

Does high proportion of old and large spawners buffer a fish stock against environmental fluctuations?

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ABSTRACT

Commercial fishing generally removes large and old individuals from fish stocks, reducing mean age and age diversity among spawners. It is feared that these demographic changes lead to lower and more variable recruitment to the stocks. A key proposed pathway is that juvenation and reduced size distribution causes reduced ranges in spawning period, spawning location and egg buoyancy. This is proposed to lead to reduced spatial distribution of fish eggs and larvae, more homogeneous ambient environmental conditions within each year-class and reduced buffering against negative environmental influences. However, few, if any, studies have confirmed a causal link from spawning stock demographic structure through egg and larval distribution to year class strength at recruitment. We here show that high mean age and size in the spawning stock of Barents Sea cod (*Gadus morhua*) is positively associated with high abundance and wide spatiotemporal distribution of cod eggs. We find, however, no support for the hypothesis that a wide egg distribution leads to higher recruitment or a weaker recruitment-temperature correlation. These results are based on statistical analyses of a spatially resolved data set on cod eggs covering a period (1959–1993) with large changes in biomass and demographic structure of spawners. The analyses also account for significant effects of spawning stock biomass and a liver condition index on egg abundance and distribution. Our results suggest that the buffering effect of a geographically wide distribution of eggs and larvae on fish recruitment may be insignificant compared to other impacts.

Keywords: fisheries; age and size truncation; population dynamics; climate effects; cod

Gadus morhua

Significance statement: It is feared that loss of old and large spawners impairs heavily fished fish stocks' reproductive capacity and increases their sensitivity to environmental fluctuations. The Barents Sea cod is the world's largest cod stock and has been reported to show increased temperature-recruitment associations in periods with predominantly young and small spawners. We here investigate the possible causal basis for the link between demographic structure and recruitment by analysing long-term egg survey data. Results support a link between demographic structure and abundance and distributional extent of eggs but not between egg distribution and recruitment. These results question whether the benefits of a wide spatiotemporal distribution of spawning are of quantitative importance for recruitment.

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INTRODUCTION

Many exploited fish stocks have shown large changes in their demographic structure over the last decades, towards a reduced age range of the spawners with fewer old and large fish (1-4). It is feared that these changes impair the reproductive potential of the stocks and make them more susceptible to effects of climate variability and change; hence, a goal of the common fisheries policy of the European Union is to reverse these changes to obtain “a population age and size distribution that is indicative of a healthy stock” (5). In some harvested stocks age and size truncation has indeed been associated with lower recruitment (i.e., population renewal, often measured as the abundance of the youngest year-class captured in the fisheries) per biomass of spawners (6-8), larger interannual variability in recruitment (9) and higher sensitivity of recruitment to environmental fluctuations (10, 11). In other stocks, however, no such links between age or size structure and recruitment have been found (9, 12, 13). There is therefore disagreement whether the value of maintaining a wide age and size distribution in managed fisheries is overemphasised (14) or underappreciated (15).

A causal basis for lower recruitment in age-truncated stocks is supported by field and experimental studies on Atlantic cod (*Gadus morhua*), a broadcast multiple batch spawner of high economic and ecological importance. These studies have shown that older and larger fish produce more eggs per biomass of spawner, as well as larger and more viable eggs compared with younger and smaller conspecifics (16, 17). A cod stock with many old and large spawners may also have a wide distribution of offspring in space and time by having an extended spawning season (16), an extended geographic range of spawning (18, 19) and/or a wide buoyancy range and hence horizontal spreading of eggs (20). This is thought to buffer effects of environmental fluctuations on recruitment (21, 22) and increase the mean and reduce the variance in recruitment (23). The mechanism proposed for this is that environmental influences

on different patches of eggs and larvae may cancel out, which reduces the variance. Reduced variance may lead to increased mean if, for example, subsequent survival is density dependent so that abundant year-classes are reduced proportionally more than poor year-classes.

We here assess whether the presumed links between the age and size distribution of the spawning stock and recruitment (1, 21-23) are supported by observations of realized egg distributions. To examine this, we utilize a unique spatially resolved egg data set that originates from 35 years (1959–1993) of dedicated Russian ichthyoplankton surveys (24). Our analyses are for the Barents Sea stock of Atlantic cod (alternatively referred to as Northeast Arctic or Arcto-Norwegian cod). Our findings are expected to be relevant also for other exploited stocks of broadcast spawners, most of which lack data to investigate such links.

While the Barents Sea cod stock currently is the world's largest, it had during 1959–1993 a period with increasing fishing mortality and relatively low spawning stock biomass (25). The mean age and weight in the spawning stock was declining (4, 11), a trend which appears to have been reversed in recent years (26). The cod spawn along the west and north coasts of Norway from mid-February to early May (27). The eggs and larvae drift north- and eastwards into the Barents Sea, the nursery area of the juveniles and the feeding area of the adult cod (Fig. 1). Offspring recruit to the fisheries at age 3. High recruitment is associated with a number of abiotic and biotic factors recently reviewed by (27), such as high temperature (e.g., 28) and good condition of the spawners (e.g., 29). Despite several studies linking spawner age, size and/or spawning experience with egg production and egg viability for this stock (27), there are no clear effects of spawning stock structure on recruitment (4). Furthermore, while the recruitment-temperature correlation for this stock has been found to be stronger during periods with low mean age and length in the spawning stock (11), multi-stock analyses have shown that such a link is not generally present and the causal basis for it remains unclear (9, 13).

We wish to answer three questions (*Q1–Q3*).

Q1: Which factors influence the total abundance of cod eggs?

We hypothesize that high abundance of eggs is associated with a high proportion of old and large individuals in the spawning stock (16, 17).

Q2: Which factors influence the distributional extent of the eggs?

We hypothesize that large distributional extent of eggs is associated with a high proportion of old and large individuals in the spawning stock (18-20).

Q3: How does the distributional extent of eggs affect survival to later stages?

We hypothesize that a wide spatial distribution of eggs is associated with high subsequent survival and a weak response of survival to temperature fluctuations (21-23).

RESULTS

Q1: Which factors influence the total abundance of cod eggs?

Analysing time-series of log-scale total cod egg abundance in April–May (EGG_{TOTAL} , Fig. S1) and alternative predictor variables (Table 1, Fig. S2) statistically, we found that egg abundance was best explained (lowest AIC_C (30)) as a function of spawning stock biomass (SSB), liver condition index ($COND$) and mean weight in the spawning stock (MW) (Table S1a, Fig. 2a). For a change in MW from 3.2 kg to 7.0 kg (which are, respectively, the 5% and 95% of MW in the study period) and mean values of SSB and $COND$, we estimate EGG_{TOTAL} to change from 1.2 to 2.5, corresponding to a 3.7-fold increase in total egg abundance. Model diagnostics (e.g., of residual autocorrelation and correlation among predictors) suggested that findings were robust to key assumptions of the model (SI Results in SI Text file).

An alternative model with mean age (MA) instead of MW as predictor was similarly supported by the data (i.e., it provided similar AIC_C) and showed a significant effect of MA (Table S1a, Fig. S3a).

Q2: Which factors influence the distributional extent of the eggs?

We then analysed associations between the same potential predictor variables and an index of the areal distributional extent of cod eggs (EGG_{EXTENT} , Fig. S1). Perhaps not surprisingly given the tight connection between abundance and distribution, the same variables that explained total egg abundance were selected as predictor variables for distributional extent (Table S1b). However, the strengths of the associations differed, with MW (Fig. 2b), or alternatively MA (Fig. S3b), being more strongly correlated with EGG_{EXTENT} than with EGG_{TOTAL} . For a change in MW from 3.2 kg to 7.0 kg and mean values of SSB and $COND$, we estimated EGG_{EXTENT} to change from 0.28 to 0.54, corresponding to a doubling in areal extent.

As high abundance of eggs usually implies a large distributional extent, predictor effects on EGG_{EXTENT} might reflect associations with total abundance, rather than with distributional extent *per se*. To assess possible independent associations between predictor variables and distributional extent, we added EGG_{TOTAL} as covariate in the analysis of EGG_{EXTENT} . SSB and $COND$ then had no significant effect, but MW , or alternatively MA , did (Table S1c). This finding suggests that the associations of SSB and $COND$ with distributional extent are fully explainable through total egg abundance. On the other hand, the result shows that a given amount of eggs has larger distributional extent with high than with low mean weight or age in the spawning stock.

Using spatiotemporal statistical analysis we found that at high MW , the spatial distribution of cod eggs expands in most directions, perhaps most strongly into offshore areas in the Norwegian Sea (Fig. 3).

Q3: How does the distributional extent of eggs affect survival to later stages?

Finally we analysed associations between EGG_{TOTAL} , EGG_{EXTENT} and time-series of year-class abundance at three later stages, i.e., as larvae/post-larvae in June–July, as age-0 juveniles in August–September and as age-3 recruits (Eq. 1 in Methods). None of the estimated coefficients

for the effect of EGG_{EXTENT} (γ , Table 2) on log-abundances of later stages were significant. The coefficients for the effects of EGG_{TOTAL} and EGG_{EXTENT} (β and γ , Table 2) are correlated ($r = -0.91$) in all three models, corresponding to a variance inflation factor (31) of 5.8. This means that effects of distributional extent and density dependence cannot be fully separated with this analysis. Models with both EGG_{TOTAL} and EGG_{EXTENT} as predictors were not significantly better than models with only EGG_{TOTAL} ($P > 0.05$, F-tests; temperature was also included as covariate, see below). Hence, the results fail to show associations between survival and egg distribution that are independent of total egg abundance.

As a rough estimate of the potential survival value of a high distributional extent at the egg stage, we used the results in Table 2 to calculate how much predicted year-class abundance at later stages changes if EGG_{EXTENT} increases by 0.26. This change in EGG_{EXTENT} is the predicted effect of an increase in MW from 3.2 kg to 7.0 kg (see Results, Q2). The predicted proportional change in cohort abundance of larvae/post-larvae in June–July was 0.04 (95 % confidence interval, c.i.: -0.65, 2.23), of age-0 cod in August–September -0.75 (c.i.: -0.97, 0.88) and of age-3 cod -0.40 (c.i.: -0.69, 0.18). We interpret the upper limits of these confidence intervals as upper limits for the potential survival effect of a high MW giving a wide distributional extent of eggs.

While temperature was generally positively associated with the abundances of later life stages (coefficient δ , Table 2), we found no evidence for stronger temperature effects when MW was low: We found no significant interaction effect between EGG_{EXTENT} and temperature (coefficient θ , Table 2; see also Fig. S4). For example, the estimated effect of a one-degree temperature increase on age-3 log-abundance at EGG_{EXTENT} values of 0.28, 0.43 and 0.54, respectively, were 0.64 (c.i.: 0.08, 1.20), 0.64 (c.i.: 0.15, 1.13) and 0.64 (c.i.: 0.11, 1.17).

DISCUSSION

Our results add to previous studies on effects of demographic structure on recruitment dynamics by presenting thorough statistical analyses of spatially explicit egg data. These results generally support the hypothesised links between age and size structure and the abundance and distribution of eggs, but not those between egg distribution and recruitment.

Q1: Which factors influence the total abundance of cod eggs?

In accordance with our *a priori* predictions, we found that total egg abundance is significantly higher in years with more old and large individuals in the spawning stock.

Several non-exclusive mechanisms may explain these associations. Firstly, older and larger cod are reported to have higher relative fecundity (16, 17). This mechanism is supported by (32), who found that potential fecundity of Barents Sea cod was best explained as a function of body weight, with no significant additional contribution of age – which parallels our findings for realized egg abundance. Secondly, inexperienced, young and small cod produce smaller than average eggs, which seem to have lower than average fertilization and survival rates [(17) and references therein]. Thirdly, young and small females are more likely to skip spawning than older and larger conspecifics (33). Hence, with low mean age and weight in the presumed spawning stock, the proportion that actually spawns in a given year may be lower than with high mean age or weight. In the field, the frequency of skipped spawning appears to range from almost zero in Baltic cod (34) to 30–40 % reported for other cod populations, including Barents Sea cod (33, 35). Finally, the proportion of females and hence the egg production rate may be reduced in years when the mean age and weight in the spawning stock is low, as females mature at a higher age and larger size than males do (36). The proportion of females in the spawning stock biomass of Barents Sea cod has been found to vary between 24 % and 68 %, and that spawning stock biomass became more female-biased and total egg production per biomass of spawners became higher as mean length of spawners increased (37).

The condition of cod is believed to influence fecundity as do size, age, feeding regime and prey availability (38). Poor recruitment to the Barents Sea cod stock occurs when the liver condition index is lower than 6 % (29), which is consistent with our findings for total egg abundance (Fig. 2a). Our results thus support a causal basis for the previously reported association between the liver condition index and recruitment (29). Cod in poor condition produce fewer eggs (39, 40), and both fecundity and condition of Barents Sea cod are reduced in years with low biomass of their key prey, capelin (*Mallotus villosus*) (32, 38). Moreover, low condition might induce mature fish to skip spawning (33, 35) and potential first-time spawners to postpone maturation (36, 41).

Our results show no significant association between abiotic environmental variables and egg abundance. The lack of significant association of temperature with egg abundance is in apparent contrast to a reported positive correlation between temperature in the pre-spawning period and potential fecundity (32). The lack of a significant association with temperature in our study could have several explanations, such as, hypothetically, high fecundity in warm years being counter-balanced by high egg mortality.

Q2: Which factors influence the distributional extent of the eggs?

As predicted, we found that a given amount of eggs is distributed over an increased area when the mean weight and age in the spawning stock is high. This is consistent with analyses of the 50-years long CalCOFI larval fish time-series off southern California, which suggest reduced area of occupancy and spatial heterogeneity of exploited populations (42).

Spatiotemporal statistical analysis might give some clues to the possible mechanisms behind this association. Such analysis showed that low mean weight in the spawning stock was associated with a contraction of the egg distribution in most directions (Fig. 3). We did not see particularly strong effects towards the southern margin of the survey area, as might be expected from the disputed hypothesis that a decrease in the average size and age in the stock leads to

reduced spawning at the southern spawning grounds (see 18, 19, 43). Several other mechanisms might be at play. For example, a wide buoyancy range of eggs from repeat spawners could contribute to wide dispersal (20) and increased survival of eggs from experienced, old and large females (17) could contribute to increased probability of finding eggs far from the spawning grounds.

Q3: How does the distributional extent of eggs affect survival to later stages?

Our results provide no support for the hypotheses that a wide spatial distribution of cod eggs, as found in years with high mean weight in the spawning stock, is associated with increased cohort survival to later stages or reduced response of cohort survival to temperature fluctuations.

The lack of significant result is likely not due to low statistical power, although the close connection between egg abundance and distribution (illustrated by the high correlation between EGG_{TOTAL} and EGG_{EXTENT}) does make it difficult to separate the unique contribution of each factor. Even the upper bounds of the confidence intervals, which account for uncertainty and correlation in egg indices, suggest low effects, especially on recruitment at age 3. While we estimate that an increase in MW from 3.2 to 7.0 kg leads to a doubling of the areal extent of cod eggs (from 28 % to 54 % of the study area), this maximally leads to 18 % higher recruitment; most likely lower. This is trivial compared to other influences on recruitment (e.g., 44) and suggests that the spatial extent of the eggs *per se* is on average of little importance for year class strength. Similarly, population modelling suggests that maternal size effects on recruit production likely have a much smaller impact on population growth than environmental conditions during early life in long-lived and highly fecund (45) and harvested (46) fish stocks such as the Barents Sea cod.

A possible explanation for a weak association between distributional extent and survival is that the survival is quite homogeneous across the distribution range of the offspring. The natural mortality of Barents Sea cod larvae appears to show large-scale spatial patterns (47) and

to correlate with local temperature and food conditions in spring (48). However, the spatial patterns in larval mortality are partly offset by temperature-dependent differences in survival to later life-stages (49). It is therefore uncertain which areas of the egg distribution contribute most to recruitment as well as how the level of heterogeneity compares with other fish stocks. Hypothetically, variable levels of spatial heterogeneity in environmental conditions could explain some of the reported among-stock differences (9) in the associations between demographic structure and recruitment, as well as cause temporal differences in such associations.

Some caveats should be mentioned. It is possible that other egg distribution indices than *EGG_{EXTENT}* would have shown associations with recruitment if they captured possible spatial differences in mean offspring survival better. We also note that our study does not investigate whether a wide seasonal distribution of spawning provides benefits for mean offspring survival (23). Finally, the statistical inference from this study should be further corroborated and tested, e.g., using coupled biophysical modelling to assess the mechanistic links between egg distribution and recruitment under different climate conditions and assumptions about spatial patterns in growth and survival (49).

Implications

Hixon et al. (15) recently reviewed the value of big old fat fecund female fish [BOFFFFs, a concept introduced by (1) and (3)] in fostering stock productivity and stability. This value can be divided into three main components (15), (i) the storage effect: BOFFFFs outlive periods unfavourable for larvae, (ii) the fecundity effect: BOFFFFs have higher relative (weight-specific) fecundity than younger females, and (iii) maternal effects: the presence of BOFFFFs provide variation in reproductive strategies because BOFFFF offspring grow faster and survive better in some environments and because BOFFFFs likely spawn at different times and places than younger females. In support of the first mechanism, results of (50) show that population

growth of Barents Sea cod and the Norwegian Spring-Spawning stock of herring *Clupea harengus* are indeed more dependent on recruitment, and hence pre-recruitment environmental conditions, in periods with an age-truncated spawning stock compared with periods with intact age-structure. Our study supports a possible role of the second mechanism by showing a statistically significant association between age and size structure and egg abundance. These results support a causal basis for findings by (8), who, in contrast to an earlier correlational study (4), estimated a positive effect of age on recruitment at age 3 for this stock. Finally, our study suggests that the benefits of a wide spatial distribution of eggs may be of low quantitative importance for the recruitment of Barents Sea cod. We hence question whether this mechanism can explain the association between age and size structure and the strength of recruitment-environment correlations reported for this stock (11), an association which has been widely used in the literature to exemplify age-truncation effects on fish stocks. Finally, we propose that future studies should investigate whether the inconsistent association between demographic structure and recruitment among stocks (e.g., 9) is related to stock differences in the benefits of a wide offspring distribution, which can be approximated by the level of spatial environmental heterogeneity in spawning, larval drift and nursery areas.

METHODS

Outline of analyses

We used spatiotemporal egg data to construct annual indices of total abundance (EGG_{TOTAL}) and distributional extent (EGG_{EXTENT}) of Barents Sea cod eggs for the period 1959–1993 (except 1964 and 1967, when survey coverage was insufficient to calculate the indices). Survey coverage in a representative year is shown in Fig. 1 and the data and the construction of the indices are described in SI Methods. These indices served as response variables in time-series analyses to assess which factors explain year-to-year differences in egg abundance ($Q1$) and egg distribution ($Q2$). The same egg indices served as predictors in time-series analyses to

assess if the distributional extent of the eggs influences survival to later stages (*Q3*). These analyses using annual indices allowed us to quantify the dynamics using well established time-series analysis methods for model selection, residual diagnostics etc. In addition we used spatiotemporal statistical analysis to visualize how the egg distribution changed depending on spawning stock structure (as part of *Q2*).

Statistical analyses

Q1. Which factors influence the total abundance of cod eggs?

We conducted a multiple linear regression analysis to explore which combination of biotic and abiotic variables best explained total egg abundance, EGG_{TOTAL} . Several potential explanatory variables were considered (Table 1), in order to account for factors that may be confounded with the variables of main interest. The potential predictor variables and the rationale for considering these are described in SI Methods. Variables were selected in a stepwise search, by adding variables one by one based on the Akaike Information Criterion corrected for small sample size, AIC_C (30). Non-significant terms ($P > 0.05$) were, however, not added even if such inclusion led to slight reduction in AIC_C . The residuals of the final model were checked for outliers and strong deviations from normality by inspecting their quantile-quantile normal plot and for positive serial autocorrelation by plotting the autocorrelation function. If residuals were significantly positively correlated, we re-estimated the parameters using a generalized least squares model with the same predictor variables and an order-1 autocorrelation structure [using the `gls` and `corAR1` functions in the `nlme` library of the programming language R (51)]. Strong correlations between some potential predictor variables (Table S2) could complicate interpretation of results as their effects may be confounded. We therefore report if alternative predictors provided similar AIC_C (<2 difference in AIC_C).

Q2: Which factors influence the distributional extent of the eggs?

We then explored to which degree the age and size distribution of the spawners influenced the spatial distributional extent of their offspring. To do so, we conducted a multiple linear regression analysis with EGG_{EXTENT} as response variable and predictor variables from Table 1 selected based on AIC_C .

To visualize the change in the spatial distribution of cod eggs under contrasting age or size structure in the spawning stock, we fitted a spatial variable-coefficient GAM (52, 53) to presence-absence data. This binomial model quantified the probability p of catching at least one egg of a given stage at a station as function of sampling day-of-year, sampling location, SSB , $COND$ and MW . The modelled effect of MW varied as a smooth function of location. See SI Methods for details.

Q3: How does the distributional extent of eggs affect survival to later stages?

We explored effects of distributional extent on survival from eggs in April–May to three later life stages:

- i. Larvae / post-larvae in June–July. An annual index of log-abundance for 1959–1993 was constructed from spatiotemporal survey data from June–July (24), analogously to the construction of EGG_{TOTAL} for April–May survey data (48).
- ii. Age-0 juveniles in August–September. An annual index of log-abundance for 1966–1993 was constructed by combining two survey-based age-0 indices with partly overlapping year coverage [(54), using data from ICES working group reports].
- iii. Age-3 recruits. We used estimates of annual log-abundance at age 3 years from extended survivors analysis based mainly on fisheries data (55).

We assumed a log-linear relationship between past and present cohort size [the ‘Gompertz’ model (56)]. In order to test if a wide spatial and temporal distribution of cod eggs was significantly associated with high survival to later stages, the model was modified by adding

the distributional extent of the eggs as predictor variable. In order to test if a wide distributional extent was significantly associated with a weak response to climate variations, we further added interaction effects of distributional extent and annual temperature (standardized to zero mean to facilitate interpretation of coefficients for other terms). The modified Gompertz model thus was:

$$(1) \log_e(n_t) = \alpha + \beta EGG_{TOTAL,t-\Delta t} + \gamma EGG_{EXTENT,t-\Delta t} + \delta TEMP_{ANN,t-\Delta t} + \theta EGG_{EXTENT,t-\Delta t} TEMP_{ANN,t-\Delta t} + \varepsilon_t$$

Here, n_t represents the observed cohort size of the given later life stage (i, ii or iii), $n_{t-\Delta t}$ represents the observed cohort size of eggs in April–May (note that $\log_e(n_{t-\Delta t}) = EGG_{TOTAL,t-\Delta t}$), $-\alpha$ represents density-independent mortality and unknown scaling of the indices with real abundance, $1 - \beta$ is density-dependent mortality and ε_t is an independent and normal distributed environmental error term with mean zero and variance σ^2 . We expected that a positive relationship between distributional extent and survival would lead to γ larger than zero. Based on previous studies (e.g. 57) we expected positive coefficients for the temperature effect, δ . If a wide distributional extent buffered the temperature effect, we expected negative coefficients for the interaction term, θ .

The models were fitted by ordinary least-squares regression. An assumption of regression models is that predictor variables are measured without errors. To quantify possible bias and additional uncertainty in model coefficients caused by errors in egg indices, we refitted the model for each of the 1000 samples from the joint bootstrap distribution (SI Methods) of EGG_{TOTAL} and EGG_{EXTENT} . The additional uncertainty was quantified as the variance of the bootstrap distribution of the coefficients. This variance component was added to the squared standard errors from the model to obtain standard errors corrected for uncertainty in egg indices.

All statistical analyses were performed with R version 3.2.4 (58). The mgcv package version 1.8-12 (53) was used for GAM analyses.

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Figures and Figure Legends.

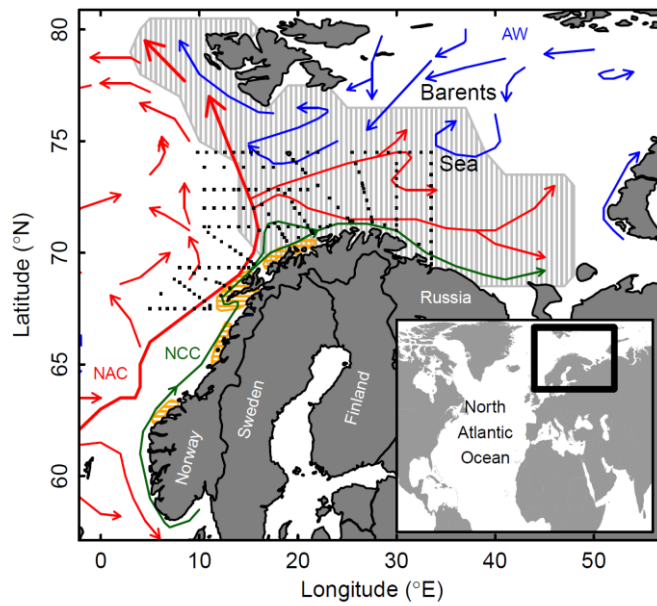


Figure 1. Study area. Horizontally hatched orange areas: main spawning grounds of Barents Sea cod. Vertically hatched grey areas: distribution of 5-months old cod juveniles in August–September. Coloured arrows: main features of the mean surface circulation pattern. NAC, North Atlantic Current. NCC, Norwegian Coastal Current. AW, Arctic Waters. Points: ichthyoplankton survey (shown for one representative year, 1988).

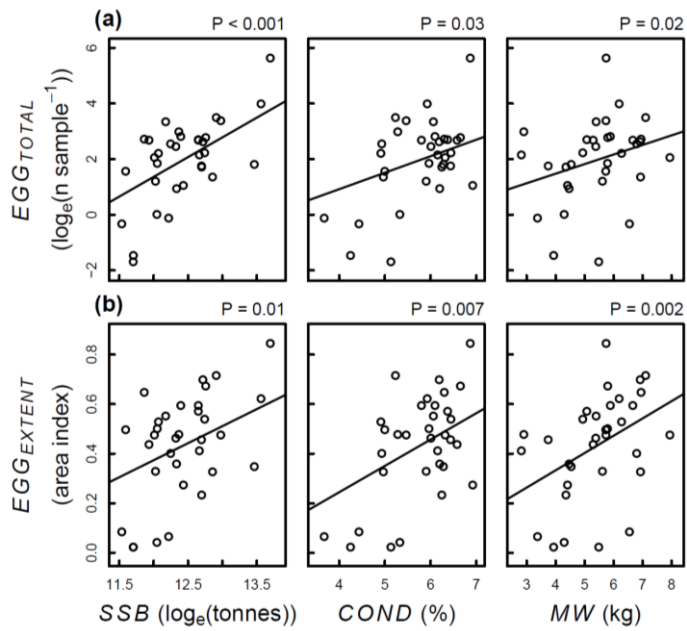


Figure 2. Predictor effects on total egg abundance (a) and egg distributional extent (b). Associations between EGG_{TOTAL} and EGG_{EXTENT} (response variables) and spawning stock biomass (SSB), liver condition index ($COND$) and mean weight in the spawning stock (MW). Superimposed on the data are regression lines from multiple linear regression analysis for each response variable (with associated P-values shown above each panel).

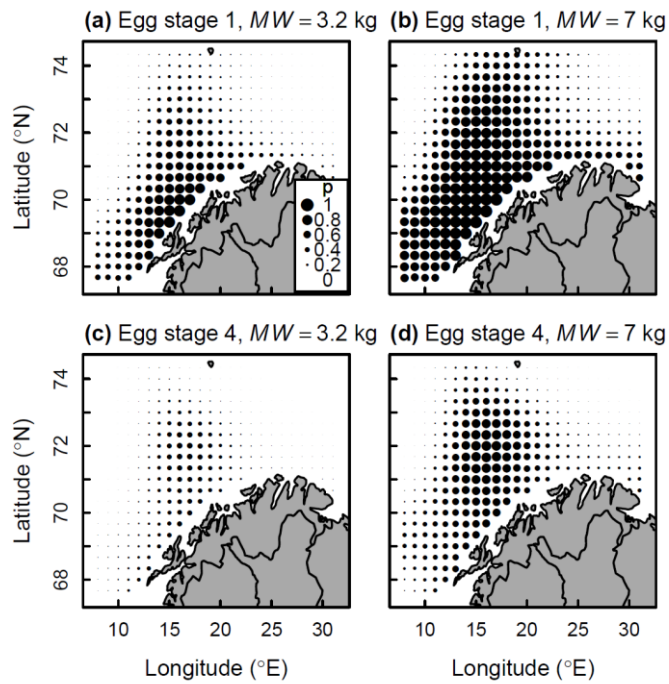


Figure 3. Associations between mean weight in the spawning stock and spatial distribution of cod eggs. The maps show estimated probabilities (p) of occurrence of eggs for years with contrasting weight structure in the spawning stock (a, c: the 5% and b, d: the 95% percentiles of MW). Predictions are for mean values of spawning stock biomass and liver condition index for egg stage 1 (a, b) and egg stage 4 (c, d) for May 6th (mean sampling day).

Table 1. Variables considered as predictors of abundance and distribution of cod eggs.

Variable name	Description
<i>SSB</i>	Spawning stock biomass (\log_e [tonnes]).
<i>MA</i>	Mean biomass-weighted age in the spawning stock (years).
<i>MW</i>	Mean biomass-weighted weight in the spawning stock (kg).
<i>AWIDTH</i>	Biomass-weighted age width (years): the difference in age between the 5 % and 95 % quantile of mature biomass-at-age.
<i>ADIV</i>	Biomass-weighted age diversity in the spawning stock, calculated as Shannon's diversity index (59) for non-zero frequencies of mature biomass-at-age.
<i>REPEAT</i>	Proportion of repeat spawners in spawning stock biomass.
<i>COND</i>	Liver condition index (%): liver wet weight as percentage of total wet weight for cod of lengths 41–70 cm for January–December the year before spawning (60).
<i>TEMP_{WIN}</i>	Winter (October–March, preceding spawning) sea temperature (°C) in the Barents Sea (0–200 m depth at the Kola section, 70.5–72.5 °N, 33.5 °E).
<i>TEMP_{SPR}</i>	Spring (April) sea temperature (°C) at the spawning grounds in the Lofoten Islands (10 m depth at Skrova, 68.1 °N, 14.7 °E).
<i>TEMP_{SUM}</i>	Summer (April–September) sea temperature (°C) in the Barents Sea.
<i>TEMP_{ANN}</i>	Annual (January–December) sea temperature (°C) in the Barents Sea.
<i>NAO_{WIN}</i>	The North Atlantic Oscillation winter index: the principal component based NAO index (61) for December–March preceding spawning.
<i>NAO_{SPR}</i>	The North Atlantic Oscillation index for March–May.

Table 2. Analysis of survival of cod eggs to later stages (Eq. 1, Methods). α , intercept, β , effect of total abundance of cod eggs, γ , effect of distributional extent of cod eggs, δ , effect of temperature, θ , interaction effect between distributional extent of cod eggs and temperature. To reduce correlation between main and interaction effect estimates, the distributional extent and temperature variables were standardized to zero mean.

Survival to stage	Parameter estimate \pm standard error					R^2
	α	β	γ	δ	θ	
Larvae / post-larvae June–July	-2.92 \pm 0.69*	0.61 \pm 0.33	0.16 \pm 2.16	0.39 \pm 0.42	0.15 \pm 1.73	0.56
Age-0 Aug.–Sep.	19.9 \pm 1.26*	1.36 \pm 0.61*	-5.32 \pm 3.95	1.57 \pm 0.74*	-0.33 \pm 2.89	0.57
Age-3	19.1 \pm 0.42*	0.37 \pm 0.20	-1.94 \pm 1.31	0.64 \pm 0.25*	0.00 \pm 1.04	0.43
Age-3 AR(1) [†]	19.0 \pm 0.42*	0.41 \pm 0.19*	-2.21 \pm 1.33	0.53 \pm 0.25*	0.02 \pm 0.93	

* $P < 0.05$

autocorrelation.

[†] Generalized least squares model which accounts for order-1 residual

1 **SI TEXT**

2 This online appendix accompanies the paper:

3 Stige LC, Yaragina NA, Langangen Ø, Bogstad B, Stenseth NC, Ottersen G (2016) Does high
4 proportion of old and large spawners buffer a fish stock against environmental
5 fluctuations? *Proc. Natl. Acad. Sci. USA*, 00(00):00-00.

6

7 Contents SI page

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13 Variables that potentially influence cod egg abundance and distribution. 6

14 Spatiotemporal statistical analysis of association between spatial distribution
15 of cod eggs and mean weight in the spawning stock. 8

16 **SI RESULTS**

17 **Model diagnostics**

18 *Q1: Which factors influence the total abundance of cod eggs?*

19 The selected model (Table S1a) included *MW*, *SSB* and *COND* as predictors of *EGG_{TOTAL}*.
20 The inclusion of *MW* as predictor improved AIC_C by 3.4 and increased R^2 from 0.50 to 0.58
21 compared to a model with only *SSB* and *COND*.

22 There was no significant ($P > 0.05$) positive autocorrelation in the residuals in the
23 selected model, which could otherwise bias uncertainty estimates. Because of positive
24 correlation between *SSB* and *COND* (Table S2) the coefficients for these effects were
25 negatively correlated ($R^2 = 0.18$). The magnitude of the confounding between *SSB* and *COND*
26 effects was estimated by the variance inflation factor [VIF (31)], which measures how much
27 the variance of the coefficients (i.e., the standard errors squared) is increased because of
28 collinearity. The correlation between *SSB* and *COND* caused a VIF of 1.2, which we
29 considered acceptably low to include both variables in the model.

30 To assess the possible influence of misclassification of eggs of cod and haddock
31 *Melanogrammus aeglefinus* (see SI Methods), we added haddock spawning stock biomass to
32 the final models of cod egg abundance (*Q1*) and distributional extent (*Q2*). No significant
33 effects of haddock were found.

34 *Q2: Which factors influence the distributional extent of the eggs?*

35 Residuals from the selected models of predictor effects on distributional extent (Table S1b–c)
36 showed no significant positive autocorrelation and besides *SSB* and *COND*, predictors were not
37 significantly correlated.

38 The spatiotemporal model (Fig. 3) did not attempt to account for all correlations in the
39 data, hence we do not present uncertainty estimates from this model.

40 *Q3: How does the distributional extent of eggs affect survival to later stages?*

41 Residuals from the analyses of the two earliest stage intervals in Table 2 showed no significant
42 positive autocorrelation, while the lag-1 autocorrelation function for age-3 was 0.39 and
43 statistically significantly ($P < 0.05$). Explicitly modelling this autocorrelation structure using a
44 generalized least squares model had little effect on parameter estimates and standard errors
45 (Table 2).

46 **SI METHODS**

47 **Ichthyoplankton data**

48 Eggs of Barents Sea cod were sampled during dedicated ichthyoplankton surveys by the Polar
49 Research Institute of Marine Fisheries and Oceanography (PINRO), Murmansk (24). The
50 survey covered main drift areas of eggs and larvae of Barents Sea cod between 67°30'N and
51 74°30'N from about 7 km (4 nautical miles) to 500 km from the coast (Fig. 1). From around
52 10 % to 25 % of the landings from the spawning fisheries in years 1959–1969 were from south
53 of the survey area (18), with the long-term trends in the proportion apparently covarying with
54 the mean age of the spawners [(19) but see (43)]. The survey was conducted in April–May [i.e.
55 0–2 months after the peak spawning of the cod (62)] each year from 1959 to 1993, except 1967,
56 when there was no survey. On average 156 stations were sampled each year, but with
57 considerable variability among years in the extent and timing of the survey (24, 48). Cod eggs
58 were classified into four developmental stages based on morphology. Stage-1 eggs could not
59 be reliably differentiated from the eggs of haddock. Stage-1 eggs were therefore classified to
60 species according to the fraction of cod compared to haddock eggs of stages 2–4 in the sample.
61 For further details on the ichthyoplankton data we refer the reader to (24) and (48).

62 **Construction of indices of abundance and distributional extent of cod eggs.**

63 *Two different indices were calculated.*

64 We used a statistical approach to construct annual indices for the abundance and distributional
65 extent of cod eggs. One index measured the total abundance of eggs (EGG_{TOTAL}). The other
66 measured the spatial distributional extent of the eggs (EGG_{EXTENT}).

67 *Sampling variation was corrected for statistically.*

68 To construct these indices we used a Generalized Additive Model (GAM, 53) regression
69 method in order to correct for variability in sampling date, sampling location and slight
70 variability in the number of samples per station (48). The models used to construct the egg
71 indices were estimated by maximum-likelihood methods with mixed-effects GAMs, using the
72 gam function in the mgcv package (version 1.7-9) in R (version 2.14.0) (53).

73 *A hurdle model separated the variation into binomial and lognormal parts.*

74 As the survey data contained many stations with no eggs, the data were considered to
75 originate from two different processes: one process determining the probability of a positive

76 tow (i.e., non-zero abundance of eggs of a given stage at a station) and another determining
 77 the abundance conditional on a positive tow (see 63). To account for the two processes we
 78 used a hurdle model approach (64), whereby a binomial model quantified the probability of a
 79 positive tow and a lognormal model quantified abundance in positive tows.

80 The binomial model quantified the probability p of catching at least one egg of a given
 81 stage at a station. Each data point represents presence (coded as 1) or absence (coded as 0) of
 82 one out of four egg developmental stages at one station in one year. Each station is thus
 83 represented by four data points in the analysis, one for each egg stage. As covariates we
 84 included sampling day-of-year (Day) and sampling location (Lon , longitude and Lat , latitude,
 85 standardised to zero mean). The probability p_{sij} was modelled as

$$86 \quad (S1) \quad \text{logit}(p_{sij}) = \alpha_s + f_s(Day_i) + g_s(Lon_i, Lat_i) + a_j + b_j Lon_i + c_j Lat_i$$

87 where the subscripts s , i and j represent stage, station and year, respectively, α_s is a stage-
 88 specific intercept and f_s and g_s are stage-specific smooth functions correcting for sampling
 89 date and location (g_s being a two-dimensional anisotropic smooth modelled as a tensor-
 90 product of two smooth basis functions with maximally 5 knots each). The random term a_j
 91 captures year-to-year variation in the intercept, that is, in the overall probability of sampling
 92 cod eggs. The random terms b_j and c_j capture year-to-year variation in the location of the
 93 eggs, b_j in the longitudinal direction and c_j in the latitudinal. By considering year as random
 94 effect, values for data-poor years are pulled towards the overall mean. Random effects were
 95 modelled as smooth terms by using the flag “bs=re” when specifying the smooth. Stage-
 96 specific smooths were modelled by using the flag “by=Stage” when specifying the smooth.
 97 The number of samples taken at the station was included as offset. This model thus quantified
 98 interannual differences in the spatial occurrence of cod eggs.

99 Similarly, we modelled the natural logarithm of cod egg abundance in positive tows,
 100 $\log_e(N)$, but using only non-zero counts and assuming a normal error distribution (ϵ). This
 101 model can be summarized as

$$102 \quad (S2) \quad \log_e(N_{sij}) = \beta_s + h_s(Day_i) + i_s(Lon_i, Lat_i) + d_j + e_j Lon_i + f_j Lat_i + \epsilon_{sij}$$

103 The notation is analogous to Eq. S1. For this analysis, the natural logarithm of the number of
 104 samples taken at the station was offset.

105 *An index of total egg abundance was calculated from the hurdle model.*

106 To combine this information into one index for cod egg abundance in all tows, EGG_{TOTAL} , we
 107 calculated predictions for a grid at fixed 1° longitude and $1/3^\circ$ latitude intervals over the
 108 study area for April 20th for each year. This date was shortly after the abundance peak of cod
 109 eggs and within the survey period most years. For each grid cell the predicted abundance of
 110 each stage in all tows was calculated as the predicted probability of a positive tow (p_{sij}) from
 111 Eq. S1 multiplied with the predicted abundance in positive tows (N_{sij}) from Eq. S2.
 112 EGG_{TOTAL} was calculated as the natural logarithm of the weighted mean number of predicted
 113 eggs (summed across stages) per grid cell for each year: $EGG_{TOTAL,j} =$
 114 $\ln\left(\frac{1}{N} \sum_i^N \sum_s^4 p_{sij} N_{sij} w_i\right)$. Here, the subscript j refers to year, i to geographic grid location and s
 115 to stage. The weights were the area (km^2) represented by each grid cell divided by their
 116 average area ($w_i = 20 \cdot 1.852 \cdot 60 \cdot 1.852 \cdot \cos(\pi \cdot \text{Lat}_i / 180) / 1275$). The weights were included
 117 to account for the fact that northern grid cells represent smaller areas than southern. To assess
 118 if results might be sensitive to choice of date for standardisation, we also calculated EGG_{TOTAL}
 119 and EGG_{EXTENT} (defined below) for 20 days earlier or later than April 20th. These alternative
 120 indices correlated highly with those used in the analyses (EGG_{TOTAL} : $r > 0.999$, EGG_{EXTENT} :
 121 $r > 0.98$), suggesting that this was not the case.

122 *An index of distributional extent was calculated from the binomial part of the model.*
 123 The index of distributional extent of cod eggs was calculated from the binomial model (Eq.
 124 S1) alone. Specifically, EGG_{EXTENT} was defined as the fraction of the study area with
 125 predicted probability $p_{ij} > 0.2$ of egg occurrence at April 20th. Here, p_{ij} refers to the
 126 probability of sampling eggs of any stage ($p_{ij} = 1 - \prod_{s=1}^{s=4} (1 - p_{sij})$). This index thus
 127 measures the areal extent of cod egg occurrence at a scale from 0 to 1 (the whole study area).

128 *How well do the modelled distributions represent the observation data?*

129 The survey data are shown in Fig. S5. The binomial model (Eq. S1) explained 42.4 % of the
 130 deviance in the data and the lognormal model (Eq. S2) explained 52.8%. The occurrence of
 131 cod eggs predicted from Eq. S1 is shown in Fig. S6 and total abundance predicted from the
 132 hurdle model (Eqs. S1 and S2) is shown in Fig. S7. For most years the model predictions
 133 appear to represent the data reasonably well. For 1964 it is clear that survey coverage is
 134 insufficient to determine egg distribution. This year was therefore excluded from all time-
 135 series analyses.

136 *Uncertainty was estimated by bootstrap.*

137 The uncertainty in the two egg indices was estimated by nonparametric bootstrap, whereby
138 1000 bootstrap data sets of the same sample size as the original data were generated by
139 sampling (with replacement) stations within years, and for each bootstrap data set refit the
140 models (Eqs. S1–S2) and calculate EGG_{TOTAL} and EGG_{EXTENT} . These uncertainty estimates
141 account for the pseudo-replication caused by entering the same station four times (one for
142 each stage) in the regression, but not for possible residual spatial autocorrelation or modelling
143 errors. Residual diagnostics for model S2 suggested no strong spatial autocorrelation: A
144 semivariogram estimated for within-year patterns in residuals showed only about 7 % increase
145 in variance of pairs of residuals from 33 km (the smallest scale estimated) to 68 km apart (the
146 second smallest scale) and no further increase at larger distances. Note that violation of model
147 assumptions, for example caused by differences among years in (logit-scale, Eq. S1, or log-
148 scale, Eq. S2) seasonal patterns, might cause additional uncertainty not captured by the
149 bootstrap.

150 **Variables that potentially influence cod egg abundance and distribution**

151 Potential predictor variables for analyses of year-to-year variation in cod egg abundance ($Q1$)
152 and distribution ($Q2$) are listed in Table 1 and shown in Fig. S2.

153 Spawning stock biomass (SSB) was included as a rough index of the potential egg
154 production. SSB data were obtained from ICES (55). SSB is computed using values for stock
155 number at age from extended survivors analysis (XSA) based mainly on fisheries data, weight-
156 at-age in the stock and maturity-at-age, calculated as weighted averages from Russian and
157 Norwegian surveys during the winter season (37, 55).

158 As five alternative measures of age and size structure in the spawning stock we
159 considered mean biomass-weighted age (MA), weight (MW), age width ($AWIDTH$), age
160 diversity ($ADIV$) and proportion of repeat spawners ($REPEAT$). This choice of indices largely
161 follows previous studies on effects of age and size structure on recruitment (4, 9, 11). By
162 weighting by biomass and not abundance of each age class, these indices represent the ages or
163 sizes that dominate the spawning stock in terms of potential egg production. Indices of
164 spawning stock structure were calculated from abundance-at-age estimated by XSA, weight-at-
165 age and maturity-at-age, all from ICES (55). These estimates are, in addition to the data from
166 the fisheries, dependent on age reading from otoliths and number of mature fish per length
167 group (maturity ogives). Systematic errors in age reading, which might in particular bias
168 estimates of MA , appear to be relatively small (65). The MA and MW indices are strongly

169 correlated with one another, but not with the other indices (Table S2). Note that *REPEAT* is a
 170 coarser index than used in some earlier studies (e.g., 16), as it is calculated mainly based on
 171 changes in maturity-at-age between years. We used the following formula to calculate *MA*, *MW*,
 172 *ADIV* and *REPEAT*:

$$173 \quad (S3) \quad MA_j = \frac{\sum_{a=3}^{a=13+} (a SSB_{aj})}{\sum_{a=3}^{a=13+} SSB_{aj}}$$

$$174 \quad (S4) \quad MW_j = \frac{\sum_{a=3}^{a=13+} (W_{aj} SSB_{aj})}{\sum_{a=3}^{a=13+} SSB_{aj}}$$

$$175 \quad (S5) \quad ADIV_j = - \sum_{a=Min(f_{aj})}^{a=Max(f_{aj})} (f_{aj} \log_e(f_{aj})) \text{ for } f_{aj} > 0$$

$$176 \quad (S6) \quad REPEAT_j = \frac{\sum_{a=3}^{a=13+} (M_{a-1j-1} / M_{aj}) SSB_{aj}}{\sum_{a=3}^{a=13+} SSB_{aj}}$$

177 where *j* is year, *a* is age (years) and *SSB_{aj}* is mature biomass-at-age:

$$178 \quad (S7) \quad SSB_{aj} = N_{aj} W_{aj} M_{aj}, \text{ and}$$

179 *N* number, *W* weight (kg), *M* proportion mature.

180 We further considered a liver condition index (*COND*), which correlates positively with the
 181 recruitment of Barents Sea cod (29), presumably through effects on egg production or viability.
 182 We considered the liver condition index calculated for cod of lengths 41–70 cm sampled by
 183 PINRO January–December the year before spawning. This size range includes first-time
 184 spawners, age 6–7 years (around 65–70 cm). The index for this size range had best data
 185 coverage and represents the spawners reasonably well: The product-moment correlation
 186 between this index and a corresponding index for 61–70 cm only was 0.93 and for 71–100 cm
 187 (available for 1968 onwards) was 0.79 (N.A. Yaragina, unpublished results). The index was
 188 lagged to the year before spawning because gonad growth is thought to start already around the
 189 time of autumnal equinox (66, 67) and a physiological “decision” to ripen or not dependent on
 190 energy acquisition might be taken even earlier. The index was calculated for
 191 January–December because liver condition data were only available as annual averages prior
 192 to 1967.

193 As abiotic variables we considered sea temperature before, during or after spawning
 194 and the North Atlantic Oscillation index (NAO, 61). High temperature has been associated
 195 with early spawning and high potential fecundity (32, 66) and also acts as proxy for various
 196 factors that may potentially influence transport, development and survival of Barents Sea cod

197 eggs (57). We considered sea temperature before, during or after spawning. High temperature
 198 during vitellogenesis (i.e., yolk deposition) is associated with high oocyte growth, early
 199 spawning and high potential fecundity (32, 66). The temperature in the Barents Sea further
 200 acts as a proxy for various factors that may potentially influence growth and survival of early
 201 life stages of Barents Sea cod (57). The *NAO* correlates positively with west wind stress and
 202 water transport in the study region (57) and with a north easterly distribution of Barents Sea
 203 cod larvae (68). Barents Sea temperature was measured by PINRO (69) and temperature at
 204 spawning grounds by IMR (70). *NAO* data were obtained from
 205 [https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-](https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based)
 206 [based](https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based).

207 **Spatiotemporal statistical analysis of association between spatial distribution of cod eggs**
 208 **and mean weight in the spawning stock.**

209 To visualize the change in the spatial distribution of cod eggs under contrasting age or size
 210 structure in the spawning stock, we fit a spatial variable-coefficient GAM (52, 53) to presence-
 211 absence data. This binomial model quantified the probability p of catching at least one egg of
 212 a given stage at a station. Each data point represents presence (coded as 1) or absence (coded
 213 as 0) of one out of four egg developmental stages at one station in one year. Each station is thus
 214 represented by four data points in the analysis, one for each egg stage. As covariates we
 215 included sampling day-of-year (*Day*) and sampling location (*Lon*, longitude and *Lat*, latitude)
 216 and predictor variables selected in time-series analysis of *EGG_{EXTENT}* (i.e., *SSB*, *COND* and *MW*;
 217 Results). Specifically, the probability p_{sij} was modelled as:

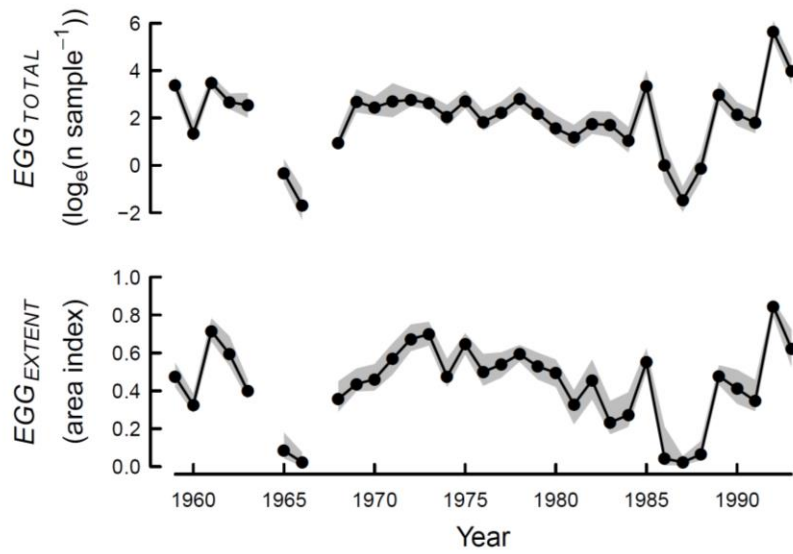
$$218 \quad (S8) \quad \text{logit}(p_{sij}) = \alpha_s + f_s(\text{Day}_i) + g_s(\text{Lon}_i, \text{Lat}_i) + \beta \text{SSB}_j + \gamma \text{COND}_j +$$

$$219 \quad h(\text{Lon}_i, \text{Lat}_i) \text{MW}_j$$

220 where subscripts s , i and j represent stage, station and year, respectively. α_s is a stage-specific
 221 intercept. f_s and g_s are stage-specific smooth functions correcting for sampling date and
 222 location (g_s being a two-dimensional anisotropic smooth modelled as a tensor-product of two
 223 smooth basis functions with maximally 5 knots each). Stage-specific smooths were modelled
 224 by using the flag “by=Stage” when specifying the smooth. β is the coefficient for the effect of
 225 *SSB* and γ the coefficient for the effect of *COND*. The coefficient for the effect of age or size
 226 structure (*MW*) is allowed to vary smoothly as a function of location. The smooth function
 227 $h(\text{Lon}, \text{Lat})$ thus gives a location-dependent coefficient that *MW* is multiplied with. The

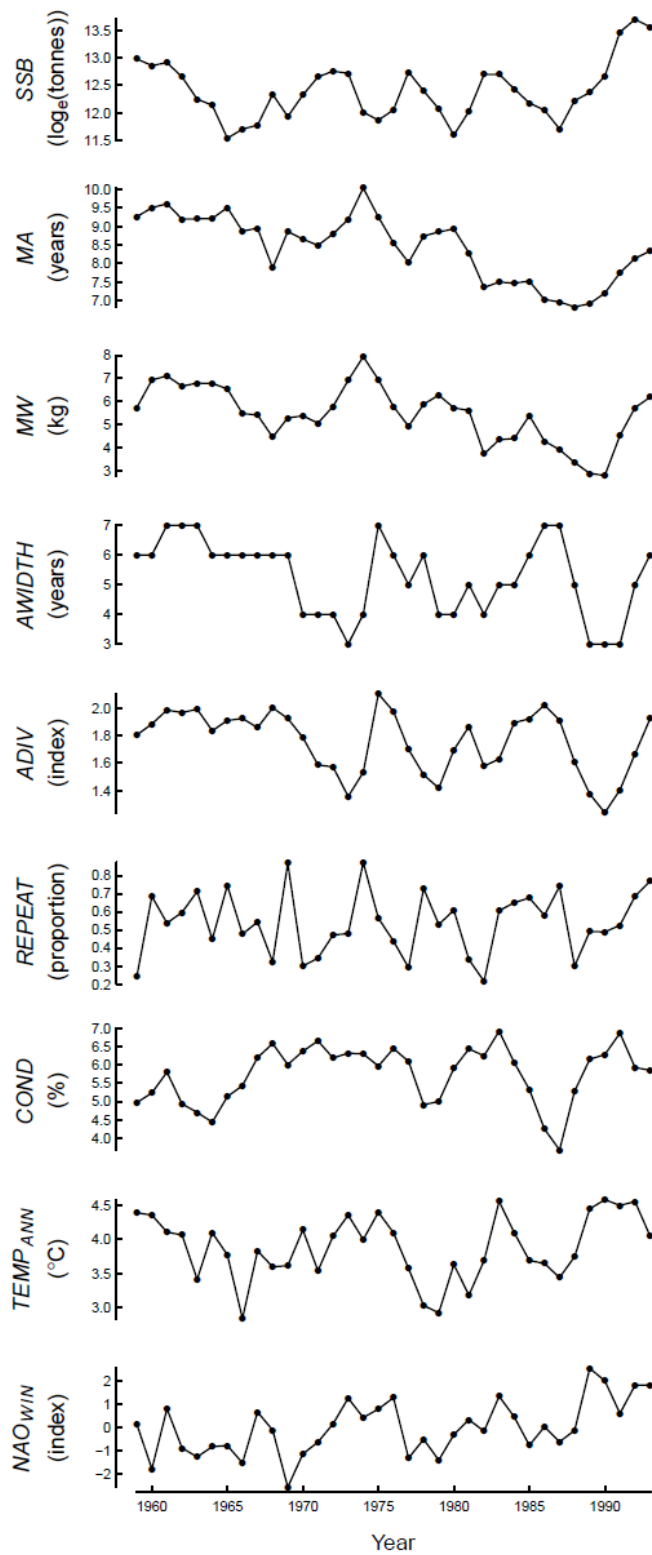
228 number of samples taken at the station was included as offset. This model was used to map
229 the probability of sampling eggs of different stages for years with low *MW* or high *MW*.

230 **SI Figures and Figure Legends.**



231

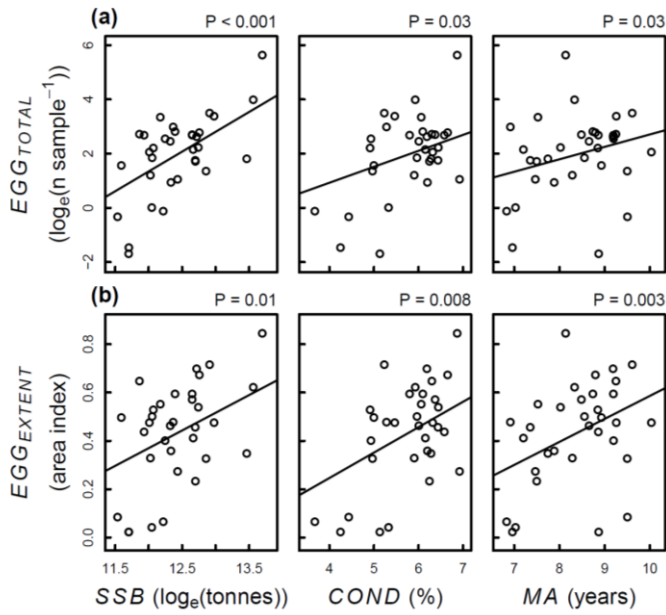
232 **Figure S1.** Annual indices of egg abundance and distribution. *EGG_{TOTAL}*, total abundance of
233 cod eggs in April–May. *EGG_{EXTENT}*, distributional extent. Shaded areas: 95% bootstrap
234 confidence intervals.



235

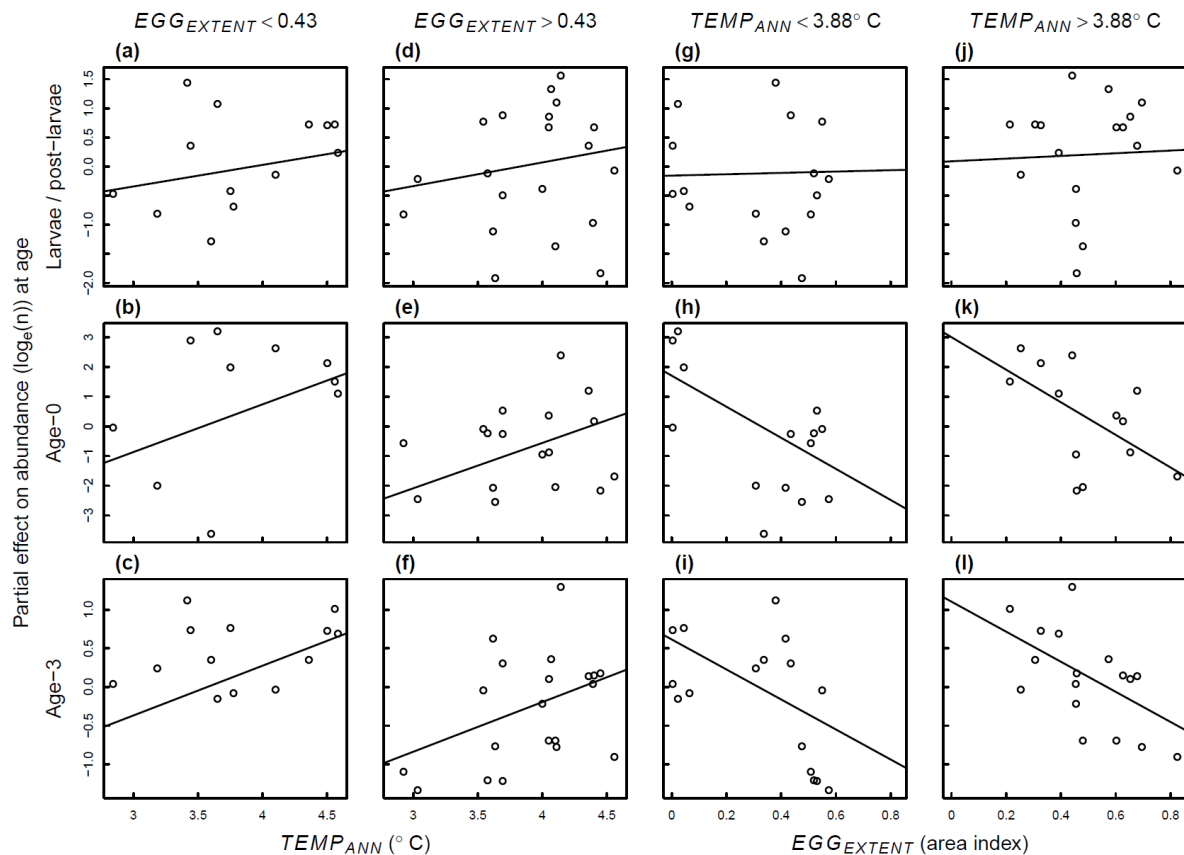
236 **Figure S2.** Main variables considered as predictors of abundance and distributional extent of
 237 cod eggs. See Table 1 and SI Methods for explanation of variables.

238



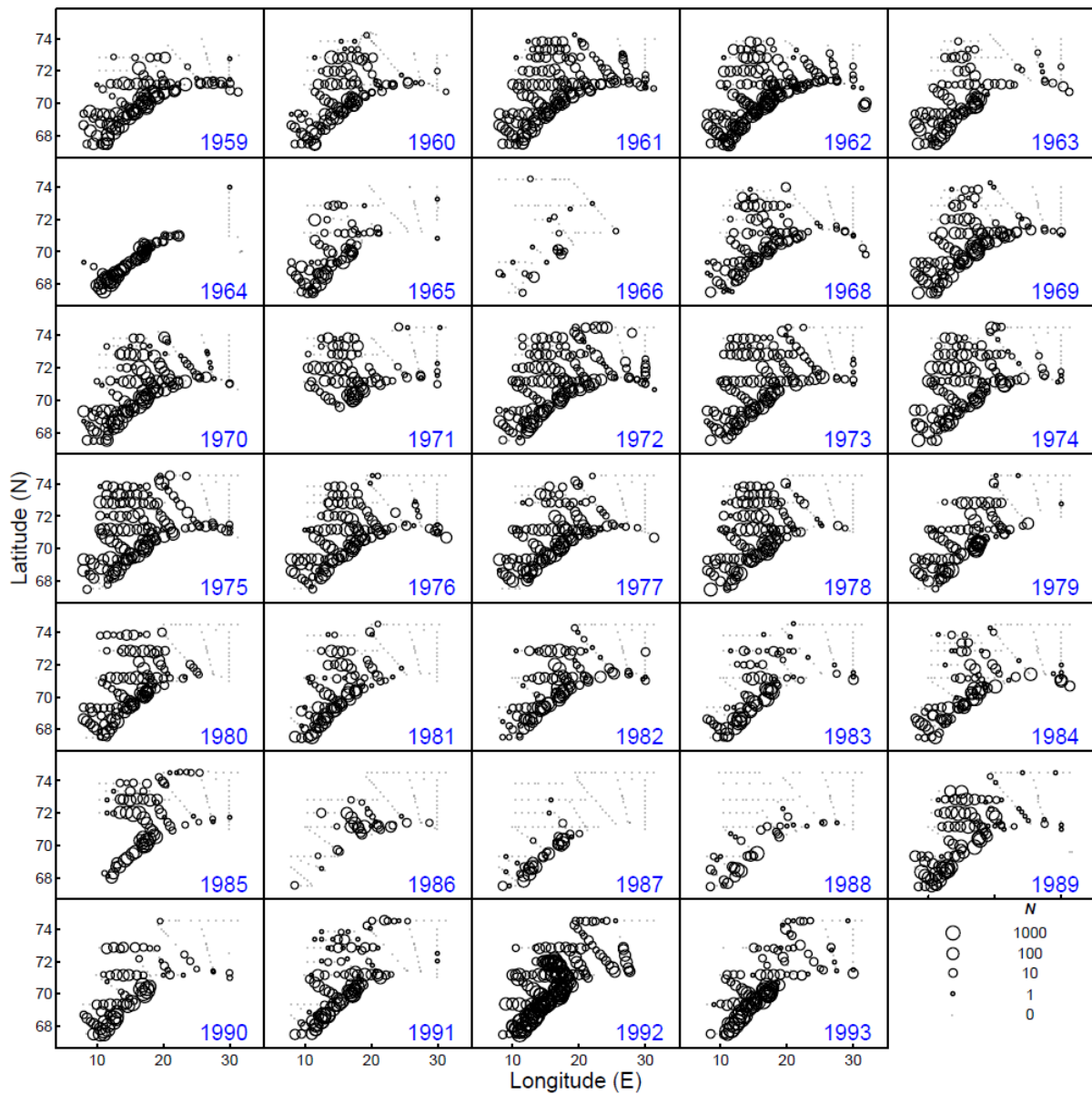
239

240 **Figure S3.** Estimated effects of *SSB*, *COND* and *MA* on total egg abundance (a) and egg
 241 distributional extent (b). Superimposed on the data are regression lines from a multiple linear
 242 regression for each response variable (with associated P-values shown above each panel).



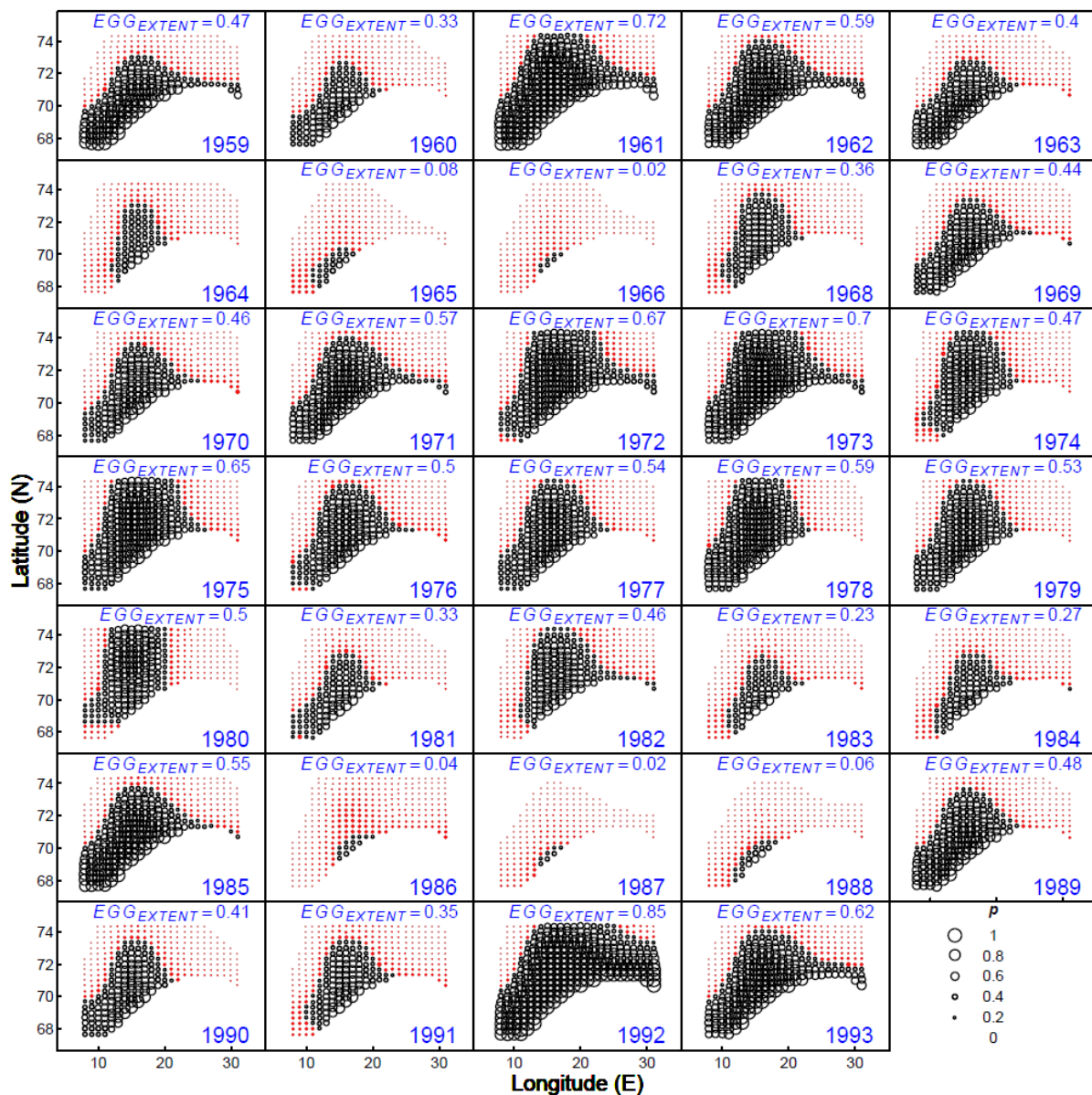
244

245 **Figure S4.** Estimated interaction effects of temperature and distributional extent on survival
 246 of cod eggs to later life stages. Panels a–c and d–f, respectively, show temperature–survival
 247 associations for years with below-average and above-average distributional extent
 248 (EGG_{EXTENT}). Panels g–i and j–l, respectively, show distributional extent–survival
 249 associations for years with below-average and above-average temperature ($TEMP_{ANN}$). Lines:
 250 predicted partial effects of the x-axis variable for the 25th percentile and 75th percentile of the
 251 grouping variable in the given panel (from continuous interaction model, Eq. 1). Points:
 252 partial residuals, accounting for initial cohort abundance. The interaction effects and the main
 253 effects of EGG_{EXTENT} were non-significant in all models ($P > 0.05$, Table 2).



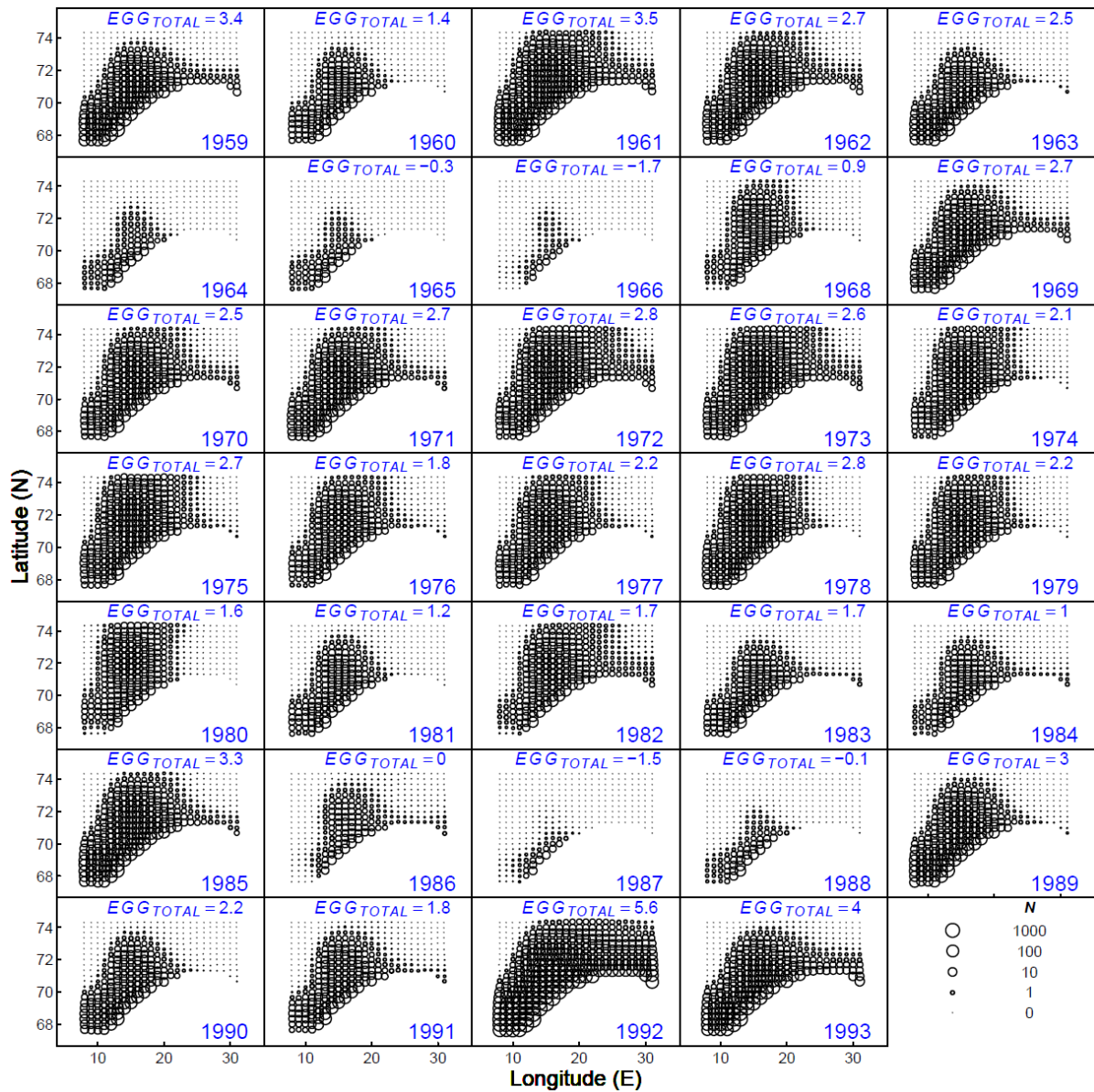
254

255 **Figure S5.** Cod egg surveys. N , total number of cod eggs sampled at a station.



257

258 **Figure S6.** Cod egg occurrence predicted from a binomial model (Eq. S1) fitted to the
 259 observation data. p , predicted probability of sampling one or more cod egg at April 20th for
 260 each year. Black: $p > 0.2$. Red: $p < 0.2$. The egg distribution index (EGG_{EXTENT}) is the annual
 261 fraction of the area having $p > 0.2$. The index is undefined for 1964 due to poor survey
 262 coverage that year (Fig. S5).



263

264 **Figure S7.** Cod egg abundance predicted from a hurdle model (Eqs. S1 and S2) fitted to the
 265 observation data. N , predicted abundance of cod eggs at April 20th for each year. The egg
 266 abundance index (EGG_{TOTAL}) is the natural logarithm of the annual sum of N across grid
 267 points. The index is undefined for 1964 due to poor survey coverage that year (Fig. S5).

268 **Table S1. Regression results. Model coefficients \pm standard errors for the models**
 269 **providing lowest AIC_C. Δ AIC_C, difference in AIC_C compared to the best model.**

					R ²	Δ AIC _C
(a) Total egg abundance						
<i>EGG_{TOTAL}</i>	= -21.0	+ 1.42 \pm 0.37 <i>SSB</i>	+ 0.59 \pm 0.25 <i>COND</i>	+ 0.34 \pm 0.14 <i>MW</i>	0.58	0
<i>EGG_{TOTAL}</i>	= -23.4	+ 1.46 \pm 0.37 <i>SSB</i>	+ 0.59 \pm 0.26 <i>COND</i>	+ 0.46 \pm 0.20 <i>MA</i>	0.57	0.7
(b) Distributional extent						
<i>EGG_{EXTENT}</i>	= -2.27	+ 0.14 \pm 0.053 <i>SSB</i>	+ 0.11 \pm 0.036 <i>COND</i>	+ 0.070 \pm 0.020 <i>MW</i>	0.57	0
<i>EGG_{EXTENT}</i>	= -2.79	+ 0.15 \pm 0.054 <i>SSB</i>	+ 0.11 \pm 0.037 <i>COND</i>	+ 0.095 \pm 0.029 <i>MA</i>	0.56	0.8
(c) Distributional extent correcting for effect of total egg abundance						
<i>EGG_{EXTENT}</i>	= -0.15	+ 0.12 \pm 0.010 <i>EGG_{TOTAL}</i>		+ 0.041 \pm 0.017 <i>MA</i>	0.85	0
<i>EGG_{EXTENT}</i>	= 0.04	+ 0.12 \pm 0.010 <i>EGG_{TOTAL}</i>		+ 0.029 \pm 0.012 <i>MW</i>	0.85	0.3

270

271 **Table S2.** Pearson's product-moment correlation (r) among variables. $|r| > 0.45$ are shown in bold. $|r| > 0.35$ and 0.45 , respectively, are
 272 statistically significant at the 5% and 1% level. N = 33 years.

	NAO_{SPR}	NAO_{WIN}	$TEMP_{ANN}$	$TEMP_{SUM}$	$TEMP_{SPR}$	$TEMP_{WIN}$	$COND$	$REPEAT$	$ADIV$	$AWIDTH$	MW	MA	SSB	EGG_{EXTENT}
EGG_{TOT}	0.18	0.34	0.44	0.41	0.28	0.27	0.54	0.07	-0.19	-0.16	0.29	0.24	0.64	0.91
EGG_{EXTENT}	0.08	0.28	0.31	0.29	0.16	0.17	0.56	0.00	-0.20	-0.20	0.42	0.38	0.51	
SSB	0.24	0.42	0.53	0.53	0.44	0.46	0.44	-0.13	-0.29	-0.23	-0.04	-0.09		
MA	-0.42	-0.32	-0.03	-0.06	0.05	0.04	-0.02	0.24	0.22	0.21	0.92			
MW	-0.43	-0.25	-0.04	-0.06	0.01	0.08	-0.01	0.36	0.32	0.33				
$AWIDTH$	-0.24	-0.34	-0.25	-0.31	-0.29	0.00	-0.30	0.29	0.88					
$ADIV$	-0.33	-0.34	-0.19	-0.23	-0.32	0.06	-0.16	0.17						
$REPEAT$	-0.16	-0.06	0.00	-0.08	0.11	0.15	-0.01							
$COND$	0.16	0.26	0.28	0.26	0.06	0.25								
$TEMP_{WIN}$	0.01	0.41	0.74	0.70	0.65									
$TEMP_{SPR}$	0.26	0.47	0.85	0.84										
$TEMP_{SUM}$	0.28	0.67	0.98											
$TEMP_{ANN}$	0.24	0.61												
NAO_{WIN}	0.51													

273

