THE EVOLUTION OF SPAWNING MIGRATIONS: STATE DEPENDENCE AND FISHING-INDUCED CHANGES

Christian Jørgensen,[1,3] Erin S. Dunlop,[1,2] Anders Frugård Opdal,[1] and Øyvind Fiksen[1]

[1]*Department of Biology, University of Bergen, Box 7803, N-5020 Bergen, Norway*
[2]*Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, Norway*

Abstract. Individuals migrate to exploit heterogeneities between spatially separated environments to modulate growth, survival, or reproduction. We devised a bioenergetics model to investigate the evolution of migration distance and its dependence on individual states. Atlantic cod *Gadus morhua* ranges from sedentary populations to stocks that migrate several thousand kilometers annually. We focused on the Northeast Arctic cod stock, which migrates south to spawn. A linear relationship between migration distance and the expected survival of offspring was assumed, here understood as the prospects for future survival and development that a fertilized egg faces at a particular spawning location. Reasons for why it may increase southward include warmer water that increases development rates, and thereby survival, along the pelagic drift trajectory.

In the model, ingested energy can either be allocated to growth or stored for migration and reproduction. When migrating, individuals forgo foraging opportunities and expend energy. Optimal energy allocation and migration strategies were found using state-dependent optimization, with body length, age, condition, and current food availability as individual states. For both a historical and contemporary fishing regime we modeled two behaviors: (1) homing cod returning to the same spawning site each year and (2) roaming cod with no such constraints.

The model predicted distinct regions of locally high spawning stock biomass. Large individuals in good condition migrated farthest, and these also tended to mature later in life. The roaming cod spread farther south as they grew larger and older. Homing cod did not have this freedom, and spawning was generally concentrated along a narrower stretch of the coastline.

Under contemporary fishing, individuals matured earlier at a smaller size, had shorter migrations, spawned over a contracted geographical range, and tended to be in poorer condition. The effects were most pronounced for the homing behavior.

Key words: energy allocation; fisheries-induced evolution; Gadus morhua; geographical distribution; life history strategy; maturation; migration; state dependence.

INTRODUCTION

By migrating, individuals exploit heterogeneities between spatially separated environments to modulate growth, survival, or reproduction. Since animal migrations are no doubt costly, there has to be adaptive advantages for the individuals who migrate, potentially mediated via their offspring (Sutherland 1996). Any benefit to growth, survival, or reproduction can in principle lead to the establishment of animal migrations. Examples of direct benefits to the migrating individual include energetics, nutrition, lowered disease-risk, and reduced predation (Dingle 1996, Buehler and Piersma 2008). With such assumptions, Alexander (1998) presented generalized equations for when migrants should move from a fixed breeding area to an over-wintering area that is favorable in terms of energy or survival. However, the adaptive basis of migrations might also be related to indirect benefits, where parents confer advantages to their offspring by mating or reproducing in certain areas. For example, area- or time-specific rates of early development and survival can provide constraints on adult life histories, and may act as selective forces for migration and phenology (Jonzén et al. 2006, Reznick et al. 2006).

The early life stages of fish at high latitudes can generally benefit from higher temperatures and plentiful food to achieve rapid development and increased survival. For pelagic larvae, growth and survival furthermore depend on how these factors integrate and can be modulated over the pelagic drift trajectory (Fiksen et al. 2007). One demonstration was provided by Mullon et al. (2002), who investigated optimal spawning locations in anchovies *Engraulis capensis* in an ocean circulation model. By assuming that pelagic larvae had to remain inshore, avoid cold water, and end up in suitable nursery grounds, their model predicted favorable spawning locations and routes of adult spawning migrations.

Although such offspring benefits may be a primary driver to establish and maintain spawning migrations, they come at a cost and are subject to trade-offs. For adults, migrations cost energy and time and can lead to lost feeding opportunities and mortality. Thus, what is a benefit to the offspring often entails a cost to the adults, and understanding such adaptations requires consideration of the entire life cycle. How parental life histories evolve under such selection pressures depends on fitness benefits for offspring, and costs of spawning at a given location.

The trade-offs between costs and benefits of migration might crucially depend on body size or condition (Forseth et al. 1999, Nøttestad et al. 1999, Block et al. 2005). This is especially important in indeterminate growers such as most fish, where life-long growth may lead to large differences in length, mass, condition, and fecundity even among individuals that have reached sexual maturity. When it comes to costs, the mass-specific cost of transport is generally reduced with increasing body size in fish (Ware 1978, Alexander 2003). In comparisons across fish species, migratory species are on average larger than nonmigratory species (Roff 1988), and there are positive relationships between migration distance and swimming efficiency (Bernatchez and Dodson 1987) and between migration distance and body size (Schaffer and Elson 1975, Roff 1988). As body size is important for migrations when viewed across populations, it might also affect migration strategies within a population (Slotte 1999, Block et al. 2005). In other words, the choice of how far to migrate to spawn is dependent on the individual's size or state (Slotte and Fiksen 2000).

The Atlantic cod (*Gadus morhua*) is an interesting species for studying the evolution of migration because of the huge between-population variation in migratory behavior. The existence of large differences within a species likely reflects local or regional adaptations, and suggests that cod has a physiological architecture and an ecological role that permits such plasticity in the evolution of migration behavior. In a comprehensive review of tagging studies in cod (Robichaud and Rose 2004), approximately 40% of the cod populations were classified as sedentary, with some moving less than 10 kilometers over a lifetime. At the other extreme, several offshore cod populations perform large and annual spawning migrations hundreds to thousands of kilometers, often returning to the same areas in subsequent years.

The Northeast Arctic (NEA) cod stock is special in that it undergoes the most extensive annual spawning migration of any cod stock (Robichaud and Rose 2004). Each spring, mature individuals migrate from offshore feeding grounds in the Barents Sea to spawning areas located along the Norwegian coast. These spawning migrations are frequently more than a thousand kilometers long and occur against the prevailing Norwegian coastal and North Atlantic currents. Once spawned, developing eggs and larvae drift back with the currents to the feeding grounds. Historically, NEA cod have spawned along the Norwegian coast, spanning a distance of almost 2000 km. The bulk of spawning takes place in Lofoten (a migration distance of approximately 800 km), with another distinct spawning concentration off Møre (migration distance ~1500 km; see Fig. 1a, b for the historical importance of selected spawning grounds). It is not known why these two areas historically have the largest spawning aggregations whereas other areas show much less spawning activity. Alternative explanations revolve around benign oceanographical features, such as currents and eddies that increase the probability that larvae drift into the Barents Sea rather than toward Arctic and unfavorable waters (Vikebø et al. 2005). Also, warmer waters farther south allow larvae to grow faster (Folkvord 2005), which may decrease their vulnerability to predation.

Another factor that could play a role in shaping the patterns of migration in NEA cod is fishing (see Plate 1). Since the onset of industrial fishing in the Barents Sea in the 1920s (Godø 2003), age and size at maturation have shown a dramatic decline (Jørgensen 1990). Similar reductions in maturation age have been attributed to fisheries-induced evolution of life history strategies in a range of species and stocks worldwide (Jørgensen et al. 2007), including the NEA cod (Heino et al. 2002). As body size has consequences for swimming costs, one can expect that migration strategies also evolve. In sockeye salmon, intense harvesting late in the season has led to progressively earlier run times (Quinn et al. 2007) and in brook charr, there is evidence that fishing of anadromous individuals promotes evolution of residency (Thériault et al. 2008). Fishing might thus be expected to alter cod migrations and the distribution of spawning along the Norwegian coast. Furthermore, geographically shifted spawning locations could have implications for larval survival probability and thereby impact recruitment and population dynamics.

In this paper, we investigate the evolution of spawning migrations in NEA cod. Our work has two main components. First, we investigate how state distribution influences the distance of spawning migrations. We accomplish this by constructing an energy allocation model predicting optimal timing of maturation and optimal migration distance depending on an individual's age, body length, and body condition. Second, we examine the effect of industrial fishing on the spatial distribution of optimal spawning locations. We also study the effect of individual behavior by allowing individuals to either choose the optimal spawning site each year independently (i.e., roaming migrants) or restricting individuals to return to the same spawning site in successive years (i.e., homing migrants). These two behaviors differ in how flexible they are: roaming cod can respond to short-term environmental fluctuations or change their spawning sites as they grow, whereas homing cod make a decision that has to hold for life.
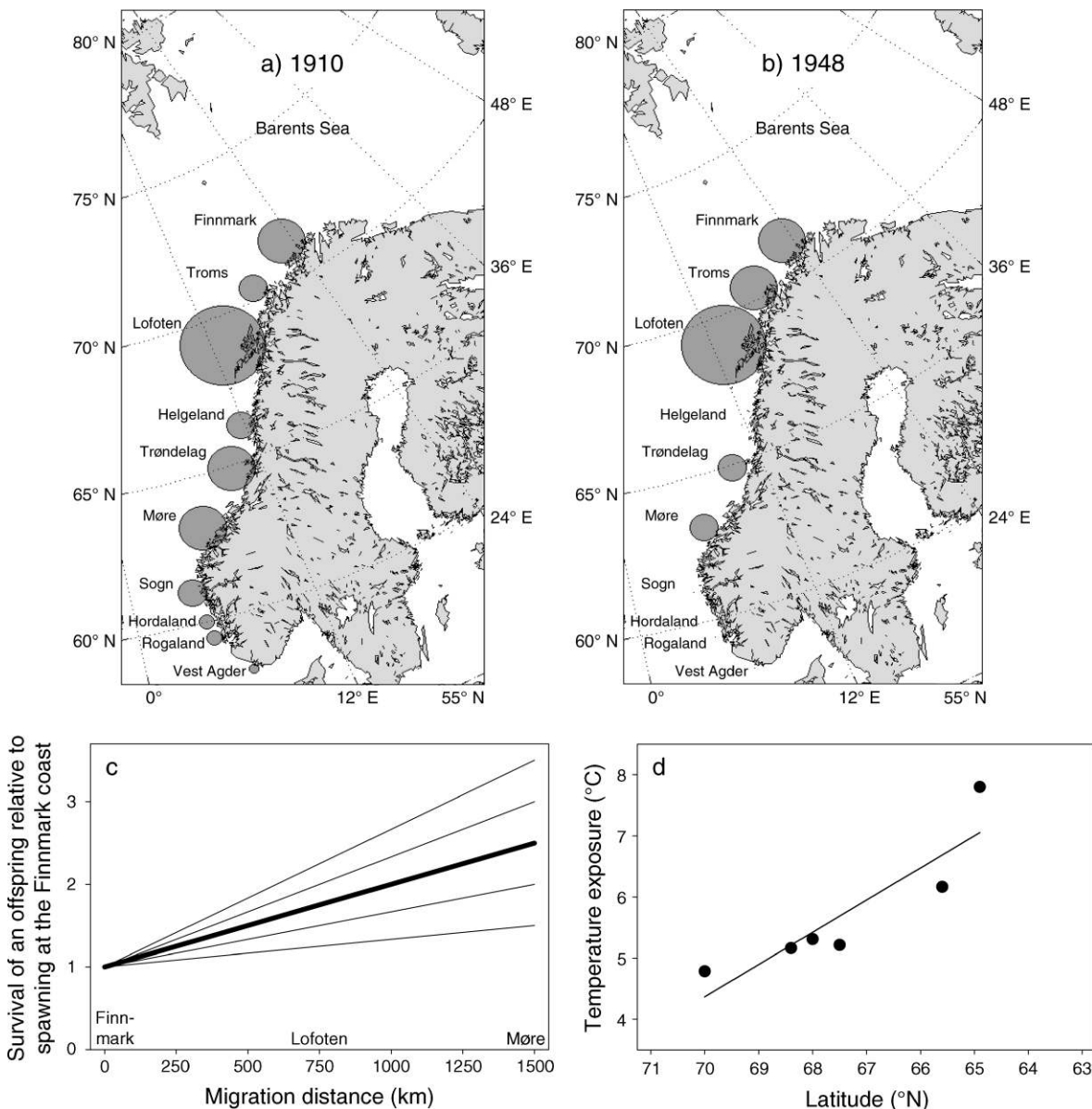
FIG. 1. Map showing fisheries catch of Northeast Arctic cod during the spawning season in (a) 1910 and (b) 1948. Data are from the Annual Norwegian Fisheries Statistics (Norges fiskerier–Grandes pêches maritimes) from the respective years. Over this period, the southernmost spawning locations have been deserted, and catches at the southern end of the cod distributional range in 1948 are lower. Catch is proportional to area of the circles. (c) Assumed survival values for Northeast Arctic cod offspring spawned along the Norwegian coastline for different values of the parameter ΔV, the proportional increased survival of an offspring spawned in Lofoten compared to survival with no migration (from bottom to top: 0.25, 0.5, 0.75, 1.00, and 1.25). (The thick line, $\Delta V = 0.75$, is used in all figures except the sensitivity analysis in Fig. 6.) (d) Simulated experienced temperature for drifting particles released from six known spawning sites along the Norwegian coast. Using an ocean circulation model, the particles were released over the course of one month around the time of peak spawning and were drifting at a fixed depth of 10 m for 100 days. Equation for the linear regression: temperature $= 41.23 - 0.523 \times$ latitude.

MODEL DESCRIPTION

Energy allocation model and life history strategies

A mechanistic and physiologically rich energy allocation model was used to obtain optimal life history strategies for each scenario. The basic model is presented in detail in Jørgensen and Fiksen (2006); here it was extended by allowing migration distance to vary with homing and roaming behavior. The model is state dependent, with the following individual states: body length, 25–200 cm in 1-cm steps; age in months, thus also including seasonal effects; stored energy, 0–100% of maximum stores in 10% steps; and relative level of food abundance in nine discrete steps. In total, there are thus

PLATE 1. The rich fishery for spawning cod in Lofoten was made famous in the thousand-year-old Norwegian viking sagas. Large fish were abundant historically, but individual fish have declined in size since industrial trawling began in the stock's offshore feeding grounds in the 1920s. Life history changes induced by heavy exploitation in the feeding grounds are predicted to promote shorter spawning migrations than before. This fishing, typically trawling, favors the evolution of earlier maturation at smaller sizes, and for smaller fish it is energetically more expensive to perform long migrations. The photo shows the fisherman Martin Fiksen (the brother of one of the authors) fishing with gillnets for spawning cod and holding what is now considered to be a good-sized individual. Photo credit: Inger Elin Kristina Ivarsdottir Utsi.

more than five million combinations of individual states, and for each of these the optimal strategy is found and stored.

The acquired amount of food varies stochastically on a monthly time scale to mimic temporal fluctuations in environmental conditions. Standard metabolism and costs of routine activity are subtracted from the energy in the ingested food, and the net energy is available for allocation between somatic growth and energy storage (in white muscle and liver). The stored energy can be spawned once per year, after the energetic costs of the spawning migration have been subtracted. The energy allocation, whether to spawn or not, and migration distance are then optimized for each state combination using dynamic programming (Houston and McNamara 1999) and stored in a matrix of optimal values. The optimality criterion is to maximize lifetime reproductive output R_0; in this model, R_0 is the expected lifetime fecundity including the survival effect depending on where offspring are spawned. A population following the optimal life history strategy is thereafter simulated, and the resulting population dynamics, averaged over 1000 years, is the basis for the results presented in this paper. The population is structured by the same individual states as the optimal life history strategies except that length and condition are treated as continuous variables. Beverton-Holt juvenile survival is

the density-dependent regulation in the population dynamics (Hilborn and Walters 1992). The model only considers females because Atlantic cod is a lekking species (Windle and Rose 2007) and little is known about the selection pressure on male body size.

Spawning and migrations

Spawning takes place annually and we assume that it has, regardless of an individual's body size, a duration of one month (Kjesbu et al. [1996] measured spawning durations of 22–48 days under experimental conditions) centered around 1 April (Pedersen 1984). We assumed that all fish engaging in reproduction had to arrive at the spawning grounds one month prior to mating (indicated, e.g., in Pedersen 1984); a steady current flowing 0.1 m/s northward (Brander 1994); and that all cod swim at a speed of 0.3 m/s through the water (Brander 1994; resulting in ground speeds of 0.2 m/s southward and 0.4 m/s northward). Swimming costs are modeled as a function of size and swimming speed as in Jørgensen and Fiksen (2006). Both large and small cod thus swim at equal speed, but with different costs. Alternatively, we could have let fish swim at optimal speeds, e.g., the speeds with the lowest transport costs. This would not have included the opportunity cost of being away from the feeding grounds, however, and a consistent approach would therefore require several assumptions

which are difficult to justify from the empirical literature.

A novelty of the energy allocation model presented in this paper is that migration distance is part of the optimization, with implications for spawning location, energetic costs, offspring survival, and the time spent migrating.

To incorporate potential temperature benefits to larvae spawned farther south, we constructed a profile of survival values where each egg has a future expected survival depending on its spawning location (Fig. 1c). ΔV is the proportional extra survival gained from spawning in Lofoten, after a migration of 750 km, relative to spawning at the coast of Finnmark. When $\Delta V = 1.0$, an offspring thus has twice the expected survival when spawned in Lofoten compared to no migration, and three times the expected survival if spawned after a migration distance of 1500 km (approximately around Møre). Although such a linear survival profile is obviously a simplification, it could result from temperature exposure, as higher temperatures farther south likely lead to higher rates of growth and development, and therefore shorter time spent in size windows vulnerable to high predation rates. Fig. 1d shows mean experienced temperature of drifting particles followed at 10 m depth, a proxy for the temperature exposure of cod larvae, simulated in an ocean circulation model (see Vikebø et al. 2007). The particles were released at known spawning locations over one month centered on the time of spawning. We also tested the sensitivity of our model predictions to varying ΔV and present further implications of this assumption in Discussion.

For every state combination, we verified all possible migration distances, ranging from no migration (corresponding for the NEA cod to the coast of Finnmark) to around 1500 km migration (corresponding to Møre) in 21 discrete steps. The optimization procedure then stored whether spawning was a superior life history option than not spawning, and if so, the optimal migration distance. We repeated this for two types of behavior. Roaming migrants were free to choose the optimal migration distance every year. This behavior is flexible, and can respond optimally to environmental variation between years and individual state-changes due to growth and ageing. Tagging studies suggest only very limited movement between spawning sites in Atlantic cod (Godø 1983, Pampoulie et al. 2006), and evidence from Atlantic bluefin tuna Thunnus thynnus (Block et al. 2005) and North Sea plaice Pleuronectes platessa (Hunter et al. 2003) suggests that fish to variable degrees are able to return to the same spawning sites in consecutive years. We therefore also implemented lifetime homing behavior (see also Robichaud and Rose 2001). These cod had to return to the same spawning site for every year they reproduced, throughout their life. Homing cod cannot change migration distance according to environmental variation or growth, and thus have less behavioral flexibility.

We modeled both the energetic and time cost of migration. This means that a short migration has a low energy cost, but also that the delayed departure and early return from the spawning grounds give more time at the feeding grounds. The resultant net energy intake is available for energy allocation between growth and energy storage as described above. This means that the optimal migration distance results from complex trade-offs on two time scales. First, there is a best use of available energy stores in the current year. This follows from the trade-off between the energy cost of migration and the increased survival value of offspring spawned farther south. Second, the optimization procedure also automatically considers the opportunity cost of being away from the feeding grounds. This opportunity cost has two components: for the near future, shorter migrations and thus more time for foraging will increase the energy available for migration and spawning. Further into the future, more energy for growth would likely lead to larger body size and higher fecundity for the remaining lifetime.

Atlantic cod presumably eat little during migration and spawning (Fordham and Trippel 1999), and we therefore assumed feeding during migration that is only sufficient to cover basic metabolic needs; in other words, feeding during migration will not provide any net energy for allocation or to cover migration and activity costs.

Effects of fishing

The model was repeated for two levels of fishing mortalities, F, one corresponding to the historical exploitation ($F_S = 0.2$ yr^{-1} at the spawning sites and during migration, $F_F = 0.1$ yr^{-1} at the feeding grounds) and one to contemporary industrial exploitation ($F_S = 0.3$ yr^{-1} and $F_F = 0.6$ yr^{-1}, respectively) (Olav Rune Godø, unpublished data from the Institute of Marine Research, Bergen, Norway). A version of the model without migration has been extensively tested for variations in F_S and F_F (Jørgensen and Fiksen 2006, Jørgensen et al. 2006), so here we present only those results for the two exploitation regimes estimated from the data. Natural mortality rate was kept constant at $M = 0.2$ yr^{-1}.

The optimization approach only finds evolutionarily stable endpoints, so the resulting life history strategies represent the situation after the populations have had time to fully adapt to the selection pressure. Since the historical exploitation had been ongoing for many centuries (Law and Grey 1989), one can argue that our historical scenario corresponds to the situation in the early 1900s, but for the contemporary scenario the process of adaptation is most probably still underway.

RESULTS

Body size has a strong influence on the bioenergetics budget of spawning migrations (Fig. 2). A fish of 50 cm body length would use 29% of its maximum energy store for migration to and from spawning in Lofoten, while a
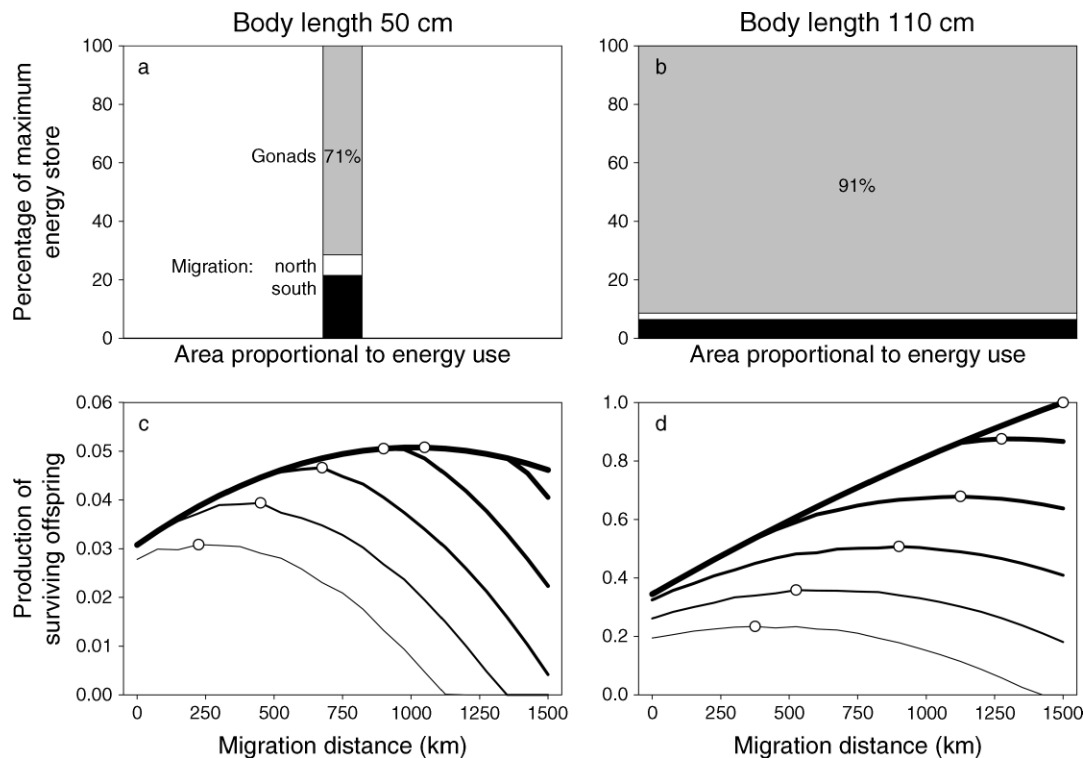
FIG. 2. The effect of body size on the bioenergetics of spawning for fish migrating to spawn in Lofoten (migration distance of 750 km) for female cod of body length (a, c) 50 cm and (b, d) 110 cm. (a, b) The area is proportional between the two graphs and represents the maximum amount of energy the fish can store in preparation for reproduction. A portion of this energy is used for swimming during migration (black, migration southward against the current; white, migration northward with the current). The remaining energy (gray area) can be used for gonads and spawning. (c, d) The resulting production of surviving offspring (relative to a 110-cm female with full stores) for female cod given that the survival of each offspring increases with migration distance ($\Delta V = 0.75$). Total offspring production is thus the product of fecundity and offspring survival. The different lines denote expected production of surviving offspring for different levels of energy stores (ranging from 0% to 100% of maximum in 20% steps from bottom [thin lines] to top [thick lines]) measured at the time when fish that migrate farthest have to depart. Fish with shorter migration distances can feed and store energy until their shorter migration must commence. For the sake of illustration, this figure does not take into account growth, so any energy in excess of what is needed for reproduction cannot be used to grow larger. The migration distance that maximized reproductive output for each condition level is indicated by an open circle. Note that the scale is different between the two panels; values are normalized so that the large cod with maximum energy stores at the optimal migration distance has a value of 1.0.

110-cm individual would use only 9%. In addition, larger fish have a much higher fecundity, and would therefore receive the fitness benefit (increased survival) for many more offspring than the smaller fish. The optimal migration distance also depends on the individual's body size and condition (Fig. 2c, d). In general, fish in good condition should migrate longer, and the optimal migration distance of a fish in maximum condition increases with body size (compare Fig. 2c, d).

We observed distinct patterns in the optimal migration distance of our modeled NEA cod population. Under the historical (i.e., low-pressure) fishing regime, there were two clear peaks where the frequency of spawners was highest: one at a distance of 750 km and one at a distance of 1125 km (Fig. 3a, b). Spawning took place farther north on the coast in the life history strategy that is optimal under contemporary fishing, with peak locations occurring at 225 km and 450 km

(Fig. 3c, d). There were also subtle differences in migration distance between roaming and homing behaviors. For the roaming cod, the peaks of the spawning aggregations were less distinct than for the homing cod, especially under the contemporary fishing regime (compare Fig. 3b to 3a). Also, the spawning distribution tended to be wider for the roaming cod than for the homing cod.

For both types of behavior and for both fishing regimes, larger and older cod tended to migrate farther (Fig. 4). The spawning population was more structured for the roaming behavior than for the homing behavior. This was because the homing behavior, where fish returned to the same spawning site for their entire lifetime, averaged out many of the differences due to growth and ageing that could influence optimal migration distance for roaming cod. In most cases, there was a positive correlation between maturation age and migra-
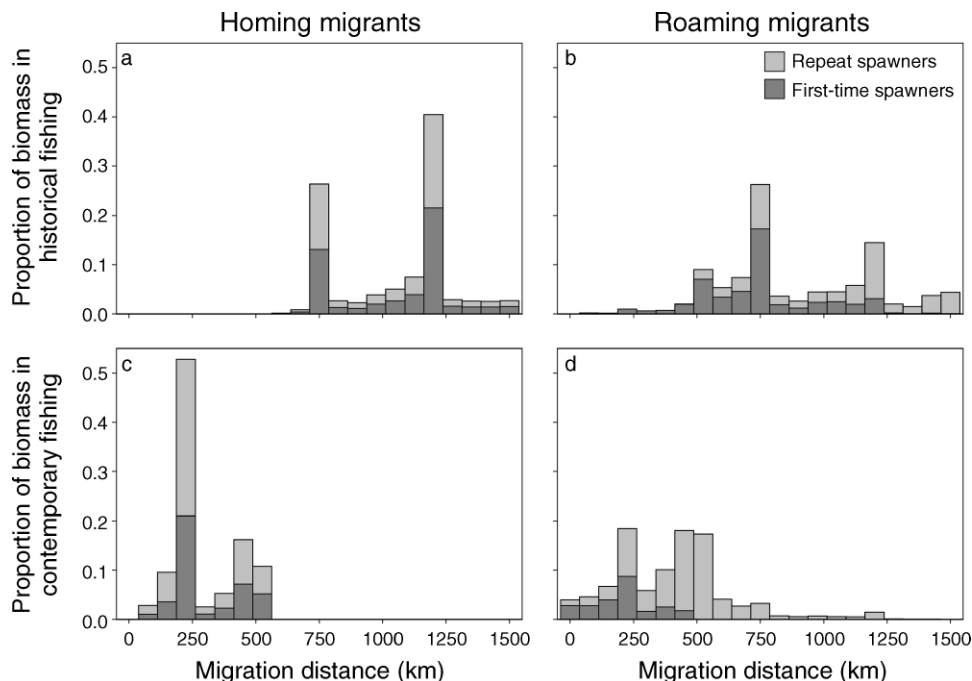
Fig. 3. Spawning distribution along a hypothetical coastline of female cod that follow optimal life history strategies. The survival value of each offspring is assumed to increase the farther the parent migrates ($\Delta V = 0.75$). Light gray bars denote total spawning biomass at that location; dark gray bars indicate first-time spawners. (a, b) Biomass distribution for historical fishing levels. (c, d) Biomass distribution for contemporary (more intensive) fishing levels. Panels (a) and (c) show the distribution of homing migrants that are constrained to return to the same spawning site each year. Panels (b) and (d) show the distribution of roaming migrants that are free choose a spawning location every year.

tion distance. This suggests that there is a life history trade-off between early maturation, small size, and short migration distances on the one hand, vs. late maturation, larger size, and longer spawning migrations on the other. For the roaming cod, the flattening of maturation age beyond a migration distance of 700 km indicates that these were basically the same fish, and the increase in age and size with longer migration distances reflects that individuals migrate farther as they age and grow (Fig. 4b).

The condition of homing migrants did not vary greatly with migration distance, whereas the condition of roaming migrants tended to increase with migration distance (Fig. 5). For both the homing and roaming migrants, contemporary fishing caused a decline in the age at maturation, body length and age, however, the decline was more pronounced for the homers (Fig. 4). The mean condition also declined with contemporary fishing for both homing and roaming migrants (Fig. 5).

Not surprisingly, the survival assigned to offspring as a function of spawning location affected optimal migration distances. When increasing ΔV, migration distances increased (Fig. 6). A survival gain in ΔV of 0.25 was insufficient to cause spawning migrations for either of the combinations of fishing regime and type of behavior investigated in this study. When $\Delta V = 0.5$, industrial fishing had little impact on the spawning locations of roaming migrants whereas for higher ΔV

values, industrial fishing caused a significant reduction in migration distances for both the homing and roaming behavior (Fig. 6).

DISCUSSION

Our results illustrate how interactions between physiology, behavior, larval ecology, and adult life history strategies create large-scale population-level patterns, and how an understanding of all these elements is necessary to fully appreciate the adaptive dimension of animal migrations. A priori, one can expect that animal migrations would not evolve unless there are adaptive benefits to the individuals who migrate, potentially coming through their offspring. We will first discuss this central assumption, and how it is applied in our model as an assumed linear increase in expected survival for each offspring spawned farther south along the coast. Second, we will focus on the emerging population-level patterns in the model and their potential implications for understanding animal migrations in general and spawning migrations in the NEA cod in particular. Finally, given the degree to which harvest may modify migration patterns, we evaluate potential consequences for population dynamics, resilience, and adaptability to new environmental conditions. This last point suggests topics for further research as well as concerns for fisheries management.
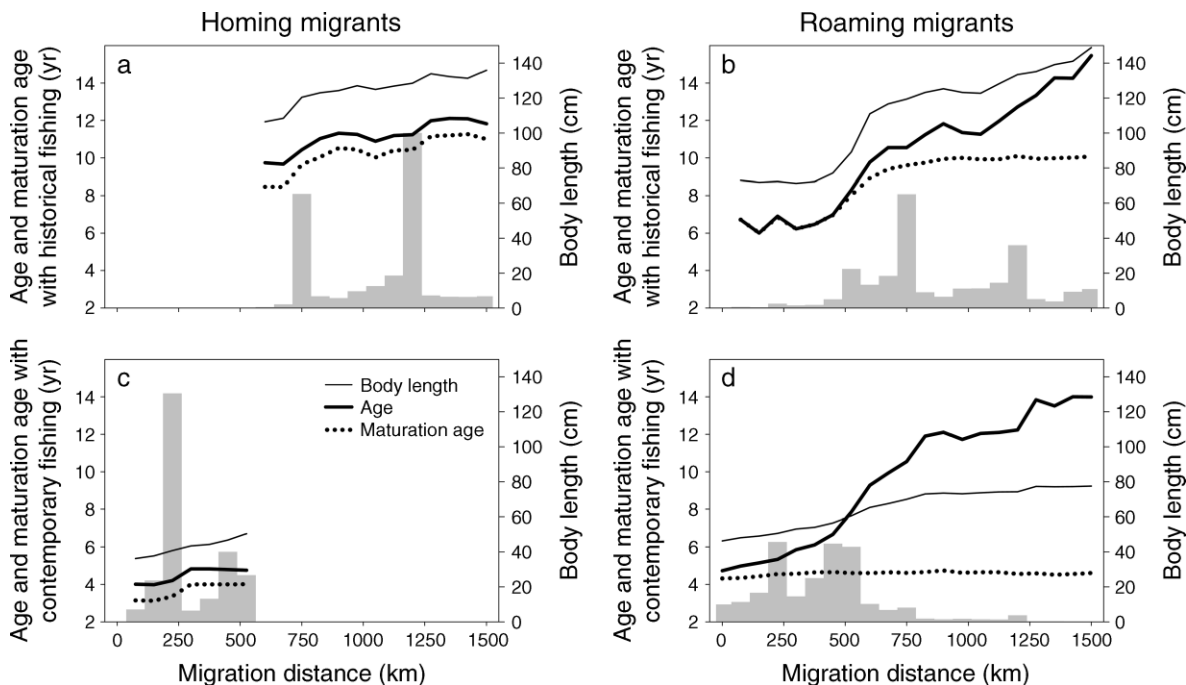
Fig. 4. State distribution in the spawning stock of a migrating cod population along a hypothetical coastline. The gray histogram in the background illustrates the distribution of spawning biomass along the coastline. The lines denote mean age (years; thick solid line), mean maturation age (years; thick dotted line), and mean body length (cm; thin line; right axis). (a, b) Life history strategies that were optimal under historical fishing. (c, d) Optimal life history strategies under the contemporary fishing regime. In panels (a) and (c), the homing migrants are constrained to return to the same spawning site each year. In panels (b) and (d), roaming migrants are free to choose the optimal spawning location each year independently.

Adaptive benefits of migrations

That species perform costly migrations points toward the existence of adaptive benefits, even though the exact benefit might not be known in each case. With spawning migrations, the benefits can either be direct, benefiting the parents (food abundance or predation risk), or indirect, with advantages for the offspring (favorable conditions for larval survival and development). We have modeled indirect benefits explicitly: the central assumption of this study was that offspring survival increases linearly with migration distance. In NEA cod,
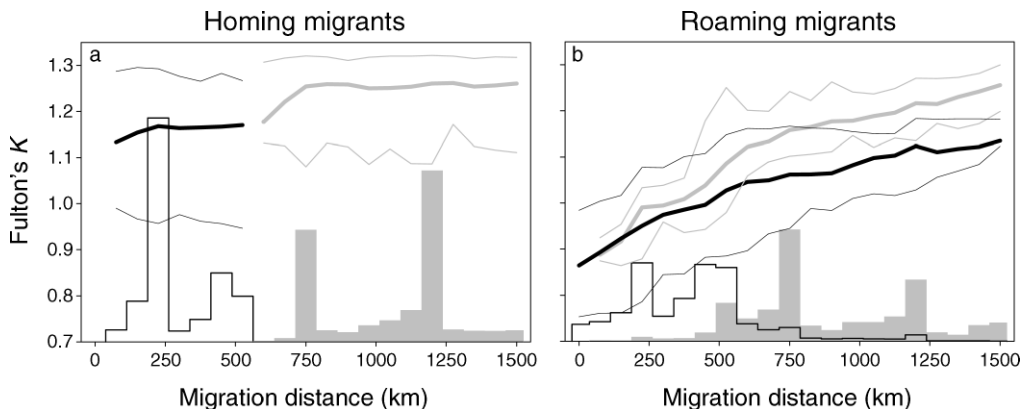

Fig. 5. The relationship between migration distance and Fulton's condition factor resulting from a life history model for the Northeast Arctic cod. Gray bars and lines relate to the life history strategy that was optimal in the historical situation prior to industrial fishing, while black lines and bars represent the life history that is optimal under contemporary and more intense exploitation. The lines are weighted mean Fulton's condition factor at that spawning location (thick line), indicating also maximum and minimum values (thin lines). The bars illustrate the distribution of the spawning stock biomass from Fig. 3. (a) Homing migrants constrained to return to the same spawning site each year. (b) Roaming migrants that are free to choose the optimal spawning location each year independently.
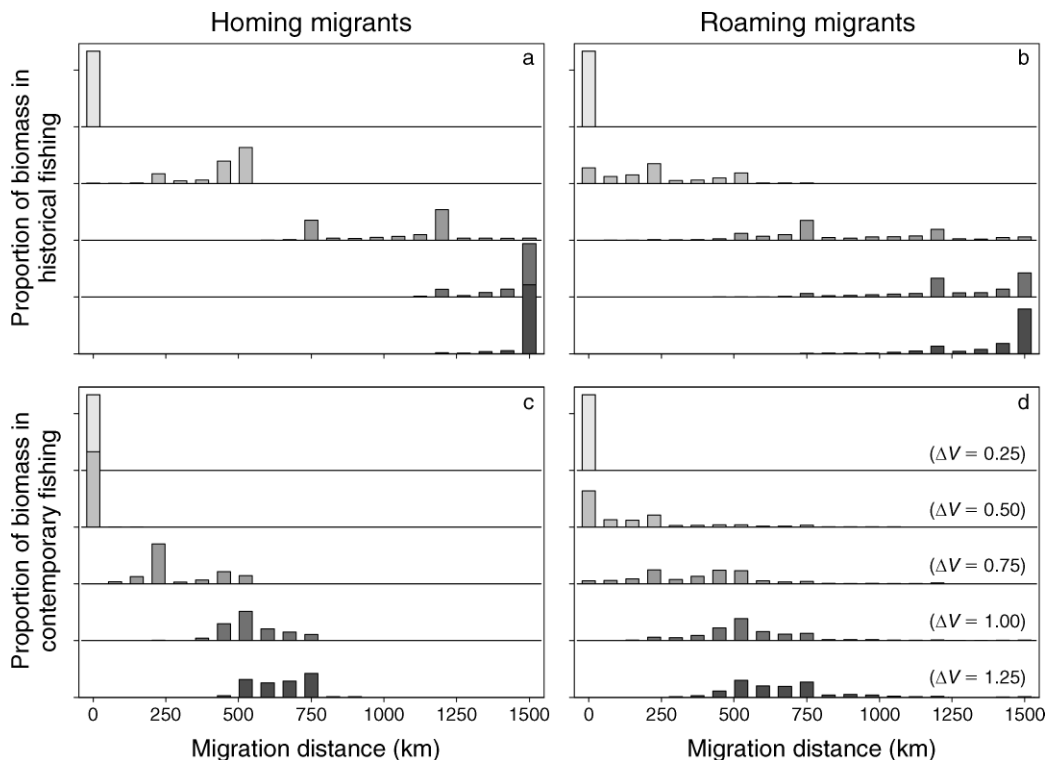
FIG. 6. Sensitivity analysis of varying the survival benefit to offspring ΔV, fishing pressure, and migratory behavior. The bars show the distribution of spawning stock biomass along the hypothetical coastline. The values of ΔV are given in panel (d); the standard value used in all other results presented is $\Delta V = 0.75$. Each value of ΔV corresponds to a different shade of gray. (a, b) Optimal life history strategies under historical fishing. (c, d) Optimal life history strategies under contemporary fishing. In panels (a) and (c), homing migrants are constrained to return to the same spawning site each year. In panels (b) and (d), roaming migrants are free to choose the optimal spawning location each year independently.

the spawning migrations take place along a north-south axis. Longer migration distances thus coincide with more southerly spawning, and any latitudinal gradient that influences spawning success has the potential to contribute to a linear relationship of the type we assumed.

The peak of spawning is just a week after spring equinox (Pedersen 1984). There is virtually no latitudinal variation in day length at that time of year, but days quickly become longer farther north, which would benefit visually feeding larvae such as cod. Sun height and twilight duration also have the potential to influence the amount and variability of available light (Mobley 1994, Suthers and Sundby 1996). In sum, these components probably benefit growth and survival farther north (Suthers and Sundby 1996), with diminishing differences as larvae from southerly spawning sites drift northward.

More important is the latitudinal variation in temperature. In spring, southerly waters are warmer, and growth and development rates are positively correlated with temperature in cod larvae (Folkvord 2005). Longer migration distances in parents thus equate to more time spent in warmer waters for their eggs and larvae, in turn accelerating development. Predation

mortality is generally high in pelagic larvae but is quickly reduced as they grow bigger (McGurk 1986). Faster growth therefore normally translates into higher survival. It is notoriously difficult to quantify mortality during the pelagic phase in field studies, and according to Sundby et al. (1989) only one out of 25 000 cod larvae would, on average, survive their first 100 days. There is thus ample opportunity for natural selection to improve survival, and modeling studies indicate that temperature differences between spawning sites only a few nautical miles apart can double survival probabilities during the pelagic drift phase in cod larvae (Fiksen et al. 2007). A link with temperature is also suggested by historical data from the spawning grounds. Sundby and Nakken (2008) reported that spawners were distributed farther south in colder years, and retracted to a narrower and more northerly range in warmer years.

A third possibility is that larvae spawned farther south have a lower probability of drifting north into Arctic areas at a life stage when they are too small to swim back into the warmer Atlantic water. Prevailing oceanographic conditions have the potential to sweep the larvae past the shallow and productive Barents Sea and into Arctic water, which is generally not preferred by cod (Ottersen et al. 1998). Such oceanographic

constraints may well be an evolutionary driver toward more southerly spawning. It has also been suggested that climate-driven changes in the thermohaline circulation pattern could lead to increased larval loss to the west of Spitsbergen and into the Arctic Ocean (Vikebø et al. 2007), which could alter the benefit of spawning farther south.

In the case of the NEA cod, it therefore seems likely that longer migrations can produce predictable benefits primarily relating to offspring survival. Naturally, spawning migrations did not arise in the model when migrating had no or only a very small benefit to offspring survival. However, when the survival probability for larvae spawned in Lofoten (750 km) was 75% higher than larvae spawned with no migration, our model's predicted distribution of spawning migrations compares well with observed patterns (Fig. 1a).

An assumption of our model is that offspring survival increases linearly as a function of migration distance. However, although the true relationship might show a general increase of offspring survival with migration distance, the actual shape of the curve is likely to be rugged and variable, conforming to geographical, oceanographical, and biological features that vary along the coastline (see also the temperature profile in Fig. 1d). For example, favorable habitat for spawning might not be available everywhere along the coast. Furthermore, meso-scale oceanographical features such as eddies and fronts can greatly influence retention and productivity. For drifting larvae, this could translate to higher temperature exposure, more abundant food, or better benthic habitats at the time of settlement (Fiksen et al. 2007). By condensing all such factors into a smooth linear relationship, our model deliberately ignores several complexities but maintains a geographical trend in offspring fitness as the primary driver. Further trade-offs from physiology and size-dependent processes act on top of this, and together they cause constraints and opportunities for the evolution of migration distance.

There are also direct benefits to the parents in one of our modeled scenarios. Although the contemporary fishing pressure is higher, harvest on the spawning grounds and along the migratory route is exerted primarily by a coastal fleet. In the contemporary scenario, migrating and spawning cod experience higher adult survival rates than feeding cod in the Barents Sea, where trawlers harvest more intensely (Godø 2003). This adds a direct benefit to longer migrations in the contemporary scenario. On the other hand, the relative strength of fishing pressures in the historical scenario is the opposite, and there is a trade-off in that longer migrations reduce adult survival. In addition, the modeled cod eat little during the migration, so a longer migration translates into less feeding time during the annual cycle. In both fishing scenarios, there is thus also a trade-off between migration distance and total annual energy intake, which in isolation would favor shorter spawning migrations. Although evidence is scarce, it has

been suggested that another direct benefit could result when migrating cod follow the Norwegian spring-spawning herring *Clupea harengus* migration southward while feeding on it (Olav Rune Godø, *personal communication*). The opportunity for concomitant foraging would thus tempt the cod to travel farther than what would be predicted from our model. It would be interesting to see studies or reanalyses of data that could explore such alternative hypotheses.

The annual fishery statistics (Norwegian Annual Fisheries Statistics 1910–1948) reported spawning NEA cod from the coast of Finnmark all the way south to Lindesnes at the southern tip of Norway, corresponding to a migration of more than 2000 km each way. The NEA cod spawning between Lindesnes (2100 km) and Hordaland (1800 km) once sustained regional fisheries, but disappeared from the commercial catch statistics around 1928. The last spawning NEA cod off Bergen (1800 km) were observed in the mid-1990s (Odd Nakken, *personal communication*). The Møre fishery (1500 km) experienced an all-time low from 1937, but improved again by the late 1940s, and was reported to be good as late as in 2007 (Olav Rune Godø, *personal communication*). The overall trend seems to be that the southernmost spawning sites disappear progressively with time.

Commercial catch statistics also report liver and roe content per 1000 fish, but no individual measures such as body length or weight (Norwegian Annual Fisheries Statistics 1910–1948). Although crude, the data clearly show that throughout the period 1910–1948, cod spawning at Finnmark had significantly less roe than more southerly distributed spawners, indicating that spawners in Finnmark were smaller or in poorer condition. For most of the time, the statistics indicate that fish off Lofoten and Møre had similar amounts of roe per biomass, but the statistics do not report differences in size.

The role of behavior

The flexibility of individual migration behavior impacted upon the spawning distribution. A more flexible behavior, in which individuals were free to choose spawning sites each year, led to more structured state dynamics and a wider distribution of spawning locations and individual states. In these roaming migrants, first-year spawners were predicted to be younger and smaller and to migrate shorter distances. However, as the mature roaming migrants aged and grew, they tended to migrate farther with each passing year. This behavior contrasted with the homing migrants, which tended to form a narrower band of spawning locations along the coast.

Although evidence is sparse, there is some indication from tagging experiments that NEA cod adults return to the same spawning locations they migrated to in their previous reproductive year (Godø 1983, 1984). Only a very small proportion of the sampled cod were

recaptured at another spawning location than they were tagged, and most often these recaptures could not be unambiguously designated to that spawning area as the cod might have been passing through on their way to a more southerly spawning site (Godø 1983, 1984). Tagging studies from other species have also demonstrated that mature adults can return to specific spawning sites in consecutive years (Ridgway et al. 2002, Hunter et al. 2003, Block et al 2005). Developments in the field of animal navigation may also contribute to understanding and testing homing vs. roaming behavior (Alerstam 2006).

It is interesting to note that an assumption about the type of migratory behavior has implications for predicted spawning distribution, maturation ages, size distribution, and condition of the individual fish. These intricate responses highlight how life history and behavioral traits evolve together to form successful life history strategies; an argument that should encourage the use of multiple traits and mechanisms in evolutionary models.

Population-level patterns and their implications

Given the assumed distribution of offspring survival along the coast, our model predicts that adult state dynamics create variation in the length of spawning migrations, scaling up to large-scale patterns of fish distribution at the population level. Larger, older spawners with higher condition have longer optimal migration distances. These longer-distance migrants sacrifice energy stores and fecundity because of the increased survival of their offspring. Smaller, younger, and poorer-conditioned spawners have lower fecundity and would not receive the same fitness gain by migrating farther. Instead, they have shorter optimal migration distances. Similar predictions to those reported here have been made for Norwegian spring-spawning herring, also migrating south along the Norwegian coast to spawn: longer optimal migration distances were associated with increasing fish length and condition (Slotte and Fiksen 2000). This pattern is also evident in data from the same herring stock (Slotte 1999).

There were spatially distinct peaks of spawning stock biomass for our modeled NEA cod. In the absence of industrial fishing, these peaks corresponded to migration distances of 750 km and 1125 km. Interestingly, the prediction of two spawning clusters qualitatively matches historical observations of the NEA cod, where Lofoten (750 km) and Møre (1500 km) have had the highest spawning aggregations. As our assumed offspring survival relationship does not include distinct geographical features, the two spawning clusters predicted by our model arise from the interplay between size-dependent physiological and ecological processes and life history strategies. The two major components in the population correspond to early-maturing life history strategies with shorter migration distances, and later-maturing cod that migrate farther south. The mecha-

nism could be that the population dynamics generate certain state combinations, for which the optimal migration distances cluster around the two spawning peaks. Similar peaks have been observed in herring (Slotte 1999). Population patterns of spawning fish also separate by body size in migrating capelin, *Mallotus villosus*, where fish size at the spawning sites declines throughout the spawning season (Vandeperre and Methven 2007).

It is generally believed that NEA cod target Lofoten and Møre because of the benign oceanographic conditions for larval development at these locations. That hypothesis assumes larval ecology is the driving force that shapes spawning distribution patterns. However, the ability of our model to predict spawning locations that qualitatively match observed patterns suggests that, in addition to any effects of larval ecology, adult state and behavior may also play a crucial role. Similarly, the northward shift of the spawning range in warmer years has been explained by oceanography and its implications for larvae (Sundby and Nakken 2008), whereas our results suggest that one should also look for the influences that warm temperatures have on individual states and the resulting trade-offs in the adult population. Similar size-driven processes can influence migration in any animal species where there is variation in body size or other individual states. In groups composed of animals of different size or condition, one could also expect that the optimal migration distance for the group as a whole would not necessarily be optimal for each individual in the group. Because cost of transport usually declines with body size, smaller individuals would, in such cases, be expected to migrate longer than their optimum, while large individuals might migrate shorter than their optimum. Of course, the outcomes of such group dynamics depend on the relative influence of the differently sized individuals and on the corresponding costs of deviating from optimal individual strategies.

Consequences of harvest

With the onset of industrial fishing in the Barents Sea, the observed mean age and size at maturation of NEA cod has dramatically declined (Jørgensen 1990, Heino et al. 2002). Our model predicted similar declines, and thus lends support to the claims that the observed trends have an evolutionary dimension. Furthermore, these evolutionary changes toward younger ages, smaller sizes, and lessened condition at spawning have altered the selection pressure acting on migration distance. Under the contemporary fishing regime, the predicted state distribution of spawners resulted in shorter optimal migration distances. A central research challenge thus becomes to identify potential consequences of a fishing-induced shift toward smaller-sized individuals and a more northerly spawning distribution. Over the last 50 years, cod recruitment has changed from being uncorrelated to becoming positively correlated with mean annual

seawater temperature in the Barents Sea (Ottersen et al. 2006). This could suggest the concomitant trend toward smaller-sized individuals has reduced the stock's ability to buffer environmental variability. Similar results were obtained in a study of skipped spawning using the same model as the one in this paper: as fishing is expected to lead to earlier maturation, the link between environment and the proportion of the mature biomass that skipped spawning in any year grew stronger (Jørgensen et al. 2006). On top of this, fishing has been shown to increase fluctuations in population dynamics (Hsieh et al. 2006). For sustainable management, it thus becomes imperative to understand to what extent fisheries-induced evolution might influence population dynamics, and what increased fluctuations imply for harvest, resilience, collapse, and recovery (Jørgensen et al. 2007).

A more concentrated spawning range with a more northerly distribution also means that in any given year, the cod stock "samples" less of the spatial environmental variation. If areas with high recruitment success change from year to year, less spatial coverage could thus lead to higher population fluctuations, increased risk of stock collapse, and reduced resilience and recovery potential. A wide spawning range also means that the cod has been exposed to, and probably harbors adaptations to, a broad set of climatic conditions. The expected shorter migration distances could thus with time erode the stock's ability to respond adaptively to climate change.

Our model suggests a rich interplay between individual size and condition on the one hand, and large-scale patterns of spawning distribution and population structuring on the other. Internal physiological trade-offs and individual life history strategies scale up to and have consequences for geographical distribution at the population level, which links spatial and temporal scales. The model also shows how exploitation not only affects life history traits of individual fish, but how harvest can induce large-scale changes in the exploited resource, changing its distribution in ways that allude to a range of unexplored potential consequences. In itself, the possibility of such large-scale effects of human intervention carry dire warning for the sustainable use of living resources, which should prompt empirical and modeling studies that identify and investigate a wider range of mechanisms potentially influenced by fishing activities.

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