Original Article

Egg mortality of northeast Arctic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*)[†]

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High and variable mortality during the egg and larval stages is thought to be an important source of interannual variability in stock size in many marine fish. However, quantitative information about the mortality during these life stages, especially interannual variability, is sparse. Here, we used a time-series covering 35 years (1959–1993) of survey data to estimate mortality during the egg stages of northeast Arctic cod (*Gadus morhua*) and Northeast Arctic haddock (*Melanogrammus aeglefinus*). Using a regression approach based on the numbers of eggs in different developmental stages, we calculated the mean instantaneous mortality rate of cod eggs to be 0.17 d^{-1} (95% CI: 0.15–0.19), which is significantly higher than that for haddock, 0.09 d^{-1} (95% CI: 0.07–0.12). Interannual variability in egg mortality ranges from ∼0.12 to ∼0.22 d^{-1} for cod and from ∼0.04 to ∼0.12 d^{-1} for haddock. The accuracy of these estimates was evaluated by the analysis of synthetic data constructed from a coupled physical–biological model, suggesting that mean mortality and the magnitude of interannual variability were estimated reliably, but not mortality for any given year.

Keywords: cod, egg mortality, generalized additive mixed models, haddock, physical–biological modelling.

Introduction

Marine organisms often show large fluctuations in productivity caused by interannual variations in recruitment, i.e. in the year-class strength as the cohort enters the fishery (e.g. Hjort, 1914). The amount of successfully spawned eggs and the cumulative result of mortalities experienced by all life stages preceding recruitment determine the year-class strength at recruitment age (e.g. Houde, 2008; Lough and O'Brien, 2012). Survival during early life stages, such as during the egg and larval stages, may have a large influence on recruitment (Myers and Cadigan, 1993), although no single life stage can, in general, be considered as the primary source of variability in recruitment (Houde, 2008).

To understand and model the processes that link variations in recruitment to variations in biomass or abundance of spawners (Miller, 2007), it is important to have good mortality estimates of all life stages preceding recruitment. Stage-specific mortalities are regularly used as input parameters in a variety of individual-based models (e.g. Heath and Gallego, 1998; Andrews et al., 2006; Opdal et al., 2011) used both to improve the understanding of ecological processes (Grimm, 1999) and for management purposes (Hinrichsen et al., 2011).

Here, we use a time-series of survey data spanning 35 years (1959–1993) to estimate mortality during the egg stages of northeast Arctic cod (*Gadus morhua*, hereafter cod) and Northeast

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Arctic haddock (*Melanogrammus aeglefinus*, hereafter haddock) as well as interannual variability in mortality. Furthermore, we construct several time-series of synthetic survey data based on a coupled physical–biological model covering 15 years (1978–1992) to assess and optimize the estimation method.

Material and methods
Data
The Russian ichthyoplankton surveys were conducted twice a year in spring (April–May) and summer (June–July) from 1959 to 1993. The 1967 spring survey was not conducted due to technical reasons; hence, the time-series for spring, the portion of the data analysed in this paper, contains 34 years of data. The surveys were conducted at different stations mainly covering an offshore region from outside the Lofoten Islands in the south to Bear Island in the north and to the western parts of the Kola Peninsula in the east (Figure 1). The survey did not cover the inner parts of the Lofoten area. The starting time of the surveys varied between 30 March and 4 May, although there was no long-term trend in the starting dates (Mukhina et al., 2003). Duration (24–58 d for the spring survey), spatial coverage, and total number of stations (100–358 for the spring survey) varied considerably between years.

At each survey station, eggs were sampled with an egg net (IKS-80) unaltered throughout the time-series. A vertical haul (from bottom or maximum depth of 500 m) and two horizontal tows at 0- and 25-m depth, each with 10-min duration, were made at each station.

The collected eggs were identified and counted. Furthermore, the cod eggs were classified into four different developmental
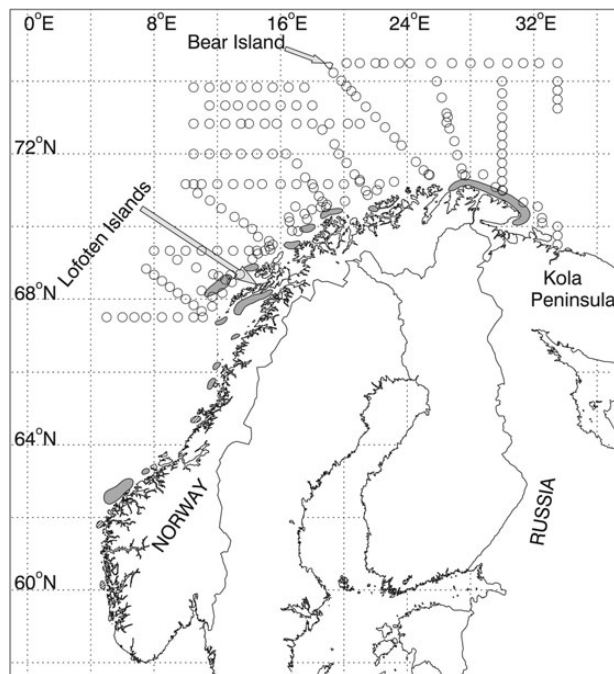

Figure 1. Coverage of survey stations for 1984 (open circles). The grey shaded polygons show the spawning grounds used in the synthetic data. The line-filled polygons show the spawning grounds with zero weight, which were not used in construction of the synthetic data.

stages [I–IV (Rass, 1946) corresponding to stages 1–10, 11–20, 21–25, and 26–30, respectively, of Russell (1976)]. The vital resident time within each stage was assumed approximately equal (5 d, of a total temperature-dependent development time of ~20 d; Ellertsen et al., 1987). Due to lack of sampling in the inner parts of the Lofoten area (leading to bias towards older eggs) and due to difficulties in distinguishing cod and haddock eggs in the first development stage, the first stage was not included in this analysis. In summary, the data contain spatio-temporal catch abundance estimates for four developmental stages (three used in the present analysis) of cod and haddock eggs. Further details about the Russian ichthyoplankton surveys are reported by Mukhina et al. (2003).

Furthermore, we analysed the time-series of cod spawning–stock biomass and the number of recruits at age 3 from virtual population analysis (1959–1990; ICES, 2012). In addition, we used annual abundance indices for eggs and larvae (1959–1990; Mukhina et al., 2003) and 5-month-old cod [1980–2008; Table 1.2 in ICES (2012)] based on pelagic trawls and indices for 10-, 22-, and 34-month-old cod (the latter representing recruitment age) from bottom-trawl surveys (1980–2008; ICES, 2012).

Methods
To estimate the overall mean and interannual variability in mortality for each species, we used a statistical regression model approach. This method exploits differences in egg density among stages, assuming 5 d between each egg stage and a total development time of 20 d, while taking into account other factors affecting density. The log-transformed stage-specific egg numbers were modelled with a generalized additive mixed model using the gam function in the mgcv library in R and treating the random effects as smooths (specified by bs = re) (Wood, 2006a, b). As covariates, we used the day of spawning (*spd*, calculated from sampling day minus egg age at the middle of the stage), sampling location (*lon*, longitude, and *lat*, latitude), and approximate egg age (*Age*, coded as −5, 0, and 5 d for egg stages II, III, and IV, respectively, to centre the model around 0). The covariates were included to account for, respectively, seasonal variation in spawning time, horizontal transport from spawning locations, and, most importantly, mortality. Specifically, the coefficient for the *Age* effect estimates −*M*, where *M* is the daily instantaneous mortality rate. Two random-effect terms were included: a random year effect and a random year by egg age effect. These random effects account for interannual variations in total egg numbers and interannual variations in mortality. We considered that several processes might account for the zeros in our data. For this reason, we removed all zeros from the data and modelled the observed numbers with a lognormal model. The model for the log-transformed stage-specific egg numbers [ln(*En*)] can be summarized as:

$$\ln(En)_{ij} = \beta_0 + f_1(spd_i) + f_2(lon_i, \, lat_i) + b_{0j} + (\beta_1 + b_{1j})\, Age_i + \varepsilon_{ij}, \tag{1}$$

where the subscripts *i* and *j* represent the station and year, respectively, β_0 and β_1 the model coefficients for fixed effects, f_1 a smoothing spline, f_2 a tensor product smooth, b_{0j} and b_{1j} the random year effects, and ε_{ij} a normally distributed error term. Cod and haddock egg numbers were modelled using the same

structure in the statistical model. To estimate confidence intervals around the point estimates, we used a bootstrapping procedure (Efron and Tibshirani, 1993) where we resampled the stations within years and re-estimated the parameters 1000 times.

To assess and optimize the mortality estimation procedure, we constructed several synthetic datasets (Aksnes and Ohman, 1996). A detailed description of the construction of synthetic data can be found in the Appendix. In short, the synthetic data were constructed to resemble the cod egg data by "sampling" particles (representing eggs) in the output of a coupled physical–biological model for the early life stages of cod at the same spatio-temporal coordinates as in the survey. Following egg release (Figure 1), the advection of eggs was calculated (Ådlandsvik and Sundby, 1994) based on 15 years (1978–1992) of simulated flowfields (Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008). We used a super-individual perspective (Scheffer et al., 1995), where each particle represented a large number of eggs that were scaled to match the sampled egg density and the reported spatial (Sundby and Nakken, 2008; Vikebø et al., 2011) and temporal (Ellertsen et al., 1989) distribution of spawning (origin of particles). In addition, the particles were given a daily instantaneous mortality (M), linking the abundance at time $t(N_t)$ to the abundance at time zero (N_0) according to:

$$N_t = N_0 e^{-Mt}. \tag{2}$$

We considered two different sets of scenarios when constructing the synthetic data. In the first set of scenarios, we constructed an array of nine different datasets with low, medium, and high mortality levels and early, medium, and late mean spawning (under the assumption of no interannual variation in the mortality rate and dates of spawning; see Table 1 for details). The influence of spawning day was explored to assess if erroneous assumptions about spawning time might influence the mortality estimates.

The second set of scenarios was constructed to explore the accuracy of the estimation method and to reveal possible biases in the estimated mortality due to interannual variability in mortality and spawning. We constructed a series of seven different datasets with different magnitudes of interannual variability in mortality. The mortality time-series were randomly generated from normal distributions with mean of 0.15 d^{-1} and with scenario-dependent standard deviation for interannual variability varying between 0 and 0.075 d^{-1}. Mean spawning day was simulated to vary randomly among years, centred at 30 March with a

standard deviation for interannual variability of 3 d (similar to observations for 1976–1986; Ellertsen et al., 1989). This time-series was kept fixed in all scenarios. The statistical model [Equation (1)] was applied to the synthetic data to test if the estimated mortality was similar to the simulated ("true") input mortality.

To explore some of the implications of our findings, we correlated the annual mortality estimates [b_{1j}, Equation (1)] for cod with indices of cohort abundance at earlier and later life stages (given at least 15 years of overlap with the mortality estimates). We also calculated the interannual variance in log-transformed cohort size at different life stages of cod (spawning–stock biomass, eggs, larvae, 5-month olds, 10-month olds, 22-month olds, 34-month olds, and recruits) for the 1959–1990 and 1980–2008 periods (depending on data availability). Because of a change in bottom-trawl gear in 1994, all variances for 1980–2008 were weighted means of variances calculated before and after this shift.

Results

We estimated an average mortality of 0.169 d^{-1} (with 95% confidence limits of 0.159–0.181) for cod eggs and 0.094 d^{-1} (with 95% confidence limits of 0.082–0.109) for haddock eggs. The annual estimates of the mortalities, with 95% confidence limits derived from the bootstrap, for the two species are shown in Figure 2. Furthermore, we estimated interannual
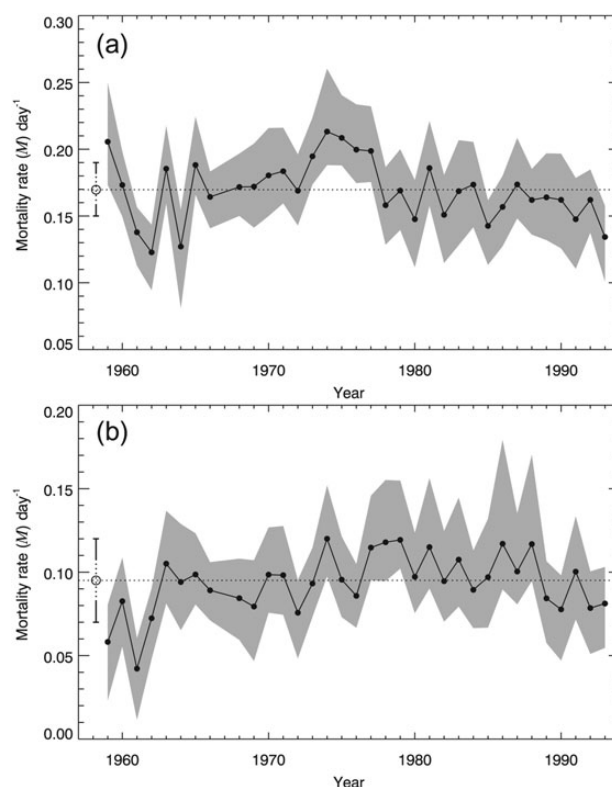

Figure 2. Instantaneous mortality rates estimated based on the relative number of eggs in different developmental stages for cod (a) and haddock (b). Filled points and grey polygon are annual estimates and 95% bootstrap CI. The open circle and the dotted vertical line are overall estimate and 95% bootstrap CI. According to the analysis of simulated data, true standard errors of the estimates may be about twice as large as the bootstrap standard errors. The solid vertical bar indicates the corrected CI for the overall mean.

Table 1. The different values of mortality and spawning times used in the nine different scenarios with constant mortality used to construct synthetic data and the resulting estimated mortalities and confidence intervals.

Spawning time	Input mortality (d^{-1})	Estimated mortality (CI) (d^{-1})
Early spawning, centred at 23 March	0.05	0.07 (0.044, 0.096)
	0.15	0.16 (0.134, 0.186)
	0.25	0.26 (0.227, 0.283)
Medium spawning centred at 30 March	0.05	0.06 (0.034, 0.078)
	0.15	0.15 (0.126, 0.174)
	0.25	0.24 (0.219, 0.271)
Late spawning, centred at 6 April	0.05	0.06 (0.034, 0.082)
	0.15	0.15 (0.126, 0.178)
	0.25	0.25 (0.218, 0.274)

standard deviation in mortality of 0.031 d^{-1} (with 95% confidence limits of 0.020–0.046) for cod and 0.025 d^{-1} (with 95% confidence limits of 0.016–0.040) for haddock. The annual egg mortality estimates for cod were not significantly correlated with indices of larval abundance ($r = -0.18$, $p > 0.1$), recruitment at age 3 ($r = -0.05$, $p > 0.1$), or indicators of initial egg abundance [spawning–stock biomass, or, alternatively, the random intercept, b_{0j}, Equation (1)] (both $r = -0.25$, $p > 0.1$).

Testing the statistical model by the analysis of synthetic data simulated under different assumptions about the mortality level and timing of spawning resulted in the estimation of mortalities usually very close to the input mortalities and always within the 95% confidence limits (see Table 1 for details). In addition, the analysis of synthetic data simulated under different assumptions about the magnitude of interannual variability in mortality resulted in the estimation of interannual standard deviations in mortality mostly within confidence limits for true input standard deviations (Figure 3). However, these tests revealed an overestimation of interannual variability when the true standard deviation was lower than ∼0.03 d^{-1}. This bias is most likely due to the low contrast in mortality compared with other factors, such as interannual variability in drift pattern, sampling, and temperature-dependent development rate. For example, according to the hydrodynamic modelling results for 1978–1992, the average stage duration may vary between warm and cold years from 4.5 to 5.9 d, which may lead to 10–15% error in the mortality estimates. Due to this bias in the estimation at low variability, we cannot set a lower limit on the estimated variability. Furthermore, correlations between simulated and estimated mortalities were fairly low. For the most realistic scenario, simulating an interannual standard deviation of 0.03 d^{-1}, this correlation was 0.22, suggesting that the statistical model could only explain ∼5% of the interannual variability in mortality. The root-mean-square prediction error of annual mortality ranged from 0.023 to 0.038 d^{-1} among the different scenarios and was higher for scenarios that simulated high interannual variability
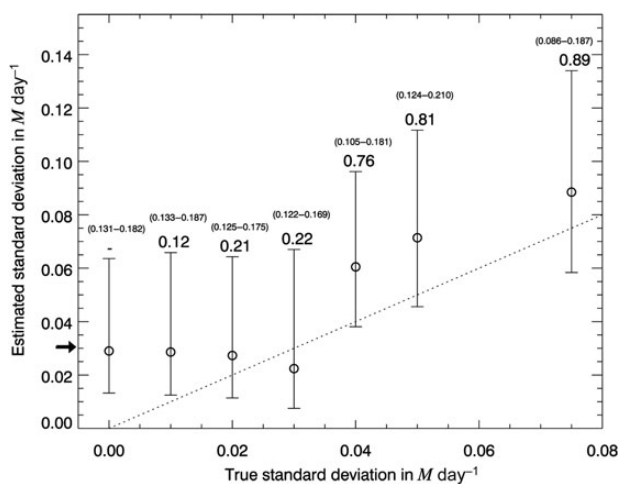
in mortality. The root-mean-square prediction error for the most realistic scenario was 0.031, which is about twice as large as the bootstrap estimate of the standard error for annual mortality (=0.015). If we apply a factor of 2 to the bootstrap standard errors, we obtain more conservative 95% confidence limits for the mean mortality for cod of 0.15–0.19 and for haddock of 0.07–0.12 that might better capture the various sources of uncertainty. Plots of the residuals (not shown) indicate that our log-normal model performed satisfactorily. Furthermore, tests with a negative binomial model to the complete dataset (including zeros) showed unsatisfactory quantile plots for large observations, and this model did not perform satisfactorily on the synthetic data (bias in average estimated mortality).

The log-transformed stage-specific interannual variances for cod show an increasing trend from early stages until 5–10-month olds. For older stages, the interannual variance decreases with age (Figure 4).

Discussion

The instantaneous mortality rate for cod eggs estimated herein (0.17 d^{-1}) is significantly higher than the previously reported 0.10 d^{-1} for the northeast Arctic cod stock (Fossum, 1988). Using the instantaneous mortality rate from Fossum (1988) for egg development time of 20 d gives a total cod egg stage survival of 11–17% (Table 2), whereas we report an average annual survival of ∼3% (95% corrected bootstrap CI: 2–5%). The present estimates were based on a long time-series and a carefully assessed method, hence making the mean mortality estimates reliable. For cod eggs, yearly cumulative egg stage survival varied between ∼1 and ∼10% over the time-series, while for haddock, the same numbers were higher and around 10 and 40%. Note, however, that testing with the synthetic data revealed that the estimates for any given year are uncertain. The lack of significant relationships between egg mortality and earlier or later cohort size might, therefore, simply be due to low statistical power. Nevertheless, we have reliably estimated an interannual standard deviation for the daily mortality rate of ∼0.03 d^{-1} (or lower) for both cod and haddock.

Figure 3. The "true" (simulated) and estimated interannual standard deviations in mortality (open circles) with 95% confidence bands (vertical bars). Numbers above bars are correlation coefficients between true and estimated annual mortalities, and numbers in brackets are confidence intervals for the estimated average mortality. The average "true" mortality was 0.15 d^{-1} for all datasets. Arrow shows the standard deviation estimated from the real data for cod.
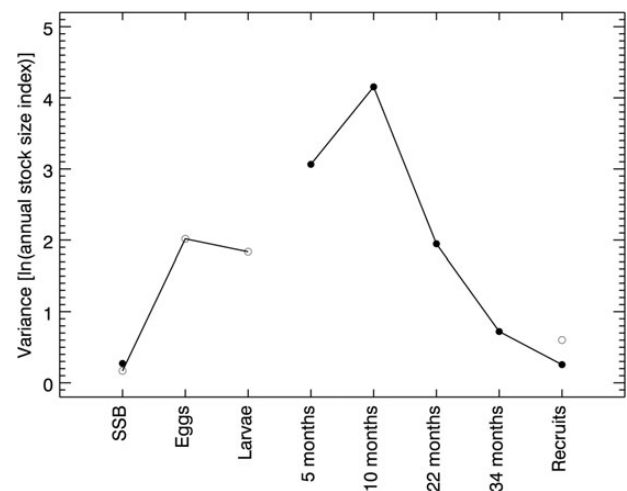

Figure 4. Interannual variance in the stock size index (ln scale) for different life stages of cod. Open circles, 1959–1990; filled circles, 1980–2008 cohorts; SSB, spawning–stock biomass (indicator of potential egg production); recruits, number of 3-year olds.

Table 2. Egg mortality rates of cod and haddock reported in this and other studies[a].

Stock	Years	Egg mortality (d^{-1}): interannual mean and range	Approximate egg stage duration (d)	Cumulative egg stage survival (%): interannual mean and range	Reference
Northeast Arctic cod	1959–1993	0.17 (0.12–0.22)	20	3.3 (1.2–9.0)	This study
Northeast Arctic cod	1983, 1984	0.10 (0.09–0.11)	20	14 (11–17)	Fossum (1988)
North Sea cod	1971, 1976, 1987, 1988	0.25 (0.14–0.41)	21	0.5 (0.02–5.3)	Rijnsdorp and Jaworski (1990) and references therein
Baltic Sea cod	1996, 2002, 2003	0.32 (0.26–0.38)	14	1.1 (0.5–2.7)	Wieland et al. (2000) and Voss et al. (2011)[b]
Irish Sea cod	1995	0.25	14	3.0	Armstrong et al. (2001)
Georges Bank cod	1979–1987, 1995–1999	0.12 (0.023–0.20)	14	19 (6.0–72)	Lough et al. (2006) and Mountain et al. (2008)
Western Scotian Shelf cod	1983–1985	0.19 (0.14–0.26)	16	4.8 (1.6–11)	Campana et al. (1989)
Northeast Arctic haddock	1959–1993	0.09 (0.04–0.12)	20	17 (9.1–45)	This study
Georges Bank haddock	1979–1987, 1995–1999	0.09 (0–0.17)	14	28 (9.3–100)	Lough et al. (2006) and Mountain et al. (2008)
Western Scotian Shelf haddock	1983–1985	0.19 (0.14–0.29)	16	4.8 (1.0–11)	Campana et al. (1989)

[a]When mortality rates for different egg stages/months were given, they were averaged for each year.
[b]Averaged for months of peak spawning, i.e. June–September 2002 and August–October 2003.

Comparing these results with those reported for other cod and haddock stocks in the North Atlantic (Table 2), we see that our estimates are comparable with previous results. Egg mortality of northeast Arctic cod appears to be similar to that of the western Scotian Shelf cod, in the upper range of that reported for the well-studied Georges Bank cod, but lower than that reported from the North Sea, the Baltic Sea, and the Irish Sea. For haddock eggs, our estimated mean mortality of 0.09 d^{-1} is similar to that reported for haddock from Georges Bank and lower than that reported from the western Scotian Shelf. The interannual range in egg mortality is difficult to compare across studies because of differences in length of the time-series and in estimation methods. For most stocks, daily mortality rates vary by a factor of ~2–3. Egg survival on Georges Bank is more variable for both cod and haddock, which may be linked to the special hydrographical conditions and resulting variable egg retention rates in this area (Lough et al., 2006).

Stage-dependent mortality has been reported in cod eggs (Campana et al., 1989). Here, we assumed equal mortality in the egg stages analysed. We tested this assumption by analysing each stage pair (stages II and III and stages III and IV) separately (results not shown). These tests did not show any significant difference from the full model; therefore, we conclude that this is a reasonable assumption.

Our results contribute to the improved modelling of the early life stages of cod and haddock. The results also provide indications of the potential importance of egg mortality to generate fluctuations in recruitment. By log-transforming and calculating the variance on both sides of Equation (2), it follows that the interannual variance in cohort size at a given age T (assumed constant) can be considered as a function of the variance in cohort size at an earlier age ($T_0 = 0$), variance in mortality, and covariance between cohort size and mortality (i.e. density-dependence):

$$\mathrm{Var}(\log N_T) = \mathrm{Var}(\log N_0) + T^2\mathrm{Var}(M)$$
$$- 2T\mathrm{Cov}(\log N_0, M). \quad (3)$$

For the sake of convenience, cohort size is here measured on a natural logarithmic scale. For northeast Arctic cod, the variance in cohort size increases up to an age of ~1 year, then decreases until the recruitment age of 3 years (Figure 4). Our interpretation of this figure is that during the first year of life, interannual variability in mortality tends to increase cohort fluctuations, while thereafter compensatory density-dependence tends to dampen cohort fluctuations, as seen in many marine species (e.g. Martino et al., 2012).

How much of this increase in cohort variability during the first year of life of cod can variable egg survival explain? With a standard deviation of the instantaneous egg mortality M of 0.03 d^{-1} and a egg stage duration T of 20 d, our results suggest that interannual fluctuations in the egg mortality rate increases cohort variance by $T^2\mathrm{Var}(M) = 0.36$. This estimate is consistent with an 11-fold difference in cumulative egg survival between years with abnormally low and high egg mortality (± 2 s.d. from the average). We can compare this estimate with the contribution from temperature-driven variability in egg-stage duration: at higher temperatures, egg-stage duration T_{egg} is shorter and cumulative survival higher (all else being equal). According to our hydrodynamic modelling results for 1978–1992 (and the most realistic egg-release scenario centred around 30 March), the interannual standard deviation in T_{egg} is 1.65 d. With a mean M of 0.17 d^{-1}, we find that temperature-driven variability in egg-stage duration increases cohort variance at the end of the egg stage by $M^2\mathrm{Var}(T_{egg}) = 0.07$. This estimate suggests a threefold difference in cumulative egg survival between years with abnormally high and low ambient temperatures (i.e. egg-stage duration ± 3.3 d or ambient temperature $\pm 1.1°$C). In comparison, instantaneous mortality during the larval stages of northeast Arctic cod has been reported to be lower, but similarly variable, as egg mortality, ranging from 0.08 to 0.15 d^{-1} in 8 years between 1979 and 1988 (Sundby et al., 1989). Because of the longer duration of the larval stages (2 months or more), cumulative survival is more variable, resulting in a 68-fold difference within the years studied (Sundby et al., 1989). Similar results, stressing the importance of

the longer duration of larval relative to egg stages, have been reported for other stocks (e.g. Sissenwine et al., 1984; Campana et al., 1989). It should be noted that larval mortality estimates by Sundby et al. (1989) were based on a 10% egg-stage survival (corresponding to an instantaneous mortality of $0.115 \, d^{-1}$). A simple calculation with the new egg mortality estimates (see Appendix) gives a larval instantaneous mortality of $0.075 \, d^{-1}$.

We conclude that interannual variability in the mortality rate or development time of cod eggs may lead to biologically significant differences in cohort survival between years, but that these effects may often be suppressed by considerable variability in survival during subsequent life stages.

Acknowledgements

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Appendix
Synthetic data

We used a coupled physical–biological model (Ådlandsvik and Sundby, 1994) to construct realistic synthetic data. As input to the model, we used the daily averaged flow, temperature, and salinity fields provided by the general circulation model, Regional Ocean Modelling System (ROMS, Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008), forced by the atmospheric and boundary conditions for 1978–1992. Furthermore, diffusivity coefficients due to salinity and temperature gradients were provided by ROMS. The circulation model covers the North Atlantic, including the North, Norwegian, Barents, and Kara seas and parts of the Arctic Ocean with a grid resolution of 4 × 4 km. Further details on the ocean circulation model setup are reported by Vikebø et al. (2010).

Each synthetic dataset was based on 15 years (1978–1992) of simulated flow fields. To construct the synthetic data, we took a super-individual perspective (Scheffer et al., 1995), where each simulated egg particle represents several thousand actual eggs. In each year, a total of 100 cod egg particles were released per spawning ground (see Figure 1) per day from the beginning of March through April. In total, more than 85 000 egg particles were released yearly. The following procedure was used to calculate realistic scaling factors to convert particle numbers to egg numbers, dependent on the release location and release time of the particles. The spatial position and extent of the spawning grounds were based on Sundby and Nakken (2008). Furthermore, the distribution of cod eggs among spawning grounds was scaled according to Table 1 in Vikebø et al. (2011). In the cases where Table 1 in Vikebø et al. (2011) did not include the same fine-scale resolution of the spawning grounds as presented by Sundby and Nakken (2008), we redistributed the weights among the subspawning grounds according to the surface area. Three spawning grounds were given zero weight and were not included in the construction of the synthetic data (see Figure 1). Interannual variation in total (simulated) egg numbers was scaled to be proportional to the spawning–stock biomass of cod (ICES, 2012). Seasonal variation in spawning was scaled using a Gaussian curve with mean depending on the scenario and a standard deviation of 8 d. Finally, total egg numbers over the simulated period (15 years) were scaled to make the synthetic data contain similar amounts of eggs as in the observed data.

Each egg particle was released at 10 m depth and was assigned a normal distributed random buoyancy, with mean of 31.25 psu (salinity at neutral buoyancy) and standard deviation of 0.69 (Sundby, 1991; Stenevik et al., 2008). The differences between egg density and ambient water density and Stokes law (for creep flow) were used to determine vertical movements according to Thygesen and Ådlandsvik (2007). Horizontal advection of particles uses a time-step of 1 h; interpolation from the daily averaged flow fields was achieved using a fourth-order Runge–Kutta method (Ramsden and Holloway, 1991). Egg particles were allowed to develop according to local ambient temperature along the particle track. We used the following relationship between ambient temperature (T_0 in Celsius) and total egg development time (D in days):

$$\ln D = 3.65 - 0.145T_0,$$

based on Ellertsen et al. (1988). The cumulative sum of the daily fraction of development determines the egg's total development. Egg particles were given a daily mortality (M) that links abundance at time t (N_t) to abundance at time zero (N_0), according to Equation (2). We considered two different sets of scenarios when constructing the synthetic data. These scenarios are described in detail in the Methods section. In short, we constructed one set of synthetic data with interannual constant mortality and spawning time, and one set where both mortality and spawning time varied interannually.

To finalize construction of the synthetic data, we used the spatio-temporal coordinates of the real survey to calculate a synthetic catch number for each of the four egg stages (0–25, 25–

50, 50–75, and 75–100% developed eggs) at each station. Since for more than 95% of the time the egg particles were horizontally advected <20 km d^{-1}, we used a circle with a radius of 20 km as the catch region surrounding each station, i.e. all egg particles within this radius during the day of the sampling were considered sampled, but not removed from the simulation. Hence, some egg particles were encountered multiple times.

Larval mortality

We calculated the instantaneous mortality in the larval stage by using the model:

$$N_{0\text{-group}} = N_{\text{egg}}e^{-(m_1 t_1 + m_2 t_2 + m_3 t_3)},$$

where $N_{0\text{-group}}$ is the number of 0-group individuals (juvenile fish 4 months after hatching), N_{egg} is the total egg production (TEP),

$t_i (i \in \{1, 2, 3\})$ is the stage duration, and m_i is the stage instantaneous mortality for the three stages (egg, larval, and early juvenile, respectively). TEP was taken from Marshall et al. (2006) and 0-group abundance was taken from ICES (2012). We used only the 14 overlapping years from 1980 to 1993 in this analysis. Stage duration was, for simplicity, assumed to be 20 d (t_1) for the egg stage and 60 d for the larval (t_2) and the early juvenile stage (t_3), in total 140 d from spawning to the 0-group stage. We used the average early juvenile mortality of $m_3 = 0.04$ d^{-1} reported by Sundby et al. (1989), since this estimate did not rely on egg mortality. Furthermore, we used the egg mortality estimated in the present paper ($m_1 = 0.17$ d^{-1}) to calculate the larval mortality (m_2). This gave an average mortality of 0.075 d^{-1} for the larval stage, with a range of 0.062–0.083 d^{-1} due to interannual variability in early juvenile mortality. Including other sources of variability would increase this range.

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