

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

3

4 **Ø. Langangen^{1‡*}, L.C. Stige^{1*}, N.Yaragina², F. Vikebø³, B. Bogstad³, Y. Gusdal⁴**

5

6 ¹*Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo,*

7 *Department of Biology, P.O. Box 1066 Blindern, N-0316 Oslo, Norway*

8 ²*Polar Research Institute of Marine Fisheries and Oceanography, 6 Knipovich St.,*

9 *Murmansk, 183763, Russia*

10 ³*Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway*

11 ⁴*Norwegian Meteorological Institute, 0313 Oslo, Norway*

12 [‡]*Corresponding author: oysteol@bio.uio.no, tel: (+47) 22854648, fax: (+47) 22854001*

13 ** Equal contribution*

14

15

16

17

18

19

20

21

22 Abstract

23 High and variable mortality during the egg and larval stages is thought to be an important
24 source of interannual variability in stock size in many marine fishes. However,
25 quantitative information about the mortality during these life stages, especially the
26 interannual variability, is sparse. Here, we used a time series covering 34 years (1959-
27 1993) of survey data to estimate the mortality during the egg stages of Northeast Arctic
28 cod and Northeast Arctic haddock. Using a regression approach based on the numbers of
29 eggs in different developmental stages, we calculated the mean instantaneous mortality
30 rate of cod eggs to be 0.17 day^{-1} (95% c.i. 0.15, 0.19), which is significantly higher than
31 that for haddock, 0.09 day^{-1} (c.i. 0.07, 0.12). **The interannual variability in egg**
32 **mortality range from about 0.12 day^{-1} to 0.22 day^{-1} for cod and from about 0.04 day^{-1}**
33 **to 0.12 day^{-1} for haddock.** The accuracy of these estimates was evaluated by analysis
34 of synthetic data constructed from a coupled physical-biological model, suggesting that
35 the mean mortality and the magnitude of the interannual variability were estimated
36 reliably, but not the mortality for any given year.

37

38 **Keywords:** *cod, egg mortality, generalized additive mixed models, haddock, physical-*
39 *biological modelling*

40

41

42 Introduction

43 Marine **organisms** often show large fluctuations in productivity caused by interannual
44 variations in recruitment, that is, in the year class strength as the cohort enters into the
45 fisheries (e.g. Hjort 1914). The amount of successfully spawned eggs and the cumulative
46 result of mortalities experienced by all life stages preceding recruitment determine the
47 year class strength at recruitment age (e.g. Houde 2008, Lough and O'Brien 2012). The
48 survival during the early life stages, such as during the egg and larval stages, may have
49 large influence on recruitment (Myers and Cadigan 1993) even though no single life
50 stage can in general be considered as the primary source for variability in recruitment
51 (Houde 2008).

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

59 Here, we use a time series of survey data spanning 34 years (1959-1993) to
60 estimate the mortality during the egg stages of Northeast Arctic cod (*Gadus morhua*,
61 from now on cod) and Northeast Arctic haddock (*Melanogrammus aeglefinus*, from now
62 on haddock) as well as the interannual variability in mortality. Furthermore, we construct
63 several time series of synthetic survey data based on a coupled physical-biological model
64 covering 15 years (1978-1992) to assess and optimize the estimation method.

65 Data

66 The Russian ichthyoplankton surveys were conducted twice per year in spring (April-
67 May) and summer (June-July) from 1959 to 1993. Note that the 1967 spring cruise was
68 not conducted due to technical reasons, hence the time series for spring, the part of the
69 data analysed in the present paper, contains 34 years of data. The surveys were conducted
70 at different stations mainly covering an offshore region from outside of the Lofoten
71 islands in the south to Bear Island in the north and to the western parts of the Kola
72 Peninsula in the east (see Figure 1). Note that the survey did not cover the inner parts of
73 the Lofoten area. The starting time of the surveys varied between 30 March and 4 May,
74 while there was no long-term trend in the starting dates (Mukhina et al. 2003). The
75 duration of the surveys (24-58 days for the spring survey), **the spatial coverage** and the
76 total number of stations (100-358 for the spring survey) varied considerably between
77 years.

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

82 The collected eggs were identified and counted. **Furthermore, the cod eggs were**
83 **classified in four different developmental stages (I-IV, Rass 1946, corresponding to**
84 **stages 1-10, 11-20, 21-25 and 26-30, respectively, of Russell 1976). The vital resident**
85 **time within each stage was assumed roughly equal (5 days, of a total temperature-**
86 **dependent development time of approximately 20 days, Ellertsen et al. 1988).** Due to
87 lack of sampling in the inner parts of the Lofoten area (leading to bias towards older

88 eggs) and due to difficulties in separation between cod and haddock eggs in the first
89 development stage of these eggs, the first stage was not included in this analysis. In
90 summary the data contain spatiotemporal catch abundances for four developmental stages
91 (three used in the present analysis) of cod and haddock eggs. For further details about the
92 **Russian ichthyoplankton** surveys the reader is referred to Mukhina et al. (2003).

93 **Furthermore, we analysed time-series of cod spawning stock biomass and**
94 **number of recruits at age three from virtual population analysis (1959-1990, ICES**
95 **2012). In addition, we used annual abundance indices for eggs and larvae (1959-**
96 **1990, Mukhina et al. 2003) and 5-month old cod (1980-2008, Table 1.2 in ICES**
97 **2012) based on pelagic trawls, and indices for 10-month-olds, 22-month-olds and 34-**
98 **month-olds (the latter representing recruitment age) from bottom trawl surveys**
99 **(1980-2008, ICES 2012).**

100

101 Methods

102 To estimate the overall mean and the interannual variability in mortality for each species
103 we used a statistical regression model approach. This method exploits the differences in
104 egg density among stages, assuming 5 days between each egg stage and a total
105 development time of 20 days, while taking other factors affecting density into account.
106 The log transformed stage specific egg numbers were modelled with a generalized
107 additive mixed model (GAMM) using the gam function in the mgcv library in R and
108 treating the random effects as smooths (**specified by ‘bs=’re’**) (Wood 2006a, b). As
109 covariates we used the day of spawning (*spd*, calculated from sampling day minus egg
110 age at the middle of the stage), sampling location (*lon*, longitude, and *lat*, latitude) and

111 approximate egg age (*Age*, coded as -5, 0 and 5 days for egg stage II, III and IV
 112 respectively to centre the model around 0). The covariates were included to account for,
 113 respectively, seasonal variation in spawning time, horizontal transport out from spawning
 114 locations and, most importantly, mortality. Specifically, the coefficient for the *Age* effect
 115 estimates $-M$, where M is the daily instantaneous mortality rate. Two random effect terms
 116 were included, a random year effect and a random year by egg age effect. These random
 117 effects account for interannual variations in total egg numbers and interannual variations
 118 in mortality. **We considered that several processes might account for the zeros in our**
 119 **data. For this reason, we removed all zeros in the data and modeled the observed**
 120 **numbers with a lognormal model.** The model for the log transformed stage specific egg
 121 numbers ($\ln(En)$) can be summarized as

122
$$\ln(En)_{ij} = \beta_0 + f_1(spd_i) + f_2(lon_i, lat_i) + b_{0j} + (\beta_1 + b_{1j}) Age_i + \varepsilon_{ij}$$

 123 Equation 1

124 where the subscripts i and j represent station and year, respectively, β_0 and β_1 are model
 125 coefficients for fixed effects, f_1 is a smoothing spline, f_2 is a tensor product smooth, b_{0j}
 126 and b_{1j} are random year effects and ε_{ij} is a normally distributed error term. Cod and
 127 haddock egg numbers were modelled using the same structure in the statistical model. To
 128 estimate confidence intervals around the point estimates we used a bootstrapping
 129 procedure (Efron and Tibshirani 1993) where we resampled the stations within years and
 130 re-estimated the parameters 1000 times.

131 To assess and optimize the mortality estimation procedure we constructed several
 132 synthetic data sets (Aksnes and Ohman 1996). A detailed description of the construction
 133 of synthetic data can be found in Appendix A. **In short, the synthetic data were**
 134 **constructed to resemble the cod egg data, by “sampling” particles (representing**

135 **eggs) in the output of a coupled physical-biological model for the early life stages of**
136 **cod at the same spatiotemporal coordinates as in the survey.** Following egg release,
137 the advection of eggs was calculated (Ådlandsvik and Sundby 1994) based on fifteen
138 years (1978-1992) of simulated flow fields (Shchepetkin and McWilliams 2005,
139 Haidvogel et al. 2008). We used a super-individual perspective (Scheffer et al. 1995),
140 where each particle represented a large number of eggs, scaled to match the sampled egg
141 density and the reported spatial (Sundby and Nakken 2008, Vikebø et al. 2011) and
142 temporal (Ellertsen et al. 1989) distribution of spawning (origin of particles). In addition,
143 the particles were given a daily instantaneous mortality (M), linking the abundance at
144 time t (N_t) to the abundance at time zero (N_0) according to

145
$$N_t = N_0 e^{-Mt}. \quad \text{Equation 2}$$

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

153 The second set of scenarios was constructed to explore the accuracy of the
154 estimation method and to reveal possible biases in the estimated mortality due to
155 interannual variability in mortality and spawning. **We constructed a series of seven**
156 **different data sets with different magnitude of the interannual variability in**
157 **mortality.** The mortality time series were randomly generated from normal distributions

158 with mean of 0.15 day^{-1} and with scenario-dependent standard deviation for the
159 interannual variability varying between 0 and 0.075 day^{-1} . The mean spawning day was
160 simulated to vary randomly among years, centred at 30th of March with a standard
161 deviation for the interannual variability of 3 days (similar to observations for 1976-1986
162 (Ellertsen et al. 1989)). This time series was kept fixed in all scenarios. The statistical
163 model (Eq.1) was applied to the synthetic data to test if the estimated mortality was
164 similar to the simulated (“true”) input mortality.

165 **To explore some of the implications of our findings, we correlated the annual**
166 **mortality estimates (b_{tj} , Eq. 1) for cod with indices of cohort abundance at earlier**
167 **and later life stages (given at least 15 years of overlap with the mortality estimates).**
168 **We also calculated the interannual variance in log transformed cohort size at**
169 **different life stages of cod (spawning stock biomass, eggs, larvae, 5-month-olds, 10-**
170 **month-olds, 22-month-olds, 34-month-olds and recruits) for the 1959-1990 and the**
171 **1980-2008 periods (depending on data availability). Because of a change in bottom**
172 **trawl gear in 1994, all variances for 1980-2008 were weighted means of variances**
173 **calculated before and after this shift.**

174 Results

175 We estimated an average mortality of 0.169 day^{-1} (with 95% confidence limits of
176 $[0.159, 0.181]$) for cod eggs and 0.094 day^{-1} (with 95% confidence limits of $[0.082,$
177 $0.109]$) for haddock eggs. The annual estimates of the mortalities, with 95 % confidence
178 limits derived from the bootstrap, for the two species are shown in Figure 2. Furthermore,
179 we estimated an interannual standard deviation in mortality of 0.031 day^{-1} (with 95%

180 confidence limits of [0.020, 0.046]) for cod and 0.025 day^{-1} (with 95% confidence limits
181 of [0.016, 0.040]) for haddock. **The annual egg mortality estimates for cod were not**
182 **significantly correlated with indices of larval abundance ($r = -0.18$, $P > 0.1$),**
183 **recruitment at age-3 ($r = -0.05$, $P > 0.1$) or indicators of initial egg abundance**
184 **(spawning stock biomass, or, alternatively, the random intercept, b_{0j} , Eq. 1) (both r**
185 **= -0.25 , $P > 0.1$).**

186 Testing the statistical model by analysis of synthetic data simulated under different
187 assumptions about the mortality level and timing of the spawning resulted in estimation
188 of mortalities usually very close to the input mortalities and always within the 95%
189 confidence limits, see Table 1 for details. In addition, the analysis of synthetic data
190 simulated under different assumptions about the magnitude of the interannual variability
191 in mortality resulted in estimation of the interannual standard deviations in mortality
192 mostly within the confidence limits for true input standard deviations (Figure 3).

193 **However, these tests revealed an overestimation of the interannual variability when**
194 **the true standard deviation was lower than about 0.03 day^{-1} . This bias is most likely**
195 **due to the low contrast in the mortality compared to other factors, such as**
196 **interannual variability in drift pattern, sampling and temperature-dependent**
197 **development rate. For example, according to the hydrodynamic modelling results**
198 **for 1978-1990, the average stage duration may vary between warm and cold years**
199 **from 4.5 to 5.9 days, which may lead to 10-15% error in the mortality estimates.**
200 **Due to this bias in the estimation at low variability we cannot set a lower limit on the**
201 **estimated variability.** Furthermore, the correlations between the simulated mortalities
202 and the estimated mortalities were fairly low: For the most realistic scenario, simulating

203 an interannual standard deviation of 0.03 day^{-1} , this correlation was 0.22, suggesting that
204 the statistical model could only explain about 5% of the interannual variability in
205 mortality. The root-mean-square prediction error of the annual mortality ranged from
206 0.023 to 0.038 day^{-1} among the different scenarios and was higher for scenarios that
207 simulated high interannual variability in mortality. The root-mean-square prediction error
208 for the most realistic scenario was 0.031, which is about twice as large as the bootstrap
209 estimate of the standard error for the annual mortality (= 0.015). If we apply a factor of
210 two to the bootstrap standard errors, we obtain more conservative 95% confidence limits
211 for the mean mortality of cod [0.15, 0.19] and haddock [0.07, 0.12] that might better
212 capture the various sources of uncertainty. **Plots of the residuals (not shown) indicate**
213 **that our lognormal model performed satisfactorily. Furthermore, tests with a**
214 **negative binomial model to the complete dataset (including the zeros) showed**
215 **unsatisfactory quantile plots for large observations and this model did not perform**
216 **satisfactorily on the synthetic data (bias in average estimated mortality).**

217 **The log transformed stage specific interannual variances for the cod show an**
218 **increasing trend from early stages up until 5- to 10-month-olds. For older stages the**
219 **interannual variance is decreasing with age (Figure 4).**

220 Discussion

221 The instantaneous mortality rate for cod eggs estimated herein (0.17 day^{-1}) is
222 significantly higher than the previously reported 0.10 day^{-1} for the Northeast Arctic cod
223 stock (Fossum 1988). Using the instantaneous mortality rate from Fossum (1988) for a
224 egg development time of 20 days gives a total cod egg stage survival of 11-17 % (**Table**
225 **2**) while we report an average annual survival of about 3% (95% corrected bootstrap c.i.

226 [2%, 5%]). The present estimates were based on a long time series and a thoroughly
227 assessed method, hence making the mean mortality estimates reliable. For cod eggs, the
228 yearly cumulative egg stage survival varied between about 1% and 10% over the time
229 series, while for haddock the same numbers were higher and around 10% and 40%. Note,
230 however, that the testing with the synthetic data revealed that the estimates for any given
231 year are uncertain. **The lack of significant relationships between egg mortality and**
232 **earlier or later cohort size might thus simply be due to low statistical power.**

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

235 Comparing these results with results reported for other stocks of cod and haddock
236 in the North Atlantic (Table 2), we see that our estimates **are comparable with** previous
237 results. Egg mortality of Northeast Arctic cod appears to be similar to that of the Western
238 Scotian Shelf cod, in the upper range of that reported for the well-studied Georges Bank
239 cod, but lower than that reported from the North Sea, the Baltic Sea and the Irish Sea. For
240 haddock eggs, our estimated mean mortality of 0.09 day^{-1} is similar to that reported for
241 haddock from the Georges Bank, and lower than that reported from the Western Scotian
242 Shelf. The interannual range in egg mortality is difficult to compare across studies
243 because of differences in the length of the time series and in estimation methods. For
244 most stocks, the daily mortality rates vary by a factor of about two to three. Egg survival
245 on the Georges Bank is more variable for both cod and haddock, which may be linked to
246 the special hydrographical conditions and resulting variable egg retention rates in this
247 area (Lough et al. 2006).

248 **Stage dependent mortality has been reported in cod eggs (Campana et al.**
249 **1989). Here, we assumed equal mortality in the egg stages analyzed. We tested this**
250 **assumption by analysing each stage pair (stage II and III, and stage III and IV)**
251 **separately (results not shown). These tests did not show any significant difference**
252 **from the full model, and hence we conclude that this is a reasonable assumption.**

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

$$260 \quad \text{Var}(\log N_T) = \text{Var}(\log N_0) + T^2 \text{Var}(M) - 2TCov(\log N_0, M), \text{ Equation 3}$$

261 Note that for the sake of convenience, cohort size is here measured on a natural-
262 logarithmic scale. For Northeast Arctic cod, the variance in cohort size increases up to an
263 age of about one year, and then decreases until the recruitment age of 3 years (Figure. 4).
264 Our interpretation of this figure is that during the first year of life, interannual variability
265 in mortality tends to increase cohort fluctuations, while thereafter; compensatory density
266 dependence tends to dampen cohort fluctuations **as seen in many marine species (see,**
267 **e.g., Martino et al. 2012).**

268 How much of this increase in cohort variability during the first year of the cod's
269 life can variable egg survival explain? With a standard deviation of the instantaneous egg
270 mortality, M , of 0.03 day^{-1} and a egg stage duration, T , of 20 days, our results suggest that

271 interannual fluctuations in egg mortality rate increases cohort variance by $T^2 Var(M) =$
272 0.36. This estimate is consistent with a 11-fold difference in cumulative egg survival
273 between years with abnormally low and high egg mortality (\pm two standard deviations
274 from the average). We can compare this estimate with the contribution from temperature-
275 driven variability in egg stage duration: At higher temperatures, the egg stage duration,
276 T_{EGG} , is shorter and the cumulative survival higher (all else being equal). According to
277 our hydrodynamic modelling results for 1978 -1992 (and the most realistic egg release
278 scenario centred around 30th of March), the interannual standard deviation in T_{EGG} is 1.65
279 days. With a mean M of 0.17 day^{-1} , we find that temperature-driven variability in egg
280 stage duration increases cohort variance at the end of the egg stage by $M^2 Var(T_{EGG}) =$
281 0.07. This estimate suggests a three-fold difference in cumulative egg survival between
282 years with abnormally high and low ambient temperatures (i.e., egg stage duration ± 3.3
283 days, or ambient temperature $\pm 1.1 \text{ }^\circ\text{C}$). In comparison, the instantaneous mortality
284 during the larval stages of Northeast Arctic cod has been reported to be lower but
285 similarly variable as the egg mortality, ranging from 0.08 to 0.15 day^{-1} in eight years
286 between 1979 and 1988 (Sundby et al. 1989). Because of the longer duration of the larval
287 stages (2 months or more), the cumulative survival is more variable, resulting in a 68-fold
288 difference within the years studied (Sundby et al. 1989). **Similar results, stressing the**
289 **importance of the longer duration of the larval compared to the egg stages, have**
290 **been reported for other stocks (e.g. Sissenwine et al. 1984, Campana et al. 1989).**
291 Note, that the larval mortality estimates by Sundby et al. (1989) were based on a 10% egg
292 stage survival (corresponding to a instantaneous mortality of 0.115 day^{-1}). A simple

293 calculation with the new egg mortality estimates (see Appendix B) gives a larval
294 instantaneous mortality of 0.075 day^{-1} .

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

299 Appendix A -Synthetic data

300 We used a coupled physical-biological model (Ådlandsvik and Sundby 1994) to construct
301 realistic synthetic data. As input to the model we used the daily averaged flow,
302 temperature and salinity fields provided by the general circulation model, Regional
303 Ocean Modelling System (ROMS, Shchepetkin and McWilliams 2005, Haidvogel et al.
304 2008), forced by the atmospheric and boundary conditions for 1978-1992. Furthermore,
305 diffusivity coefficients due to salinity and temperature gradients were provided by
306 ROMS. The circulation model covers the north Atlantic, including the North, Norwegian,
307 Barents and Kara seas and parts of the Arctic Ocean with a grid resolution of $4 \times 4 \text{ km}$.
308 For further details on the ocean circulation model setup the reader is referred to Vikebø et
309 al. (2010).

310 Each synthetic data set was based on fifteen years (1978-1992) of simulated flow
311 fields. To construct the synthetic data we took a super-individual perspective (Scheffer et
312 al. 1995), where each simulated egg particle represents several **thousand** actual eggs. In
313 each year a total of 100 cod egg particles were released per spawning ground (see Figure
314 1) per day from the beginning of March throughout April. In total more than 85000 egg
315 particles were released yearly. The following procedure was used to calculate realistic

316 scaling factors to convert particle numbers to egg numbers, dependent on the release
317 location and -time of the particles. The spatial position and extent of the spawning
318 grounds were based on Sundby and Nakken (2008). Furthermore, the distribution of cod
319 eggs among spawning grounds was scaled according to Table 1 in Vikebø et al. (2011).
320 In the cases where Table 1 in Vikebø et al. (2011) did not include the same fine-scale
321 resolution of the spawning grounds as presented by Sundby and Nakken (2008), we
322 redistributed the weights among the sub-spawning grounds according to the surface area.
323 Note that three spawning grounds were given zero weight, hence not included in the
324 construction of the synthetic data (see Figure 1). The interannual variation in total
325 (simulated) egg numbers was scaled to be proportional to the spawning stock biomass of
326 cod (ICES 2012). The seasonal variation in spawning was scaled using a Gaussian curve
327 with mean depending on the scenario and a standard deviation of 8 days. Finally, the total
328 egg numbers over the simulated period (15 years) were scaled to make the synthetic data
329 contain similar amounts of eggs as in the observed data.

330 Each egg particle was released at 10 meters depth and was assigned a normal
331 distributed random buoyancy with a mean of 31.25 psu (salinity at neutral buoyancy)
332 with a standard deviation of 0.69 (Sundby 1991, Stenevik et al. 2008). The difference
333 between the egg density and the ambient water density and Stokes law (for creep flow)
334 were used to determine vertical movements according to Thygesen and Ådlandsvik
335 (2007). The horizontal advection of particles uses a time step of one hour; interpolation
336 from the daily averaged flow fields was achieved using a 4th order Runge-Kutta method
337 (Ramsden and Holloway 1991). The egg particles were allowed to develop according to

338 the local ambient temperature along the particle track. We used the following relation
339 between ambient temperature (T_0 in Celsius) and total egg development time (D in days)

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

340 based on Ellertsen et al. (1988). The cumulative sum of the daily fraction of development
341 determines the eggs total development. The egg particles were given a daily mortality
342 (M), that link the abundance at time t (N_t) to the abundance at time zero (N_0) according to
343 Eq.2. We considered two different sets of scenarios when constructing the synthetic data.
344 These scenarios are described in detail in the main text (Methods section), in short we
345 constructed one set of synthetic data with interannual constant mortality and spawning
346 time, and one set where both mortality and spawning time varied interannually.

347 To finalize the construction of the synthetic data, we used the spatiotemporal
348 coordinates of the real survey to calculate a synthetic catch number for each of the four
349 egg stages (0-25%, 25-50%, 50-75% and 75-100% developed eggs) at each station. Since
350 for more than 95% of the time the egg particles were horizontally advected less than 20
351 km per day, we used a circle of radius 20 km as catch region surrounding each station.
352 I.e., all egg particles within this radius during the day of the sampling were considered
353 sampled, but not removed from the simulation. Hence, some egg particles were
354 encountered multiple times.

355 Appendix B -Larval mortality

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

$$357 N_{0-group} = N_{egg} e^{-(t_1 \cdot m_1 + t_2 \cdot m_2 + t_3 \cdot m_3)},$$

358 where $N_{0-group}$ are the number of 0-group individuals (juvenile fish 4 month after
359 hatching), N_{egg} are the total egg production (TEP), t_i ($i \in \{1,2,3\}$) are the stage duration

360 and m_i are the stage instantaneous mortality for the three stages (egg, larval and early
361 juvenile, respectively). TEP was taken from Marshall et al. (2006) and 0-group
362 abundance was taken from ICES (2012). We used only the 14 overlapping years from
363 1980-1993 in this analysis. Stage duration was for simplicity taken as 20 days (t_1) for the
364 egg stage and 60 days for the larval (t_2) and the early juvenile stage (t_3), in total 140 days
365 from spawning to the 0-group stage. We used the average early juvenile mortality of $m_3 =$
366 0.04 day^{-1} reported by Sundby et al. (1989), since this estimate did not rely on the egg
367 mortality. Furthermore, we used the egg mortality estimated in the present paper ($m_1 =$
368 0.17 day^{-1}) to calculate the larval mortality (m_2). This gave an average mortality of 0.075
369 day^{-1} for the larval stage, with a range of $[0.062-0.083] \text{ day}^{-1}$ due to interannual variability
370 in early juvenile mortality. Including other sources of variability would increase this
371 range.

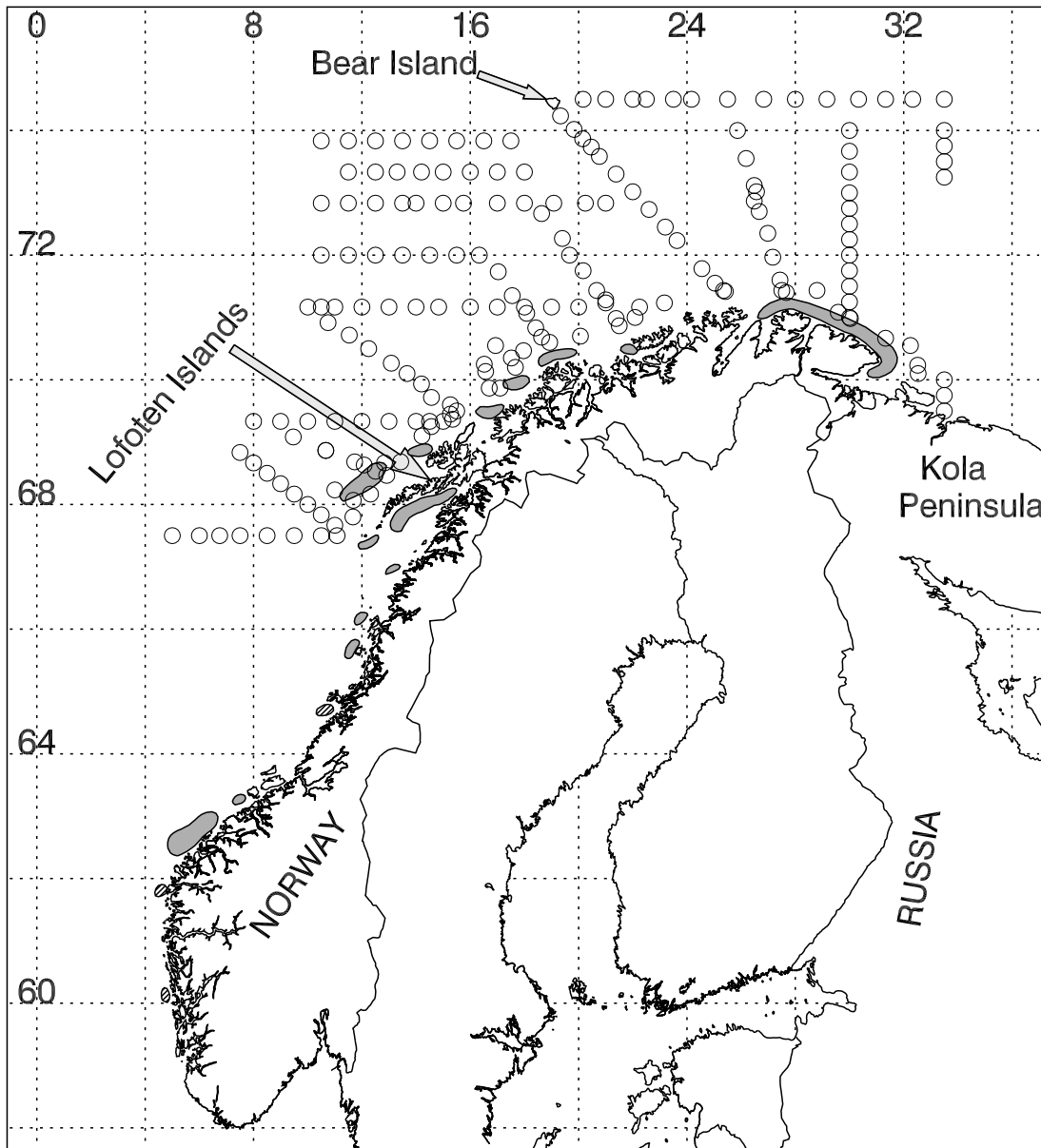
372 Acknowledgements

373 We thank Dag Hjermann for valuable comments on the manuscript. Furthermore, we
374 thank the Norwegian Research Council (NRC) for support through the SVIM project
375 (project no. 196685). This work is a contribution to the NRC PETROMAKS program -
376 SYMBIOSES (BIP project #ES468602). The SYMBIOSES project is a cooperation of 15
377 research partners, financed by the NRC, BP Exploration Operating Company Limited,
378 ConocoPhillips Skandinavia, ExxonMobil Upstream Research Company, Eni Norway,
379 Shell Technology Norway, Statoil Petroleum and Total E&P Norway. Computational
380 resources for ocean circulation simulations were granted by the Norwegian Metacenter
381 for Computational Science (NOTUR) under contract nn9146k.

382

383

384

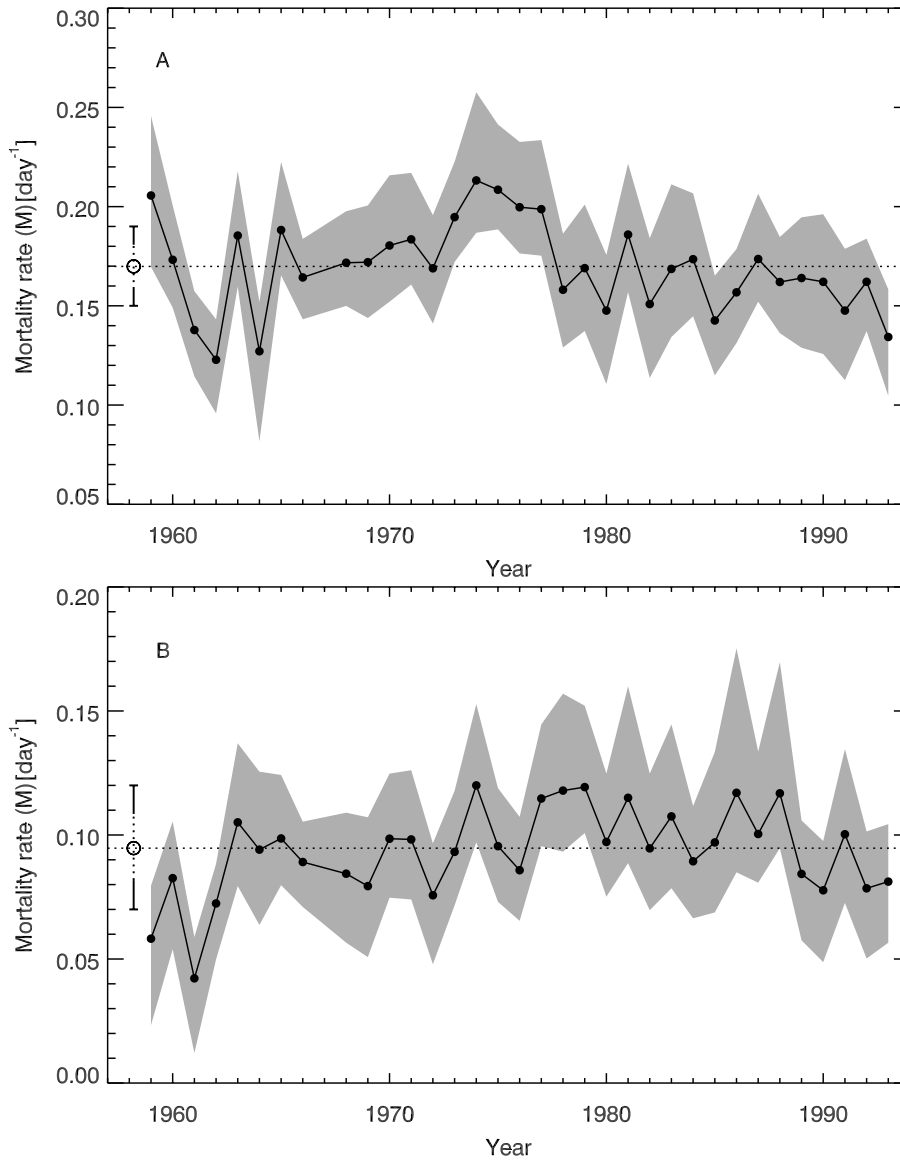


385

386 **Figure 1.** The coverage of the survey stations for the year 1984 (open circles). The grey

387 shaded polygons show the spawning grounds used in the synthetic data. The line filled

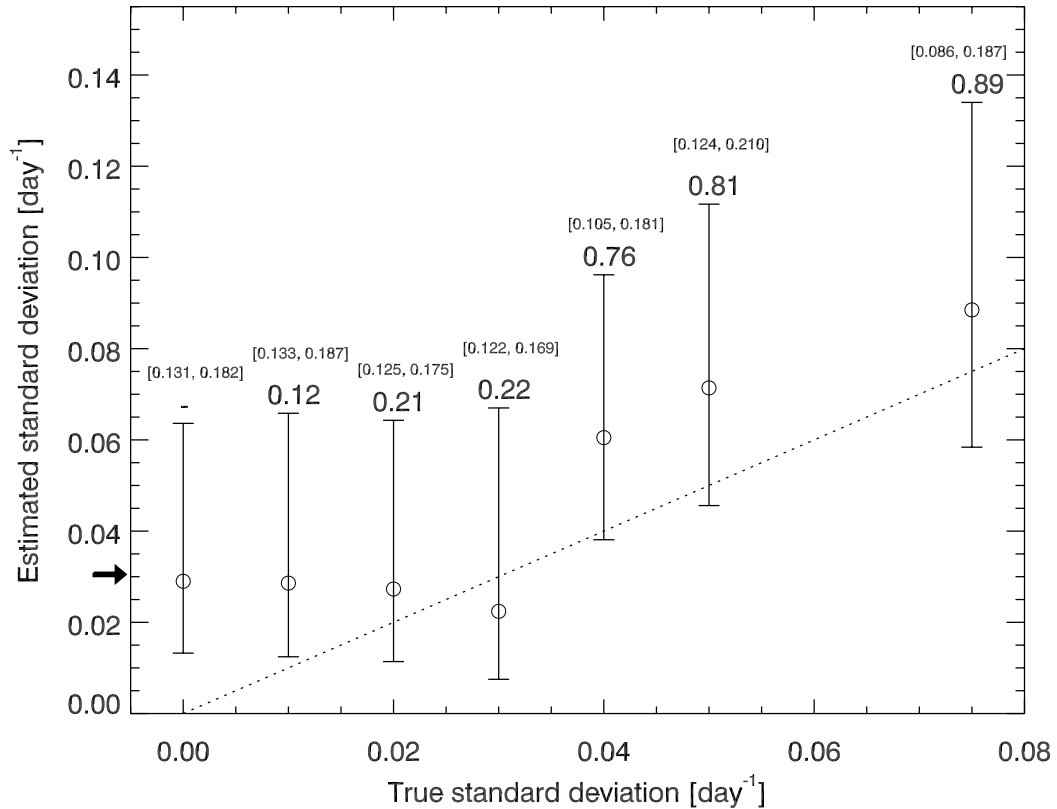
388 polygons show the spawning grounds with zero weight, and hence not used in
389 construction of the synthetic data.



390

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

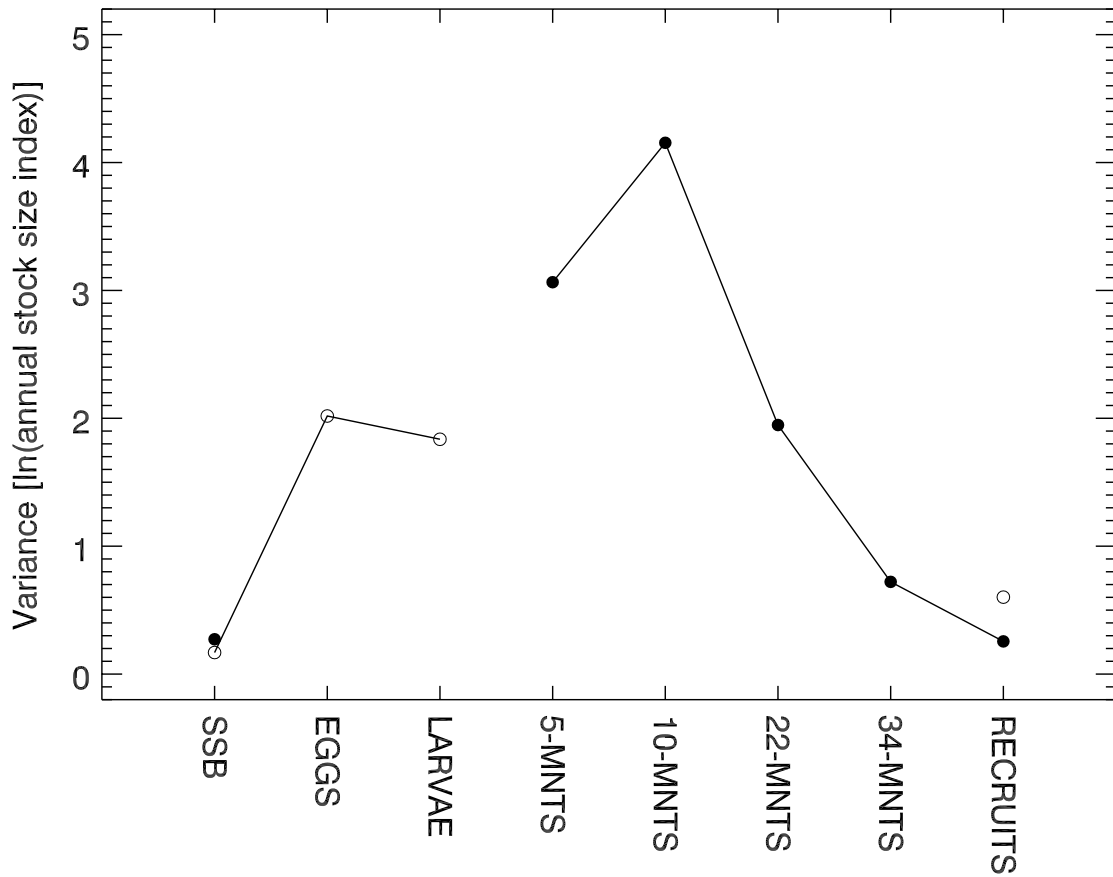
396 times as large as the bootstrap standard errors. The solid vertical bar indicates the
 397 corrected c.i. for the overall mean.



398

399 **Figure 3.** The “true” (simulated) and estimated interannual standard deviations in
 400 mortality (open circles) with 95% confidence bands (vertical bars). Numbers above bars:
 401 correlation coefficients between the true and estimated annual mortalities **and (in**
 402 **brackets) confidence bands for the estimated average mortality.** The average “true”
 403 mortality was 0.15 day⁻¹ for all data sets. Arrow: the standard deviation estimated from
 404 the real data for cod.

405



406

407 **Figure 4.** The interannual variance in cohort abundance (ln-scale) for different life stages
408 of cod. Open circles: 1959-1990, filled circles: 1980-2008 cohorts. **SSB: spawning stock**
409 **biomass (indicator of potential egg production). Recruits: number of 3-year-olds.**

410

411 **Table 1.** The different values of mortality and spawning times used in the 9 different
 412 scenarios with constant mortality used to construct synthetic data, and the resulting
 413 estimated mortalities and confidence intervals.

	Input mortality	Estimated mortality [Confidence intervals]
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]

414

415

416

417

418 **Table 2.** Egg mortality rates of cod and haddock reported in this and other studies¹.

Stock	Years	Egg mortality (day ⁻¹): Interannual mean and range	Approx. egg stage duration (days)	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 & Jaworski (1990) and ref. therein
Baltic Sea cod	1996, 2002, 2003	0.32 [0.26 – 0.38]	14	1.1 [0.5 – 2.7]	Wieland et al. (2000), Voss et al. (2011) ²
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), 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), 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)

419 ¹When mortality rates for different egg stages / months were given, these were averaged for each year.

420 ²Averaged for months of peak spawning, i.e., June-September 2002, August-October 2003

422 Literature cited

- 423 Aksnes DL, Ohman MD (1996) A vertical life table approach to zooplankton mortality
424 estimation. *Limnology and Oceanography* 41:1461–1469
- 425 Andrews JM, Gurney WS, Heath MR, Gallego A, O'Brien CM, Darby C, Tyldesley G
426 (2006) Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the
427 European continental shelf. *Can J Fish Aquat Sci* 63:1027–1048
- 428 Armstrong MJ, Connolly P, Nash R, Pawson MG, Alesworth E, Coulahan PJ, Dickey-
429 Collas M, Milligan SP, O'Neill MF, Witthames PR, Woolner L (2001) An
430 application of the annual egg production method to estimate the spawning biomass of
431 cod (*Gadus morhua* L.), plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) in
432 the Irish Sea. *ICES Journal of Marine Science* 58:183–203
- 433 Ådlandsvik B, Sundby S (1994) Modelling the transport of cod larvae from the Lofoten
434 area. *Cod and climate change ICES marine science symposium* 198:379–392
- 435 Campana SE, Frank KT, Hurley P, Koeller PA, Page FH, Smith PC (1989) Survival and
436 Abundance of Young Atlantic Cod (*Gadus Morhua*) and Haddock (*Melanogrammus*
437 *Aeglefinus*) as Indicators of Year-Class Strength. *Can J Fish Aquat Sci* 46:171–182
- 438 Efron B, Tibshirani R (1993) *An Introduction to the Bootstrap*. Chapman & Hall, Boca
439 Raton
- 440 Ellertsen B, Fossum P, Solemdal P, Sundby S (1989) Relation between temperature and
441 survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.).
442 *Rapports et Procès-Verbaux Des Réunions Du Conseil International pour*
443 *l'Exploration de la Mer* 191:209–219
- 444 Ellertsen B, Fossum P, Solemdal P, Sundby S, Tilseth S (1988) The effect of biological
445 and physical factors on the survival of Arcto-Norwegian cod and the influence on
446 recruitment variability. *Proceedings of the Third Soviet–Norwegian Symposium,*
447 *Murmansk 26-28 May 1986:101–126*
- 448 Fossum P (1988) A Tentative Method to Estimate Mortality in the Egg and Early Fish
449 Larval Stages, with Special Reference to Cod (*Gadus Morhua* L.).
450 *Fiskeridirektoratets skrifter / Serie havundersøkelser* :1–35
- 451 Grimm V (1999) Ten years of individual-based modelling in ecology: what have we
452 learned and what could we learn in the future? *Ecological Modelling* 115:129–148
- 453 Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Di Lorenzo E,
454 Fennel K, Geyer WR, Hermann AJ, Lanerolle L, Levin J, McWilliams JC, Miller AJ,
455 Moore AM, Powell TM, Shchepetkin AF, Sherwood CR, Signell RP, Warner JC,
456 Wilkin J (2008) Ocean forecasting in terrain-following coordinates: Formulation and
457 skill assessment of the Regional Ocean Modeling System. *Journal of Computational*

- 458 Physics 227:3595–3624
- 459 Heath M, Gallego A (1998) Bio-physical modelling of the early life stages of haddock,
460 *Melanogrammus aeglefinus*, in the North Sea. Fisheries Oceanography 7:110–125
- 461 Hinrichsen HH, Dickey-Collas M, Huret M, Peck MA, Vikebø FB (2011) Evaluating the
462 suitability of coupled biophysical models for fishery management. ICES Journal of
463 Marine Science 68:1478–1487
- 464 Hjort J (1914) Fluctuations in the great fisheries of Northern Europe viewed in the light
465 of biological research. Rapports et Procès-Verbaux Des Réunions Du Conseil
466 International pour l'Exploration de la Mer 20:1–237
- 467 Houde ED (2008) Emerging from Hjort's Shadow. J Northw Atl Fish Sci 41:53–70
- 468 ICES (2012) Report of the Arctic Fisheries Working Group (AFWG) 20 - 26 April 2012,
469 ICES Headquarters, Copenhagen. ICES CM 2012/ACOM:05.
- 470 Lough RG, O'Brien L (2012) Life-stage recruitment models for Atlantic cod (*Gadus*
471 *morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank. Fishery
472 Bulletin
- 473 Lough RG, Hannah CG, Berrien P, Brickman D, Loder JW, Quinlan JA (2006) Spawning
474 pattern variability and its effect on retention, larval growth and recruitment in
475 Georges Bank cod and haddock. Mar Ecol Prog Ser 310:193–212
- 476 Marshall CT, Needle CL, Thorsen A, Kjesbu OS, Yaragina NA (2006) Systematic bias in
477 estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock:
478 implications for stock-recruit theory and management. Can J Fish Aquat Sci 63:980–
479 994
- 480 **Martino EJ, Houde ED, Marshall CT (2012) Density-dependent regulation of year-**
481 **class strength in age-0 juvenile striped bass (*Morone saxatilis*). Can J Fish Aquat**
482 **Sci 69:430–446**
- 483
- 484 Miller TJ (2007) Contribution of individual-based coupled physical-biological models to
485 understanding recruitment in marine fish populations. Mar Ecol Prog Ser 347:127–
486 138
- 487 Mountain D, Green J, Sibunka J, Johnson D (2008) Growth and mortality of Atlantic cod
488 *Gadus morhua* and haddock *Melanogrammus aeglefinus* eggs and larvae on Georges
489 Bank, 1995 to 1999. Mar Ecol Prog Ser 353:225–242
- 490 Mukhina NV, Marshall CT, Yaragina NA (2003) Tracking the signal in year-class
491 strength of Northeast Arctic cod through multiple survey estimates of egg, larval and
492 juvenile abundance. Journal of Sea Research 50:57–75
- 493 Myers RA, Cadigan NG (1993) Density-Dependent Juvenile Mortality in Marine

- 494 Demersal Fish. Can J Fish Aquat Sci 50:1576–1590
- 495 Opdal AF, Vikebø FB, Fiksen Ø (2011) Parental migration, climate and thermal exposure
496 of larvae: spawning in southern regions gives Northeast Arctic cod a warm start. Mar
497 Ecol Prog Ser 439:255–262
- 498 Ramsden D, Holloway G (1991) Timestepping lagrangian particles in two dimensional
499 eulerian flow fields. Journal of Computational Physics 95:101–116
- 500 **Rass, T.S. (1946). Ontogenesis Stages of Fishes(in Russian). Zoological Journal,**
501 **25, 127–148.**
502
- 503 Rijnsdorp AD, Jaworski A (1990) Size-Selective Mortality in Plaice and Cod Eggs - a
504 New Method in the Study of Egg Mortality. Journal Du Conseil 47:256–263
- 505 **Russell, F.S. (1976). The eggs and planktonic stages of British marine fishes.**
506 **Academic Press, New York.**
507
- 508 Scheffer M, Baveco JM, DeAngelis DL, Rose KA, van Nes EH (1995) Super-individuals
509 a simple solution for modelling large populations on an individual basis. Ecological
510 Modelling 80:161–170
- 511 Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS):
512 a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean
513 Model 9:347–404
- 514 **Sissenwine, M.P., Cohen, E.B. & Grosslein, M.D. (1984). Structure of the georges**
515 **bank ecosystem. Rapports et Proces-Verbaux des Reunions Conseil**
516 **International pour l'Exploration de la Mer, 183, 243–254.**
517
- 518 Stenevik EK, Sundby S, Agnalt AL (2008) Buoyancy and vertical distribution of
519 Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast.
520 ICES Journal of Marine Science 65:1198–1202
- 521 Sundby S (1991) Factors affecting the vertical distribution of eggs. ICES Mar Sci Symp
522 192:33–38
- 523 Sundby S, Nakken O (2008) Spatial shifts in spawning habitats of Arcto-Norwegian cod
524 related to multidecadal climate oscillations and climate change. ICES Journal of
525 Marine Science 65:953–962
- 526 Sundby S, Bjørke H, Soldal A, Olsen S (1989) Mortality rates during the early life stages
527 and year-class strength of northeast Arctic cod (*Gadus Morhua L.*). ICES Marine
528 Science Symposia 191:351–358
- 529 Thygesen UH, Ådlandsvik B (2007) Simulating vertical turbulent dispersal with finite

- 530 volumes and binned random walks. *Mar Ecol Prog Ser* 347:145–153
- 531 Vikebø FB, Ådlandsvik B, Albretsen J, Sundby S, Stenevik EK, Huse G, Svendsen E,
532 Kristiansen T, Eriksen E (2011) Real-Time Ichthyoplankton Drift in Northeast Arctic
533 Cod and Norwegian Spring-Spawning Herring (M Peck, Ed.). *PLoS ONE* 6:e27367
- 534 Vikebø FB, Husebø Å, Slotte A, Stenevik EK, Lien VS (2010) Effect of hatching date,
535 vertical distribution, and interannual variation in physical forcing on northward
536 displacement and temperature conditions of Norwegian spring-spawning herring
537 larvae. *ICES Journal of Marine Science* 67:1948–1956
- 538 Voss R, Hinrichsen HH, Stepputtis D, Bernreuther M, Huwer B, Neumann V, Schmidt
539 JO (2011) Egg mortality: predation and hydrography in the central Baltic. *ICES*
540 *Journal of Marine Science* 68:1379–1390
- 541 Wieland K, Hinrichsen HH, Gronkjaer P (2000) Stage-specific mortality of Baltic cod
542 (*Gadus morhua* L.) eggs. *J Appl Ichthyol* 16:266–272
- 543 Wood SN (2006a) *Wood: Generalized additive models: an introduction with R*. Chapman
544 & Hall, Boca Raton
- 545 Wood SN (2006b) Low-Rank Scale-Invariant Tensor Product Smooths for Generalized
546 Additive Mixed Models. *Biometrics* 62:1025–1036
- 547
- 548