Egg mortality of Northeast Arctic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus)

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Abstract

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 fishes. However, quantitative information about the mortality during these life stages, especially the interannual variability, is sparse. Here, we used a time series covering 34 years (1959-1993) of survey data to estimate the mortality during the egg stages of Northeast Arctic cod and Northeast Arctic haddock. 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 day\(^{-1}\) (95% c.i. 0.15, 0.19), which is significantly higher than that for haddock, 0.09 day\(^{-1}\) (c.i. 0.07, 0.12). The interannual variability in egg mortality range from about 0.12 day\(^{-1}\) to 0.22 day\(^{-1}\) for cod and from about 0.04 day\(^{-1}\) to 0.12 day\(^{-1}\) for haddock. The accuracy of these estimates was evaluated by analysis of synthetic data constructed from a coupled physical-biological model, suggesting that the mean mortality and the magnitude of the interannual variability were estimated reliably, but not the 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, that is, in the year class strength as the cohort enters into the fisheries (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). The survival during the early life stages, such as during the egg and larval stages, may have large influence on recruitment (Myers and Cadigan 1993) even though no single life stage can in general be considered as the primary source for variability in recruitment (Houde 2008).

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

Here, we use a time series of survey data spanning 34 years (1959-1993) to estimate the mortality during the egg stages of Northeast Arctic cod (*Gadus morhua*, from now on cod) and Northeast Arctic haddock (*Melanogrammus aeglefinus*, from now on haddock) as well as the 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.
Data

The Russian ichthyoplankton surveys were conducted twice per year in spring (April-May) and summer (June-July) from 1959 to 1993. Note that the 1967 spring cruise was not conducted due to technical reasons, hence the time series for spring, the part of the data analysed in the present paper, contains 34 years of data. The surveys were conducted at different stations mainly covering an offshore region from outside of the Lofoten islands in the south to Bear Island in the north and to the western parts of the Kola Peninsula in the east (see Figure 1). Note that 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, while there was no long-term trend in the starting dates (Mukhina et al. 2003). The duration of the surveys (24-58 days for the spring survey), the spatial coverage and the total number of stations (100-358 for the spring survey) varied considerably between years.

At each survey station, eggs were collected by the use of an egg net (IKS-80) unaltered throughout the time series. The eggs were collected in a vertical haul (from the bottom or from maximum depth of 500 m) and two horizontal tows at 0 and 25 meters depth each with duration of ten minutes at each survey station.

The collected eggs were identified and counted. Furthermore, the cod eggs were classified in four different developmental 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 roughly equal (5 days, of a total temperature-dependent development time of approximately 20 days, Ellertsen et al. 1988). Due to lack of sampling in the inner parts of the Lofoten area (leading to bias towards older
eggs) and due to difficulties in separation between cod and haddock eggs in the first development stage of these eggs, the first stage was not included in this analysis. In summary the data contain spatiotemporal catch abundances for four developmental stages (three used in the present analysis) of cod and haddock eggs. For further details about the Russian ichthyoplankton surveys the reader is referred to Mukhina et al. (2003).

Furthermore, we analysed time-series of cod spawning stock biomass and number of recruits at age three 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-month-olds, 22-month-olds and 34-month-olds (the latter representing recruitment age) from bottom trawl surveys (1980-2008, ICES 2012).

Methods

To estimate the overall mean and the interannual variability in mortality for each species we used a statistical regression model approach. This method exploits the differences in egg density among stages, assuming 5 days between each egg stage and a total development time of 20 days, while taking other factors affecting density into account. The log transformed stage specific egg numbers were modelled with a generalized additive mixed model (GAMM) 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 days for egg stage 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 out 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 in the data and modeled the observed numbers with a lognormal model. The model for the log transformed stage specific egg numbers ($\ln(En)$) can be summarized as

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

Equation 1

where the subscripts $i$ and $j$ represent station and year, respectively, $\beta_0$ and $\beta_1$ are model coefficients for fixed effects, $f_1$ is a smoothing spline, $f_2$ is a tensor product smooth, $b_{0j}$ and $b_{1j}$ are random year effects and $\epsilon_{ij}$ is 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 data sets (Aksnes and Ohman 1996). A detailed description of the construction of synthetic data can be found in Appendix A. 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 spatiotemporal coordinates as in the survey. Following egg release, the advection of eggs was calculated (Ådlandsvik and Sundby 1994) based on fifteen years (1978-1992) of simulated flow fields (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, 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

$$N_t = N_0 e^{-Mt}.$$  

Equation 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 data sets with low, medium and high mortality levels and early, medium and late mean spawning (under the assumption of no interannual variation in mortality rate and dates of spawning, see Table 1 for details).** The influence of spawning day was explored to assess if erroneous assumptions about the 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 data sets with different magnitude of the interannual variability in mortality.** The mortality time series were randomly generated from normal distributions
with mean of 0.15 day\(^{-1}\) and with scenario-dependent standard deviation for the interannual variability varying between 0 and 0.075 day\(^{-1}\). The mean spawning day was simulated to vary randomly among years, centred at 30th of March with a standard deviation for the interannual variability of 3 days (similar to observations for 1976-1986 (Ellertsen et al. 1989)). This time series was kept fixed in all scenarios. The statistical model (Eq.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 \((b_{ij}, \text{Eq. 1})\) 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 the 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 day\(^{-1}\) (with 95% confidence limits of [0.159, 0.181]) for cod eggs and 0.094 day\(^{-1}\) (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 an interannual standard deviation in mortality of 0.031 day\(^{-1}\) (with 95%
confidence limits of $[0.020, 0.046]$) for cod and 0.025 day$^{-1}$ (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, $b_0j$, Eq. 1) (both $r = -0.25, P>0.1$).

Testing the statistical model by analysis of synthetic data simulated under different assumptions about the mortality level and timing of the spawning resulted in 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 the interannual variability in mortality resulted in estimation of the interannual standard deviations in mortality mostly within the confidence limits for true input standard deviations (Figure 3).

However, these tests revealed an overestimation of the interannual variability when the true standard deviation was lower than about 0.03 day$^{-1}$. This bias is most likely due to the low contrast in the mortality compared to other factors, such as interannual variability in drift pattern, sampling and temperature-dependent development rate. For example, according to the hydrodynamic modelling results for 1978-1990, the average stage duration may vary between warm and cold years from 4.5 to 5.9 days, 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, the correlations between the simulated mortalities and the estimated mortalities were fairly low: For the most realistic scenario, simulating
an interannual standard deviation of 0.03 day$^{-1}$, this correlation was 0.22, suggesting that
the statistical model could only explain about 5% of the interannual variability in
mortality. The root-mean-square prediction error of the annual mortality ranged from
0.023 to 0.038 day$^{-1}$ 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 the annual mortality (= 0.015). If we apply a factor of
two to the bootstrap standard errors, we obtain more conservative 95% confidence limits
for the mean mortality of cod [0.15, 0.19] and haddock [0.07, 0.12] that might better
capture the various sources of uncertainty. Plots of the residuals (not shown) indicate
that our lognormal model performed satisfactorily. Furthermore, tests with a
negative binomial model to the complete dataset (including the 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 the cod show an
increasing trend from early stages up until 5- to 10-month-olds. For older stages the
interannual variance is decreasing with age (Figure 4).

Discussion

The instantaneous mortality rate for cod eggs estimated herein (0.17 day$^{-1}$) is
significantly higher than the previously reported 0.10 day$^{-1}$ for the Northeast Arctic cod
stock (Fossum 1988). Using the instantaneous mortality rate from Fossum (1988) for a
egg development time of 20 days gives a total cod egg stage survival of 11-17 % (Table
2) while we report an average annual survival of about 3% (95% corrected bootstrap c.i.
The present estimates were based on a long time series and a thoroughly assessed method, hence making the mean mortality estimates reliable. For cod eggs, the yearly cumulative egg stage survival varied between about 1% and 10% over the time series, while for haddock the same numbers were higher and around 10% and 40%. Note, however, that the 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 thus simply be due to low statistical power.

Nevertheless, we have reliably estimated an interannual standard deviation for the daily mortality rate of about 0.03 day\(^{-1}\) (or lower) for both cod and haddock.

Comparing these results with results reported for other stocks of cod and haddock 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 day\(^{-1}\) is similar to that reported for haddock from the 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 the length of the time series and in estimation methods. For most stocks, the daily mortality rates vary by a factor of about two to three. Egg survival on the 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 analyzed. We tested this assumption by analysing each stage pair (stage II and III, and stage III and IV) separately (results not shown). These tests did not show any significant difference from the full model, and hence we conclude that this is a reasonable assumption.

Our results contribute to 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 Eq. 2, it follows that the interannual variance in cohort size at a given age $T$ (assumed constant) can be considered 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):

$$Var \log N_T = Var \log N_0 + T^2 Var(M) - 2TCov(\log N_0, M), \quad \text{Equation 3}$$

Note that 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 about one year, and 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 (see, e.g., Martino et al. 2012).

How much of this increase in cohort variability during the first year of the cod’s life can variable egg survival explain? With a standard deviation of the instantaneous egg mortality, $M$, of 0.03 day$^{-1}$ and a egg stage duration, $T$, of 20 days, our results suggest that
interannual fluctuations in egg mortality rate increases cohort variance by $T^2Var(M) = 0.36$. This estimate is consistent with a 11-fold difference in cumulative egg survival between years with abnormally low and high egg mortality (± two standard deviations from the average). We can compare this estimate with the contribution from temperature-driven variability in egg stage duration: At higher temperatures, the egg stage duration, $T_{EGG}$, is shorter and the 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\textsuperscript{th} of March), the interannual standard deviation in $T_{EGG}$ is 1.65 days. With a mean $M$ of $0.17\text{ day}^{-1}$, we find that temperature-driven variability in egg stage duration increases cohort variance at the end of the egg stage by $M^2Var(T_{EGG}) = 0.07$. This estimate suggests a three-fold difference in cumulative egg survival between years with abnormally high and low ambient temperatures (i.e., egg stage duration ±3.3 days, or ambient temperature ±1.1 °C). In comparison, the instantaneous mortality during the larval stages of Northeast Arctic cod has been reported to be lower but similarly variable as the egg mortality, ranging from 0.08 to 0.15 day$^{-1}$ in eight years between 1979 and 1988 (Sundby et al. 1989). Because of the longer duration of the larval stages (2 months or more), the 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 the larval compared to the egg stages, have been reported for other stocks (e.g. Sissenwine et al. 1984, Campana et al. 1989).

Note, that the larval mortality estimates by Sundby et al. (1989) were based on a 10% egg stage survival (corresponding to a instantaneous mortality of $0.115 \text{ day}^{-1}$). A simple
calculation with the new egg mortality estimates (see Appendix B) gives a larval
instantaneous mortality of 0.075 day\(^{-1}\).

We conclude that interannual variability in 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 swamped up by the considerable variability in
survival during the subsequent life stages.

Appendix A - 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.
For further details on the ocean circulation model setup the reader is referred to Vikebø et
al. (2010).

Each synthetic data set was based on fifteen 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 throughout April. In total more than 85000 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 -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 sub-spawning grounds according to the surface area. Note that three spawning grounds were given zero weight, hence not included in the construction of the synthetic data (see Figure 1). The interannual variation in total (simulated) egg numbers was scaled to be proportional to the spawning stock biomass of cod (ICES 2012). The seasonal variation in spawning was scaled using a Gaussian curve with mean depending on the scenario and a standard deviation of 8 days. Finally, the 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 meters depth and was assigned a normal distributed random buoyancy with a mean of 31.25 psu (salinity at neutral buoyancy) with a standard deviation of 0.69 (Sundby 1991, Stenevik et al. 2008). The difference between the egg density and the ambient water density and Stokes law (for creep flow) were used to determine vertical movements according to Thygesen and Ådlandsvik (2007). The horizontal advection of particles uses a time step of one hour; interpolation from the daily averaged flow fields was achieved using a 4th order Runge-Kutta method (Ramsden and Holloway 1991). The egg particles were allowed to develop according to...
the local ambient temperature along the particle track. We used the following relation
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 eggs total development. The egg particles were given a daily mortality
($M$), that link the abundance at time $t$ ($N_t$) to the abundance at time zero ($N_0$) according to
Eq.2. We considered two different sets of scenarios when constructing the synthetic data.
These scenarios are described in detail in the main text (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 the construction of the synthetic data, we used the spatiotemporal
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 less than 20
km per day, we used a circle of radius 20 km as 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.

Appendix B - Larval mortality

We calculated the instantaneous mortality in the larval stage by using the model
\[ N_{0-group} = N_{egg} e^{- (t_1m_1 + t_2m_2 + t_3m_3)}, \]
where $N_{0-group}$ are the number of 0-group individuals (juvenile fish 4 month after
hatching), $N_{egg}$ are the total egg production (TEP), $t_i (i \in \{1,2,3\})$ are the stage duration
and $m_i$ are 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 1980-1993 in this analysis. Stage duration was for simplicity taken as 20 days ($t_1$) for the egg stage and 60 days for the larval ($t_2$) and the early juvenile stage ($t_3$), in total 140 days from spawning to the 0-group stage. We used the average early juvenile mortality of $m_3 = 0.04 \text{ day}^{-1}$ reported by Sundby et al. (1989), since this estimate did not rely on the egg mortality. Furthermore, we used the egg mortality estimated in the present paper ($m_1 = 0.17 \text{ day}^{-1}$) to calculate the larval mortality ($m_2$). This gave an average mortality of 0.075 day$^{-1}$ for the larval stage, with a range of [0.062-0.083] day$^{-1}$ due to interannual variability in early juvenile mortality. Including other sources of variability would increase this range.

Acknowledgements

We thank Dag Hjermann for valuable comments on the manuscript. Furthermore, we thank the Norwegian Research Council (NRC) for support through the SVIM project (project no. 196685). This work is a contribution to the NRC PETROMAKS program - SYMBIOSES (BIP project #ES468602). The SYMBIOSES project is a cooperation of 15 research partners, financed by the NRC, BP Exploration Operating Company Limited, ConocoPhillips Skandinavia, ExxonMobil Upstream Research Company, Eni Norway, Shell Technology Norway, Statoil Petroleum and Total E&P Norway. Computational resources for ocean circulation simulations were granted by the Norwegian Metacenter for Computational Science (NOTUR) under contract nn9146k.
Figure 1. The coverage of the survey stations for the year 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, and hence not used in construction of the synthetic data.

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

Figure 3. The “true” (simulated) and estimated interannual standard deviations in mortality (open circles) with 95% confidence bands (vertical bars). Numbers above bars: correlation coefficients between the true and estimated annual mortalities and (in brackets) confidence bands for the estimated average mortality. The average “true” mortality was 0.15 day$^{-1}$ for all data sets. Arrow: the standard deviation estimated from the real data for cod.
Figure 4. The interannual variance in cohort abundance (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 1. The different values of mortality and spawning times used in the 9 different scenarios with constant mortality used to construct synthetic data, and the resulting estimated mortalities and confidence intervals.

<table>
<thead>
<tr>
<th>Spawning Time</th>
<th>Input mortality</th>
<th>Estimated mortality</th>
<th>[Confidence intervals]</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Early spawning</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centred at 23. March</td>
<td>0.05</td>
<td>0.07</td>
<td>[0.044, 0.096]</td>
</tr>
<tr>
<td></td>
<td>0.15</td>
<td>0.16</td>
<td>[0.134, 0.186]</td>
</tr>
<tr>
<td></td>
<td>0.25</td>
<td>0.26</td>
<td>[0.227, 0.283]</td>
</tr>
<tr>
<td><strong>Medium spawning</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centred at 30. March</td>
<td>0.05</td>
<td>0.06</td>
<td>[0.034, 0.078]</td>
</tr>
<tr>
<td></td>
<td>0.15</td>
<td>0.15</td>
<td>[0.126, 0.174]</td>
</tr>
<tr>
<td></td>
<td>0.25</td>
<td>0.24</td>
<td>[0.219, 0.271]</td>
</tr>
<tr>
<td><strong>Late spawning</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centred at 6. April</td>
<td>0.05</td>
<td>0.06</td>
<td>[0.034, 0.082]</td>
</tr>
<tr>
<td></td>
<td>0.15</td>
<td>0.15</td>
<td>[0.126, 0.178]</td>
</tr>
<tr>
<td></td>
<td>0.25</td>
<td>0.25</td>
<td>[0.218, 0.274]</td>
</tr>
</tbody>
</table>
Table 2. Egg mortality rates of cod and haddock reported in this and other studies\(^1\).

<table>
<thead>
<tr>
<th>Stock</th>
<th>Years</th>
<th>Egg mortality (day(^{-1})): Interannual mean and range</th>
<th>Approx. egg stage duration (days)</th>
<th>Cumulative egg stage survival (%): Interannual mean and range</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northeast Arctic cod</td>
<td>1959-1993</td>
<td>0.17 [0.12 – 0.22]</td>
<td>20</td>
<td>3.3 [1.2 – 9.0]</td>
<td>This study</td>
</tr>
<tr>
<td>North Sea cod</td>
<td>1971, 1976, 1987, 1988</td>
<td>0.25 [0.14 – 0.41]</td>
<td>21</td>
<td>0.5 [0.02 – 5.3]</td>
<td>Rijnsdorp &amp; Jaworski (1990) and ref. therein</td>
</tr>
<tr>
<td>Baltic Sea cod</td>
<td>1996, 2002, 2003</td>
<td>0.32 [0.26 – 0.38]</td>
<td>14</td>
<td>1.1 [0.5 – 2.7]</td>
<td>Wieland et al. (2000), Voss et al. (2011)(^2)</td>
</tr>
<tr>
<td>Irish Sea cod</td>
<td>1995</td>
<td>0.25</td>
<td>14</td>
<td>3.0</td>
<td>Armstrong et al. (2001)</td>
</tr>
<tr>
<td>Western Scotian Shelf cod</td>
<td>1983-1985</td>
<td>0.19 [0.14 – 0.26]</td>
<td>16</td>
<td>4.8 [1.6 – 11]</td>
<td>Campana et al. (1989)</td>
</tr>
<tr>
<td>Northeast Arctic haddock</td>
<td>1959-1993</td>
<td>0.09 [0.04 – 0.12]</td>
<td>20</td>
<td>17 [9.1 – 45]</td>
<td>This study</td>
</tr>
<tr>
<td>Western Scotian Shelf haddock</td>
<td>1983-1985</td>
<td>0.19 [0.14 – 0.29]</td>
<td>16</td>
<td>4.8 [1.0 – 11]</td>
<td>Campana et al. (1989)</td>
</tr>
</tbody>
</table>

\(^1\) When mortality rates for different egg stages / months were given, these were averaged for each year.

\(^2\) Averaged for months of peak spawning, i.e., June-September 2002, August-October 2003
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