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**Reproductive strategy of a migratory fish stock:
implications of spatial variations in natural mortality**

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1 **Reproductive strategy of a migratory fish stock: implications of spatial**
2 **variations in natural mortality**

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20 **Running header:** Spatiotemporal mortality and implications for spawning

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Abstract

We investigate how the reproductive strategy in a migratory marine fish may be influenced by spatial variations in mortality in early life-stages. In particular, we examine how spawning time and location affect offspring survival and growth. A drift model for early life-stages (eggs to age 1) of the Barents Sea cod is combined with empirical estimates of spatial variation in mortality at two different life-stages. We examine seasonal and inter-annual differences in survival and growth in offspring originating from two spawning grounds, with the central site requiring higher migration distance and hence cost than the northern. When accounting for spatially explicit mortality fields, central and northern spawned offspring have about equal survival, as do early and late spawned offspring. Furthermore, central spawned offspring grow faster and are likely to reach a larger size compared to northern spawned offspring. Our results indicate that the fitness benefit of southward migration in the Barents Sea cod is not mainly due to higher early survival of offspring, but rather due to effects of offspring acquiring a larger size.

Keywords: Spawning migration – Barents Sea cod – Early life stages – Physical-biological drift model – Spatial variation in natural mortality

40 **Introduction**

41 Conditions experienced during early life-stages may result in long lasting effects on
42 individuals and may have important implications at the population level (Metcalf and
43 Monaghan 2001, Beckerman et al. 2002, Vindenes and Langangen 2015). Maternal
44 effects, typically defined as non-genetic reproductive traits, are often considered to be
45 adaptive responses to a heterogeneous environment and can be important in shaping the
46 fitness of the offspring (Mousseau and Fox 1998). Theory on reproductive strategy
47 suggests that there is often a trade-off between offspring fitness and parental cost,
48 including maternal effects (Lack 1954). In marine fish, maternal effects may affect the
49 offspring through egg condition such as size, fat content and buoyancy, but also
50 spawning location and time (Green 2008). For many populations, the optimization of
51 timing and location of spawning involves extensive parental migration. For such
52 migrations to be beneficial, the cost of the migration must be outweighed by payoff in,
53 e.g., increased survival and growth of the offspring.

54 Spatial variation in survival was identified as an important factor in determining
55 year-class-strength of marine fish already more than a century ago, for example in Hjort's
56 aberrant drift hypothesis (Hjort 1914). Further development of these ideas include the
57 member-vagrant (Sinclair 1988, Sinclair and Iles 1989) and migration triangle hypotheses
58 (Harden-Jones 1968, Cushing 1975, Secor 2002). These hypotheses state that spatial
59 dynamics, to a large extent driven by the ocean currents, may have pronounced impact on
60 early survival. More recently, spatial effects on survival have been reported on smaller
61 spatial scales and on specific life stages (Ciannelli et al. 2007, Langangen et al. 2014a).
62 The combined effects of variable drift trajectories and spatial variations in natural

mortality on recruitment are still unclear, but may potentially be significant in shaping recruitment variations.

Opdal et al. (2011) demonstrated that for Barents Sea (BS) cod (often denoted Northeast Arctic cod or alternatively Arcto-Norwegian cod) the north-south differences in cumulative mortality probability due to temperature regulated time spent in the larval life stage are larger than the inter-annual variations. They conclude that increased survival of the larvae from the central and southern spawning locations (including Lofoten, Møre and spawning grounds further south, Figure 1) may explain the long and costly southwards migration of the parents. They, however, do not account for differences in mortality due to, e.g., spatial variability in predation or food-limitation, which are likely to be present in the early life stages of the BS cod (Ciannelli et al. 2007, Langangen et al. 2014a). The study is limited to variations in average survival of offspring spawned over the whole spawning season and to a limited number of life stages (eggs and larvae). It has been pointed out that differentiating between multiple life-stages may be essential when investigating pre-recruitment dynamics (Houde 2008).

Here, we investigate the possible offspring fitness benefits of long and energetically costly adult spawning migration in a marine fish. In particular we investigate the survival and growth the first year of life of BS cod offspring originating from a northern and a central spawning ground. Our study builds upon Opdal et al. (2011), but is extended to include additional life stages (eggs, larvae, pelagic juvenile and 0-group fish). Furthermore, we account for spatially resolved empirically estimated mortality fields separately for the summer and winter of the first year of life, thereby

extending the analysis to include effects of spatial differences in mortality due to, e.g., predation and starvation.

Materials and methods

Study system

The BS cod inhabit the arcto-boreal Barents Sea situated to the north of mainland Norway and western Russia. Mature BS cod undertake a major contranatal spawning migration in winter and early spring to spawning grounds situated along the Norwegian coast (Bergstad et al. 1987, Yaragina et al. 2011), from Finnmark in the north to Møre (and in periods beyond) in the south (Figure 1). The major spawning concentration is found in the Lofoten/Vesterålen area, and the spawning takes place from around early March to the end of April (Bergstad et al. 1987). The pelagic eggs and larvae are transported along the Norwegian coast and to a large extent into the Barents Sea. By fall, the so-called 0-group fish start to become more demersal. The distribution of young fish is fairly stationary until around age 2 (Baranenkova 1957, Maslov 1960, Ottersen et al. 1998). The life-cycle is completed with BS cod reaching maturity (around the age of 5-9 years), when they start their annual southward spawning-migration. For a detailed review of the early life history dynamics of the BS cod we refer to Ottersen et al. (2014).

Ocean model

We use the SVIM hydrographic archive (Lien et al. 2013, 2014) to drive the off-line particle drift. In short, the SVIM archive was constructed using the Regional Ocean Modeling System (ROMS, Shchepetkin and McWilliams 2005, Haidvogel et al. 2008), with a setup covering the North, Norwegian, Barents and Kara Seas and parts of the

Arctic Ocean. The spatial resolution is 4 by 4 km horizontally and consists of 32 layers vertically with the resolution in meters varying with the bottom depth. We do not consider additional diffusion in the drift model, as the relatively high spatial resolution of the model allows for realistic modeling of relevant features. The model archive has been extensively validated with available current and hydrographic data (Lien et al. 2013). We use daily averaged flow, temperature and salinity fields as input in the individual based drift model.

Individual based model for early life stages

The individual based model accounts for egg development according to ambient temperature and the vertical distribution is determined by buoyancy and turbulence (Sundby 1997, Thygesen and Ådlandsvik 2007). The eggs hatch into larvae of length 4.0 mm, based on reported length two days after hatch (Otterlei et al. 1999), and weight of 0.0448 mg, after about 20 days (D) depending on the ambient temperature (T in °Celsius) according to $\ln D = 3.65 - 0.145T$ (Ellertsen et al. 1987). The larvae grow according to an *ad libitum* feeding growth curve (Folkvord 2005) determined by the ambient temperature. The specific growth of the larvae (*SGR*) is given by

$$SGR = a_0 + b_0T + b_1T \log(DW) + b_2T \log(DW)^2 + b_3T \log(DW)^3,$$

where $a_0 = 1.08$, $b_0 = 1.79$, $b_1 = -0.074$, $b_2 = -0.0965$, $b_3 = 0.0112$ and *DW* is the dry weight in mg. At the pelagic juvenile period, we use the *ad libitum* feeding growth model of Björnsson et al. (2007). Note that by using an *ad libitum* feeding growth model, we assume no variations in growth of the larvae due to, e.g., spatial variations in food availability. We follow the method presented by Castaño-Primo et al. (2014) and allow

for a smooth transition between the larval and pelagic juvenile growth models at a weight of 400 mg. For the pelagic juveniles, the specific growth (SGR) is given by

$$SGR = \exp(a_{juv} + b_{juv}T + c_{juv}T^2 + (d_{juv} + e_{juv}T) \cdot \log(WW)),$$

where $a_{juv}=0.7620$, $b_{juv}=0.3982$, $c_{juv}=-0.0128$, $d_{juv}=-0.1500$, $e_{juv}=-0.0239$ and WW are the wet weight in grams. To account for differences between wet weight and dry weight we use a conversion factor of 0.217 (Peck et al. 2003).

In the larval and pelagic juvenile stages, the vertical behavior is determined by seasonal, latitudinal and depth dependent light conditions (downward movement during high light conditions and vice versa) to simulate diel vertical migration of the offspring (Lough and Potter 1993). Given the vertical position of the egg, larval or juvenile particle, the horizontal advection is calculated at hourly time steps, using a Runge-Kutta method for temporal interpolation (Ramsden and Holloway 1991). For an extensive description of the individual based model we refer to, e.g., Opdal et al. (2011) and Langangen et al. (2014a).

Spawning grounds, particle release and calculation of offspring survival

The spawning grounds of the BS cod are distributed along the coast of mid and northern Norway, with Lofoten/Vesterålen as the core spawning region (Figure 1, Bergstad et al. 1987, Sundby and Nakken 2008, Ottersen et al. 2014). In recent decades, the spawning has shifted towards the north, with most spawning taking place in the Lofoten area and northwards (Bogstad 2009).

In the present study, we investigate offspring survival and growth based on two selected spawning grounds, Moskenesgrunnen outside the Lofoten archipelago (from

now on denoted the central spawning ground) and Breivikbotn in western Finnmark (from now on denoted the northern spawning ground), see Figure 1. These two spawning grounds were selected to examine potential latitudinal differences in cumulative mortality probability, hence contrasting the physical environment experienced by the eggs, larvae and juvenile fish, as well as the potential dissimilar spatial mortality experienced by the offspring. In addition, the two spawning grounds exemplify the dissimilarity in adult migration cost, as the spawners at the central spawning ground in Lofoten face an additional approximately 400 km of contranant migration.

Each day, throughout March and April, we release 750 egg particles, considered to represent multiple eggs (on the order millions or more) in a super-individual perspective (Scheffer et al. 1995), on each of the two spawning grounds. In total, more than 90 000 particles are tracked each year. To account for seasonal variation in spawning intensity, we weigh the particles according to a Gaussian function centered on 1 April with a standard deviation of 14 days (cf. Pedersen 1984). About 14 days delay in peak spawning at the northern compared to the central spawning ground has been reported (Sundby and Bratland 1987). The results presented here do not change qualitatively when spawning is shifted to later in the season on the northern spawning ground (see Supplementary Data A).

Mortality is applied according to stage, with instantaneous rates of 0.17 day^{-1} for eggs and 0.075 day^{-1} for larvae (Langangen et al. 2014b) and we fix the mortality for the pelagic juvenile period to 3.6 (Sundby et al. 1989). We set the instantaneous mortality over the first winter (from the beginning of October until the beginning of March the next year) to 0.9, which corresponds to an average survival (e^{-m}) of about 40% (Ohlberger et

al. 2014). When applying the instantaneous mortality, we assume that the metamorphosis from larvae to pelagic juveniles takes place at 18 mm length. The stage durations as eggs and larvae are temperature dependent and hence variable between the particles. Because the variations in the duration of the pelagic juvenile period are largely unknown, we allow the drift period to last until 1 October and set a fixed mortality of this period to 3.6.

In addition to the average stage specific mortalities until the end of the 0-group stage (first year of life), we also optionally apply two empirically estimated spatial mortality fields, one in the summer applied mainly at the larval stage (Langangen et al. 2014a) and one over the winter applied at the end of the pelagic juvenile period (0-group fish, Ciannelli et al. 2007). Here, we investigate the consequences for survival until age 1 if the mortality varies in space according to the estimated mortality field averaged over the years. The spatial mortality field in the summer is applied according to the location (longitude and latitude) of each particle at the end of June. This relatively simple method to correct for spatial variation in mortality is used to be consistent with the estimation method for the spatial mortality field; the estimated field represents the cumulative mortality probability of particles at these locations and date (Langangen et al. 2014a). The mortality field accounts for spatial variation in mortality over roughly the past 45 days of drift. The 0-group spatial mortality is applied according to the location of each particle at the end of the pelagic juvenile period assumed to be at the beginning of October. Interpolation of the natural mortality field over the winter to the particle locations is done in a similar fashion as in the summer (Langangen et al. 2014a). In short we fit a spatial generalized additive model (GAM, Wood 2006) to the spatially explicit empirical data points used by Ciannelli et al. (2007). We use the model,

$m(lon, lat) \sim s(lon, lat) + \varepsilon$, where m is the spatial mortality at longitude (lon) and latitude (lat), s is a smoothing spline and ε a Gaussian error term ($r^2=0.31$). The spatial coverage of the two estimated mortality fields and an illustration of the spatial variations in mortalities are shown in Figure 1. In the relatively few cases where the particles are situated outside the spatial coverage of the mortality fields (Figure 2), we apply no spatially explicit mortality (see Supplementary Data B for tests of relaxing this assumption). Note that we have not included the more southern spawning grounds in the Møre region (Figure 1), as eggs released here would very often not reach the area of interest where the spatial variable mortality fields are available. We focus the analysis on the years when data used to estimate both the annual average summer mortality fields (1959-1993) and winter mortality fields (1980-2004) are available, the 14 years 1980-1993.

Results

We calculate the yearly average mortality until the end of the larval stage, first assuming spatially uniform natural mortality (Figure 3, *upper panel*) and secondly accounting for the spatially variable natural mortality in the summer (Figure 3, *lower panel*). When assuming a spatially uniform survival, in which case temperature dependent development accounts for all inter-annual variability in survival, we get a clear advantage for the central spawned larvae as compared to northern spawned larvae (Figure 3, *upper panel*, survival in the north on average 42 % of survival in the central area). The differences in mortality probability between the two spawning grounds, in this case, are driven by variable stage duration due to differences in temperature. The average egg stage duration

is 18.3 days for the central spawned eggs and 21.8 days for the northern spawned eggs. For the larval stage, the stage duration is on average 61.2 days for the central spawned offspring and 65.3 days for the northern spawned offspring. However, when we in addition to the stage specific mortality also account for the spatial variations in natural mortality the advantage of central spawning is almost fully compensated (Figure 3, *lower panel*, survival in north on average 94 % of survival in central area).

Moreover, when assuming spatially homogeneous mortality, we find a distinctly lower survival of early spawned offspring compared to late spawned offspring at both spawning grounds (Figure 4). This within season advantage of late over early spawned eggs is significantly reduced when accounting for the spatial variations in mortality (Figure 4), as early spawned central eggs have about the same survival as late spawned (with somewhat lower survival for intermediate spawned eggs), while the northern spawned eggs have almost constant survival over the season. The significant alteration of the survival when accounting for spatial variation in natural mortality is due to an indirect “seasonal” effect. Since the early spawned eggs at any given time in general will have drifted farther than the late spawned, they will in general occupy different areas (Figure 2). This difference in area gives the early spawned eggs a higher survival compared to the late spawned eggs, due to the spatial structure in the mortality field (Figure 1) and the particle distributions (Figure 2). Average survival until the end of the larval stage for offspring spawned at the central spawning ground is reduced from 5.4×10^{-4} to 4.4×10^{-4} when accounting for spatial variation in mortality while the average survival for larvae spawned at the northern spawning ground correspondingly is increased from 2.3×10^{-4} to 4.0×10^{-4} .

In addition, we find that accounting for spatial variation in natural mortality over the first winter further increases the survival of the northern spawned offspring relative to the central spawned offspring (Figure 5). The average survival of the fish originating from the central spawning ground is 1.1×10^{-5} while the fish originating from the northern spawning ground has a survival of 1.7×10^{-5} when accounting for spatial variations in natural mortality in both summer and winter. On the other hand, the average survival is 6.0×10^{-6} for the central spawned fish while the northern spawned fish have an average survival of 2.6×10^{-6} when not accounting for spatial variation in natural mortality in summer and winter.

Beyond the direct effects on offspring mortality, we also find an offspring size advantage of central spawning. In the beginning of October, the weight of the central spawned offspring is about 20 % higher than that of the northern spawned offspring (centrally spawned offspring have an average weight of about 1.3 g compared to about 1.1 g for northern spawned offspring). We also note that this advantage is variable between the years, but still is consistently in favor of central spawning in all years. In mid July, the simulated length of the centrally spawned offspring is 27.4 mm, while the northern spawned offspring is 24.7 mm long. The temperature driven increased growth for the central spawned offspring also results in a shorter developmental time from spawning until the end of the larval stage. The developmental time is on average more than 7 days shorter for the offspring spawned at the central spawning ground (Figure 4). Furthermore, in the beginning of October, the center of the distribution of central spawned fish (23.2° E, 71.5° N) is considerably further west in the Barents Sea compared to that of the northern spawned fish (27.4° E, 70.9° N).

270

271 **Discussion**

272 Our results imply that spatial variations in offspring survival may, over generations,
273 impact the development of spawning strategy including the use of spawning grounds for
274 marine fish. Specifically, accounting for spatial variations in mortality may significantly
275 affect the estimated survival of offspring through the first year of life. This is
276 demonstrated in our example, where the advantage of a longer migration distance for
277 offspring survival is significantly reduced or even cancelled when accounting for this
278 variation. In addition, our results highlight the importance of accounting for the many
279 factors that contribute to spatial heterogeneity in survival of offspring in order to make a
280 more accurate evaluation of the migration benefits. This includes abiotic factors, such as
281 temperature, turbulence and drift patterns, as well as biotic factors such as food
282 availability and predation pressure. Using the empirically estimated mortality fields, we
283 have implicitly accounted for most of these factors.

284 Theory suggests that the reproductive strategy (choice of spawning location) is an
285 optimization between the parental cost, including migration, and offspring survival (i.e.
286 Lack's principle, Lack 1954). For a recent review of evolutionary and ecological
287 constraints of spawning habitat in fish, see Ciannelli et al. (2015). Since it is well
288 established that the main spawning of the BS cod takes place in the Lofoten area
289 (including the Moskenesgrunnen, Bergstad et al. 1987, Sundby and Nakken 2008), there
290 should be a benefit of spawning in terms of increased offspring survival, growth and/or
291 fecundity in these locations compared to the less used northern locations
292 (e.g., Breivikbotn), which would involve less parental investment to reach. The energetic

cost of the spawning migration in BS cod was investigated by Jørgensen et al. (2008), suggesting state (size and nutritional condition) dependent migration costs. Increased survival in the south due to higher temperatures causing reduced stage duration has been suggested by Opdal et al. (2011) to be the main offspring benefit. However, a possible limitation of this analysis is the lack of empirical input into the scenarios. For example, if the main driver of survival is stage duration, late spawning would always be favored (Figure 4). However, when a larva is spawned later in the season, it will in general have less time for growth until the end of the growing season (e.g., in the fall for the BS cod). Based upon empirically estimated mortality fields and a coupled physical-biological drift model incorporating multiple life-stages, we find that there is only a small survival benefit for central compared to northern spawned offspring at the end of the larval stage. The increase in survival is on average less than 10% compared to more than 130 % increase when assuming spatially homogeneous mortality. Our results, albeit based on only two spawning grounds in the central and northern part of the distribution, indicate a larger variation in survival between years compared to between the spawning grounds. This result indicates that environmental variations (biotic and abiotic, often denoted cohort effects, Beckerman et al. 2002), may have a larger influence on early offspring survival than spawning location for BS cod (Sundby and Nakken 2008). Note that these results largely hold when using year specific mortality fields (Supplementary Data C).

Furthermore, we find that in the first spring (age 1 fish) the direct benefit of central spawning for early offspring survival may have vanished completely. However, the survival until age 1 is uncertain, due to unknown scaling of the variance in the spatial variation of the mortality field over the first winter. Note, that if we scale the 0-group

survival with an average instantaneous mortality of 0.9 over the first winter (Ohlberger et al. 2014) and a spatial standard deviation of 0.3 (to avoid negative mortality, which has been allowed for when directly using the estimated spatial variation in mortality with a standard deviation of about 2.7), offspring originating from the central spawning ground have almost equal survival to age 1 as compared to the northern spawning ground. Nevertheless, whatever we choose as a scaling of the spatial variation in the 0-group fish mortality field, the two mortality fields both point towards increased survival of northern compared to central spawned offspring. We note that variations in survival in the larval stage have a larger potential to affect the overall survival compared to survival over the first winter, as the larval stage has an average mortality of about 4.5 or more compared to the 0-group mortality of just below 1 (Ohlberger et al. 2014, Langangen et al. 2014b). However, variations in survival after the 0-group stage are likely significant, as year-class-strength may change considerably between settlement and recruitment at age 3 (Bogstad et al. 2015).

The relatively small differences in mean survival between the two spawning grounds, including years with better survival prospects for the northern compared to the central spawned offspring (Figures 3 and 5), indicate that there may be other offspring benefits beyond early survival to compensate the extra cost of migration to the Lofoten area. We suggest two effects that are likely to further contribute to extra offspring benefit (increased survival, growth and/or fecundity) in the Lofoten area. First, the central spawned offspring are likely to be significantly bigger than the northern spawned offspring already in the fall, and in addition central spawned offspring tend to settle in more westerly parts of the Barents Sea compared to the more northern spawned offspring.

Due to the colder bottom conditions in the eastern Barents Sea, the fish settling in the eastern Barents Sea are likely to experience reduced growth compared to more westerly settled fish (Helle et al. 2002). It has been shown that the distribution of young BS cod (until at least age 2) is fairly stationary (Baranenkova 1957, Maslov 1960, Ottersen et al. 1998), which together with the temperature differences may lead to further size differences between offspring originating from the different spawning grounds. Such spatial impacts on size may result in long lasting effects, possibly affecting the fish throughout life. Long lasting effects of conditions experienced during early life stages can be very important also at the population level (Metcalf and Monaghan 2001, Beckerman et al. 2002, Vindenes and Langangen 2015). Second, early survival from spawning to spring (i.e., prior to the period the larval mortality field applies) may be higher in the central area, possibly due to higher probability of a good match with the main zooplankton prey (*Calanus finmarchicus*) in the critical first feeding period of the fish larvae (match-mismatch, Cushing 1990, Durant et al. 2007). These points taken together are likely to significantly contribute to the overall benefit of the centrally spawned offspring and hence are probably an important component in understanding the patterns and drivers of the spawning migration of BS cod (Sundby and Nakken 2008, Opdal 2010, Opdal and Jørgensen 2014). Based on the current study we can not conclude which factor is the main driver in the observed northward shift in spawning location in recent years: demography (Opdal 2010, Opdal and Jørgensen 2014) or temperature (Sundby and Nakken 2008).

The mortality fields were estimated assuming density independence. However, the mortality field estimated in the summer show a positive correlation with density

(Langangen et al. 2014a). It is conceivable that the increased mortality in the central area and the decreased mortality in the north may be due to compensatory density dependence possibly due to, e.g., resource competition and/or spatial aggregation of predators. Indeed, Ciannelli et al. (2007) suggest incohort density dependence in mortality over the first winter (demersal 0-group fish), attributing this to cannibalism. Whatever the driver behind the density dependence, such effects may result in an overestimation of the benefit of northern spawning as the empirical estimate was based on a period when the spawner density in this region was fairly low (Sundby and Nakken 2008, Opdal 2010). Even if the spatial scales are quite large, we would expect a distribution among the spawning grounds that makes fitness of spawners of a given size fairly equal (cf., ideal free distribution, Fretwell and Lucas 1969).

The simulated size of the offspring is low compared to estimates from field data on larvae in June (Stige et al. 2015) and pelagic early juveniles in July (Suthers and Sundby 1993, Hallfredsson and Pedersen 2007). Comparing the simulated length directly with the field data is not straight forward as we only simulate two spawning grounds whereas the larvae sampled in the field may originate from a broad spectrum of spawning grounds. Stige et al. (2015) performed a full statistical comparison between observed and modeled larval lengths for larvae originating from spawning grounds situated along the coast of Norway using the same model as used here. They concluded that the model captures the spatiotemporal variations in length fairly well ($r^2=0.23$) but there was a consistent underestimation of about 4.5 mm. Possible explanations for the underestimated lengths include a bias in temperature in the drift model (Lien et al. 2013), too low

hatching length of the larvae or possibly stronger size dependence in mortality (see Supplementary Data D for further discussion).

Our results are fairly robust to the general assumptions made (see Supplementary Data A-D); nevertheless there are some weaknesses. One possible limitation of the current analysis is the lack of spatially resolved mortality fields over the whole early life period in question (eggs to age 1). For example, spatial differences in survival from spawning to spring (about 40 days) and from summer to fall (about 90 days) may have different impact on offspring survival among the spawning grounds. As discussed above, in the spring possible mismatch with the main prey may lead to higher survival for offspring originating from the central compared to the northern spawning ground. In the period from July to the end of September the spatial variation in natural mortality is unknown and can be fairly uniform or favor any of the two spawning grounds. However, we have included spatial mortality fields for two time periods (summer and winter, a total time of about 7.5 months), which consistently point toward increased survival of the northern compared to central spawned offspring. Another limitation, which may somewhat influence our results, is the incomplete spatial coverage of the two mortality fields. We have assumed that the relatively few particles not within the coverage area (Table S1) experience average mortality (no explicit variations in spatial mortality), but relaxing this assumption does not significantly alter the results (Supplementary Data B). Note that we assume that the offspring only exhibit self-propelled swimming in the vertical direction. Hence, horizontal swimming behavior, which may be significant in the pelagic early juvenile period, is a source of uncertainty in the estimated offspring location towards the end of the drift period in early October.

In this study we have assumed *ad libitum* feeding conditions. Hence, we have not accounted for, e.g., effects of spatial variations in food quality and availability on growth. Such variability in space may potentially affect the growth of offspring differently between the spawning grounds. As discussed above, it is likely that the feeding conditions are favorable for centrally spawned offspring due to better match with the main zooplankton prey, which would likely enhance the offspring size benefit of longer southwards migration.

Errors in the drift model may also potentially affect the results presented here, as the spatial location of the offspring has a large impact on the survival. For example, if the drift speed is too low in the simulation (Lien et al. 2013), the benefit of northern spawning may possibly be overestimated, as these particles are released close to areas with high survival in the summer (Figure 1). On the other hand, low drift speed may also result in low abundance in the offshore direction where estimated survival is high. Finally, we note that the estimated mortality fields are associated with several sources of uncertainty, which are discussed in detail by Ciannelli et al. (2007) and Langangen et al. (2014a). For example, the summer mortality field is more uncertain in some areas with sparse data coverage (e.g., north-eastern parts of the summer survey area, Langangen et al. 2014a). The winter mortality field may miss important patterns due to sampling challenges, such as ice coverage and shallow sampling compared to the possible depth distribution of the 0-group fish (Ciannelli et al. 2007).

Despite some caveats, this simulation study clearly demonstrates that accounting for spatial differences in survival across multiple life stages may be very important when evaluating the reproductive strategy of a migratory marine fish. Specifically, our results

indicate that the fitness benefit of southwards migration and spawning in BS cod is not mainly due to higher offspring survival the first months of life, but rather due to beneficial effects of the offspring acquiring a large size.

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Figure 1 Overview of the study area. The two spawning grounds studied (1. Moskenesgrunnen and 2. Breivikbotn, black polygons), coverage of the estimated mortality anomaly fields in summer (light grey shaded polygon with dashed black outline) and in winter (dotted polygon with solid black outline) are outlined. The time and intensity of spawning are illustrated in the upper left corner. Illustration of the two mortality fields (summer and winter) are shown on the small maps in the upper and lower right corners. Dark color indicates high mortality, while light color indicates low mortality.

Figure 2 Example of particle drift from the two spawning grounds in 1982 (1. The central spawning ground: *Moskenesgrunnen*, left panels and 2. The northern spawning ground: *Breivikbotn*, right panels). Early released particles (*blue*) and late released particles (*red*) are shown separately. The upper panels show the locations of the particles in late June, while the lower panels show the locations of the particles in the beginning of October, the times when the summer and winter spatial mortality fields are applied respectively. The solid lines outline the coverage of the spatial mortality fields for the respective seasons.

468

469 **Figure 3 The survival probability of the offspring to the end of the pelagic early**
470 **larval stage for the two spawning grounds (1. The central spawning ground:**
471 **Moskenesgrunnen, *solid lines with diamonds* and 2. The northern spawning ground:**
472 **Breivikbotn, *dotted lines with circles*) are shown. The upper panel shows survival**
473 **probability varying only due to temperature dependent variation in stage-duration,**
474 **while the lower panel shows survival probability when also spatially explicit**
475 **variation in survival (due to e.g. variable predation pressure and food levels) is**
476 **accounted for.**

Figure 4 The survival probability from spawning to larval length of 18 mm averaged over the 14 years for different spawning days, for the centrally spawned offspring (*red*) and the northern spawned offspring (*blue*), spatially homogeneous mortality (*dotted lines*) and spatially variable mortality (*solid lines*), are shown. In addition, differences in developmental time to larval length of 18 mm between the two spawning grounds are shown (*black solid line*).

Figure 5 The survival probability of the fish originating from the two spawning grounds (1. The central spawning ground: Moskenesgrunnen, *solid lines with diamonds* and 2. The northern spawning ground: Breivikbotn, *dotted lines with circles*) to spring the second year of life. Spatial variations in mortality in both summer and winter are accounted for.

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Example of particle drift from the two spawning grounds in 1982 (1. The central spawning ground: Moskenesgrunnen, left panels and 2. The northern spawning ground: Breivikbotn, right panels). Early released particles (blue) and late released particles (red) are shown separately. The upper panels show the locations of the particles in late June, while the lower panels show the locations of the particles in the beginning of October, the times when the summer and winter spatial mortality fields are applied respectively. The solid lines outline the coverage of the spatial mortality fields for the respective seasons.
241x241mm (300 x 300 DPI)

The survival probability from spawning to larval length of 18 mm averaged over the 14 years for different spawning days, for the centrally spawned offspring (red) and the northern spawned offspring (blue), spatially homogeneous mortality (dotted lines) and spatially variable mortality (solid lines), are shown. In addition, differences in developmental time to larval length of 18 mm between the two spawning grounds are shown (black solid line).
143x103mm (300 x 300 DPI)

Supplementary Data

A: Effect of late spawning in the north

As suggested by (Sundby & Bratland 1987), the fish spawning in Breivikbotn are likely to spawn later in the season compared to more central spawning grounds (e.g., Moskenesgrunnen). To test the effect of such late spawning on our results, we have applied a later spawning intensity to the northern compared to the central spawned eggs, as shown in figure S1.

Figure S1 The spawning intensity applied to the central spawned eggs (dotted line) and the delayed spawning intensity applied to the northern spawned eggs (solid line) are shown.

The resulting estimated mortalities are shown in figure S2. Based on this test, we conclude that late spawning does not change the main conclusion in this work, namely that survival of offspring spawned in Breivikbotn has about equal survival as offspring spawned in Moskenesgrunnen. If anything, this late spawning seems to increase the

survival of the northern spawned offspring compared to the central spawned offspring (compare with figure 3 in the main text.).

Figure S2 The survival probability of the offspring to the end of the pelagic early larval stage for the two spawning grounds (1. The central spawning ground: Moskenesgrunnen, *solid lines with diamonds* and 2. The northern spawning ground: Breivikbotn, *dotted lines with circles*) are shown. The upper panel shows survival probability varying only due to temperature dependent variations in stage-duration, while the lower panel shows survival probability when also explicit spatial variations in survival (due to e.g., variable predation pressure and food levels) are accounted for. Here we accounted for delayed spawning intensity in the north, see figure S1.

B: Effect of particles residing outside area with mortality field

The drift of the particles sometimes leads to particles residing outside the areas where we have empirically estimated mortality fields (e.g., Figure 3 in the main text). To quantify this effect, we give the percentage of particles residing outside these areas in Table S1. Usually, the percentage of particles residing outside the areas with information on the spatial variable mortality field is small. However, there are a few cases where there are a relative high number of particles outside these areas, especially for particles originating from the central spawning ground in the winter. This is due to a relatively high component of particles drifting along the shelf edge up along Svalbard/Spitsbergen. In the main text we give these particles an average survival value. Here we relax this assumption by extrapolating the mortality field in the summer, to capture possible higher survival even further east in the Barents Sea. Hjort (1914) suggested that larvae advected to too deep areas at the time of settlement would not survive. To test how this may affect our results, we assume that juveniles settling in deeper water than 500 m in the winter experience 100 % mortality and if the juveniles settle at less than 500 m depth north of 77°N we assign twice the mortality rate over the first winter (1.8). The result of this test is shown in Figures S3 and S4. These results are directly comparable to Figures 3 and 5 in the main text.

Also, we have extrapolated the mortality fields into the shore, as we consider this our best knowledge of how the mortality field varies in these areas. However, it is possible that the mortality in the near shore area is higher due to e.g., predation mortality due to sea birds and pelagic fishes. As shown in figure S5 by extrapolating the mortality field, the mortality increases towards land. To further test the impact of an even higher

mortality in the area close to shore around Breivikbotn, we gave all particles residing outside the observation area (light grey region in figure S5) and at the same time north of 70 °N and west of 30 °E a mortality of 3.0. The result of such a test is shown in figure S6.

Based on these tests, we conclude that spatial extrapolation of the summer mortality field only has a minor influence on the calculated mortalities, and hence is unlikely to influence the main conclusion of the current work.

Table S1 Percentage of particles from the two spawning grounds outside of the empirically estimated mortality fields in summer and in winter for the 14 years of interest.

	Central		North	
	Summer	Winter	Summer	Winter
1980	3 %	13 %	3 %	0.2 %
1981	6 %	19 %	6 %	2 %
1982	8 %	16 %	11 %	2 %
1983	6 %	35 %	4 %	2 %
1984	6 %	19 %	22 %	5 %
1985	8 %	50 %	6 %	0.6 %
1986	14 %	20 %	10 %	1 %
1987	9 %	18 %	3 %	0.3 %
1988	2 %	22 %	6 %	0.9 %
1989	5 %	9 %	4 %	2 %
1990	2 %	8 %	3 %	0.1 %
1991	5 %	13 %	3 %	2 %
1992	7 %	29 %	5 %	0.4 %
1993	3 %	30 %	3 %	0.2 %

Figure S3 The survival probability of the eggs to the end of the pelagic early larval stage for the two spawning grounds (1. Moskenesgrunnen, *solid lines with diamonds* and 2. Breivikbotnen, *dotted lines with circles*) are shown. The spatially resolved mortality is accounted as before for the particles inside the area of interest, while we extrapolate the mortality field for particles outside the area of interest.

Figure S4 The survival of the fish to the beginning of spring the second year. The survival is based on accounting for spatial variations in both summer and winter, where we extrapolate particles missing the area of interest in the summer and applying high mortality to the particles ending up in deep water (deeper than 500m) in the winter.

Figure S5 Overview of the area of data coverage in summer (light grey shaded region). The solid vertical line indicates the curve where we extract the mortality shown in the upper right corner. The two spawning grounds are shown in black.

Figure S6 Same as figure 3 in the main text, but with increased mortality in the near shore areas around Breivikbotn.

C: Effect of year specific mortality fields

We tested the sensitivity of the results to using the average spatial mortality field by redoing the analysis using year specific mortality fields in the summer. The results are shown in Figure S7. We conclude that the main results of the paper are fairly stable to this assumption since the results of the test are fairly similar to the results presented in the main text. However, there are some indications of even higher survival in the northern spawning ground compared to the central spawning ground. The estimated survival from the year 1992 (and possibly 1993) seems high for the northern spawned larvae and this survival should be considered with care. The large difference in survival between the two spawning grounds is largely due to increased survival of offspring originating from the northern spawning ground. Northern spawned offspring reside in spatial areas with high survival, as is also the case when the average mortality field for 1992 but not in 1993. This illustrates that there is quite some variability between years (and between the average and year specific mortality fields) in the spatially resolved mortality field. Nevertheless, we conclude that the main results (e.g., about equal survival of offspring originating from the two spawning grounds) are fairly robust to the use of average or year specific mortality fields.

Figure S7 This figure is similar to figure 3 in the main text. The survival probabilities from spawning to the end of the pelagic early larval stage for the two spawning grounds are shown. The upper panel assumes homogeneous mortality, while the lower panel shows survival when accounting for year specific spatial mortality.

D: Further testing of the modelled growth

To further test how the bias in modelled temperature, the hatching length of the larvae and stronger size dependence of mortality may affect the modelled length we performed a simple test for the year 1988 (same year as data are available for pelagic juveniles in mid July (Suthers & Sundby 1993)). In this test, we increased the ambient temperature experienced by the particles by 0.5 degrees Celsius and increased the hatching length from 4 mm to 4.5 mm. In such a simulation, the mean length of pelagic juveniles in mid July was 28.9 mm, which is much closer to the reported lengths around 30 mm. The remaining differences may be explained by for example field-sampled larvae originating from warmer spawning grounds (e.g., Innersiden where the particles will experience more retention compared to Moskenessgrunnen) or stronger contribution from early spawned offspring due to e.g., stronger size specific survival. We note that early spawned offspring (before 1 April) had a length of 32.0 mm compared to a length of 25.7 mm for late spawned offspring. In this simulation we find a very similar pattern in the changes in survival in 1988 as compared to the simulation presented in the main paper. In the center, survival until summer is reduced from about 0.39 to 0.23 ‰ when accounting for spatial variations in mortality and in the north survival until summer is elevated from 0.15 to 0.17 ‰. Similar numbers for the year 1988 in the main simulation was a reduction from 0.44 to 0.26 ‰ in the centre and an increased survival from 0.16 to 0.18 ‰ in the north. Based on these results we conclude that these issues are not likely to affect the main conclusion of this work.

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