (25% of data), and all sub-models contained in the selected model with  
246 the lowest AICc value were run on the training data to estimate the model parameters and  
247 subsequently predict the remaining test data. We then calculated the root mean squared  
248 prediction error (RMSE) as our performance metric:

$$249 \quad \text{RMSE} = \sqrt{\frac{\sum_1^n (\hat{y} - y)^2}{n}}, \quad (12)$$

250 where  $\hat{y}$  and  $y$  are model-predicted and observed  $\ln(\text{recruits}/\text{SSB})$  in each year, respectively, and  
251  $n$  is the number of years. This procedure was repeated 1000 times by randomly drawing the  
252 training and test datasets from the observations. The median root mean squared prediction errors

253 across runs were compared among all sub-models to assess which of the models would produce  
254 the best out-of-sample predictions, i.e. smallest median prediction errors. Code for the statistical  
255 analyses is provided as supporting information (Data S1) and is available online in Zenodo at:  
256 <https://doi.org/10.5281/zenodo.5851638>.

## 257 **RESULTS**

258 Over the past 75 years, spawning stock biomass of NEA cod has varied between 0.1 and 2.64  
259 million tons with an average of 0.62 million tons, and recruitment at age-3 has varied between  
260 0.11 and 2.59 billion recruits with an average of 0.75 billion recruits (Fig. 2). Population  
261 productivity measured as  $\ln(\text{recruits}/\text{SSB})$  has varied considerably over time and was particularly  
262 low during the 2010s when spawning stock biomass was high.

263 Population age structure was an important predictor of population productivity in NEA cod.

264 Several of the age structure metrics performed similarly well in terms of AICc and model  
265 predictive ability (Appendix S1: Table S4; Fig. S2), and our model selection showed support for  
266 including the same covariates in models with alternative age structure metrics. In addition to  
267 spawning stock biomass, the final models included the biomass of age 3-6 cannibals, mean  
268 temperature, and one of the age structure metrics:

$$269 \ln\left(\frac{R_{y+3}}{S_y}\right) = \alpha + \beta_0 S_y + \beta_1 A_y + \beta_2 C_{y+1} + \beta_3 T_y + \epsilon_y,$$

270 where  $A_y$  is the age structure metric in year  $y$ ,  $C_{y+1}$  is biomass of potential cannibals in the  
271 following year, and  $T_y$  is mean environmental temperature in year  $y$  from July to December.  
272 Time series of selected covariates are presented in Fig. 2. Productivity of NEA cod was not  
273 associated with any of the abundance or biomass indices of the interacting species that we

274 considered in the model. We did not find evidence for the inclusion of model weights to explain  
275 the variance structure in the data.

276 We found that population productivity was negatively associated with spawning stock biomass  
277 (mature fish age 6 or older) and the biomass of potential cannibals (mostly immature fish ages 3-  
278 6), and positively associated with mean temperature and the age structure metrics (Fig. 3). While  
279 spawner mean age performed best in terms of model predictive ability, other age structure  
280 metrics resulted in similar prediction errors and AICc values (Appendix S1: Table S4; Fig. S2).  
281 Specifically, the log ratio of the proportion of old individuals (ages 15+) in the population and  
282 spawner age diversity were similarly good predictors of population productivity (Fig. 3).

283 The AICc-based model selection of covariates resulted in competing models with similar AICc  
284 support (Appendix S1: Table S2). The more complex model included an interaction effect  
285 between temperature and the age structure metric as categorical variable (e.g. spawner mean age  
286 with a threshold at the 0.7 quantile, Appendix S1: Fig. S3). However, the simpler model received  
287 support based on the model cross-validation due to lower root mean squared prediction errors  
288 and was selected as the most parsimonious model (Appendix S1: Fig. S4). Residuals suggested  
289 no violation of assumptions of normality and homoscedasticity and model predictions captured  
290 much of the trends and interannual variability in population productivity (Appendix S1: Fig. S5).  
291 The estimated model coefficients (per unit standard deviation) are provided in Appendix S1:  
292 Table S3. The standard deviation of the normal random error was 0.54, and the autocorrelation  
293 coefficient was 0.47 (mean age model). While spawning stock biomass, metrics of spawner age  
294 structure, and cannibal biomass are intrinsic population metrics, pairwise correlations between  
295 covariates of the fitted models were low (Pearson correlation coefficients  $<0.4$ ), and a variance  
296 inflation factor analysis of the selected covariates raised no concern of multicollinearity (all

297 values  $<1.2$ ). Inclusion of alternative age structure metrics did not appreciably alter the estimated  
298 coefficients for spawning stock biomass, biomass of cannibals, and mean temperature (Fig. 3).  
299 The selected models were used to predict  $\ln(\text{recruits}/\text{SBB})$  as a function of spawning stock  
300 biomass for different values of the age structure metrics while setting other covariates (cannibal  
301 biomass and temperature) to median values. We used the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of spawner  
302 mean age, log ratio of the proportion plus group, and the spawner age diversity index that have  
303 been observed over the past 75 years. The predictions illustrated the large effect that spawner age  
304 structure has on expected recruits per spawning stock biomass (Fig. 3). For example, the ratio of  
305 model-predicted recruits/SBB at the highest compared to the lowest mean age was 3.04. A  
306 spawning stock with a mean age of about 11 years is expected to produce three times as many  
307 recruits per unit spawner biomass compared to a spawning stock with a mean age of about 7  
308 years. We further found that the effects of spawner age structure were slightly weaker when the  
309 biomass of age 3-6 cod was not included in the model. Dropping cannibal biomass from the  
310 model resulted in smaller effect sizes of spawner age structure, and reduced model predictive  
311 ability (Appendix S1: Fig. S4, Fig. S6).

## 312 **DISCUSSION**

313 We find evidence that the mean age of spawners, or alternatively age diversity or the proportion  
314 of old individuals in the population, has a positive effect on population productivity, measured as  
315 recruits per spawning stock biomass. Our results suggests a three-fold difference in population  
316 productivity between the lowest and highest mean ages of spawners that have been observed  
317 over the past 75 years. In addition, we find evidence that the biomass of potential cannibals  
318 negatively affects population productivity, and that increasing temperatures have a positive effect  
319 on the productivity of this high-latitude cod population.



320 Previous work has evaluated the effect of spawner age structure on cod population recruitment.  
321 Ottersen (2008) analyzed data on NEA cod and found no clear link between the mean age of  
322 spawners and subsequent recruitment. Brunel (2010) studied multiple stocks of Atlantic cod and  
323 found that the effects of spawner mean age and age diversity on recruitment were positive but  
324 non-significant for most cod stocks, including NEA cod. Shelton et al. (2015) used stock-recruit  
325 relationships that included maternal age structure to model the recruitment of several stocks of  
326 Atlantic cod and found that in many stocks a model with a maternal age effect was preferred,  
327 though they reported a relatively weak effect for NEA cod. However, these studies did not  
328 account for potential cannibalism of pre-recruits by older juveniles that have recruited to the  
329 fishery but are not part of the spawning stock. Because NEA cod rarely mature before age 6, and  
330 predation by 3-6 year-olds accounts for most of the cannibalism mortality among pre-recruits  
331 (Bogstad et al. 1994; Yaragina et al. 2009), the majority of potential cannibals are not part of the  
332 spawning stock. We therefore included cannibal biomass as an additional variable in our model.  
333 Ignoring this component of intrinsic population regulation likely affects inferences about other  
334 factors affecting productivity, especially because cannibalism in NEA cod appears to be more  
335 pronounced than in other stocks (Holt et al. 2019). This is in line with our finding that the effect  
336 of spawner age structure was weaker when the biomass of age 3-6 cod was not included in the  
337 model. It should be noted that our analysis relies on data from a stock-assessment model that are  
338 assumed to represent true values. The NEA stock assessment model considers cannibalism  
339 mortality, in addition to a fixed natural mortality, and the underlying estimation of consumption  
340 of cod by cod based on stomach content data is uncertain and affected by temperature (ICES  
341 2020). This might introduce bias into our model estimates, in particular the cannibalism effect.

342 The higher recruitment success per unit spawner biomass of an older and more age diverse  
343 spawning stock is in part caused by an increase in mass-specific reproductive investment with  
344 female body size. Hyperallometric scaling of reproductive output is commonly observed in  
345 marine fishes, including Atlantic cod (Barneche et al. 2018), and interannual variation in relative  
346 fecundity is associated with variation in the size composition of the spawning stock in NEA cod  
347 (Marshall et al. 2006). While the approach applied here does not allow us to quantify the  
348 contributions of different mechanisms, our findings suggest that other factors linked to maternal  
349 effects contribute to increased population productivity of an older spawning stock, because  
350 productivity was more strongly linked to the mean age of spawners than the mean weight of  
351 spawners. Maternal effects may arise from various mechanisms, including differences between  
352 young and old spawners in the duration of spawning, frequency of skipped spawning, and factors  
353 such as larger eggs that can result in higher offspring survival (Solemdal et al. 1995; Kjesbu et  
354 al. 1996; Nissling et al. 1998; Vallin and Nissling 2000; Jørgensen et al. 2006). Other  
355 mechanisms appear to be less important, for instance, a broader spatial distribution of eggs has  
356 little effect on recruitment in NEA cod (Stige et al. 2017; Langangen and Stige 2021).

357 We found a positive but relatively weak link between NEA cod productivity and temperature, as  
358 reported previously (Ottersen and Loeng 2000; Stige et al. 2010; Ohlberger et al. 2014). Higher  
359 temperatures likely increase growth and survival during early life-stages. Impacts of warming  
360 may also differ between life-stages (Peck et al. 2009), and manifest through various mechanisms,  
361 including changes in the abundance and distribution of predators and prey (Ohlberger 2013;  
362 Ottersen et al. 2014). In NEA cod, higher temperatures also appear to be linked to spawning at  
363 higher latitudes (Sundby and Nakken 2008; Langangen et al. 2019; but see Opdal and Jørgensen  
364 2015). Importantly, climate warming can affect populations of the same species differently. The

365 relationship between environmental temperature and recruitment of Atlantic cod varies by  
366 population, with positive effects at higher latitudes and negative effects at lower latitudes  
367 (Drinkwater 2005). Interestingly, we found similar support for a model that included an  
368 interaction between temperature and age structure (as a categorical variable), which suggested a  
369 positive temperature effect at low mean age, age diversity or proportion plus group, but no effect  
370 at high values. While that model was not selected as the most parsimonious due to its lower  
371 predictive performance, such an interaction would be consistent with previous work that  
372 suggested a strengthening of the climate-recruitment link during the second half of the 20<sup>th</sup>  
373 century (Ottersen et al. 2006).

374 The reduction in population productivity associated with shifting spawner age structure is of  
375 particular importance because fisheries increase mortality and often selectively remove large  
376 individuals from the spawning populations. Fishing commonly leads to population age structures  
377 shifting towards younger and smaller fish (Anderson et al. 2008; Sharpe and Hendry 2009) and  
378 may result in evolutionary changes toward earlier maturation (Kuparinen and Merilä 2007;  
379 Heino et al. 2015). While evidence exists that changes in the age structure of NEA cod largely  
380 occurred in response to exploitation (Ottersen 2008; Eikeset et al. 2016), it is conceivable that  
381 increasing temperatures contribute to reduced mean age of spawners via effects on growth and  
382 maturation (Forster et al. 2012; Baudron et al. 2014; Huss et al. 2019). Our results thus suggest  
383 that intense capture fisheries can affect the productivity of the populations they depend on, not  
384 only via changes of total spawner abundance, but also by altering the age structure of the  
385 spawning stock. Changes related to species life-histories, such as shifting spawner age structures,  
386 are increasingly recognized to impact population recruitment (Shelton et al. 2015). Our study  
387 shows that age structure can have significant impacts on fish stock productivity, which in turn

388 might affect the long-term sustainable yield of commercial fisheries and the livelihoods that  
389 depend on these fisheries. A model including spawner mean age had a slightly better predictive  
390 ability compared to models including alternative age structure metrics in our study. While mean  
391 age has been criticized as a poor descriptor of the age composition of a population and is difficult  
392 to link to individual-level traits (Shelton et al . 2015), spawner mean age appears to capture the  
393 shift in age composition of the NEA cod spawning stock (Appendix S1: Fig. S1), likely because  
394 these shifts are associated with changes in age at first maturation. Alternative metrics such as the  
395 proportion of old individuals in the population may be better suited to reflect age structure  
396 changes in other exploited populations, for example those that have not experienced long-term  
397 changes in maturation schedules.

398 Our findings highlight the potential of preserving spawner age structure as a tool to sustaining  
399 population productivity. Shifting age structures of fish populations can also cause increased  
400 variability in abundance and reduced population resilience (Anderson et al. 2008; Hsieh et al.  
401 2010; Shelton and Mangel 2011). Incorporating demographic information into the fishery  
402 management process could help preserve an older and more diverse age structure and thereby  
403 facilitate fisheries sustainability. Whether the best approach to preserving spawner age structure  
404 is via size or weight limits, spatial fishery closures, or reduced fishing mortality, likely depends  
405 on the ecology of the exploited population as well as fishing methods and current management  
406 practices (Berkeley et al. 2004; Kjesbu et al. 2014; Ahrens et al. 2020). For instance, the NEA  
407 cod fishery is currently managed via a harvest control rule that is used to set the total allowable  
408 catch each year based on reference points for spawning stock biomass and fishing mortality. This  
409 rule was designed to ensure that the stock is harvested sustainably (ICES 2009; Eikeset et al.  
410 2013), and its implementation in the mid-2000s appears to have contributed to increased spawner

411 biomass and mean age (Kjesbu et al. 2014; Fig. 1). In addition to biomass or fishing mortality  
412 limits, harvest control rules could adopt reference points based on the demographic status of a  
413 population to further ensure that population reproductive capacity is maintained.

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#### 417 **LITERATURE CITED**

418 Ahrens R. N. M., M. S. Allen, C. Walters, and R. Arlinghaus. 2020. Saving large fish through  
419 harvest slots outperforms the classical minimum-length limit when the aim is to achieve  
420 multiple harvest and catch-related fisheries objectives. *Fish and Fisheries* 21:483–510.

421 Andersen K. H., N. S. Jacobsen, and P. D. van Denderen. 2019. Limited impact of big fish  
422 mothers for population replenishment. *Canadian Journal of Fisheries and Aquatic  
423 Sciences* 76:347–349.

424 Anderson C. N. K., et al. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*  
425 452:835–839.

426 Anderson J., and R. S. Gregory. 2000. Factors regulating survival of northern cod (NAFO  
427 2J3KL) during their first 3 years of life. *ICES Journal of Marine Science* 57:349–359.

428 Audzijonyte A., et al. 2020. Fish body sizes change with temperature but not all species shrink  
429 with warming. *Nature Ecology & Evolution* 4:809–814.

430 Barneche D. R., D. R. Robertson, C. R. White, and D. J. Marshall. 2018. Fish reproductive-  
431 energy output increases disproportionately with body size. *Science* 360:642–644.

- 432 Barnett L. A. K., T. A. Branch, R. A. Ranasinghe, and T. E. Essington. 2017. Old-growth fishes  
433 become scarce under fishing. *Current Biology* 27:2843–2848.
- 434 Baudron A. R., C. L. Needle, A. D. Rijnsdorp, and T. Marshall C. 2014. Warming temperatures  
435 and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global  
436 Change Biology* 20:1023–1031.
- 437 Beamish R. J., G. A. McFarlane, and A. Benson. 2006. Longevity overfishing. *Progress in  
438 Oceanography* 68:289–302.
- 439 Berkeley S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via  
440 protection of age structure and spatial distribution of fish populations. *Fisheries  
441 Oceanography* 29:23–32.
- 442 Birkeland C., and P. Dayton. 2005. The importance in fishery management of leaving the big  
443 ones. *Trends in Ecology & Evolution* 20:356–358.
- 444 Bogstad B., G. R. Lilly, S. Mehl, O. K. Palsson, and G. Stefansson. 1994. Cannibalism and year-  
445 class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents  
446 Sea, Iceland, and eastern Newfoundland). *ICES Marine Science Symposia* 198:576–599.
- 447 Botsford L. W., M. D. Holland, J. C. Field, and A. Hastings. 2014. Cohort resonance: a  
448 significant component of fluctuations in recruitment, egg production, and catch of fished  
449 populations. *ICES Journal of Marine Science* 71:2158–2170.
- 450 Brunel T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast  
451 Atlantic fish stocks. *ICES Journal of Marine Science* 67:1921–1930.
- 452 Brunel T., and G. J. Piet. 2013. Is age structure a relevant criterion for the health of fish stocks?  
453 *ICES Journal of Marine Science* 70:270–283.

- 454 Burnham K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference, Second  
455 edition edn (eds Burnham KP, Anderson DR). Springer-Verlag, New York, NY.
- 456 Daufresne M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in  
457 aquatic ecosystems. *Proceedings of the National Academy of Sciences USA* 106:12788–  
458 12793.
- 459 Denderen D., H. Gislason, J. Heuvel, and K. H. Andersen. 2020. Global analysis of fish growth  
460 rates shows weaker responses to temperature than metabolic predictions. *Global Ecology  
461 and Biogeography* 29:2203–2213.
- 462 Drinkwater K. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change.  
463 *ICES Journal of Marine Science* 62:1327–1337.
- 464 Eikeset A. M., E. S. Dunlop, M. Heino, G. Storvik, N. C. Stenseth, and U. Dieckmann. 2016.  
465 Roles of density-dependent growth and life history evolution in accounting for fisheries-  
466 induced trait changes. *Proceedings of the National Academy of Sciences USA*  
467 113:15030–15035.
- 468 Forster J., A. G. Hirst, and D. Atkinson. 2012. Warming-induced reductions in body size are  
469 greater in aquatic than terrestrial species. *Proceedings of the National Academy of  
470 Sciences USA* 109:19310–19314.
- 471 Gardner J. L., A. Peters, M. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a  
472 third universal response to warming? *Trends in Ecology & Evolution* 26:285–291.
- 473 Hamre J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents  
474 Sea ecosystem. *Biodiversity and Conservation* 3:473–492.

- 475 Heino M., B. Díaz Pauli, and U. Dieckmann. 2015. Fisheries-Induced Evolution. Annual Review  
476 of Ecology and Systematics 46:461–480.
- 477 Hixon M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of  
478 conserving old-growth age structure in fishery populations. ICES Journal of Marine  
479 Science 71:2171–2185.
- 480 Hjermann D. Ø., B. Bogstad, A. M. Eikeset, G. Ottersen, H. Gjøsæter, and N. C. Stenseth. 2007.  
481 Food web dynamics affect Northeast Arctic cod recruitment. Proceedings of the Royal  
482 Society B: Biological Sciences 274:661–669.
- 483 Holt R. E., and C. Jorgensen. 2014. Climate warming causes life-history evolution in a model for  
484 Atlantic cod (*Gadus morhua*). Conservation Physiology 2:cou050.  
485 <https://doi.org/10.1093/conphys/cou050>
- 486 Holt R. E., B. Bogstad, J. M. Durant, A. V. Dolgov, and G. Ottersen. 2019. Barents Sea cod  
487 (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic  
488 patterns. ICES Journal of Marine Science 76:1641–1652.
- 489 Hsieh C.-H., A. Yamauchi, T. Nakazawa, and W. F. Wang. 2010. Fishing effects on age and  
490 spatial structures undermine population stability of fishes. Aquatic Sciences 72:165-178.
- 491 Huss M., M. Lindmark, P. Jacobson, RM. van Dorst, and A. Gårdmark. 2019. Experimental  
492 evidence of gradual size-dependent shifts in body size and growth of fish in response to  
493 warming. Global Change Biology 25:2285–2295.
- 494 ICES. 2009. Report of the ICES Advisory Committee 2009. ICES Advice 2009.
- 495 ICES. 2020. Arctic Fisheries Working Group (AFWG). ICES Scientific Reports 2:52.  
496 <http://doi.org/10.17895/ices.pub.6050>



- 497 Jørgensen T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus*  
498 *morhua* L.). ICES Journal of Marine Science 46:235-248
- 499 Jørgensen C., et al. 2007. Ecology: managing evolving fish stocks. Science 318:1247–1248.
- 500 Jørgensen C., B. Ernande, Ø. Fiksen, and U. Dieckmann. 2006. The logic of skipped spawning in  
501 fish. Canadian Journal of Fisheries and Aquatic Sciences 63:200–211.
- 502 Kjesbu O. S., P. Solemdal, P. Bratland, M. Fonn. 1996. Variation in annual egg production in  
503 individual captive Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and  
504 Aquatic Sciences 53:610–620.
- 505 Kjesbu O. S., B. Bogstad, J. A. Devine, H. Gjøsæter, D. Howell, R. B. Ingvaldsen, R. D. M.  
506 Nash, and J. E. Skjæraasen. 2014. Synergies between climate and management for  
507 Atlantic cod fisheries at high latitudes. Proceedings of the National Academy of Sciences  
508 USA 111:3478–3483.
- 509 Köster F. W., E. A. Trippel, and J. Tomkiewicz. 2013. Linking size and age at sexual maturation  
510 to body growth, productivity and recruitment of Atlantic cod stocks spanning the North  
511 Atlantic. Fisheries Research 138:52–61.
- 512 Langangen Ø., J. Ohlberger, L. C. Stige, J. M. Durant, E. Ravagnan, N. C. Stenseth, and D. Ø.  
513 Hjermann. 2017. Cascading effects of mass mortality events in Arctic marine  
514 communities. Global Change Biology 23:283–292.
- 515 Langangen Ø., et al. 2019. Ticket to spawn: Combining economic and genetic data to evaluate  
516 the effect of climate and demographic structure on spawning distribution in Atlantic cod.  
517 Global Change Biology 25:134–143.

- 518 Langangen Ø., and L. C. Stige. 2021. Shedding light on the link between the spatial distribution  
519 of eggs and survival in Northeast Arctic cod. *Fisheries Oceanography* 30:429–436.
- 520 Law R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57:  
521 57:659–668.
- 522 Marshall C. T., C. L. Needle, A. Thorsen, O. S. Kjesbu, and N. A. Yaragina. 2006. Systematic  
523 bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock:  
524 implications for stock-recruit theory and management. *Canadian Journal of Fisheries and*  
525 *Aquatic Sciences* 63:980–994.
- 526 Marshall D. J., M. Bode, M. Mangel, R. Arlinghaus, and E. J. Dick. 2021. Reproductive  
527 hyperallometry and managing the world’s fisheries. *Proceedings of the National*  
528 *Academy of Sciences USA* 118:e2100695118.
- 529 Marteinsdottir G., and K. Thorarinsson. 1998. Improving the stock-recruitment relationship in  
530 Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal*  
531 *of Fisheries and Aquatic Sciences* 55:1372–1377.
- 532 Murawski S. 2001. Impacts of demographic variation in spawning characteristics on reference  
533 points for fishery management. *ICES Journal of Marine Science* 58:1002–1014.
- 534 Nissling A., R. Larsson, L. Vallin, and K. Frohland. 1998. Assessment of egg and larval viability  
535 in cod, *Gadus morhua*: methods and results from an experimental study. *Fisheries*  
536 *Research* 38:169–186.
- 537 Ohlberger J. 2013. Climate warming and ectotherm body size - from individual physiology to  
538 community ecology. *Functional Ecology* 27:991–1001.

- 539 Ohlberger J., L. A. Rogers, and N. C. Stenseth. 2014. Stochasticity and determinism: How  
540 density-independent and density-dependent processes affect population variability. PLoS  
541 ONE 9:e98940.
- 542 Ohlberger J., et al. 2020. The reproductive value of large females: consequences of shifts in  
543 demographic structure for population reproductive potential in Chinook salmon.  
544 Canadian Journal of Fisheries and Aquatic Sciences 77:1292–1301.
- 545 Olsen E., S. Aanes, S. Mehl, J. C. Holst, A. Aglen, and H. Gjøsæter. 2010. Cod, haddock, saithe,  
546 herring, and capelin in the Barents Sea and adjacent waters: A review of the biological  
547 value of the area. ICES Journal of Marine Science 67:87–101.
- 548 Opdal A. F., and C. Jørgensen. 2015. Long-term change in a behavioural trait: truncated  
549 spawning distribution and demography in Northeast Arctic cod. Global Change Biology  
550 21:1521–1530.
- 551 Ottersen G. 2008. Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian  
552 cod (*Gadus morhua*) and possible consequences for recruitment. Canadian Journal of  
553 Fisheries and Aquatic Sciences 65:523–534.
- 554 Ottersen G., and H. Loeng. 2000. Covariability in early growth and year-class strength of  
555 Barents Sea cod, haddock, and herring: the environmental link. ICES Journal of Marine  
556 Science 57:339–348.
- 557 Ottersen G., D. Ø. Hjermann, and N. C. Stenseth. 2006. Changes in spawning stock structure  
558 strengthen the link between climate and recruitment in a heavily fished cod (*Gadus*  
559 *morhua*) stock. Fisheries Oceanography 15:230–243.

- 560 Ottersen G., and N. C. Stenseth. 2001. Atlantic climate governs oceanographic and ecological  
561 variability in the Barents Sea. *Limnology and Oceanography* 46:1774-1780.
- 562 Ottersen G., L. C. Stige, J. M. Durant, K.-S. Chan, T. A. Rouyer, K. F. Drinkwater, and N. C.  
563 Stenseth. 2013. Temporal shifts in recruitment dynamics of North Atlantic fish stocks:  
564 effects of spawning stock and temperature. *Marine Ecology Progress Series* 480:205–  
565 225.
- 566 Ottersen G., B. Bogstad, N. A. Yaragina, L. C. Stige, F. B. Vikebø, and P. Dalpadado. 2014. A  
567 review of early life history dynamics of Barents Sea cod (*Gadus morhua*). *ICES Journal*  
568 *of Marine Science* 71:2064–2087.
- 569 Peck L. S., M. S. Clark, S. A. Morley, A. Massey, and H. Rossetti. 2009. Animal temperature  
570 limits and ecological relevance: effects of size, activity and rates of change. *Functional*  
571 *Ecology* 23:248–256
- 572 R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for  
573 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 574 Ricker W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*  
575 11:559–623.
- 576 van Rijn I., Y. Buba, J. DeLong, M. Kiflawi, and J. Belmaker. 2017. Large but uneven reduction  
577 in fish size across species in relation to changing sea temperatures. *Global Change*  
578 *Biology* 23:3667–3674.
- 579 Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients.  
580 *Methods in Ecology and Evolution* 1:103–113.

- 581 Scott B. E., G. Marteinsdottir, G. A. Begg, P. J. Wright, and O. S. Kjesbu. 2006. Effects of  
582 population size/age structure, condition and temporal dynamics of spawning on  
583 reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling* 191:383–415.
- 584 Sharpe D. M. T., and A. P. Hendry. 2009. Life history change in commercially exploited fish  
585 stocks: an analysis of trends across studies. *Evolutionary Applications* 2:260–275.
- 586 Shelton A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects  
587 of fishing. *Proceedings of the National Academy of Sciences USA* 108:7075–7080.
- 588 Shelton A. O., J. A. Hutchings, R. S. Waples, D. M. Keith, H. R. Akçakaya, N. K. and Dulvy.  
589 2015. Maternal age effects on Atlantic cod recruitment and implications for future  
590 population trajectories. *ICES Journal of Marine Science* 72:1769–1778.
- 591 Solemdal P. 1997. Maternal effects - a link between the past and the future. *Journal of Sea*  
592 *Research* 37:213-227.
- 593 Stige L. C., K. Ø. Kvile, B. Bogstad, and Ø. Langangen. 2018. Predator-prey interactions cause  
594 apparent competition between marine zooplankton groups. *Ecology* 25:151–10.
- 595 Stige L. C., et al. 2010. Direct and indirect climate forcing in a multi-species marine system.  
596 *Proceedings of the Royal Society B: Biological Sciences* 277:3411–3420.
- 597 Stige L. C., N. A. Yaragina, Ø. Langangen, B. Bogstad, N. C. Stenseth, and G. Ottersen. 2017.  
598 Effect of a fish stock's demographic structure on offspring survival and sensitivity to  
599 climate. *Proceedings of the National Academy of Sciences USA* 114:1347-1352.
- 600 Sundby S., and O. Nakken. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod  
601 related to multidecadal climate oscillations and climate change. *ICES Journal of Marine*  
602 *Science* 65:953-962.

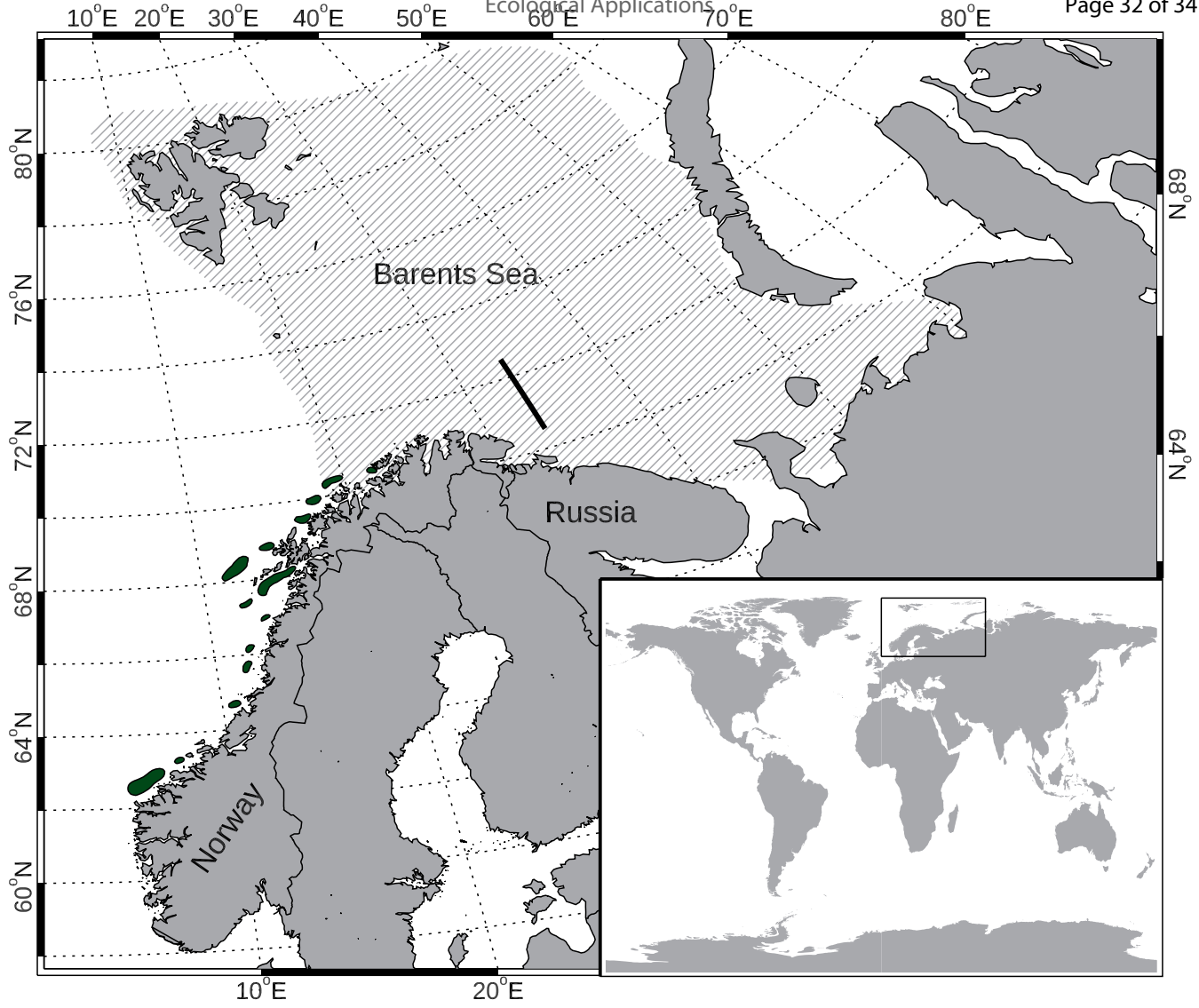
- 603 Swain D., A. Sinclair, and M. Hanson J. 2007. Evolutionary response to size-selective mortality  
604 in an exploited fish population. *Proceedings of the Royal Society B: Biological Sciences*  
605 274:1015-1022.
- 606 Tereschenko V. V. 1996. Seasonal and year-to-year variations of temperature and salinity along  
607 the Kola meridian transect. *ICES CM 1996/C:11*.
- 608 Vallin L., and A. Nissling. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod,  
609 *Gadus morhua*: implications for stock structure effects on recruitment. *Fisheries*  
610 *Research* 49:21–37.
- 611 Wright P. J., and E. A. Trippel. 2009. Fishery-induced demographic changes in the timing of  
612 spawning: consequences for reproductive success. *Fish and Fisheries* 10:283–304.
- 613 Yaragina N. A., B. Bogstad, and Y. A. Kovalev. 2009. Variability in cannibalism in Northeast  
614 Arctic cod (*Gadus morhua*) during the period 1947–2006. *Marine Biology Research*  
615 5:75–85.
- 616 Zhukova N. G., V. N. Nesterova, I. P. Prokopchuk, and G. B. Rudneva. 2009. Winter distribution  
617 of euphausiids (*Euphausiacea*) in the Barents Sea (2000–2005). *Deep Sea Research II*  
618 56:1959–1967.
- 619 Zuur A. F., E. Ieno, and C. Elphick. 2010. A protocol for data exploration to avoid common  
620 statistical problems. *Methods in Ecology and Evolution* 1:3–14.

621 **FIGURE CAPTIONS**

622 **Fig. 1: Map showing the spawning locations and general distribution of NEA cod.** Juvenile  
623 and adult NEA cod are mostly distributed in the Barents Sea (shaded area). The fish perform  
624 annual migrations to the spawning grounds (dark gray) along the Norwegian coast. Also  
625 indicated is the Kola section (station 3-7) in the Barents Sea (thick black line).

626 **Fig. 2: Time series data.** Shown are (a) spawning stock biomass (SSB, million tons) and  
627 recruitment (billions), (b) biomass of age 3-6 cod that are considered cannibals on pre-recruits,  
628 (c) temperature of the Kola section in the Barents Sea (red and blue indicate temperatures above  
629 and below the long-term average of 4.8°C, respectively), and (d) three age structure metrics:  
630 biomass-weighted mean age of the spawning stock (blue), the log ratio of the proportion of old  
631 individuals (age 15+) in the population (green), and the Shannon index of spawner age diversity  
632 (orange).

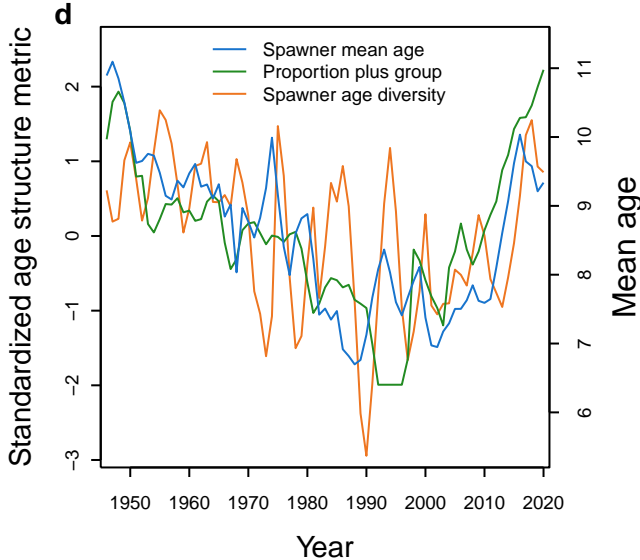
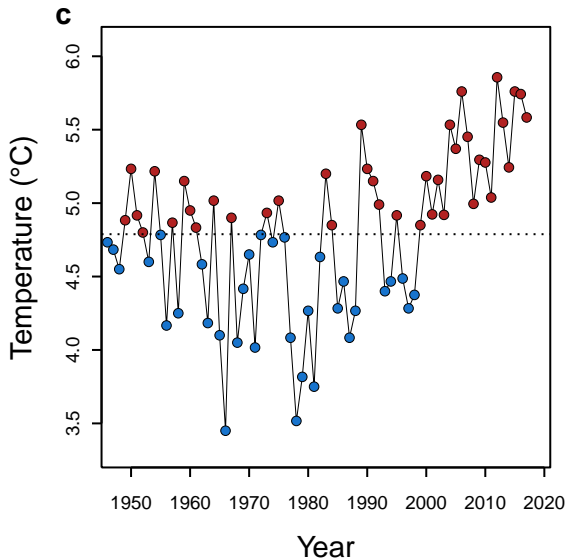
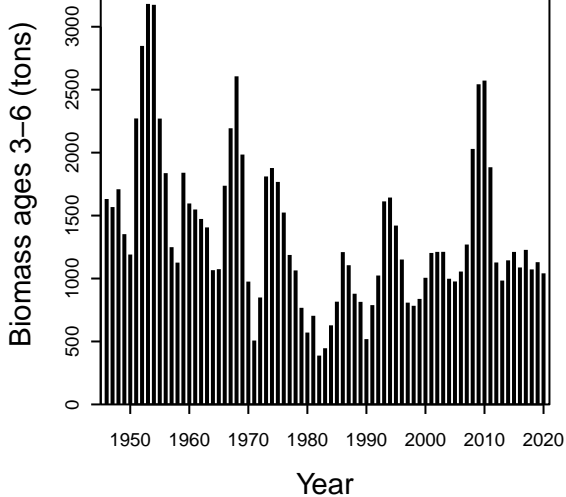
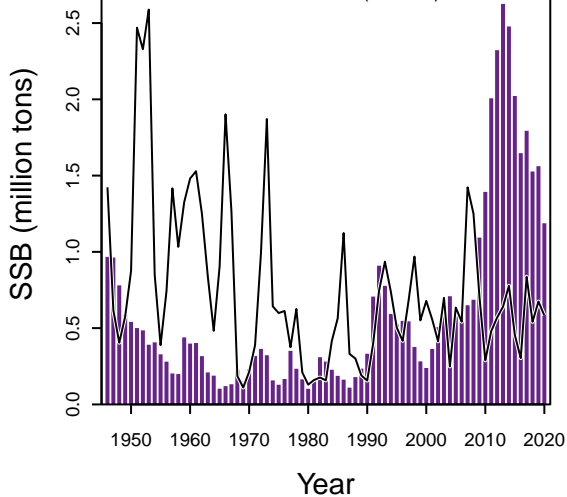
633 **Fig. 3: Estimated covariate effects and spawner-recruit predictions for models including**  
634 **alternative age structure metrics.** Shown are standardized effect size estimates of all covariates  
635 in the three alternative models, including total spawner biomass, biomass of age 3-6 cannibals,  
636 mean temperature, and the age structure metric, where lines are 95% confidence intervals (**a-c**),  
637 partial effects on  $\ln(\text{recruits}/\text{SSB})$  of the age structure metrics, where shaded polygons are 95%  
638 confidence intervals (**d-f**), and predicted relationships between spawning stock biomass (million  
639 tons) and recruitment (billions) for the alternative age structure metrics (**g-i**). Predictions were  
640 made for two different values of the respective age structure metric, taken as the 2.5th and 97.5th  
641 percentiles, and assuming median values for the other predictors in the model (biomass of age 3-  
642 6 cod and mean temperature). Thin dashed lines represent two times the standard error of the  
643 predictions.



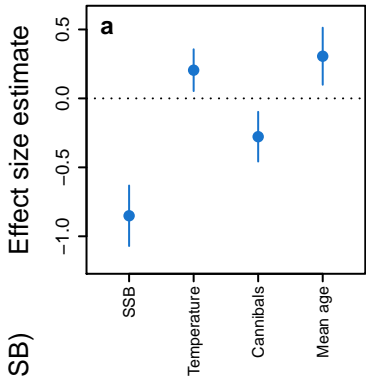


— Recruits (billions)

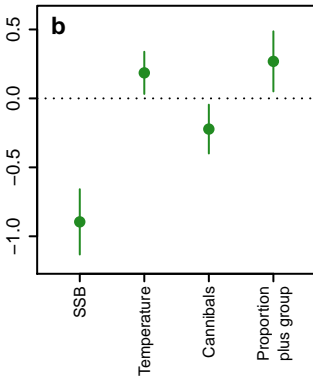
Ecological Applications



### Mean age model



### Proportion plus group model



### Age diversity model

