

# Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate

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**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 with other impacts.**

fisheries | age and size truncation | population dynamics | climate effects | *Gadus morhua*

Many exploited fish stocks have shown large changes in their demographic structure over the past decades, toward 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 overemphasized (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 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 use a unique spatially resolved egg data set that originates from 35 y (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.

Although 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

## Significance

**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 analyzing 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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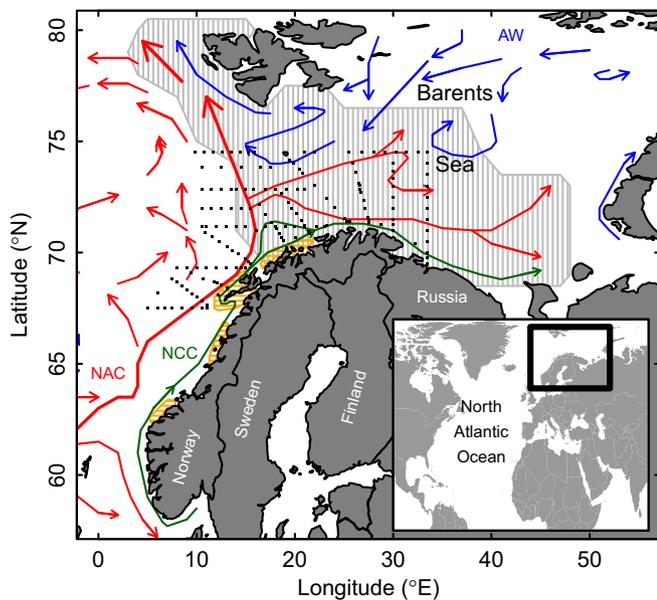
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**Fig. 1.** Study area. Horizontally hatched orange areas: main spawning grounds of Barents Sea cod. Vertically hatched gray areas: distribution of 5-mo-old cod juveniles in August–September. Colored arrows: main features of the mean surface circulation pattern. AW, Arctic waters (blue); NAC, North Atlantic current (red); NCC, Norwegian coastal current (green). Points: ichthyoplankton survey (shown for one representative year, 1988).

age and weight in the spawning stock was declining (4, 11), a trend that 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 eastward 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 Ottersen et al. (27), such as high temperature (28) and good condition of the spawners (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, although 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), multistock

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**

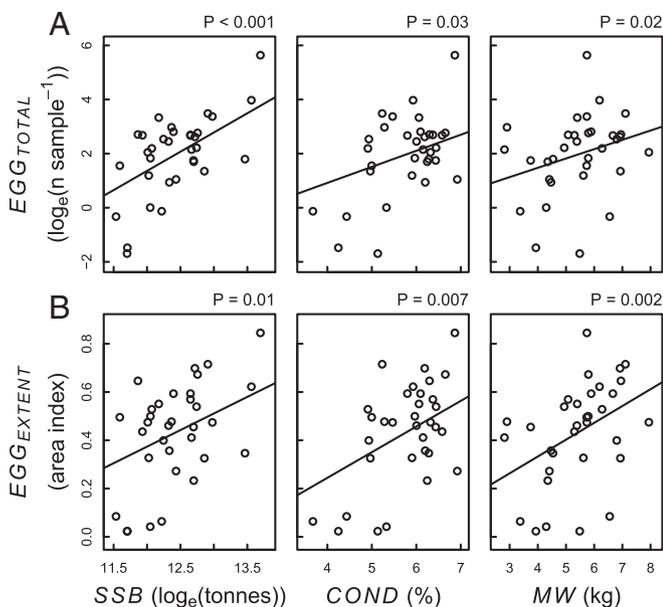
**Q1: Which Factors Influence the Total Abundance of Cod Eggs?** Analyzing time-series of log-scale total cod egg abundance ( $EGG_{TOTAL}$ ) in April–May (Fig. S1) and alternative predictor variables (Table 1 and Fig. S2) statistically, we found that egg abundance was best explained [lowest Akaike Information Criterion corrected for small sample size ( $AIC_C$ )] (30) as a function of spawning stock biomass ( $SSB$ ), liver condition index ( $COND$ ), and mean weight in the spawning stock ( $MW$ ) (Table S1 and Fig. 2A). For a change in  $MW$  from 3.2 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).

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 S1 and Fig. S3A).

**Q2: Which Factors Influence the Distributional Extent of the Eggs?** We then analyzed 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 S2). However, the strengths of the associations differed, with  $MW$  (Fig. 2B) or, alternatively,  $MA$

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

| Variable     | Description  |
|--------------|--|
| $SSB$        | Spawning stock biomass ( $\log_e$ [tons])  |
| $MA$         | Mean biomass-weighted age in the spawning stock (y)  |
| $MW$         | Mean biomass-weighted weight in the spawning stock (kg)  |
| $AWIDTH$     | Biomass-weighted age width (y): the difference in age between the 5% and 95% quantile of mature biomass-at-age   |
| $ADIV$       | Biomass-weighted age diversity in the spawning stock, calculated as Shannon’s diversity index (59) for nonzero frequencies of mature biomass-at-age                          |
| $REPEAT$     | Proportion of repeat spawners in spawning stock biomass  |
| $COND$       | 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)                 |
| $TEMP_{WIN}$ | Winter (October–March, preceding spawning) sea temperature ( $^{\circ}C$ ) in the Barents Sea (0–200 m depth at the Kola section, 70.5–72.5 $^{\circ}N$ , 33.5 $^{\circ}E$ ) |
| $TEMP_{SPR}$ | Spring (April) sea temperature ( $^{\circ}C$ ) at the spawning grounds in the Lofoten Islands (10 m depth at Skrova, 68.1 $^{\circ}N$ , 14.7 $^{\circ}E$ )                   |
| $TEMP_{SUM}$ | Summer (April–September) sea temperature ( $^{\circ}C$ ) in the Barents Sea  |
| $TEMP_{ANN}$ | Annual (January–December) sea temperature ( $^{\circ}C$ ) in the Barents Sea   |
| $NAO_{WIN}$  | North Atlantic Oscillation (NAO) winter index: the principal component-based NAO index (61) for December–March preceding spawning  |
| $NAO_{SPR}$  | NAO index for March–May  |



**Fig. 2.** Predictor effects on total egg abundance (A) and egg distributional extent (B). Spawning stock biomass (SSB), liver condition index (COND), and mean weight in the spawning stock (MW) were selected as predictors in both analyses. Superimposed on the data are regression lines from multiple linear regression analysis for each response variable (with associated  $P$  values shown above each panel).

(Fig. S3B), being more strongly correlated with  $EGG_{EXTENT}$  than with  $EGG_{TOTAL}$ . For a change in MW from 3.2 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.

Because 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 a covariate in the analysis of  $EGG_{EXTENT}$ . SSB and COND then had no significant effect, but MW or, alternatively, MA, did (Table S3). This finding suggests that the associations of SSB and COND with distributional extent are fully explainable through total egg abundance. However, 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 analyzed associations among  $EGG_{TOTAL}$ ,  $EGG_{EXTENT}$ , and time-series of year-class abundance at three later stages, i.e., as larvae/postlarvae in June–July, as age-0 juveniles in August–September, and as age-3 recruits (Eq. 1). None of the estimated coefficients for the effect of  $EGG_{EXTENT}$  ( $\gamma$ ; Table 2) on log abundances of later stages were significant. The coefficients for the effects of  $EGG_{TOTAL}$  and  $EGG_{EXTENT}$  ( $\beta$  and  $\gamma$ ; Table 2) are correlated ( $r = -0.91$ ) in all three models, corresponding to a variance inflation factor (31) of 5.8, which 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 a covariate, see below). Hence, the results fail to show associations between survival and egg distribution that are independent of total egg abundance.

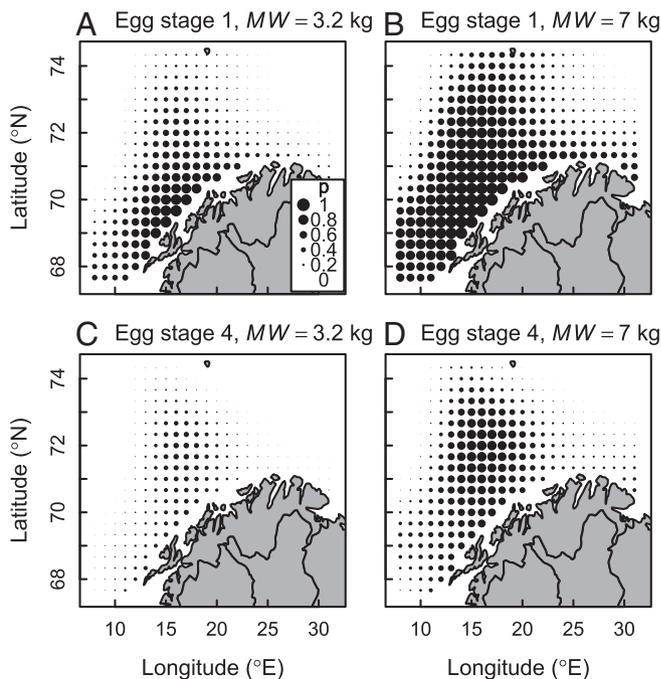
As a rough estimate of the potential survival value of a high distributional extent at the egg stage, we used the results in Table 2 to calculate how much predicted year-class abundance at later stages changes if  $EGG_{EXTENT}$  increases by 0.26. This change in  $EGG_{EXTENT}$  is the predicted effect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

Although temperature was generally positively associated with the abundances of later life stages (coefficient  $\delta$ ; 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  $\theta$ ; Table 2 and Fig. S4). For example, the estimated effect of a  $1^\circ$  temperature increase on age-3 log-abundance at  $EGG_{EXTENT}$  values of 0.28, 0.43, and 0.54, respectively, were 0.64 (CI: 0.08, 1.20), 0.64 (CI: 0.15, 1.13), and 0.64 (CI: 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 hypothesized 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



**Fig. 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 [5th percentile (A and C) and 95th percentile (B and D) of MW]. Predictions are for mean values of spawning stock biomass and liver condition index for egg stage 1 (A and B) and egg stage 4 (C and D) for May 6 (mean sampling day).

**Table 2. Analysis of survival of cod eggs to later stages (Eq. 1)**

| Survival to stage           | Parameter estimate ± SE |              |              |              |              |       |
|-----------------------------|-------------------------|--------------|--------------|--------------|--------------|-------|
|                             | $\alpha$                | $\beta$      | $\gamma$     | $\delta$     | $\theta$     | $R^2$ |
| Larvae/postlarvae June–July | -2.92 ± 0.69*           | 0.61 ± 0.33  | 0.16 ± 2.16  | 0.39 ± 0.42  | 0.15 ± 1.73  | 0.56  |
| Age 0 August–September      | 19.9 ± 1.26*            | 1.36 ± 0.61* | -5.32 ± 3.95 | 1.57 ± 0.74* | -0.33 ± 2.89 | 0.57  |
| Age 3                       | 19.1 ± 0.42*            | 0.37 ± 0.20  | -1.94 ± 1.31 | 0.64 ± 0.25* | 0.00 ± 1.04  | 0.43  |
| Age 3 autoregressive model† | 19.0 ± 0.42*            | 0.41 ± 0.19* | -2.21 ± 1.33 | 0.53 ± 0.25* | 0.02 ± 0.93  |       |

$\alpha$ , intercept;  $\beta$ , effect of total abundance of cod eggs;  $\gamma$ , effect of distributional extent of cod eggs;  $\delta$ , effect of temperature; and  $\theta$ , 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.

\* $P < 0.05$ .

†Generalized least-squares model, which accounts for order-1 residual autocorrelation.

abundance is significantly higher in years with more old and large individuals in the spawning stock.

Several nonexclusive mechanisms may explain these associations. First, older and larger cod are reported to have higher relative fecundity (16, 17). This mechanism is supported by Kjesbu et al. (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. Second, inexperienced, young, and small cod produce smaller-than-average eggs, which seem to have lower-than-average fertilization and survival rates (ref. 17 and references therein). Third, 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, because females mature at a higher age and larger size than males (36). The proportion of females in the spawning stock biomass of Barents Sea cod has been found to vary between 24% and 68%, and 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 is 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. 24). 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 prespawning 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 counterbalanced 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 finding is consistent with analyses of 50-y-long 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 toward 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 (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  $EGG_{TO}$  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. Although 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, and most likely lower. This effect is trivial compared with other influences on recruitment (44), and suggests that the spatial extent of the eggs per se is on average of little importance for year-class strength. Similarly, population modeling 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 highly 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—for example, by using coupled biophysical modeling 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 [BOFFFF; a concept introduced by Berkeley et al. (1) and Law (3)] in fostering stock productivity and stability. This value can be divided into three main components (15): (i) the storage effect: BOFFFF outlive periods unfavorable for larvae; (ii) the fecundity effect: BOFFFF have higher relative (weight-specific) fecundity than younger females; and (iii) maternal effects: the presence of BOFFFF provide variation in reproductive strategies because BOFFFF offspring grow faster and survive better in some environments and because BOFFFF likely spawn at different times and places than younger females. In support of the first mechanism, results of Rouyer et al. (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 prerecruitment 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 Shelton et al. (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 that 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 (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* and *Figs. S5–S7*. 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), 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  $AIC_C$  (30). Nonsignificant 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 reestimated 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 S4) could complicate interpretation of results because 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 this, 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 generalized additive model (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 modeled 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/postlarvae 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 (ref. 54, using data from ICES working group reports). (iii) Age-3 recruits. We used estimates of annual log abundance at age 3 y 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)]. To test if a wide spatial 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 a predictor variable. 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:

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

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  $\varepsilon_t$  is an independent and normal distributed environmental error term with mean zero and variance  $\sigma^2$ . We expected that a positive relationship between distributional extent and survival would lead to  $\gamma$  larger than zero. Based on previous studies (57), we expected positive coefficients for the temperature effect,  $\delta$ . If a wide distributional extent buffered the temperature effect, we expected negative coefficients for the interaction term,  $\theta$ .

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 1,000 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 SEs from the model to obtain SEs 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. All time series and computer code are available upon request. Restrictions apply to the raw data used.

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# Supporting Information

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## SI Results

**Q1: Which Factors Influence the Total Abundance of Cod Eggs?** The selected model (Table S1) included *MW*, *SSB*, and *COND* as predictors of *EGG<sub>TOTAL</sub>*. The inclusion of *MW* as predictor improved  $AIC_C$  by 3.4 and increased  $R^2$  from 0.50 to 0.58 compared with a model with only *SSB* and *COND*.

There was no significant ( $P > 0.05$ ) positive autocorrelation in the residuals in the selected model, which could otherwise bias uncertainty estimates. Because of positive correlation between *SSB* and *COND* (Table S4), the coefficients for these effects were negatively correlated ( $R^2 = 0.18$ ). The magnitude of the confounding between *SSB* and *COND* effects was estimated by the variance inflation factor (VIF) (31), which measures how much the variance of the coefficients (i.e., the SEs squared) is increased because of collinearity. The correlation between *SSB* and *COND* caused a VIF of 1.2, which we considered acceptably low to include both variables in the model.

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

**Q2: Which Factors Influence the Distributional Extent of the Eggs?** Residuals from the selected models of predictor effects on distributional extent (Tables S2 and S3) showed no significant positive autocorrelation and besides *SSB* and *COND*, predictors were not significantly correlated.

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

**Q3: How Does the Distributional Extent of Eggs Affect Survival to Later Stages?** Residuals from the analyses of the two earliest stage intervals in Table 2 showed no significant positive autocorrelation, whereas the lag-1 autocorrelation function for age 3 was 0.39 and statistically significantly ( $P < 0.05$ ). Explicitly modeling this autocorrelation structure using a generalized least-squares model had little effect on parameter estimates and SEs (Table 2).

## SI Methods

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

## Construction of Indices of Abundance and Distributional Extent of Cod Eggs.

**Two different indices were calculated.** We used a statistical approach to construct annual indices for the abundance and distributional extent of cod eggs. One index measured the total abundance of eggs (*EGG<sub>TOTAL</sub>*), the other measured the spatial distributional extent of the eggs (*EGG<sub>EXTENT</sub>*).

**Sampling variation was corrected for statistically.** To construct these indices we used a GAM (53) regression method to correct for variability in sampling date, sampling location, and slight variability in the number of samples per station (48). The models used to construct the egg indices were estimated by maximum-likelihood methods with mixed-effects GAMs, using the gam function in the mgcv package (version 1.8–12) in R (version 3.2.4) (53).

**A hurdle model separated the variation into binomial and lognormal parts.** Because the survey data contained many stations with no eggs, the data were considered to originate from two different processes: one process determining the probability of a positive tow (i.e., nonzero abundance of eggs of a given stage at a station) and another determining the abundance conditional on a positive tow (63). To account for the two processes, we used a hurdle model approach (64), whereby a binomial model quantified the probability of a positive tow and a lognormal model quantified abundance in positive tows.

The binomial model quantified the probability  $P$  of catching at least one egg of a given stage at a station. Each data point represents presence (coded as 1) or absence (coded as 0) of one of four egg developmental stages at one station in 1 y. Each station is thus represented by four data points in the analysis, one for each egg stage. As covariates we included sampling day-of-year (*Day*) and sampling location (*Lon*, longitude; *Lat*, latitude, standardized to zero mean). The probability  $P_{sij}$  was modeled as

$$\text{logit}(P_{sij}) = \alpha_s + f_s(\text{Day}_i) + g_s(\text{Lon}_i, \text{Lat}_i) + a_j + b_j \text{Lon}_i + c_j \text{Lat}_i, \quad [\text{S1}]$$

where the subscripts  $s$ ,  $i$ , and  $j$  represent stage, station, and year, respectively;  $\alpha_s$  is a stage-specific intercept, and  $f_s$  and  $g_s$  are stage-specific smooth functions correcting for sampling date and location ( $g_s$ , a 2D anisotropic smooth modeled as a tensor product of two smooth basis functions with maximally 5 kn each). The random term  $a_j$  captures year-to-year variation in the intercept, that is, in the overall probability of sampling cod eggs. The random terms  $b_j$  and  $c_j$  capture year-to-year variation in the location of the eggs,  $b_j$  in the longitudinal direction and  $c_j$  in the latitudinal. By considering year as random effect, values for data-poor years are pulled toward the overall mean. Random effects were modeled as smooth terms by using the flag “bs = re” when specifying the smooth. Stage-specific smooths were modeled by using the flag “by = Stage” when specifying the smooth. The number of samples taken at the station was included as offset. This model thus quantified interannual differences in the spatial occurrence of cod eggs.

Similarly, we modeled the natural logarithm of cod egg abundance in positive tows,  $\log_e(N)$ , but using only nonzero counts and assuming a normal error distribution ( $\epsilon$ ). This model can be summarized as

$$\log_e(N_{sij}) = \beta_s + h_s(\text{Day}_i) + i_s(\text{Lon}_i, \text{Lat}_i) + d_j + e_j \text{Lon}_i + f_j \text{Lat}_i + \epsilon_{sij}. \quad [\text{S2}]$$

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

**An index of total egg abundance was calculated from the hurdle model.** To combine this information into one index for cod egg abundance in all tows,  $EGG_{TOTAL}$ , we calculated predictions for a grid at fixed  $1^\circ$  longitude and  $1/3^\circ$  latitude intervals over the study area for April 20 for each year. This date was shortly after the abundance peak of cod eggs and within the survey period most years. For each grid cell the predicted abundance of each stage in all tows was calculated as the predicted probability of a positive tow ( $P_{sij}$ ) from Eq. S1 multiplied with the predicted abundance in positive tows ( $N_{sij}$ ) from Eq. S2.  $EGG_{TOTAL}$  was calculated as the natural logarithm of the weighted mean number of predicted eggs (summed across stages) per grid cell for each year:  $EGG_{TOTAL, j} = \ln\left(\frac{1}{N} \sum_i \sum_s P_{sij} N_{sij} w_i\right)$ .

Here, the subscript  $j$  refers to year,  $i$  to geographic grid location, and  $s$  to stage. The weights were the area ( $\text{km}^2$ ) represented by each grid cell divided by their 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 to account for the fact that northern grid cells represent smaller areas than southern. To assess if results might be sensitive to choice of date for standardization, we also calculated  $EGG_{TOTAL}$  and  $EGG_{EXTENT}$  (defined below) for 20 d earlier or later than April 20. These alternative indices correlated highly with those used in the analyses ( $EGG_{TOTAL}$ :  $r > 0.999$ ;  $EGG_{EXTENT}$ :  $r > 0.98$ ), suggesting that this was not the case. **An index of distributional extent was calculated from the binomial part of the model.** The index of distributional extent of cod eggs was calculated from the binomial model (Eq. S1) alone. Specifically,  $EGG_{EXTENT}$  was defined as the fraction of the study area with predicted probability  $P_{ij} > 0.2$  of egg occurrence at April 20. Here,  $P_{ij}$  refers to the probability of sampling eggs of any stage,  $P_{ij} = 1 - \prod_{s=1}^4 (1 - P_{sij})$ . This index thus measures the areal extent of cod egg occurrence at a scale from 0 to 1 (the whole study area).

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

**Uncertainty was estimated by bootstrap.** The uncertainty in the two egg indices was estimated by nonparametric bootstrap, whereby 1,000 bootstrap data sets of the same sample size as the original data were generated by sampling (with replacement) stations within years, and for each bootstrap data set refit the models (Eqs. S1 and S2) and calculate  $EGG_{TOTAL}$  and  $EGG_{EXTENT}$ . These uncertainty estimates account for the pseudoreplication caused by entering the same station four times (one for each stage) in the regression, but not for possible residual spatial autocorrelation or modeling errors. Residual diagnostics for model S2 suggested no strong spatial autocorrelation: A semivariogram estimated for within-year patterns in residuals showed only about 7% increase in variance of pairs of residuals from 33 km (the smallest scale estimated) to 68 km apart (the second smallest scale), and no further increase at larger distances. Note that violation of model assumptions, for example caused by differences among years in (logit-scale, Eq. S1; or log-scale, Eq. S2) seasonal patterns, might cause additional uncertainty not captured by the bootstrap.

**Variables That Potentially Influence Cod Egg Abundance and Distribution.** Potential predictor variables for analyses of year-to-year variation in cod egg abundance (Q1) and distribution (Q2) are listed in Table 1 and shown in Fig. S2.

$SSB$  was included as a rough index of the potential egg production.  $SSB$  data were obtained from the International Council for the Exploration of the Sea (ICES) (55).  $SSB$  is computed using

values for stock number at age from extended survivors analysis (XSA) based mainly on fisheries data, weight at age in the stock, and maturity at age, calculated as weighted averages from Russian and Norwegian surveys during the winter season (37, 55).

As five alternative measures of age and size structure in the spawning stock, we considered mean biomass-weighted age ( $MA$ ), weight ( $MW$ ), age width ( $AWIDTH$ ), age diversity ( $ADIV$ ), and proportion of repeat spawners ( $REPEAT$ ). This choice of indices largely follows previous studies on effects of age and size structure on recruitment (4, 9, 11). By weighting by biomass and not abundance of each age class, these indices represent the ages or sizes that dominate the spawning stock in terms of potential egg production. Indices of spawning stock structure were calculated from abundance at age estimated by XSA, weight at age, and maturity at age, all from ICES (55). These estimates are, in addition to the data from the fisheries, dependent on age reading from otoliths and number of mature fish per length group (maturity ogives). Systematic errors in age reading, which might in particular bias estimates of  $MA$ , appear to be relatively small (65). The  $MA$  and  $MW$  indices are strongly correlated with one another, but not with the other indices (Table S4). Note that  $REPEAT$  is a coarser index than used in some earlier studies (16), because it is calculated mainly based on changes in maturity at age between years. We used the following formula to calculate  $MA$ ,  $MW$ ,  $ADIV$ , and  $REPEAT$ :

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

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

$$ADIV_j = - \sum_{a=3}^{a=13+} (f_{aj} \log_e(f_{aj})) \quad \text{For } f_{aj} > 0 \quad [S5]$$

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

where  $j$  is year,  $a$  is age (y),  $N$  is number,  $W$  is weight (kg),  $M$  is proportion mature,  $SSB_{aj}$  is mature biomass at age:

$$SSB_{aj} = N_{aj} W_{aj} M_{aj} \quad [S7]$$

$N$  is number,  $W$  is weight (kg),  $M$  is proportion mature, and  $f$  is frequency of mature biomass at age.

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

As abiotic variables we considered sea temperature before, during, or after spawning and the North Atlantic Oscillation (NAO)

index (61). High temperature has been associated with early spawning and high potential fecundity (32, 66) and also acts as proxy for various factors that may potentially influence transport, development, and survival of Barents Sea cod eggs (57). High temperature during vitellogenesis (i.e., yolk deposition) is associated with high oocyte growth, early spawning, and high potential fecundity (32, 66). The temperature in the Barents Sea further acts as a proxy for various factors that may potentially influence growth and survival of early life stages of Barents Sea cod (57). The NAO correlates positively with west wind stress and water transport in the study region (57) and with a northeasterly distribution of Barents Sea cod larvae (68). Barents Sea temperature was measured by PINRO (69) and temperature at spawning grounds by Institute of Marine Research (70). NAO data were obtained from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based>.

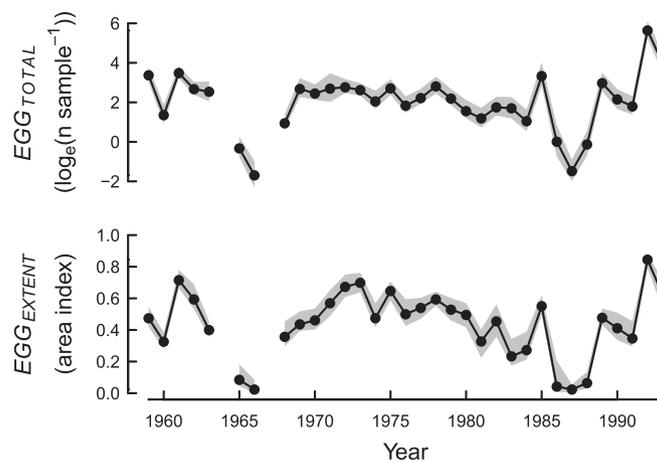
#### Spatiotemporal Statistical Analysis of Association Between Spatial Distribution of Cod Eggs and Mean Weight in the Spawning Stock.

To visualize the change in the spatial distribution of cod eggs under contrasting age or size structure in the spawning stock, we fit 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. Each data point represents presence (coded as 1) or absence (coded as 0) of one of four egg developmental stages at one station in 1 y. Each station is

thus represented by four data points in the analysis, one for each egg stage. As covariates we included sampling day of year ( $Day$ ) and sampling location ( $Lon$ , longitude;  $Lat$ , latitude) and predictor variables selected in time-series analysis of  $EGG_{EXTENT}$  (i.e.,  $SSB$ ,  $COND$ , and  $MW$ ; *Results*). Specifically, the probability  $P_{sij}$  was modeled as

$$\text{logit}(P_{sij}) = \alpha_s + f_s(Day_i) + g_s(Lon_i, Lat_i) + \beta SSB_j + \gamma COND_j + h(Lon_i, Lat_i)MW_j, \quad [S8]$$

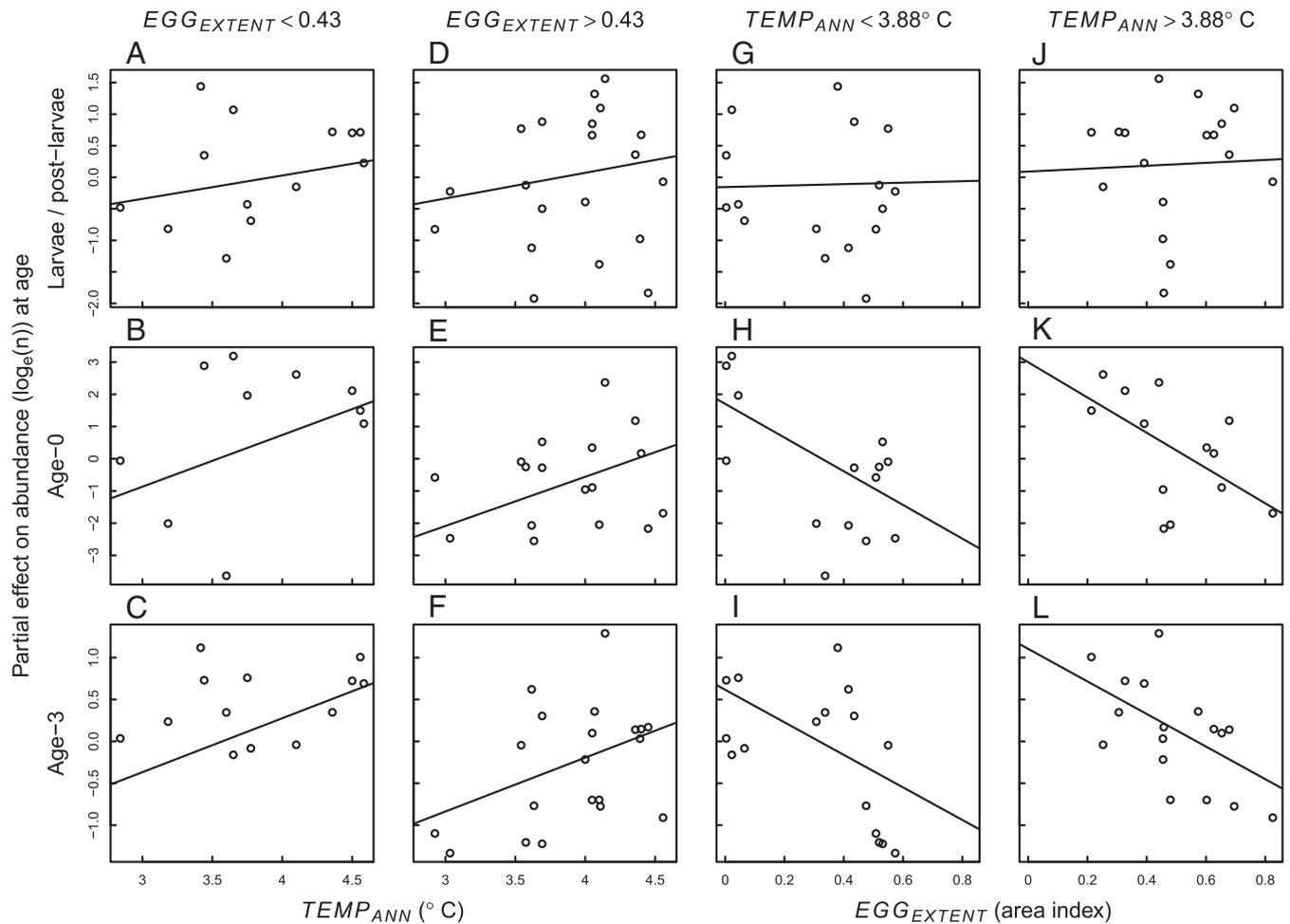
where subscripts  $s$ ,  $i$ , and  $j$  represent stage, station, and year, respectively.  $\alpha_s$  is a stage-specific intercept.  $f_s$  and  $g_s$  are stage-specific smooth functions correcting for sampling date and location ( $g_s$  being a 2D anisotropic smooth modeled as a tensor product of two smooth basis functions with maximally 5 kn each). Stage-specific smooths were modeled by using the flag “by = Stage” when specifying the smooth.  $\beta$  is the coefficient for the effect of  $SSB$ , and  $\gamma$  the coefficient for the effect of  $COND$ . The coefficient for the effect of age or size structure ( $MW$ ) is allowed to vary smoothly as a function of location. The smooth function  $h(Lon, Lat)$  thus gives a location-dependent coefficient that  $MW$  is multiplied with. The number of samples taken at the station was included as offset. This model was used to map the probability of sampling eggs of different stages for years with low  $MW$  or high  $MW$ .



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







**Fig. S4.** Estimated interaction effects of temperature and distributional extent on survival of cod eggs to later life stages. Temperature–survival associations for years with below-average (A–C) and above-average (D–F) distributional extent ( $EGG_{EXTENT}$ ). Distributional extent–survival associations for years with below-average (G–I) and above-average (J–L) temperature ( $TEMP_{ANN}$ ). Lines: predicted partial effects of the  $x$ -axis variable for the 25th and 75th percentile of the grouping variable in the given panel (from continuous interaction model, Eq. 1). Points: partial residuals, accounting for initial cohort abundance. The interaction effects and the main effects of  $EGG_{EXTENT}$  were nonsignificant in all models ( $P > 0.05$ ; Table 2).







**Table S1. Total egg abundance regression results**

| Model coefficients $\pm$ SEs for the models providing lowest AIC <sub>C</sub>     | R <sup>2</sup> | $\Delta$ AIC <sub>C</sub> |
|---|----------------|---------------------------|
| $EGG_{TOTAL} = -21.0 + 1.42 \pm 0.37 SSB + 0.59 \pm 0.25 COND + 0.34 \pm 0.14 MW$ | 0.58           | 0                         |
| $EGG_{TOTAL} = -23.4 + 1.46 \pm 0.37 SSB + 0.59 \pm 0.26 COND + 0.46 \pm 0.20 MA$ | 0.57           | 0.7                       |

$\Delta$ AIC<sub>C</sub> difference in AIC<sub>C</sub> compared with the best model.

**Table S2. Distributional extent regression results**

| Model coefficients $\pm$ SEs for the models providing lowest AIC <sub>C</sub>          | R <sup>2</sup> | $\Delta$ AIC <sub>C</sub> |
|--|----------------|---------------------------|
| $EGG_{EXTENT} = -2.27 + 0.14 \pm 0.053 SSB + 0.11 \pm 0.036 COND + 0.070 \pm 0.020 MW$ | 0.57           | 0                         |
| $EGG_{EXTENT} = -2.79 + 0.15 \pm 0.054 SSB + 0.11 \pm 0.037 COND + 0.095 \pm 0.029 MA$ | 0.56           | 0.8                       |

$\Delta$ AIC<sub>C</sub> difference in AIC<sub>C</sub> compared with the best model.

**Table S3. Distributional extent regression results correcting for effect of total egg abundance**

| Model coefficients $\pm$ SEs for the models providing lowest AIC <sub>C</sub> | R <sup>2</sup> | $\Delta$ AIC <sub>C</sub> |
|---|----------------|---------------------------|
| $EGG_{EXTENT} = -0.15 + 0.12 \pm 0.010 EGG_{TOTAL} + 0.041 \pm 0.017 MA$      | 0.85           | 0                         |
| $EGG_{EXTENT} = 0.04 + 0.12 \pm 0.010 EGG_{TOTAL} + 0.029 \pm 0.012 MW$       | 0.85           | 0.3                       |

$\Delta$ AIC<sub>C</sub> difference in AIC<sub>C</sub> compared with the best model.

**Table S4. Pearson's product-moment correlation (r) among variables**

| Variable              | NAO <sub>SPR</sub> | NAO <sub>WIN</sub> | TEMP <sub>ANN</sub> | TEMP <sub>SUM</sub> | TEMP <sub>SPR</sub> | TEMP <sub>WIN</sub> | COND        | REPEAT | ADIV        | AWIDTH | MW          | MA    | SSB         | EGG <sub>EXTENT</sub> |
|-----------------------|--------------------|--------------------|---------------------|---------------------|---------------------|---------------------|-------------|--------|-------------|--------|-------------|-------|-------------|-----------------------|
| EGG <sub>TOT</sub>    | 0.18               | 0.34               | 0.44                | 0.41                | 0.28                | 0.27                | <b>0.54</b> | 0.07   | -0.19       | -0.16  | 0.29        | 0.24  | <b>0.64</b> | <b>0.91</b>           |
| EGG <sub>EXTENT</sub> | 0.08               | 0.28               | 0.31                | 0.29                | 0.16                | 0.17                | <b>0.56</b> | 0.00   | -0.20       | -0.20  | 0.42        | 0.38  | <b>0.51</b> |                       |
| SSB                   | 0.24               | 0.42               | <b>0.53</b>         | <b>0.53</b>         | 0.44                | <b>0.46</b>         | 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   | <b>0.92</b> |       |             |                       |
| 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   | <b>0.88</b> |        |             |       |             |                       |
| 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 <sub>WIN</sub>   | 0.01               | 0.41               | <b>0.74</b>         | <b>0.70</b>         | <b>0.65</b>         |                     |             |        |             |        |             |       |             |                       |
| TEMP <sub>SPR</sub>   | 0.26               | <b>0.47</b>        | <b>0.85</b>         | <b>0.84</b>         |                     |                     |             |        |             |        |             |       |             |                       |
| TEMP <sub>SUM</sub>   | 0.28               | <b>0.67</b>        | <b>0.98</b>         |                     |                     |                     |             |        |             |        |             |       |             |                       |
| TEMP <sub>ANN</sub>   | 0.24               | <b>0.61</b>        |                     |                     |                     |                     |             |        |             |        |             |       |             |                       |
| NAO <sub>WIN</sub>    | <b>0.51</b>        |                    |                     |                     |                     |                     |             |        |             |        |             |       |             |                       |

|r| > 0.45 are shown in bold. |r| > 0.35 and 0.45, respectively, are statistically significant at the 5% and 1% level. n = 33 y.