Dynamics of spawning migrations in Northeast Arctic cod

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SCIENTIFIC ENVIRONMENT

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FOREWORD

On my very first day as a doctorate student, my supervisor Øyvind Fiksen introduced me to one of my new colleagues, Christian Jørgensen, who enthusiastically told me about his fascination with the Northeast Arctic cod's spawning migrations. I was immediately intrigued by his eager approach, but most of all by the simplicity of the research question that would form the basis of this thesis. Why on earth would some cod choose to swim all the way from the Barents Sea to Møre, or even to Bergen, to spawn their eggs, when there were perfectly good spawning grounds in Lofoten or Troms, much closer to the Barents Sea? General evolutionary theory would predict that the individuals who undertook spawning migrations several times longer than their conspecifics must be getting something in return. Otherwise, it would be an evolutionary cul-de-sac.

Impatiently I started sifting through all the literature I could find, from online articles via obscure reports from the Directorate of Fisheries, to joint Norwegian-Russian conference proceedings from the early 80s, forgotten in someone's bottom drawer. Still early in my work, Odd Nakken, a retired fisheries scientist, held an inspiring lecture commemorating 100 years of research on the Northeast Arctic cod, and introduced me to a wonderful untapped world of commercial fisheries statistics. In retrospect, I'd rather not think about how many hours I've spent in the cellar of the Faculty of History library, reading, scanning, and punching catch weights from dissolving leather-bound fisheries' statistics reports, printed sometime in the mid eighteen hundreds.

At around the same time, Christian took me on board on his modelling project on the evolution of spawning migrations, where the fruits of my library hours came to bear for the first time. Later, Frode Vikebø and Øyvind introduced me to oceanographic modelling and the role of individual behaviour, even at the very early life stages. I was fascinated by it all, and I must admit that those first months came to influence, direct, and inspire me through the rest of my doctorate period.

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Thanks to Agur, Loic and Nico for making computer scripts less of a headache, for reading manuscripts, and for teaching me how complicated statistics can be. Thanks to my cousin Richard for learning me how to write English, and to Nicolas for your eager to discuss fisheries management and real life politics in a research group heavily biased by ecological theory, numerical modelling and cycling.

I would also like to thank David for inviting me to his lab at the Scripps Institute of Oceanography in La Jolla, California, and to the EvoFish and Modelling group at UiB, for creating such a great environment to work in, and for all the fun discussions we've had around the lunch table.

My ever supporting parents, Wenche and Martin, are thanked for convincing me that an academic education perhaps wasn't such a bad idea, as opposed to becoming a carpenter (my childhood dream). Though sometimes, I'm not so sure. Also, I thank Reidar and Katrine for being delightfully uninterested in my career, making our time together much more fun.

Finally, I thank my lovely wife, Hilde, for keeping up with such a nerdy husband, and for encouraging me in everything that I do. Ylva and Lars, you are the greatest kids in the world. I love you to death, and you make me want to leave work early every day!

Bergen, December 2010,

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The evolution of spawning migrations: state dependence and fishing-induced changes. *Ecology* **89**:3436-3448

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Historical changes in spawning grounds of Northeast Arctic cod outweigh role of climatic variation for early life thermal exposure. *Manuscript*

SUMMARY

The Northeast Arctic (NA) cod is known to undertake long southbound spawning migrations from their feeding grounds in the Barents Sea, to various spawning grounds along the Norwegian coast. Hence it's native Norwegian name "skrei", meaning to move or to travel. The spawned eggs and larvae subsequently drift northwards along with the prevailing currents, eventually reaching the Barents Sea as juveniles. From commercial fisheries statistics we see that these spawning grounds once spanned across nearly 2000 km of the west coast of Norway, from Finnmark in the north to Vest-Agder at the very south. Today the latitudinal range of the spawning grounds is significantly reduced, with only a marginal part of the stock spawning as far south as Møre, some 1500 km from the Barents Sea. Coarse estimates from the Institute of Marine Research suggest that around 90 - 95 % of the spawning stock spawn from Lofoten and northwards, utilizing only a third of their original expanse. Also, recent scientific surveys have found that during the last decade, the NA cod have to a great extent stopped spawning at their major traditional grounds in Vestfjorden, Lofoten, and have relocated to more northbound areas. Historically, scientists have shown little interest in the changes in spawning grounds, but due to the major impact this recent shift has had on local fishermen and landing ports, the topic currently attracts noticeable interest from fisheries scientists as well as climate scientists. The NA cod's previous widespread spawning distribution, together with its historical and contemporary northbound shifts has spurred two major research questions addressed in this thesis. First, why does spawning take place over such a vast geographical area, implying that certain parts of the population undergo spawning migrations several thousands of kilometres further than their conspecifics? Secondly, what has caused the northbound shift in spawning grounds?

From general evolutionary theory, we would expect that individuals undertaking longer spawning migrations, thus leaving less time to forage in the Barents Sea, as well as increasing their energetic cost of migration, would achieve a comparable return benefit. If not, such a life history strategy could simply not hold through the

course of natural selection. The benefit need not target the spawning individual directly, but can also be mediated through increased fitness to their progeny, essentially through increased survival probability.

Using a simplistic assumption that fitness benefit increases linearly with migration distance, we developed a model simulating a population of individuals which finds optimal solutions to the trade-off between growth and reproduction, depending on physiological condition and ecological constraints. Overall, the model predict that larger individuals and individuals in better condition gain higher fitness benefit from longer spawning migrations compared to smaller and less fit individuals. These findings are partly due to a nonlinear relationship between hydrodynamic friction and individual size, meaning that relatively, larger fish spend less energy on swimming compared to smaller individuals. More interestingly, when simulating historical fishing pressure at the spawning grounds, there is selection for large late-maturing fish and longer migrations, whilst a contemporary trawl fishery, typically located at the feeding areas in the Barents Sea, select for small and early-maturing fish with shorter optimal migration distances. The latter case is consistent with observational studies, and indicates that fisheries' induced evolution have not only lowered the maturation age of NA cod, but may also be causing the northbound shift in spawning ground distribution.

To test the validity of our initial assumption that southerly spawning grounds are in fact associated with higher fitness benefits, we employed different general circulation models to track virtual fish eggs and larvae released at various spawning grounds along the Norwegian coast. From their drift trajectories towards the Barents Sea, we found that eggs and larvae released from more southerly spawning grounds experienced higher average temperature exposures, generally thought to promote faster growth and consequently reduce mortality in early life stages. However, the southernmost spawning grounds generally also experienced more retention in local fjord systems. In addition, seasonal and inter-annual variation in drift trajectories, as well as overall temperature exposure, growth and survival was evident, indicating that climatic conditions may also play a role for offspring success. Overall, the latitudinal effect on larval temperature exposure was significantly stronger than the climatic variability.

Finally, by utilizing empirical data from commercial catch statistics dating back to 1866, our initial theory, that shifts in spawning grounds are caused by a size-selective industrial trawl fishery in the Barents Sea, was tested against alternative explanatory factors such as density dependence and climate change. In total, 104 years of landing data were compiled for the entire Norwegian coast, revealing large fluctuations in spawning ground distributions, but also showing trends towards more northbound spawning after the 1920s. Climatic variation was found only partially to explain the variation, whilst rapidly increasing landings from the trawl fishery in the Barents Sea starting around 1923, clearly coincided with the northbound shifts in spawning grounds.

RATIONALE

In 1878, fisheries scientist G.O. Sars unveiled a long kept secret on where the cod spawning along the Norwegian coast in early spring came from, namely the Barents Sea (see Mohn and Sars 1880). Then, as now, fisheries scientists were particularly concerned about the fluctuating cod fishery in Lofoten, also known as the NA cod, or Lofoten-cod, given that the majority of spawning cod was predominantly located there. The fact that the NA cod actually spawned along the entire Norwegian coast is poorly reflected in scientific literature, despite the fact that there were years when the majority of NA cod actually spawned on the southwest coast of Norway, and not in Lofoten. Fisheries scientists had made important discoveries on the particular conditions, such as at what temperatures and depths fish eggs and larvae need to grow and proliferate (e.g. Sars 1866, Gade 1894, Hjort 1895, 1905). These findings eventually culminated in the classical work by Hjort (1914), who linked early life survival, year class strength and stock recruitment in the NSS herring. The concept that fishes in general, and the NA cod and NSS herring in particular, utilize specific life history strategies to maximize their reproductive success, must therefore have been relatively well understood. However, in the case of the NA cod, the cost of spawning migration differed widely between individuals spawning off the Finnmark coast and the ones that spawned more than 2000 km further south, outside Vest-Agder. These differences in spawning locations, known through the commercial fisheries statistics (Anon. 1866-1976), were never considered to be variations in spawning strategies, but thought to be a somewhat “natural distribution” (i.e. Sætersdal and Hylen 1964), without any particular link to life history theory. Thus, when the spawning ground distribution shifted northwards in the 1930s to half its historical expanse, no questions were asked.

Since the mid 1900s much has changed in the field of life history evolution and animal behaviour, predominantly due to the advancement in the field of evolutionary ecology in the 1960s and 70s (e.g. MacArthur and Pianka 1966, MacArthur 1972). Then, the predominant conception was that the evolution of life history adaptations evolved over thousands or millions of years. In recent decades, scientists have found that humans can induce evolution on much shorter timescales, even within the course of a lifetime, also known as contemporary evolution (reviewed by Reznick and Ghalambor 2001). More interestingly, it is also found that human impacts such as hunting and fishing can promote rapid evolution through direct and intense targeting of certain traits like large horns (Coltman et al. 2003) or body sizes (e.g. Jørgensen et al. 2007).

In the case of fisheries, today, humans are probably the most influential actor in the world's marine ecosystems. The FAO report "State of world fisheries and aquaculture" (2008), claims that the majority of existing marine resources are either fully or over-exploited (but see Worm et al. 2009). A highly efficient fishing fleet primarily targeting high trophic level species is also consecutively shifting to smaller sized- and lower trophic level species, as previously targeted species are either depleted or too scarce to fish efficiently (Pauly et al. 1998). This oversized and heavily subsidized industry (Clark 2006) not only depletes fish stocks, but also has adverse effects on their population structure, and can in turn make them even more vulnerable to fishing. Typically, highly size-selective gear, most commonly used in modern fisheries, influences species' phenotypic plasticity (Ernande et al. 2004), alters the age and size structure of a population (Jørgensen 1990), as well as causing genetic and evolutionary changes (Heino et al. 2002). Certain traits or phenotypes may become less common if targeted heavily by the fishery, affecting the diversity of reproductive and life history strategies and adaptations in the population, possibly making it more vulnerable towards factors such as climate change (Ottersen et al. 2006), harvesting (Jørgensen et al. 2007), alterations in prey and predator abundance or composition, and environmental variability (Neutel et al. 2002). These statements represent well documented concerns regarding fish stocks across the globe, and it is obvious that determining the variables that shape life history adaptations in harvested marine species is paramount to making informed and coherent decisions towards sustainable fisheries management.

LIFE HISTORY AND SIZE-SELECTIVE HARVEST

> "… it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*."
>
> Charles Darwin, 1859

Living organisms as we observe them today are the products of countless adaptations acquired through the course of natural selection. The essence of life history theory is to determine the adaptations of which a living organism consists, and why they have evolved in such a way. These adaptations take place at the individual level, but individuals aggregate in populations which again are actors in trophic relationships in the ecosystems we live in, and heavily depend on. The different life history traits that make up a life cycle are closely linked, in such a way that adaptations in early life harbour both constraints and opportunities for strategies in later life stages. Understanding the mechanics and physiology behind individual life-history strategies is necessary in order to understand ecology, the impact of human influence, and how to manage living resources.

REPRODUCTIVE STRATEGIES

Parental investment in their offspring can take many forms, and is often traded off against their own survival and future reproduction (Lack 1947). In marine ecosystems, reproductive strategies are as diverse as the species themselves. In fish, these strategies range from mouth brooding guppies via parasitic male anglerfish to broadcast spawners such as the Atlantic cod. No matter how diverse these life history strategies may seem, in the end they are all solutions to the evolutionary algorithm as first described by Charles Darwin in 1859; to maximize the number of viable offspring through the course of life.

For migrating fish, determining an optimal reproductive strategy which maximises fitness is a complex decision circling around trade-offs between interdependent variables such as migration (Jørgensen and Fiksen 2006), timing (Hjort 1914, Cushing 1986), spawning ground location, retention of offspring (Sinclair and Iles 1989), ambient temperature (Otterlei et al. 1999), turbulence (Lasker 1981, MacKenzie and Kiørboe 2000), and predator (Bailey and Houde 1989) and prey (Cushing 1990) abundance. More direct benefits of migratory behaviour can also include factors such as lowered disease risk and reduced predation (Dingle 1996). Changes in one variable is likely to cascade through other variables, and reproductive strategies may be found across multiple combinations of trade-offs.

THE ROLE OF FISHING

Today, the majority of the worlds marine ecosystems are heavily exploited (FAO 2008), and most of them are also experiencing global warming (e.g. Harvell et al. 1999, Edwards and Richardson 2004, Perry et al. 2005). For instance, size-selective fishing has been shown to trigger phenotypic plasticity (Ernande et al. 2004), and in the case of the NA cod, it has altered the age and size structure of the population (Jørgensen 1990). Fishing is also shown to cause genetic and evolutionary change in terms of younger age at maturation in both NA cod (Heino et al. 2002) and Northern cod (Olsen et al. 2004). Certain traits or phenotypes typically become less common when targeted heavily by the fisheries, and can in turn affect the diversity of the life history strategies in the population. This could possibly make populations more vulnerable to factors such as climate change (Ottersen et al. 2006) and fisheries (Jørgensen et al. 2007), but also to alterations in prey and predator abundance or composition, as well as environmental variability (Neutel et al. 2002). However, for populations such as the northern cod, it is in dispute whether climate change (deYoung and Rose 1993, Rose et al. 1994) or fisheries (Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1996) caused its collapse.

OPTIMAL STRATEGIES AND BEHAVIOURAL TRADE-OFFS

As discussed above, contemporary selection pressures such as intense size-selective harvesting and climate change, cause populations such as the NA cod to mature and reproduce at a younger age. In the case of NA cod, these changes are shown to have several negative consequences in terms of life history strategies, and in particular for the maximization of reproductive value, or fitness. Here I present reproductive strategies as a product of, and trade-off between, three main components, namely I) spawning area, II) timing of spawning, and III) energy investment. Although the components are not independent, I will first explain them separately, discuss how they might interlink, and then propose some methods to quantify them.

I) SPAWNING AREA

> ”Det lange dunkle Spørgsmaal om, hvorfra Lofotskreien kommer, maa saaledes nu ved vor Expeditions Arbeider siges at have faaet sin endelige og tilfredstillende Løsning, og en vigtig Basis for de fremtidige Undersøgelser af dette Fiskeri er herved vundet.”
>
> “The long obscure question concerning where the Lofoten-cod comes from, must as of now, due to our expeditions work, be said to have come to a satisfactory solution, and an important basis for future investigations of this fishery is hereby accomplished.” (free translation).
>
> Georg Ossian Sars, 1878

For many species, the ideal nursery areas for their offspring are often less profitable or even completely unsuitable as habitats for the parents. A vast number of species, both on land and in the sea, are capable of performing astonishing migrations to overcome such conflicting interests. Finding a spawning location which maximises fitness is therefore a complex decision circling around the trade-off between parental cost and offspring benefit (Sutherland 1996).

General theory suggests that spawning strategies, including migration length and choice of spawning ground, are optimized decisions based on individual size or physiological state (Dodson 1997). This has been suggested for pelagic species in general (Nøttestad et al. 1999), as well as for specific species such as herring (Slotte and Fiksen 2000), trout (Forseth et al. 1999) and tuna (Block et al. 2005). However, alterations of spawning areas within fish stock or population are often attributed to depleting abundance and density dependence, resulting in reduced distribution when abundance decreases (e.g. MacCall 1990). More specifically, such relationships have been found for several clupeoid species including North Sea Herring (Bailey et al. 1998) and NSS herring (Dragesund et al. 1997), as well as gadoids such as the northern cod (deYoung and Rose 1993) and Icelandic cod (Begg and Marteinsdottir 2000).

The collapse of the NSS herring stock in the 1960s was followed by severe truncation of both overwintering and spawning areas (Dragesund et al. 1997), though even long after its recovery, the NSS herring have only showed sporadic spawning on southern grounds – indicative of increased distribution. For the NA cod, changes in spawning ground distribution have received only modest scientific attention. Although severe reductions in spawning ground distribution was observed by Sætersdal and Hylen as early as 1964, it was given little thought, and was assumed to be the result of “natural change”. More recently, Sundby and Nakken (2008) suggested that climate variability was the main cause for changes in spawning ground distribution in NA cod. In fact, the fluctuating stock abundance of NA cod has typically received substantial scientific attention (Sætersdal and Hylen 1964, Garrod 1967, Nakken 1994, Godø 2003, Hjermann et al. 2004), while little effort has been directed towards the variation and truncation of spawning ground distribution.

II) TIMING OF SPAWNING

> "It is considered that, through the action of natural selection, the breeding season of each species coincides with the time of year when offspring can be raised with greatest success."
>
> David Lack, 1950

For animals inhabiting polar or sub-polar regions experiencing strong seasonal variations in climate and ecology, survival and reproductive success depends strongly on the timing of important life history events such as reproduction, feeding and overwintering (Varpe et al. 2007). Within populations the optimal timing of reproductive events varies between individuals, for instance with size and condition, and is considered to be crucial for reproductive success in animals as diverse as copepods (Varpe et al. 2007, Varpe and Fiksen 2010), birds (Verhulst and Tinbergen 1991) and fish (Lasker 1981, Cushing 1990).

Timing of reproductive events is shown to be an important response to environmental variability and predator-prey interactions in marine ecosystems (Cushing 1990), as well as for ecosystems in general (Visser and Both 2005). Interestingly, timing of spawning also determines when adult NSS herring start their feeding migration and thereby also the timing of trophic interactions in the Norwegian Sea, such as the important interaction between NSS herring and its dominant prey, the copepod *Calanus finmarchicus* (Varpe et al. 2005, Varpe and Fiksen 2010). For the NA cod, individuals spawning further south, which undergo longer migrations, also spawn earlier in the season (Sund 1933), thus leaving less time for foraging in the Barents Sea due to both longer migration time and earlier spawning. From evolutionary theory, migratory behaviour inducing both shorter feeding time and increased migration cost, should also include return benefits in terms of reproductive success (Dodson 1997)

In an environment with strong seasonal and inter-annual variation, spawning areas are rarely static in terms of larval growth and survival, and both geographic locations and the timing of reproductive events are expected to vary between years. Most boreal and Arcto boreal fishes are seemingly well adapted to the challenges of a seasonal environment and spawn during a relatively short period in late winter and early spring. For species relying on nursery areas in the Barents Sea, this assures larval drift northwards along the coast in time for the seasonal development of phytoplankton and zooplankton. Certain spawning grounds for NA cod are thought to be utilized only under specific climatic conditions due to altered distributions of adult feeding areas (Sundby and Nakken 2008, Drinkwater et al. 2010), whilst spawning grounds for NSS herring may only provide favourable retention or current regimes for eggs and larvae at certain times of the season (Vikebø et al. 2010). Survey studies of mature NSS herring from 1983 to 2003 have also revealed that between 1 and 14 % of the spawning stock are autumn spawners (Husebø et al. 2005), despite their apparent adaptation to spring spawning. Other surveys in the Norwegian Sea have also found newly hatched NSS herring larvae in autumn, possibly originating from autumn-spawning NSS herring (Fossum and Moksness 1993). This diversity in spawning time illustrates the flexibility to adapt to local optimal solutions in terms of light, temperature, availability of prey, and predator abundance, and can be interpreted in terms of fitness, and how spawning strategies may maximize reproductive value (e.g. Varpe et al. 2007, 2009, Varpe and Fiksen 2010).

III) ENERGY INVESTMENT

> "… expenditures on reproductive processes must be in functional harmony with each other and worth the costs, in relation to the long-range reproductive interest."
>
> George C. Williams, 1966

Energy is a limited resource, and its allocation to reproduction is meticulously weighed against other vital processes such as somatic growth and energy storage. Parental investment towards offspring is typically traded off against the parent's own survival and its prospects for future reproduction (Williams 1966). However, when prospect of future survival is bleak, more energy is allocated towards reproduction rather than growth or storage (Stearns 1992). This can be due to resource deficiency, high predation, heavy harvest pressure, or all of the above. Conversely, parents can also postpone reproductive investment, and choose to invest in own immediate survival or energy build-up through skipped spawning (Jørgensen et al. 2006), atresia (Kjesbu et al. 1991, Kurita et al. 2003) or simply by delaying spawning until later in the season (e.g. Varpe et al. 2007).

Both the NA cod and the NSS herring have historically distributed across spawning areas over a vast latitudinal range (Sætersdal and Hylen 1964, Dragesund et al. 1997), implying that parts of the population undergo longer migrations than others. Long distance migrators must therefore allocate more energy to migration than their short distance migrating conspecifics, consequently leaving less energy to egg production (i.e. Jørgensen and Fiksen 2006). As discussed earlier, density dependence alone cannot explain the variation in spawning ground distribution. General life history theory (e.g. Fisher 1930) predicts that the parental cost of migrating to more distant spawning areas should be considered a reproductive investment, implying a fitness benefit associated with distant spawning grounds. For the NSS herring, Fiksen and Slotte (2000) suggested that individuals in good condition perform longer migrations to more southbound spawning grounds, trading off fecundity for increased offspring survival. By assuming that offspring growth and survival would increase with warmer waters found at more southerly and distant spawning grounds, they found that optimal spawning grounds varied with parental body length and condition, and that fish in better condition spawned further south. Their predictions were comparable to observed dynamics in spawning ground distribution, and suggested that the NSS herring’s spawning ground distribution is a trade-off between parental cost and offspring benefits.

THE THESIS APPROACH

Up to this point I have discussed the components of space, time and energy as single entities in life history, and explained how they must be seen as dimensions working together towards the maximisation of reproductive fitness. Life history strategies have evolved through the constant balancing of these components, producing an array of strategies, each optimized to accommodate a string of life history factors such as age, length, physiological condition, prey and predator abundance, disease risk, and environmental conditions. The picture becomes even more complex when considering that strategies in early life might aim to increase success late in life, and that strategies among adults inherit constraints from earlier life stages. A behavioural strategy at a single point in life is not necessarily immediately optimal, but is merely a link in a chain of strategies that form the life history, for which success can only be measured at the very end of the life cycle.

Impressive and innovative modelling techniques that capture optimal life history strategies over the course of entire life cycles have been developed in recent years. The technique, termed “annual routines” by McNamara and Houston (2008), finds optimal annual routines from the trade-offs between strategies at different life stages. In this thesis I focus on only two of these life stages, the early life stages and the spawning adult, which in turn could lead to future modelling of life history strategies of fish from the full life cycle perspective.

RESEARCH QUESTIONS

1. What are the underlying reasons for the northbound truncation of spawning grounds in the NA cod?
2. What potential fitness benefits could promote long distance migrations?
3. How are parental costs and offspring benefits traded off in relation to spawning ground location?

In what follows, I discuss the approaches used in this thesis and how they contribute to solving the research questions. The approaches mainly consist of three methods of providing answers to different parts of the same question, but also offering alternative perspectives as well as generating new hypotheses.

PARENTAL COST AND OFFSPRING BENEFITS

For any animal, migration, both for feeding or reproduction, must harbour a central evolutionary as well as ecological criterion to comply with general life history theory; that the migratory cost is compensated through either long or short term gains in overall fitness (e.g. Fisher 1930). However, reproductive cost and fitness benefits are hard to quantify, and even harder to compare. The energetic cost for a spawning migrator like the NA cod typically includes egg production and swimming costs (Law and Grey 1989, Jørgensen and Fiksen 2006), but there are other more elusive costs, such as shorter foraging time due to the time-consuming migration. Costs in time and energy can in some sense be transposed to equivalent units, considering that lost time may have a particular energetic value if spent feeding rather than migrating. In general, parental benefits are mostly associated with reduced mortality due to predator avoidance or in some cases also lowered disease risk (Dingle 1996, Buehler and Piersma 2008). The offspring benefits are related more to factors such as increased prey availability, faster growth and ultimately increased survival (Sutherland 1996). However, this is not always the case. Some marine mammals, such as the Baleen whale, migrate thousands of kilometres to nurse its offspring in nutrient poor, but warm and predator scarce tropical waters (Corkeron and Connor 1999). The fitness benefit is increased survival of offspring due to low predation, while the direct parental cost is seven months without food.

Today, dynamic state-variable life history models can capture optimal strategies in distinct life stages based on an individual's internal state (Houston and McNamara 1999, Clark and Mangel 2000). Here, behaviour emerges from the optimal solutions regarding energetic trade-offs between growth and reproduction, and allows strategies to evolve through physiological constraints rather than top-down assumptions such as growth rate or age at maturation. This allows for the incorporation of factors such as starvation, natural mortality and fishing mortality that determine age at maturation and reproductive investment (Jørgensen and Fiksen 2006), as well as decisions on skipped spawning (Jørgensen et al. 2006).

We developed a dynamic state-variable optimization model for the NA cod (**paper I**). By applying the logic of general evolutionary ecology together with observations that NA cod spawn on a broad latitudinal range along the coast (Anon. 1866-1976), a simplistic assumption was made, that the fitness value of a spawning ground was increased linearly with its distance from the parents' feeding ground in the Barents Sea. This assumption, which was later investigated using a general circulation model (**paper II and IV**), together with the assumption that migration cost, excluding the standard metabolic rate, is drawn from energy storage (Rollefsen 1933) (but see Michalsen et al. 2008), resulted in a wide range of optimal life history strategies depending on internal physiological cues and external forces such as location of fishing efforts. The model reproduced observed spawning ground distribution both during historical fishing at the spawning grounds and with a more size-selective fishery in the Barents Sea. **Paper I** illustrates the link between offspring benefits and parental strategies, suggesting that a contemporary size-selective fishery in the Barents Sea promotes earlier maturation (Heino et al. 2002), smaller body size (Jørgensen 1990) and consequentially less energy storage leading to shorter spawning migrations (**paper III**). This view differs from the more widely held belief that changes in spawning grounds in the NA cod are mostly climate related (Sundby and Nakken 2008, Bogstad 2009, Drinkwater et al. 2010). These two hypotheses are discussed more thoroughly in the section "Fisheries and climate".

THE LARVAL PERSPECTIVE

In the early life stages of a fish, such as the egg stage and yolk sack larval stage, the fate of an individual is closely linked to its surroundings. However, an individual's ability to withstand and counteract environmental forces significantly improves with age and size, mostly due to increased swimming abilities and improved predatordetection capabilities (Houde 2002). The NA cod spawn their eggs in the free water masses above banks along the Norwegian coast, intersected by prevailing currents, local eddies and winds, which under the right conditions will transport them to their future nursery areas in the Barents Sea. The principle is simple, but as a reproductive strategy it depends heavily on the ambient oceanographic conditions, and as the larvae grows, also its own behaviour (e.g. Fiksen et al. 2007, Kristiansen et al. 2009). The ocean is constantly changing, and although large scale dynamics may prove stable, small scale features such as local eddies and turbulence vary strongly between years, seasons, and even days. To determine the impact of such variability on life histories, biophysical models have proved a useful tool in coupling a variable environment to individual behaviour, and investigating them in relation to each other on continuous temporal as well as spatial scales.

Environmental variability has for many populations been shown to be equally or more important than spawning stock biomass in determining recruitment success. Biophysical models have long been used to simulate the linkage between recruitment, spawning stock and environmental variables based on distribution of the spawning stock, individual based models (IBM) and oceanographic flow fields (Heath and Gallego 1998, Hinrichsen et al. 2002). Also, pure particle tracking models have been used to find drift probabilities of eggs and larvae spawned at different depths, areas and times (Hinckley et al. 1996, Vikebø et al. 2005, Brickman et al. 2007), as well as to find evolutionary stable spawning areas (Mullon et al. 2002). More recently, IBMs simulating larval behaviour with rule based mechanics (Vikebø et al. 2007) or state dependence (Fiksen et al. 2007) have been coupled to oceanographic flow fields emphasising the role of individual behaviour for drift trajectories, survival and recruitment.

For the NA cod, a regional ocean model system (ROMS) together with a particle tracking model (LADIM) were first used by Ådlandsvik and Sundby (1994), tracing particle drift trajectories from Vestfjorden in the Lofoten area, and comparing their successive distribution in the Barents Sea to 0-group survey data. Subsequently, several studies have explored the roles different fixed depths and individual behaviours elicit on drift trajectories, in turn, influencing temperature exposure, growth and distribution (Vikebø et al. 2005, Fiksen et al. 2007, Vikebø et al. 2007). However, these studies have focussed on one or two spawning grounds around the Lofoten archipelago, and did not consider the vast distribution of both contemporary and historical spawning grounds. Today, there are strong indications that most of the cod spawning in Vestfjorden are in fact Coastal cod (see reports by Thesen 2007-2009), and that an increasing proportion of the NA cod stock are spawning east and north of the Lofoten area (Mehl 2004, Bogstad 2009). Also, historically, a significant part of the spawning stock migrated south of Lofoten to spawning grounds off Møre (Sætersdal and Hylen 1964, Godø 2003, Sundby and Nakken 2008), and according to fisheries statistics (Anon. 1866-1976), even as far south as Vest-Agder on the southern tip of Norway (**paper III**).

An improved version of the ROMS model presented in Vikebø et al. (2007) allowed us to explore drift trajectories and temperature exposures from a range of spawning grounds from Finnmark (~70 °N) to Nord-Trøndelag (~65 °N) (**paper II**), and later also from more southern spawning grounds such as Møre (~63 °N) and Vest-Agder (~58 °N) (**paper IV**). In the latter case the use of a ROMS model with 20 years' of forcing data made it possible to determine the inter-annual variation in fitness values for a NA cod egg and larva of historically significant spawning grounds. This has been important in improving our understanding of a spawning cod's energy trade-off between migration and egg production, as first modelled by Jørgensen and Fiksen (2006) for a single spawning ground, and later expanded to include multiple spawning grounds in **paper I**.

FISHERIES AND CLIMATE – EMPIRICAL ANALYSES

A common controversy in fisheries science is the importance of climatic compared to fisheries' effects on stock fluctuations and geographical distributions. In many cases, their relative effects on stock depletions are difficult to disentangle, and the dubious honour is often shared between them, as shown for populations such as the NSS herring (Toresen and Østvedt 2000) and the North Sea cod (O'Brien et al. 2000). In a review of the state of the world’s fisheries, Pauly et al. (2002) point out that environmental effects on stock declines are often exaggerated, allowing fisheries to continue “business as usual” until complete collapse eventually occurs.

In the wake of the northern cod’s collapse, and the subsequent fishing moratorium in 1992, a debate emerged as to whether or not changes in ocean temperatures where responsible for its collapse, and spurred highly polarized views. The debate was initiated by “the right site hypothesis" (deYoung and Rose 1993, Rose et al. 1994), stating that cold ocean temperatures caused a more southern spawning which resulted in more offshore advection of offspring and consequently poor recruitment and stock collapse. Soon thereafter, a series of studies rejected this hypothesis (Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1996), claiming that there was no distributional shift of the spawning stock, but merely a fishing-down of its northern component, and that fishing mortality was the sole cause of the collapse. Hutchings (1994) also warned policy makers and management against attributing stock collapse to poorly understood, and perhaps non-existent, environmental causes. However, later analysis of variables such as prey availability, vertebral counts and antifreeze levels gave enhanced support to the “right site hypothesis” (Atkinson et al. 1997, Rose et al. 2000, Rose 2005). Additionally, Drinkwater (2002) showed that cold climatic conditions prior to the time of collapse caused slower growth and reduced size at age, thereby reducing the spawning stock’s reproductive potential, evidently leading to it’s collapse.

Despite a heated debate as to whether climate and/or if overfishing caused of the collapse, it is important to note that a general agreement exists that a collapse could not have happened without intensive fishing (reviewed in Sinclair and Murawski 1997), and that overall, heavily fished or depleted stocks are more vulnerable to climatic changes (O'Brien et al. 2000, Rose 2004, Ottersen et al. 2006, Brander 2010).

Climate induced changes in distribution, as suggested for the northern cod by deYoung and Rose (1993), have also been shown for a number of fish species in the North Sea (Perry et al. 2005), as well as for several other trophic levels worldwide (Ottersen et al. 2010). In the Barents Sea/Norwegian Sea ecosystem, Dragesund (1997) found that a decreasing population of NSS herring, which has partially been attributed to climate (Toresen and Østvedt 2000), caused a more northerly distribution of spawning grounds. Also, for the same area, Sundby and Nakken (2008) advocate that spatial shifts of the NA cod's spawning grounds are related to decadal climate oscillations and climate change. The latter finding is somewhat different to results presented in **paper III**, and is discussed in the following section.

To date, only two studies have endeavoured to investigate the underlying mechanisms that drive the spawning ground distribution of the NA cod, namely the work of Sundby and Nakken (2008) and **paper III**. On one side, the study of Sundby and Nakken (2008) show that roe indices (total volume of roe/total landed catch weight) on northern spawning grounds are positively correlated with increasing sea temperatures, and are negatively correlated on a southern spawning ground. This pattern is suggested to climatic fluctuations. They present two main mechanisms suggested to lie behind the correlations. The first mechanism is, that during warm periods "... a larger proportion of the mature fish is moving north", causing roe indices to increase in the north and decrease in the south. For the sake of clarity, it is worth noting that the fish are not effectively moving from south to north, but are actually migrating from the Barents Sea to spawning grounds located further north. The second mechanism is, that warmer climate generates higher productivity in the Barents Sea, and consequently higher egg production and increased roe indices. However, because roe index and temperature is negatively correlated at the southern spawning ground, the second mechanism is thought to be of less importance there.

On the other side, **paper III** suggests that shifts in spawning grounds is not an effect of climate alone, and that a size-selective trawl fishery in the Barents Sea have played a more important role. Here, I discuss the findings of Sundby and Nakken, and challenge their statement that "… mature fish is moving north" in warm periods, and south in colder periods. The statement can be interpreted in several ways, depending on how one regards the composition of the spawning stock. I will analyse three possible scenarios.

First, we may assume that all fish migrating to the spawning grounds are mature. In which case, a random increase in the proportion of fish using more northerly spawning grounds would not affect the roe index on any spawning ground. This is because roe index is a measure of the relative relationship between roe volume and body weight and does not change by randomly adding or subtracting mature fish to or from a spawning ground. It can therefore not be used to measure either population fecundity or spawning intensity. In fact, a single fish is sufficient to produce a high or low roe index.

Secondly, assuming that both immature and mature fish perform spawning migrations, and that mature fish migrate shorter distances and spawn further north in warm periods, then roe indices would increase in the north and decrease in the south during warm periods. However, no mechanism is presented as to why immature individuals (roe index = 0) would migrate further than their mature conspecifics in warm periods, and vice versa during cold periods.

The last possible scenario is that the spawning stock consists of a variety of individuals with different individual fecundities. In order to explain an increasing roe index in the north and a decrease in the south during warm years, one would have to assume that only the most fecund individuals spawn on the northerly grounds during warm years. Consequently, the least fecund individuals would have to perform longer migrations to spawn further south during warm periods, and further north in cold periods. Or alternatively, the least fecund individuals are not affected by climatic changes, and spawn at the same spawning grounds every year.

A functional relationship between climate, roe indices and the distribution of the spawning grounds is missing, and so far, no plausible explanation has been suggested as to why certain parts of the spawning stock should react differently to climate change than others.

In this thesis I have compiled evidence using a broad range of methods supporting the hypothesis that a size-selective trawl fishery in the Barents Sea has altered the spawning ground distribution of the NA cod. From a dynamic state-variable model (**paper I**) we show that a "feeder fishery" promote earlier age at maturation compared to a historic "spawner fishery", and that due to physiological changes to the spawning stock, optimal spawning grounds will shift north, despite a given fitness benefit of southern spawning. This assumed fitness benefit is followed up in **paper II** and **paper IV**, which papers give support for faster offspring growth potential and reduced mortality at southern spawning grounds. In **paper IV** we also propose that latitudinal effects on survival outweigh inter-annual climatic influence, suggesting that location of spawning grounds could be more important than climatic variability in determining ambient larval conditions. Thus, it is plausible that a reduced distribution of spawning grounds would strengthen the link between climate and recruitment. Finally, by analysing commercial fisheries catch data from 1866 to 1969 (**paper III**), it is suggested that the influence of climatic periods on spawning ground distribution becomes negligible when factoring in the onset, and rapid increase, of the trawl fishery in the Barents Sea (feeder fishery).

FUTURE PERSPECTIVES

Evolutionary theory has taught us that most behavioural actions are not random, but are successfully evolved traits, refined through the course of natural selection. Through this perspective, I argue that the present and historical use of different spawning grounds along the coast does, and did not occur by mere chance, but is the product of the maximization of individual reproductive success governed by internal physiological cues, as well as external forcing. The models and data analysis presented in this thesis focus on behavioural strategies in single life stages, and can only speculate on the consequences these behaviours have in the perspective of a lifetime. A natural progression would be to include optimal dynamics in all life stages, presenting a more realistic view on how life history is the sum of strategies through a lifetime, and not isolated events at different life stages.

The next step should be to integrate behavioural and life history models of both larval and adult life stages to form complete life-cycle models for the NA cod. First, state-dependent models of early life stages (i.e. Fiksen et al. 2007) may be implemented in general oceanographic circulation models (i.e. **paper II** and **IV**), which would integrate large-scale oceanographic processes with the fate of offspring. Secondly, models of optimal annual routines could be used to link life history theory, behaviour, and phenology in a consistent and coherent framework (Varpe et al. 2007, McNamara and Houston 2008). By coupling these two approaches it would be possible to develop an integrated approach, linking basin-wide environmental dynamics via individual effects to fully consistent species' life cycle.

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PAPER I

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

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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.

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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.

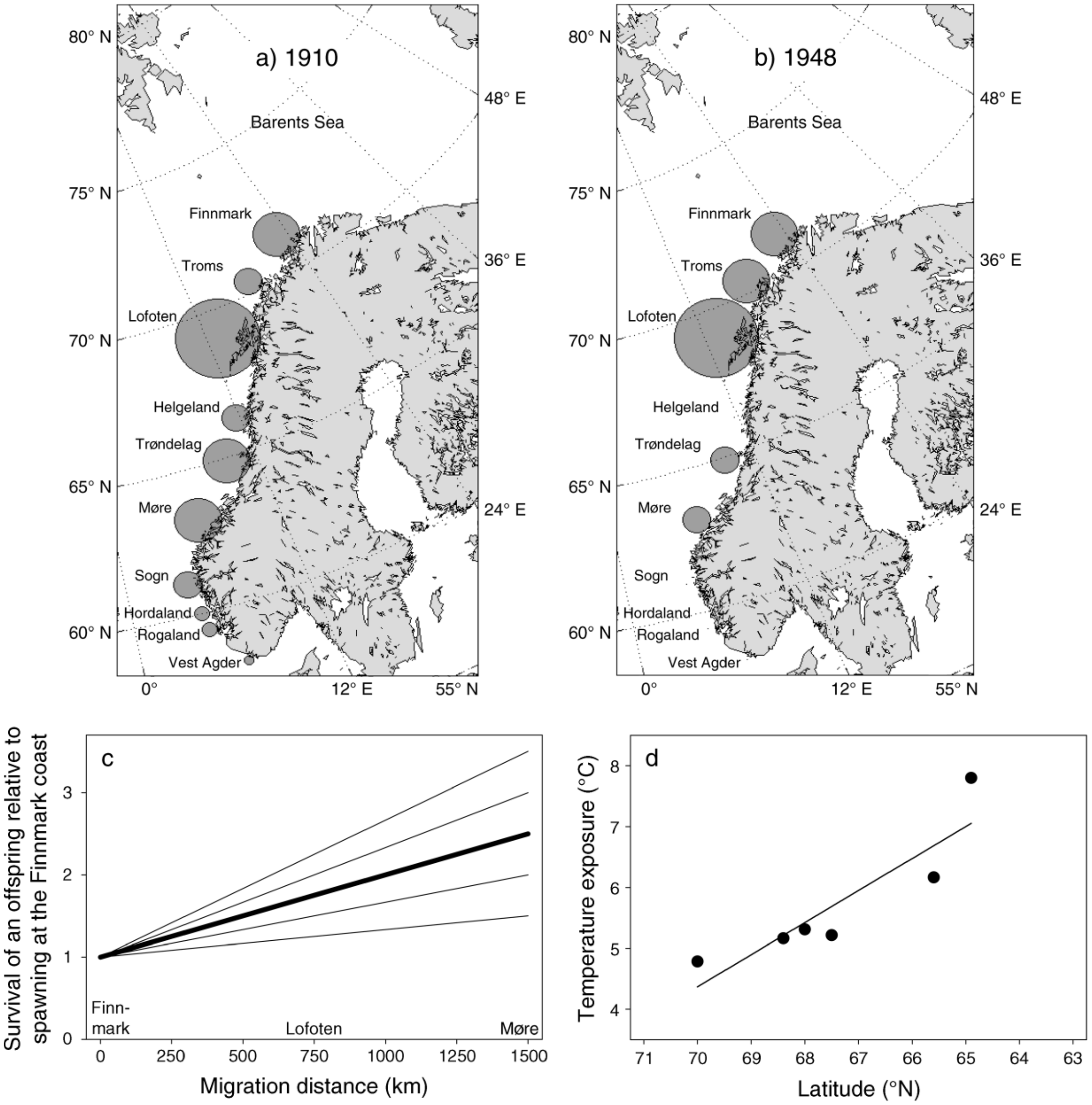

FIG. 1. Map showing fisheries catch of Northeast Arctic cod during the spawning season in (a) 1910 and (b) 1948. Data are from the Annual Norwegian Fisheries Statistics (Norges fiskerier–Grandes pêches maritimes) from the respective years. Over this period, the southernmost spawning locations have been 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 × 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

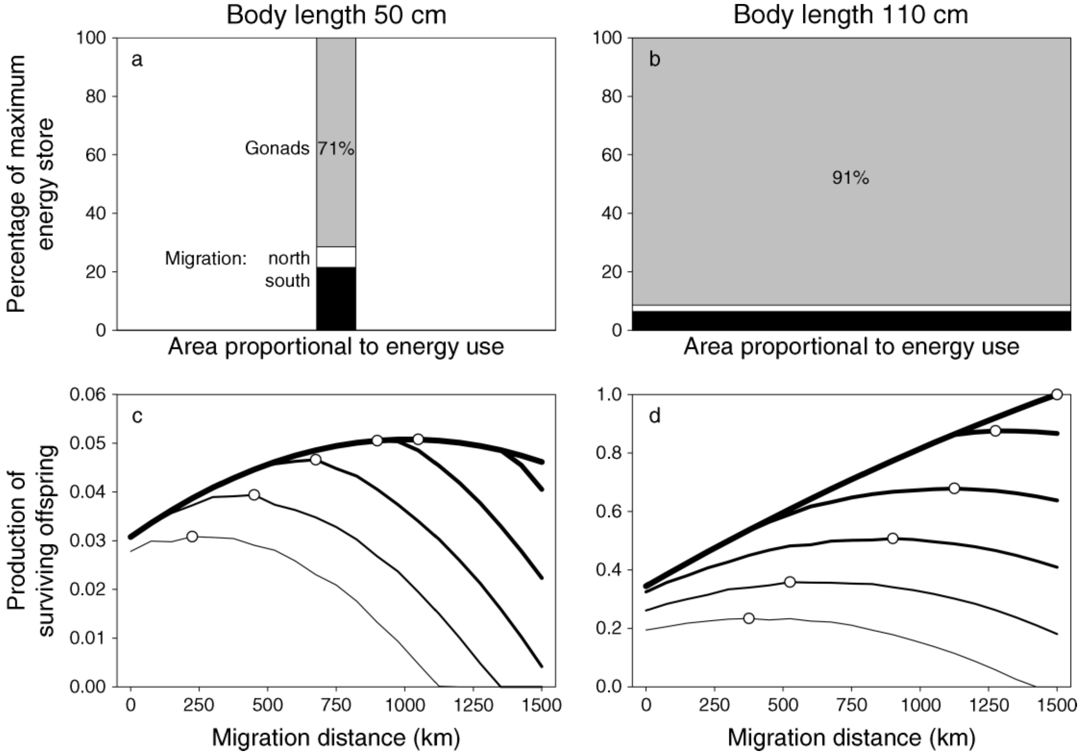

FIG. 2. The effect of body size on the bioenergetics of spawning for fish migrating to spawn in Lofoten (migration distance of 750 km) for female cod of body length (a, c) 50 cm and (b, d) 110 cm. (a, b) The area is proportional between the two graphs and represents the maximum amount of energy the fish 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-

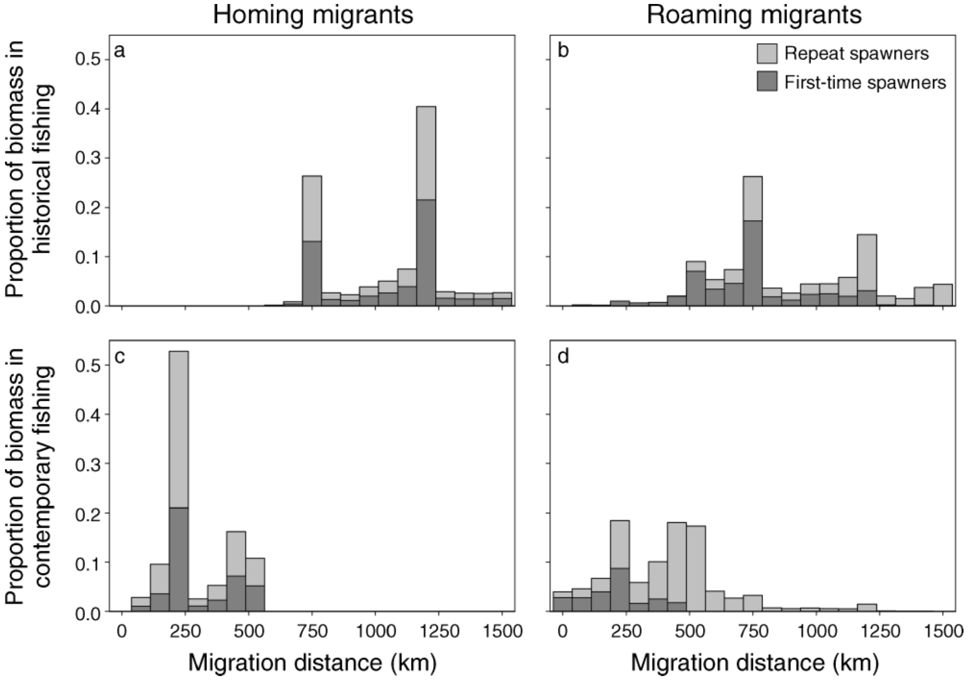

FIG. 3. Spawning distribution along a hypothetical coastline of female cod that follow optimal life history strategies. The survival value of each offspring is assumed to increase the farther the parent migrates ($\Delta V = 0.75$). Light gray bars denote total spawning biomass at that location; dark 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.

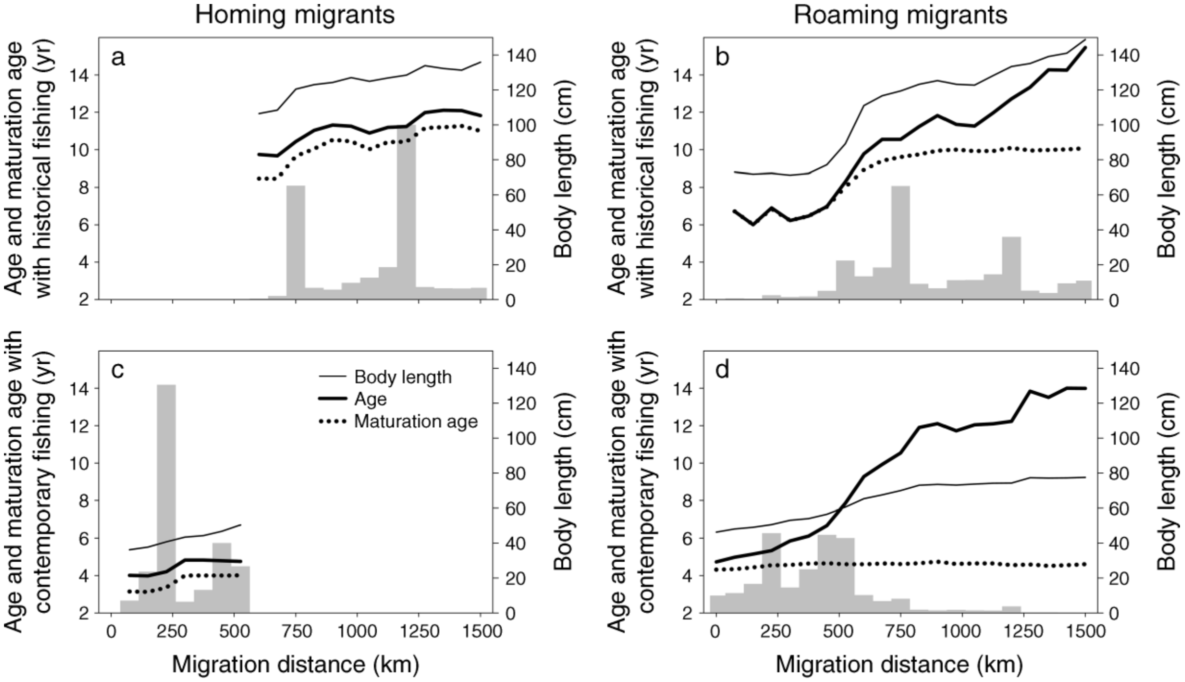

FIG. 4. State distribution in the spawning stock of a migrating cod population along a hypothetical coastline. The gray histogram in the background illustrates the distribution of spawning biomass along the coastline. The lines denote mean age (years; thick solid line), mean maturation age (years; thick 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,

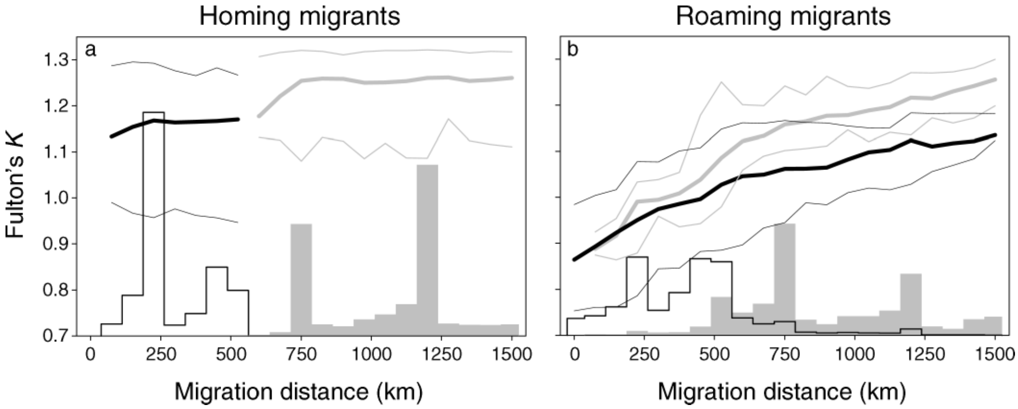

FIG. 5. The relationship between migration distance and Fulton's condition factor resulting from a life history model for the Northeast Arctic cod. Gray bars and lines relate to the life history strategy that was optimal in the historical situation prior to industrial fishing, while black lines and bars 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.

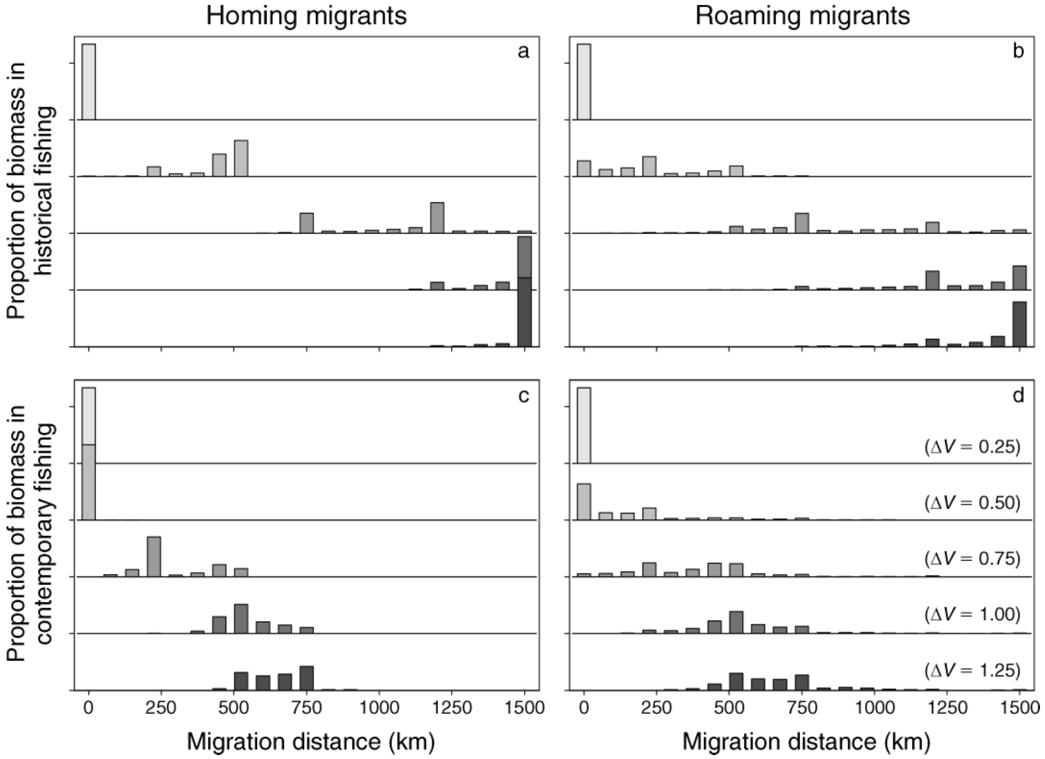

FIG. 6. Sensitivity analysis of varying the survival benefit to offspring ΔV, fishing pressure, and migratory behavior. The bars show the distribution of spawning stock biomass along the hypothetical coastline. The values of ΔV are given in panel (d); the standard value used in all other results presented 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 mechanism 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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PAPER II

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Relationships between spawning ground identity, latitude and early life thermal exposure in Northeast Arctic cod. *Journal of Northwest Atlantic Fishery Science* **49**:13-22.

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Relationships Between Spawning Ground Identity, Latitude and Early Life Thermal Exposure in Northeast Arctic Cod

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Abstract

The Northeast Arctic cod (*Gadus morhua*), is well known for extensive upstream migrations from its feeding grounds in the Barents Sea to various spawning banks along the Norwegian coast. Prior to the 1990s these banks were located on a wide latitudinal range from Finnmark (~71º N) to Møre (~63º N), or even to the south-western parts of Norway (~60º N), with the highest densities around Lofoten (~69º N). The migration is energetically costly, but may be profitable if offspring experience warmer water, higher growth rates and lower mortality. To investigate if such a temperature-benefit-hypothesis is plausible, we utilize a regional oceanographic model system (ROMS) and a particle tracking model to trace the drift of particles (virtual cod larvae) released at six important spawning grounds along a north-south gradient. We did this for two years with contrasting oceanographic conditions, and we assume the integrated ambient temperature of each particle determines growth potential during the northbound drift. In the model, particles released at the most southerly bank generally do experience significantly higher temperatures than particles released at more northern spawning grounds. This is caused by a combination of higher sea-temperatures and higher retention above and around the southern spawning ground. However, particles released at the important spawning grounds in Vestfjorden are exposed to the lowest temperatures of all. Our results suggest that offspring temperature exposure is not simply a function of latitude, but that other factors such as retention, larval prey availability and potential energetic costs of parents may modify the profitability of the spawning migration.

Key words: general circulation model, larval fish, northeast Arctic cod, retention, temperature

Introduction

Parents invest in offspring quality in many ways; spanning from mate choice, through careful selection of nursery areas, to parental care. Parental investment towards offspring quality is typically traded off against their own survival and future reproduction (Williams, 1966). For many species, the ideal nursery areas for their offspring may often be less profitable or even completely unsuitable habitats for the parents. A vast number of animals, both on land and in the sea, are capable of performing astonishing migrations to overcome such conflicting interests. Extensive spawning migrations are performed by a variety of species from catfish in the Amazon River (*e.g.* Jones, 2002) to cod in the Barents Sea (Hjort, 1914). However, finding a spawning location which maximises fitness is a complex decision including favourable retention of offspring (Sinclair and

Iles, 1989), temperature (Otterlei *et al.*, 1999), timing (Hjort, 1914; Cushing, 1986), turbulence (Lasker, 1981; MacKenzie and Kiørboe, 2000), predator (Bailey and Houde, 1989) and prey abundance (Cushing, 1990). Biophysical models have been used to simulate the linkage of these variables based on distribution of the spawning stock and oceanographic flow fields (Heath and Gallego, 1998; Hinrichsen *et al.*, 2002; Brickman *et al.*, 2007). Continuous advancements in computer technology has now made it possible to generate high resolution flow fields, and to model not only large scale ocean currents, but also to incorporate smaller features such as local eddies and turbulence. These mesoscale processes, often generating favourable current schemes around spawning or nursery areas, have long been thought to be of great importance in early larval stages (Hjort, 1914). Based on the pioneering larval-recruitment work of Hjort (1914), Sinclair and Iles (1989) introduced what later became known as the member-vagrant hypothesis, advocating the importance of retention of larvae in favourable areas during the early stages. Retention has been known to be important for recruitment for a long time (Bigelow, 1926), and more recent studies have found retention to be crucial for fish recruitment in both tropical and boreal waters (*e.g.* Sammarco and Andrews, 1988; Lough *et al.*, 2006). Here, we investigate interactions between ocean circulation patterns, retention and temperature, and how these vary with latitude in Northeast Arctic (NEA) cod.

The NEA cod perform extensive southbound upstream migrations from feeding grounds in the Barents Sea to various spawning banks outside the Norwegian coast. In recent decades its spawning migrations have been reduced to a fraction of its historical expansion (Jørgensen *et al.*, 2008). Prior to the 1990s these banks where located on a latitudinal range from the Finnmark Coast (~71° N) to the Møre Coast (~63° N), with the highest spawning density around the Lofoten area at about 69° N. During the last 30 years, cod have abandoned their southernmost spawning banks outside the Møre coast, and concentrate almost solely around the Lofoten area, and also spawning further north, at the Finnmark Coast (Anon., 1910–1976; Mehl, 2004; Sundby and Nakken, MS 2005). Modern fisheries in the Barents Sea have truncated the size distribution, reduced the fraction of older and larger individuals (Ottersen, 2008), and favoured increased energy allocation to reproduction (Sætersdal and Hylen, 1964; Jørgensen, 1990; Jørgensen *et al.*, 2007). There is a strongly held belief that these changes alter the NEA cod's spawning migrations (Godø, 2003).

After spawning, eggs and larvae undergo a 2–3 month northbound downstream drift back into the Barents Sea where they eventually settle to the bottom as 5–6 months old juveniles. While these simple population-level processes have been known for nearly a century (Hjort, 1914), it is still unknown what might motivate spawning migrations up to twice the distance of their conspecifics, and exposing their offspring to an equivalently long return journey. Potential advantages to offspring could be associated with food availability, predation pressure and/or temperatures. Jørgensen *et al.* (2008) developed an optimality model suggesting that the fitness benefit to parents (females) from migration is state dependent, since larger or fatter females (better condition) will benefit more from spawning further south relative to smaller and more lean females.

Temperature is important to growth of larval cod (Otterlei *et al.*, 1999; Folkvord, 2005), and several studies have suggested an increased recruitment of NEA cod during warm compared to cold years (Ottersen *et al.*, 2006). We explore the hypothesis that eggs and larvae spawned at southern locations will experience higher integrated ambient temperatures during their early drift phase, and subsequently also have a potential for faster growth. If this is the case, individuals investing in longer southbound migrations could gain a potential fitness benefit by providing more favourable conditions for their offspring. Using an oceanographic model, ROMS, together with a particle tracking model we trace the downstream drift of particles released at six important spawning grounds along the Norwegian coast. The model simulation is run for the years 1985 and 1986 due to their differences in abundance, distribution and growth of the 0-group cod (Ådlandsvik and Sundby, 1994). The total abundance of 0-group cod was higher in 1985 than 1986, the distribution covered a larger area, and the centre of biomass was farther to the west. The average length and weight (Ellertsen *et al.*, 1989), was also significantly higher in 1985 than in 1986 (Ottersen and Loeng, 2000).

The Models

Our main focus in this study has been to single out variation in temperature exposure of eggs or larvae (particles) drifting from different spawning locations along the coast. By using a general ocean circulation model (Haidvogel *et al.*, 2007) and a Lagrangian particle-tracking model (Ådlandsvik and Sundby, 1994) we released batches of individual particles above various spawning grounds and tracked their drift trajectories at fixed depths over a few months. Each individual was assigned with initial horizontal coordinates and depth. A forward integration in time according to modelled ocean circulation provided temperature exposure, from which temperature-dependent growth potential for larval cod could be estimated. Because the particles are suspended at fixed depths and are subjected to passive drift throughout the simulation period, it is irrelevant whether we address them as eggs or larvae with regards to drift and temperature exposure.

We know that vertical and horizontal swimming behaviour is likely to influence the dispersal of particles released in this region (Vikebø *et al.*, 2005, 2007). However, there is limited information about behaviour of larvae in the field, and we assume particles drift passively with the prevailing ocean currents at fixed depths. The reason for this is twofold. Firstly, the particle trace will then return the drift trajectories and temperature exposure at each discrete depth, rather than from a mixture of several depths depending on vertical behaviour. Secondly, we avoid errors introduced through the implementation of vertical behaviour. Although keeping larvae in fixed depths is incorrect, it appears more parsimonious for our purpose here. For the same reasons we do not discriminate between the banks in terms of prey and predator abundance.

Similar modelling studies have had their main focus on the spread and distribution of released particles (Ådlandsvik and Sundby, 1994; Vikebø *et al.*, 2005), and/or the ability of virtual larvae to influence growth and survival by encompassing various behavioural traits (Vikebø *et al.*, 2007). These studies have solely concentrated on particles released from a few places around Lofoten, and the consecutive northbound drift. In this study we explore the explicit effect different spawning grounds and latitudes have on the particle drift, as well as temperature exposure and successive larval growth potential.

Materials and Methods

Ocean Model

The circulation model used in this study is the Regional Ocean Modelling System (ROMS), version 2.0 (Haidvogel *et al.*, 2007). This is a free-surface, hydrostatic, primitive equation ocean model that uses stretched terrain-following coordinates in the vertical and orthogonal curvilinear coordinates in the horizontal.

Monthly mean climatological values of velocity, temperature, salinity, and water elevation in addition to four dominant tidal constituents (M2, S2, K1, and N2) are used to specify the initial conditions and the lateral boundary conditions (Engedahl *et al.*, 1998). Hence, no interannual variation is imposed at the lateral boundaries. The model forcing also includes daily NCEP/NCAR reanalysed wind-stress, air pressure, and ocean-atmosphere heat exchange for the years 1985 and 1986 (Kalnay *et al.*, 1996). The shortwave radiation is multiplied by a factor, which decreases linearly from 1.0 at the southernmost boundary to 0.5 at the northernmost boundary, in order to reproduce measured temperature distributions. The rationale behind this is that the NCEP/NCAR cloud cover for the Barents Sea seems to be too low (Budgell, 2005). Additional forcing is given by prescribed river run-off from 12 freshwater sources along the coast. The vertical model grid consists of 25 sigma-layers. The horizontal resolution increases from about 3.8 km in the southernmost parts, 5.3 km in the Vestfjord, and up to 8.5 km in the northernmost parts of the model domain. The bottom topography is taken from Etopo2, which gives a horizontal resolution of about 3.5 km. A general evaluation of the model shows that it reproduces the observed hydrography and current metre measurements at stations and sections (Vikebø, 2005).

Particle Release and Tracking

The particles are released from six known spawning grounds along the Norwegian coast (Rollefsen, 1960) covering a latitudinal range of more than 650 km (Fig. 1). The chosen grounds are, from south to north, Vikna, Vega, Røst, Vestfjorden, Moskenesgrunnen and Malangsgrunnen. Particles are moved forward by the daily mean updated velocity fields from the "Lagrangian advection and diffusion" hydrodynamic model (Ladim: Ådlandsvik and Sundby, 1994). Earlier work included a random component in addition to advection to parameterize Fickian diffusion (Csanady, 1973; Ådlandsvik and Sundby, 1994), but this is not included in this study, reducing the spread of particles. With decreasing grid size, the need for diffusion is reduced, as the range of resolved eddies and velocity shear is increased, leading to greater spreading of the particles also in deterministic realisations of the model.

Particles are released from 2 March, and tracked for 100 days. During the first 60 days of the simulation period, batches of 25 particles are released every third day. They are released simultaneously at all spawning grounds and at four different depths (5, 10, 20 and 30 m) to cover the upper water column where eggs and larvae are observed. A total of 12 000 particles are traced for each year. This ensures a representative estimate of dispersal from each spawning ground, although climatological forcing is highly variable through the spawning period. We also get to trace each particle for a minimum of 100 days after release.

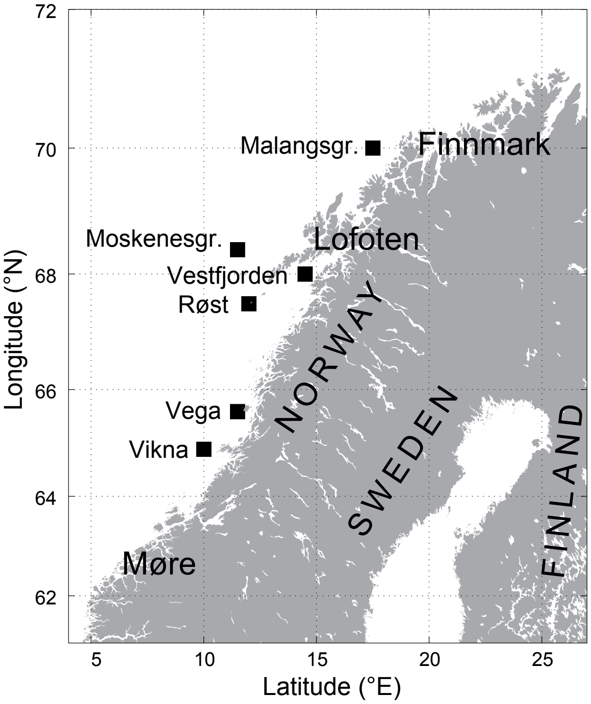

Fig. 1. Geographical placement of the six known Northeast Arctic cod spawning grounds off the northwest coast of Norway used as release points for the virtual larvae in the model.

Temperature-dependent Growth

For each particle we record standard length, growth, and spatial coordinates. We ignore mortality, and individual specific growth rate (SGR, d^{-1}) is an empirical function of body mass and ambient temperature for larval cod fed ad libitum, reared under laboratory conditions (Folkvord, 2005):

$$SGR = 1.08 + 1.79T - 0.074T\, ln\, DW - 0.0965T\left(ln\, DW\right)^2 + 0.0112T\left(ln\, DW\right)^3, \quad (1)$$

where T is temperature (°C) and DW is body mass in grams dry weight. All individuals are initialized with a dry weight of 0.03 mg, and a length of 3.53 mm (Otterlei *et al.*, 1999). This is used to illustrate how variable growth can be from various spawning locations, and it is not an attempt to simulate any kind of existing prey fields. We acknowledge that temperature-dependence in egg-stage duration has not been included explicitly; therefore our estimation of temperature-effects at early age may be slightly biased. However, growth rates during egg stages are also closely coupled to sea temperatures, and any relative deviations from the larval growth function should not influence our overall results to any significant degree.

Results

We present examples of typical particle drift routes from the spawning grounds of Northeast Arctic cod towards the Barents Sea. Furthermore we show how dispersion, and thus drift trajectories are significantly influenced by seasonality, and also how this affects the retention at the spawning banks. Finally we explore how integrated temperature exposure is dependent on all these factors, and how this governs growth potential

Drift Trajectories and Driving Forces

Through the simulation period we released in total 12 000 particles over six banks and four depths, all comprising individual drift trajectories. Rather than plotting all these trajectories in one figure, we present an example of typical drift routes of particles released on 11 March 1985 (Fig. 2). The figure shows drift trajectories of 25 particles released at 10 m depth from each of the six spawning grounds. Although trajectories change through the season and from day to day, it is clear that particles from all spawning grounds follow the prevailing North-Atlantic current, or the Norwegian coastal current north towards the Barents Sea. There are differences in retention at and around the spawning grounds, and Vikna and Røst appear to have notably stronger retention than the rest. This is quantified as the distance each particle has drifted from its origin during the first four days (Fig. 3). Here we notice a clear relationship between time of release and particle retention above their respective banks. For both 1985 and 1986 particles released early in the season experience rapid advection away from the bank compared to later in the season.

Temperature Exposure and Related Growth

Each individual drift trajectory has a unique temperature signature. The mean temperature exposure for particles released at 10 meters from all banks have been plotted as a function of time since release (particle age) both for 1985 and 1986 (Fig. 4). The standard deviation has been plotted for the spawning grounds with highest and lowest temperature (Vestfjorden and Vikna, respectively) (Fig. 4). It is apparent that particles released at Vikna experience the highest temperatures. Particles released at Vestfjorden experience low temperatures at early age, though the spread in temperatures between all grounds, excluding Vikna, is moderate, especially in 1986.

The effects of latitude and release dates on the particles' mean temperature exposure are presented in Fig. 5. The highest temperatures are observed at the southern

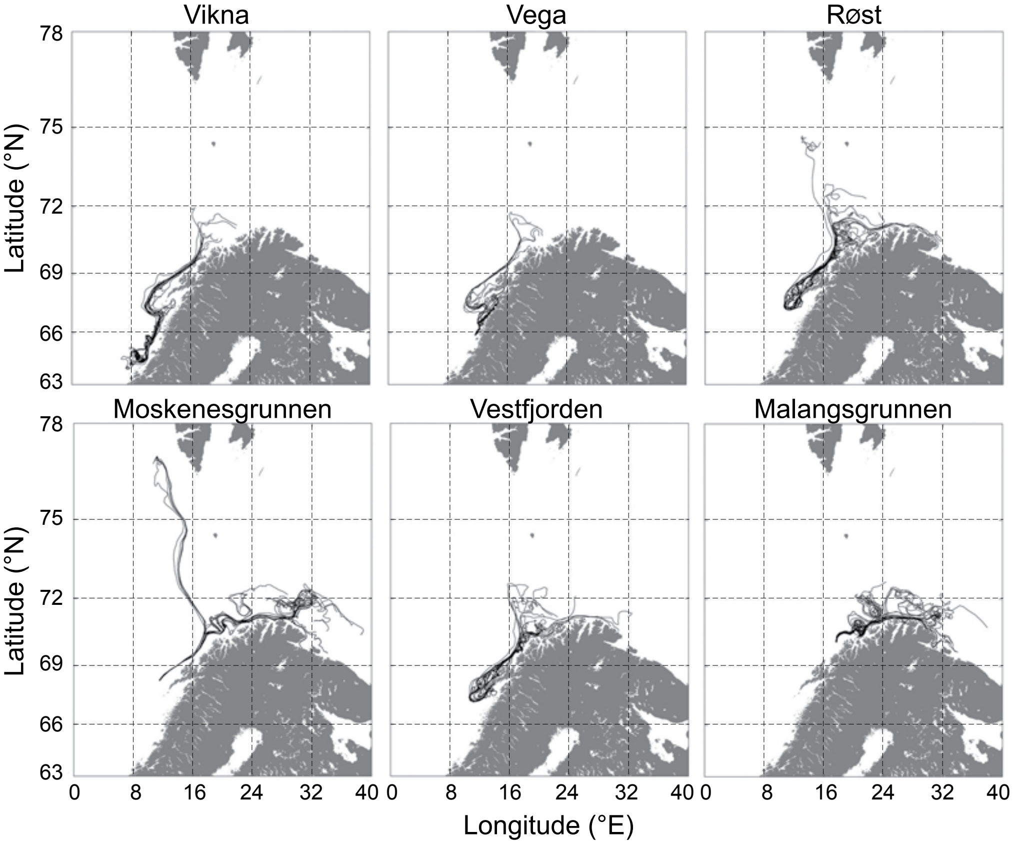

Fig. 2. Examples of drift trajectories for 25 virtual cod larvae released at 10 m depth on each of the six different spawning grounds on March 11 1985 illustrating some of the typical model-predicted dispersions and drift routes.

spawning ground, Vikna (64.9º N), apart from 5 m depth in 1986, which seems to be colder across the entire latitudinal range. Particles released later in the season also experience higher temperatures.

To translate the temperature-exposure into relative difference in larval growth-potential over latitude, we have standardized larval weight, averaged over all particles released at a given time and location at the age of 100 days. This was done simply by dividing the size of larvae from each spawning ground with the maximum average value at each date of release. This has been plotted as a function of latitude and release date (Fig. 6). We observe that the southern-most spawning ground (Vikna at 64.9º N) generally has the highest daily growth throughout the simulation period. However, in 1986 at 5 m depth there are tendencies of relatively high growth across the entire latitudinal range.

Discussion

It is evident that this study has brought to light some of the many complexities that even a simple question can raise. Apparently, different spawning grounds encompass properties important to fitness in NEA cod offspring. We observe that temperature exposure of drifting particles may be affected by local retention, which in turn is dependent on local tides, topography, frontal structures and weather conditions. Furthermore, important spawning grounds such as Vestfjorden did not provide the best temperature exposure. Possibly, these areas have a richer supply of food, or other benefits that the model does not include, or, it may be due to a trade-off between adult costs of migrating further and the risk of offspring dispersing too far north if spawning takes place further north (Jørgensen *et al.*, 2008). The strong seasonal variation in drift trajectories, and corresponding temperature exposure, suggest close links to wind driven processes.

Several modelling studies have tracked particles (larvae) from spawning grounds along the Norwegian coast to the Barents Sea (*e.g.* Ådlandsvik and Sundby, 1994; Vikebø *et al.*, 2007) These studies have mainly focused on one or two spawning grounds with large-scale drift processes, some with vertically and/or horizontally

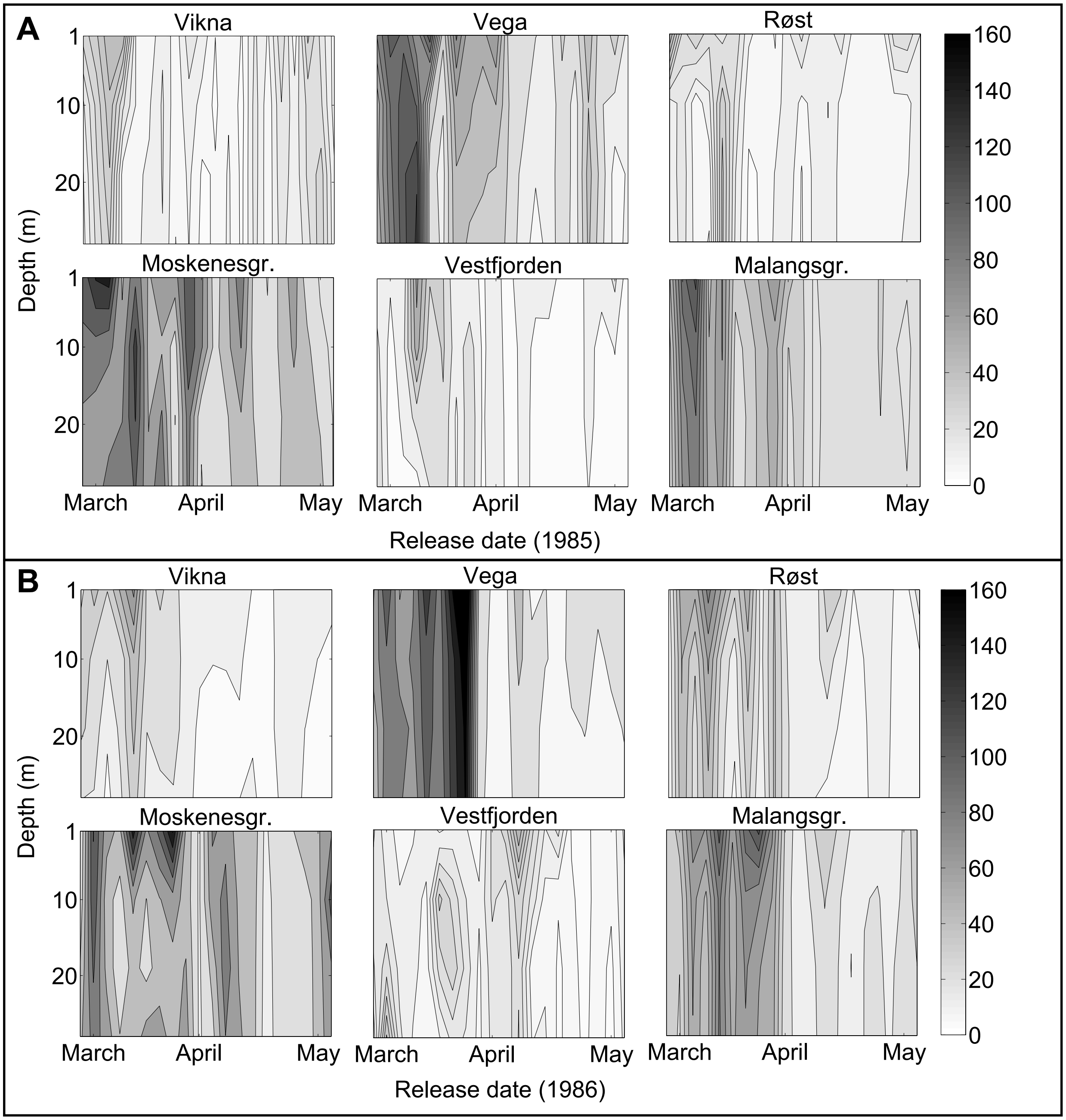

Fig. 3. A contour plot showing the distance (km) the cod larvae have drifted away from their respective spawning grounds during the first four days as a function of depth and time of release, for the years (**A**) 1985 and (**B**) 1986.

mobile larvae. Here we have focused on how ambient temperature for offspring differ for alternative spawning grounds at a wide latitudinal range. Our simulation predicted that a significant proportion of all particles released, at all depths and spawning grounds, were advected north by the prevailing currents, eventually ending up in the Barents Sea. This prediction is consistent with earlier studies, *i.e.*, a significant proportion of eggs spawned at southern spawning grounds end up in the Barents Sea recruiting to the NEA cod population. (Godø, 1984; Robichaud and Rose, 2004). However, some particles, especially those released near the coast, might never reach the Barents Sea, but end up in various fjord systems. Vikebø *et al*. (2007) show in their simulation of particle drift from the Lofoten and Moskenes banks that particles distributed deeper in the water column experienced a more easterly distribution in the Barents Sea than those inhabiting shallower water, which drifted further north. They also found that particles released closer to the core of the North Atlantic current are

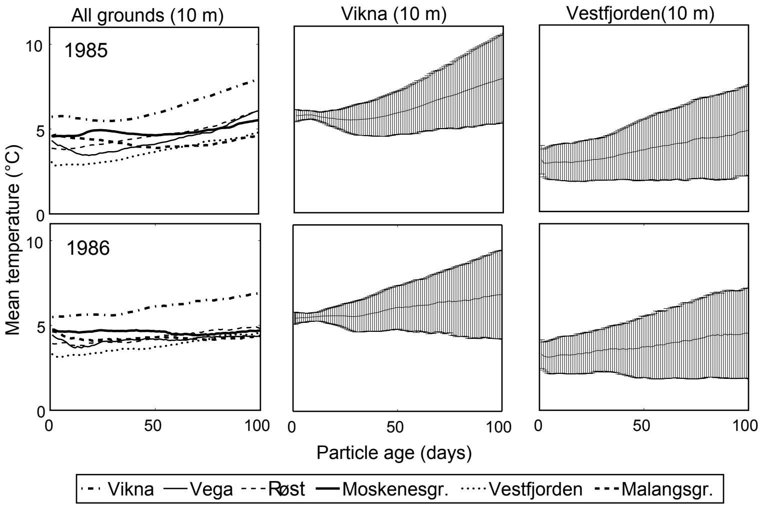

Fig. 4. Mean temperature exposures for particles released at all cod spawning grounds (left panels), with the standard deviation plotted for the highest (centre panels) and lowest (right panels) mean temperature trajectories for the years 1985 (upper panels) and 1986 (lower panels).

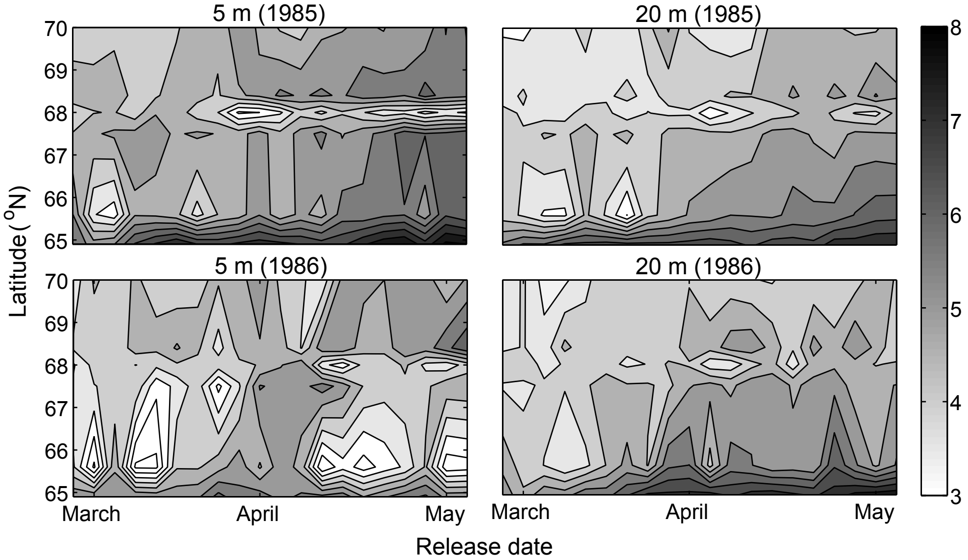

Fig. 5. Contour plot illustrating the particles mean temperature exposure throughout the simulation as a function of latitude and release date. The latitudes (°N) for the different spawning grounds are from south to north; Vikna (64.9), Vega (65.6), Røst (67.5), Vestfjorden (68.0), Moskenesgrunnen (68.4) and Malangsgrunnen (70.0).

more likely to end up in the northern and western parts of the Barents Sea. In our study we see in fact particles at the same depth divide into the two main drift trajectories when passively following prevailing currents (Fig. 2). However, we observe large variation in the dispersion and distribution of the particles depending on season, and on a day to day basis. Vikebø (2005) found that absolute wind stress, indicating input of kinetic energy to the circulation model, is significantly decreasing between March and May for the year 1985, and on average between 1980 and 1990. In the field, larvae exposed to strong winds may sink deeper to avoid strong turbulence (Visser *et al.*, 2001), reducing the effect of wind on their drift trajectories. Fiksen *et al.* (2007) showed in a similar model setup that larvae swimming 1–3 body-length s^{-1} might determine whether they end up in the eastern or northern parts of the Barents Sea by constant, directional swimming.

Seasonality and wind stress do not only influence the terminal destination of the drift trajectories, but also play a crucial role in retention at spawning banks. Retention of larvae in warm favourable conditions is known to be important for recruitment to the stock (Sinclair and Iles, 1989). Hinrichsen *et al*. (2001) also found that wind driven circulation is a central component in determining the dispersion, and thus recruitment, of the Baltic cod larvae. In our simulations particles released early in the season were generally prone to little retention and consecutive fast northbound drift (Fig. 3). We hypothesize that wind stress is an important factor, perhaps not in generating the retaining circulation itself, but for advecting larvae out of favourable current schemes and potentially exposing them to lower temperatures and reduced growth potential (Figs. 5 and 6).

Conversely, retention does not provide an unconditional recipe for recruitment success. Vestfjorden, known to be an important spawning area for NEA cod, reveals high retention and very low sea temperatures for both 1985 and 1986 in our model and reflect suboptimal temperature conditions for larval survival. However, our model temperatures are consistent with actual observations (Vikebø, 2005). The general circulation in Vestfjorden is cyclonic, and would normally enhance advection out of the fjord (Mitchelson-Jacob and Sundby, 2001). However, frequent low pressure fields early in the season may temporarily mediate these circulation patterns and enhance retention. The spawning grounds in Vestfjorden are known to be of great importance to NEA cod, supporting spawning for a significant proportion of the stock. Thus we must assume that factors such as low predation or high prey abundance (Furnes and Sundby, 1981) may compensate for the suboptimally low sea temperatures.

Disentangling the effects that season, wind stress, retention and drift trajectories have on larval temperature exposure is difficult considering that the variables themselves are inter-dependent. However, the spawning grounds stand out as perhaps the single most important independent variable for determining temperature exposure and growth. Other external drivers might mediate or enhance the effects of the spawning ground, but do not to any profound extent alter their significance to the temperature exposure (Fig. 5). It is clear that larvae released above the southernmost spawning ground, Vikna, experience the highest temperatures and subsequent growth not only as a result of a southern location, but also because of favourable retention schemes – especially in the

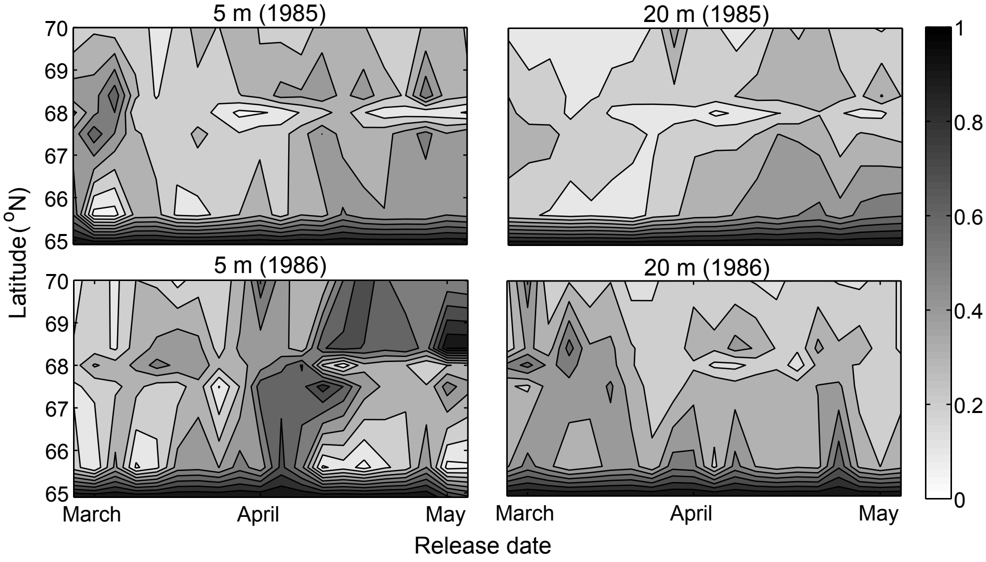

Fig. 6. Contour plot showing the cod larval weight (after 100 days) standardized relative to the highest average body weight (at day 100) at each day of release (this removes the effect of season, and highlights latitudinal differences), as a function of latitude and date of release. The latitudes (°N) for the different spawning grounds are from south to north; Vikna (64.9), Vega (65.6), Røst (67.5), Vestfjorden (68.0), Moskenesgrunnen (68.4) and Malangsgrunnen (70.0).

late season. This positive effect of retention on growth potential at Vikna is somewhat corroborated by the relatively lower temperature at Vega, only 0.7 degrees further north and accompanying slower growth. This suggests that a mere north-south gradient in temperature exposure and thereby growth potential is highly inaccurate, suggesting that a spawning ground's latitudinal position is not always closely connected to offspring success. However, at a larger scale, considering the historical spawning migration to western and southern parts of Norway, we think the upstream spawning migration by NEA cod is partly associated with temperature benefits to offspring. To further resolve this question, we need to include flow-fields all the way to the southern tip of Norway, and preferably, for a longer time period than two years.

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PAPER III

Opdal, A.F. (2010)

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Fisheries change spawning ground distribution of northeast Arctic cod

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Prior to the 1920s, the northeast Arctic (NA) cod were caught at spawning grounds ranging from the southernmost to the northernmost parts of the Norwegian coast, but have for the last 50 yr mainly been caught around the Lofoten archipelago and northwards. The NA cod have their feeding and nursery grounds in the Barents Sea, and migrate south towards the Norwegian coast in the winter to spawn. This study uses commercial fisheries' data from landing ports along the entire Norwegian coast during the period 1866–1969 as evidence of long-term truncation and northerly shift of spawning grounds. Nearly all spawning grounds south of Lofoten have been abandoned, while an increasing proportion of the spawning stock only uses the northernmost areas of the Norwegian coast, Troms and Finnmark. The truncation can hardly be attributed to long-term climatic variations, but may result from an intensive size-selective trawl fishery in the Barents Sea causing a sudden increase in fishing mortality, probably altering the size structure and migratory capacity of the stock.

Keywords: northeast Arctic cod; fisheries; spawning migration

1. INTRODUCTION

Much concern has been raised on how organisms respond to climate variability, climate change and human interventions such as harvesting (e.g. Walther *et al.* 2002; Jørgensen *et al.* 2007), and long time series are often our main source of information about long-term ecological changes. The northeast Arctic (NA) cod undergo extensive migrations from their feeding and nursery areas in the Barents Sea to their spawning areas off the Norwegian coast. During the last 150 yr, the NA cod have undergone striking fluctuations in abundance, and also substantial contraction in spawning ground distribution. While the fluctuating stock abundance has received substantial scientific attention (Sætersdal & Hylen 1964; Garrod 1967; Nakken 1994; Hylen 2002; Godø 2003; Hjermann *et al.* 2004), there has been little focus on the long-term truncation of spawning ground distribution.

Norwegian Fisheries Statistics (Anon. 1866–1899, 1900–1976) show that until the 1930s yearly commercial landings of NA cod were registered along the entire West Coast of Norway, from Finnmark to Vest-Agder (figure 1). From the mid-1920s the latitudinal range of spawning grounds has steadily decreased, with progressively less migration to more southerly spawning grounds. The reasons for the past widespread distribution of spawning grounds are poorly known, and few studies have addressed the issue.

However, recent northward shifts in the spawning ground of Lofoten have attracted popular as well as scientific attention (Jørgensen *et al.* 2008; Sundby & Nakken 2008). Sundby & Nakken (2008) argue that sea temperatures and spawning ground distributions are correlated, indicating that recent northward shifts in the Lofoten spawning ground are caused by climate warming.

Considering the energetic cost of migration, it is plausible that longer migrations provide a reward in terms of fitness. Jørgensen *et al.* (2008) assumed a linear increase in fitness benefits with decreasing latitudes. From a state-dependent optimization model, they suggest that spawning migration distance is strongly related to body size and physiological state, implying that larger fish and fish in better condition prior to the migration will profit from longer southbound spawning migrations. Smaller fish and fish in poorer condition have a lower fecundity, and would not receive the same fitness gain by longer migration (Jørgensen *et al.* 2008). A possible fitness benefit could be retention within favourable environments above certain spawning banks further south (Opdal *et al.* 2008), prolonging the larva's exposure to warmer waters, and thus faster growth (Folkvord 2005). In turn, fast growth commonly leads to reduction in offspring mortality rates (Houde 1989).

It is thought that after the onset of trawl fisheries in the Barents Sea in the 1920s (Sætersdal & Hylen 1964; Godø 2003), age and body size of the spawning stock has decreased (Jørgensen 1990), possibly leaving a spawning biomass comprised of smaller individuals destined to shorter spawning migrations (Jørgensen *et al.* 2008).

In this study I present catch data for NA cod from 1866 to 1969 both from spawning ground fisheries and offshore fisheries, providing evidence that the northwards truncation of the NA cod's spawning ground distribution could be caused by a size-selective trawl fishery in the Barents Sea.

2. MATERIAL AND METHODS

The commercial catch data for the NA cod (1866–1969) are found in the yearly publications of 'Fisheries of Norway' (Anon. 1866–1899, 1900–1976), originally recorded by the Supervisor of the Lofoten Fishery and county governors along the entire West Coast of Norway. After 1969 the fisheries' statistics no longer distinguish between the NA cod and the coastal cod landings, thus catch data beyond this year are not included in the study. Landings for Finnmark are only available after 1907, as the statistics did not separate between the spawning ground fisheries in the winter and the spring/summer fishery for NA cod feeding on capelin before this. After Norway's involvement in World War II, from 1941 to 1945, there were considerable restrictions to the fisheries, particularly in the north, and data from this period should be treated accordingly. It is reasonable to assume that for the years before and after World War II the recorded catch statistics are strongly associated with the actual fish abundance. There have been no management restrictions on the coastal fisheries in the studied time period (Anon. 1866–1899, 1900–1976), and there is no reason to believe that certain areas have experienced disproportionate changes in fishing effort relative to other areas.

Throughout the time series, catch data are organized by county, and then by district within each county. In the first period (1866–1937) catches were recorded as numbers of individuals, though from 1905 and onwards catches from Troms and Finnmark

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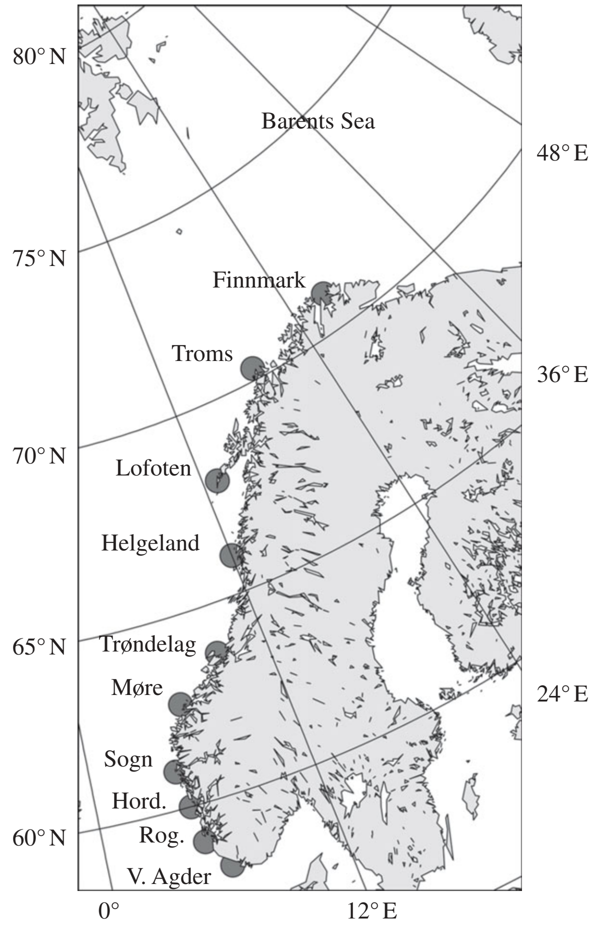

Figure 1. Map indicating the approximate midpoint of each spawning area along the Norwegian coast (adapted from Jørgensen *et al.* (2008)).

were noted as gutted weight. This refers to the fish wet weight excluding head and intestines. After 1937, gutted weight was used for all counties. In an overlapping period of 8 yr (1929–1937) catch data were presented as both gutted weight and numbers of individuals. Numbers of individuals are converted to gutted weight by extrapolating along the linear regression line between numbers and gutted weight during the overlapping period (1929–1937). All regressions are highly significant with $r^2 > 0.90$ and p-values < 0.01. The landings are assigned to their respective counties—from north to south (figure 1).

All catch statistics for the Barents Sea are extracted as total landed gutted weight (tons) from the official Norwegian catch statistics (Anon. 1900–1976).

To test the effect of the climatic periods (Godø 2003) and the presence of the Barents Sea fishery (BSF) on the spawning ground distribution, a simple analysis of variance (ANOVA) on the relative contribution of catches south of Lofoten was performed.

3. RESULTS

It is evident that the spawning grounds used by the NA cod have changed markedly through the years, and that Lofoten remains the single most important spawning area for the NA cod throughout the time period, with the exception of the years around 1915 when the Lofoten catches were exceeded by the total catch from spawning areas south of Lofoten (figure 2). Catches south of Lofoten drop below the historical average in the mid-1920s shortly after an abrupt, sixfold increase in total catch caused by the onset of trawl fisheries in the Barents Sea in 1923. The fisheries south of Møre ceased around 1938, along with a rapid decline in the Møre fishery. From the late-1930s and onwards, catches south of Lofoten are generally low, while simultaneously increasing in the northernmost areas, Troms and Finnmark. After the onset of the BSF, the relative contribution in the south decreased 13 per cent on average (ANOVA, $p > 0.05$), while during cold climatic periods the relative contribution increased 10 per cent (ANOVA, $p > 0.05$). By including an interaction between climatic periods and the presence of BSF in the model, the effect of climate during times of BSF becomes negligible (0.4%; ANOVA, $p > 0.05$).

4. DISCUSSION

The spawning distribution of NA cod along the Norwegian coast has been highly variable during the period 1866–1969, and through time the proportion of total catches in the spawning ground fisheries have been increasing in the north and decreasing in the south.

Observation of the fluctuating spawning distribution is not new. Sætersdal & Hylen (1964) noticed the rapid decline in catches on the southern spawning grounds in the 1920s and stated that the southern NA cod fishery had been insignificant since the 1930s. They argued that the decline was not caused by reduced effort, but rather a natural change in the spawning ground distribution. More recently, Sundby & Nakken (2008) studied the shifts in spawning ground distribution between Finnmark and Møre during the time period 1905–1969. They correlated smoothed sea temperature and the NA cod's roe indices, and suggested that spawning ground distribution is climate-driven, and that warm periods favour more northbound spawning compared with cold periods.

However, the present study demonstrates that there is also a strong effect of fishery on the spawning ground distribution, and that after the onset of the BSF the influence of the climatic periods is undetectable. The severe truncation of spawning ground distribution after the mid-1920s appears to take place just after the onset of the trawling fishery in the Barents Sea. The trawl fishery in the Barents Sea has a sigmoid selection curve causing higher fishing mortality for the larger individuals, contrary to the traditional line and gill net fishery taking place at the spawning grounds (Huse *et al.* 2000). Over some time this may have truncated the size distribution of NA cod, and influenced the relative abundance of spawners along the large latitudinal gradient of alternative spawning grounds. This hypothesis is supported by a recent state-variable modelling experiment, predicting that larger and older NA cod in better condition should perform longer migrations than individuals in relatively poorer condition (Jørgensen *et al.* 2008). Also, we have released and tracked particles in a general circulation model simulating the fate of larvae spawned at different known spawning areas for NA cod (Opdal *et al.* 2008). This model demonstrated that spawning grounds further south provide better offspring conditions in terms of favourable temperatures and retention schemes.

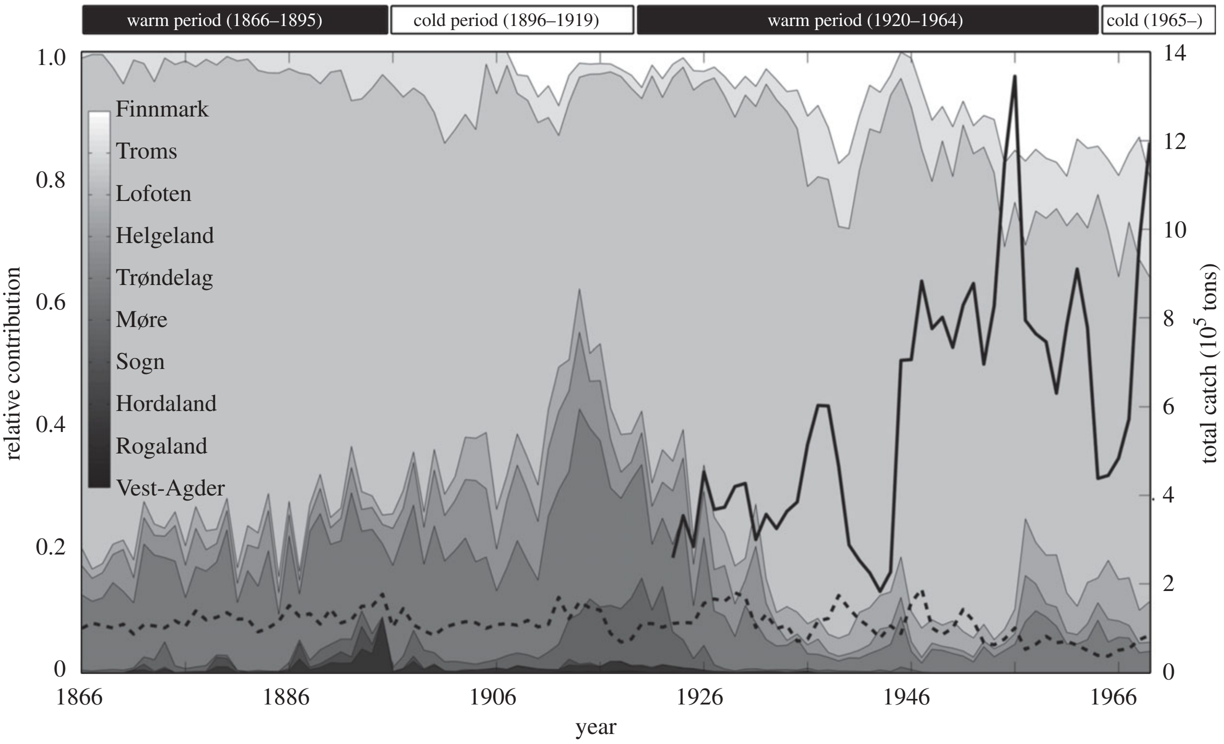

Figure 2. The proportion of the total catch of northeast Arctic cod caught at the different spawning grounds along the coast. The shaded areas represent the relative contribution from each spawning ground to the total catch from the spawning grounds, and are stacked on top of each other from south in Vest-Agder (bottom, black) to north in Finnmark (top, white). The hatched black line indicates the total catches from the spawning ground fishery, and the continuous black line indicates the total catches from the offshore trawl fishery in the Barents Sea, starting in 1923. The top panels denote the different climatic periods as described in Godø (2003). There is a missing data point for Finnmark in 1945 owing to World War II.

The present study suggests that early trawl fishery in the Barents Sea not only caused a sixfold increase in total fishing mortality within a few years, but also truncated the size distribution of the stock. This in turn reduced the abundance of large individuals in the stock, again causing the decline in, and successive disappearance from, the southern spawning grounds. The hypothesis is supported by our earlier modelling studies, and by the time-series data presented here.

Truncation and northward shift in spawning grounds has heavily reduced the latitudinal range of offspring nursery areas, possibly making recruitment processes less resilient towards climatic changes, and could provide further support for the climate-cod recruitment link that has appeared during the last decades (Ottersen *et al.* 2006). In the long run, high fishing mortalities will also increase allocation to reproduction, and reduce allocation to migration (Jørgensen *et al.* 2008).

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Correction

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Fisheries change spawning ground distribution in northeast Arctic cod

Anders Frugård Opdal

The three ANOVA tests presented at the end of §3 have p-values mislabelled as $p > 0.05$. The correct p-values should be $p < 0.05$.

PAPER IV

Opdal, A.F., Vikebø, F.B. and Fiksen, Ø.

Historical changes in spawning grounds of Northeast Arctic cod outweigh role of climatic variation for early life thermal exposure. *Manuscript*

HISTORICAL CHANGES IN SPAWNING GROUNDS OF NORTHEAST ARCTIC COD OUTWEIGH ROLE OF CLIMATIC VARIATION FOR EARLY LIFE THERMAL EXPOSURE

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ABSTRACT

During the last 150 years, the Northeast Arctic cod have experienced a substantial reduction in spawning ground distribution. Prior to the 1930s, Northeast Arctic cod were caught at spawning grounds ranging from the southernmost to the northernmost parts of the Norwegian coast, but have for the last 50 years mainly been caught around the Lofoten archipelago and northwards. We ask why, historically, certain parts of the stock would undertake spawning migrations up to 2000 km longer than their conspecifics. Potential differences in fitness benefits between historical and contemporary spawning grounds are analysed by employing a general circulation model coupled with an individual based model to track virtual eggs and larvae released along the entire Norwegian coast. The simulations are run with 20 years of forcing data (1989–2008), resulting in spatial and temporal variations in individual drift routes, distribution and temperature exposures. We find that egg and larval temperature exposure and consequently temperature dependent growth potential and survival probability increase with more southerly spawning grounds. The latitudinal effects on survival, by far outstrip the inter-annual climatic influence, suggesting that location of spawning grounds could be more important than climatic variability in determining ambient larval conditions.

Keywords: Northeast Arctic cod, spawning migration, general circulation model, larval fish, temperature

INTRODUCTION

Since the idea of a “critical period” was conceived by Hjort (1914), the concept that fast growth and large size greatly increases survival probabilities for early stages of fish is close to becoming a paradigm (McGurk 1986, Miller et al. 1988, Bailey and Houde 1989, Meekan and Fortier 1996, Houde 1997, Leggett and Frank 2008), (but see Litvak and Leggett 1992). From a parental perspective, this means providing spawning conditions that maximises offspring growth and survival, most commonly realized through an adaptive choice of spawning time and area (Lasker 1981, Bailey and Houde 1989, Sinclair and Iles 1989, Cushing 1990, Jørgensen et al. 2008).

Also for the Northeast Arctic (NA) cod, the selection of spawning ground and time of spawning has been suggested to be an important key to offspring survival (Opdal et al. 2008). In late winter, mature individuals migrate southwards from the feeding grounds in the Barents Sea, countering the northbound North Atlantic Slope Current and Norwegian Coastal Current, and arrive at spawning grounds along the Norwegian coast in late winter or early spring. The variation in the distribution of spawners across the different spawning grounds, their particular geographical locations and the timing of spawning, has given rise to research questions of evolutionary (Heino et al. 2002), as well as behavioural (Godø 1983), physiological (Kjesbu et al. 1996) and oceanographic (Ådlandsvik and Sundby 1994) origin.

At present, the majority of spawning by NA cod takes place around the Lofoten archipelago (~68 °N) and northwards (Bogstad 2009), but historic records suggest that spawning has taken place as far south as Vest-Agder (~59 °N), more than 1000 km south of Lofoten (Opdal 2010). In a study utilizing a time series of roe indices (1900-1969), Sundby and Nakken (2008) hypothesise that variation in spawning grounds operate on a multi-decadal time scale, coinciding with climatic fluctuations. Opdal (2010) propose that shifts in spawning grounds might not be caused by climate alone. From an extended time series of catch data (1866-1969), Opdal (2010) hypothesise that a size selective trawl fishery in the Barents Sea could also cause significant changes in the spawning ground distribution. Also, the date of peak spawning is fluctuating, showing a tendency towards later spawning with time, possibly caused by changes in the size-distribution of the spawning stock (Pedersen 1984), but could also be a result of lower temperatures.

Providing a favourable offspring habitat often requires a cost to the parent, and in the case of NA cod, the bulk of this cost is energy used for migration between the Barents Sea and the Norwegian coast. The spawning migration is found to encompass both time- and energetic costs (Jørgensen and Fiksen 2006), both increasing with migration distance (Jørgensen et al. 2008). Evolutionary theory predicts that a costly parental investment warrants a concurrent advantage in order to balance costs with potential fitness benefits (e.g. Williams 1966). Although empirical data on the spatial and temporal distribution of the spawning stock, including eggs and larvae, are available on a remarkably fine scale compared to most other fish stocks, questions concerning how fitness benefits are associated with spawning time and space can practically be addressed only through numerical methods.

The links between spawning grounds, time of year, and potential for offspring survival has previously been explored using a regional ocean model (ROMS) coupled with an individual based model (IBM) (Ådlandsvik and Sundby 1994, Vikebø et al. 2005, Vikebø et al. 2007), though on a limited geographical range around the Lofoten archipelago. Vikebø et al. (2005, 2007), found that modelled fish larvae released from two spawning grounds in the Lofoten area could significantly alter their drift trajectories towards the Barents Sea through subtle differences in vertical positioning in the water column, a process thought to be important in determining larval growth and survival probabilities. Similarly, Fiksen et al. (2007) showed that directional horizontal swimming or fine-scaled vertical habitat selection by fish larvae released at the same spawning ground, could cause settlement in completely different parts of the Barents Sea.

In a state dependent optimization model, assuming a linear increase in larval survival with more southerly spawning grounds, Jørgensen at al. (2008) found that larger fish and fish in better condition prior to spawning migration would profit more from spawning further south. Using a general circulation model Opdal et al. (2008) explored temperature exposures for particles released at several spawning grounds along the Norwegian coast, from West-Finnmark (~70 °N) to Helgeland (~65 °N), for two consecutive years (1985 and 1986). Assuming that higher temperature exposure enhance larval growth (Otterlei et al. 1999, Folkvord 2005) and therefore reduce mortality through reduced stage duration (McGurk 1986, Houde 1989), they found fitness benefits of spawning further south, but emphasised that the ideal spawning time may not be equal for all spawning grounds. These results were drawn from a model domain covering only the northern part of the Norwegian coast, and an expanded model domain and time period is needed to include all relevant spawning grounds and climatic conditions in the analysis.

Now we have access to an expanded model domain (see Vikebø et al. 2010) that includes all potential spawning grounds along the Norwegian coast, nearly doubling the latitudinal range of the simulations. Here we test the proposal presented in Opdal et al. (2008), that an increased latitudinal range of spawning grounds similar to that observed in historical fisheries statistics (Anon. 1866-1976) may reveal an even clearer connection between temperature benefits for offspring, and the latitude on which they are spawned. In other words, offspring spawned at low latitudes will experience higher ambient temperatures and consequently increase their growth potential compared to those spawned in the north. Fast growth may also increase survival through the critical stage of early life. By running the model simulation for 20 consecutive years we can now track long term as well as inter-annual variations in particle drift trajectories and temperature exposure, ultimately providing us with a time-space fitness landscape for all spawning grounds along the Norwegian coast.

MATERIALS AND METHODS

Our primary objective, to study the fitness benefits associated with different historic and contemporary spawning grounds along the coast, is important to understand the benefits of long spawning migrations, historically commonplace in the NA cod. A similar analysis was in part presented in Opdal et al. (2008), where a general circulation model was used to track particles released at four fixed depths and from six different spawning grounds north of 65 °N, with forcing data for 1985 and 1986. Here, we use an expanded model domain covering spawning grounds along the entire Norwegian coast from 58 °N and northwards, and with forcing data from 1989 to 2008. In addition, vertical positioning of released eggs are dependent on buoyancy (Thygesen and Ådlandsvik 2007), whilst the hatched larvae perform size-dependent diel vertical migration (e.g. Lough and Potter 1993).

THE OCEAN MODEL

We utilize a three-dimensional hydrodynamic model (ROMS; Haidvogel et al. 2008; www.myroms.org), with a model domain covering the North Sea, the Norwegian Sea, the Barents sea and partly the Arctic. This model domain has recently become available with improved resolution (4 by 4 km), and was first presented in Vikebø et al. (2010), where a more elaborate description of the model parameters and performance is available. They found that the model performed well compared to observed salinity and temperature transects along the Norwegian coast, and was also shown to accurately reproduce known oceanographic features. The model uses stretched terrain-following coordinates in the vertical, and orthogonal curvilinear coordinates in the horizontal. Monthly mean lateral boundary conditions are taken from a global version of ROMS in the North Atlantic and Arctic (~20 km resolution), and includes velocity, temperature, salinity and water elevation. To include inter-annual variation in sea surface height and barotropic flow, eight dominant tidal constituents (TPXO 7.0; Egbert et al. 1994, Egbert and Erofeeva 2002) are added at the lateral boundaries. A Lagrangian particle-tracking model (Ådlandsvik and Sundby 1994) is used to track drift trajectories, depth and temperature exposure of the virtual eggs and larvae released at the different spawning grounds.

SPAWNING GROUNDS AND LARVAL DRIFT

Prior to the 1930s, NA cod was known to spawn over a large range of spawning grounds outside the south-western parts of the Norwegian coast (Opdal 2010). To assess the potential fitness benefits associated with these spawning grounds, and consequently the long spawning migrations, we compare drift trajectories and temperature exposures of virtual eggs and larvae released at the historical as well as contemporary grounds (Fig 1). The exact locations of major spawning grounds from Møre (~63 °N) and northwards to West Finnmark (~70 °N) are relatively well known, and include, from north to south, Breivikbotn (West Finnmark), Malangsgrunnen, Moskenesgrunnen, Røstbanken, Vestfjorden, Vega, Vikna, Yttergrunnen and Buagrunnen (Møre) (Sundby and Godø 1994). North and east of Breivikbotn, spawning grounds are not as pronounced, and we have subjectively assigned one spawning ground in Central Finnmark, and another in East-Finnmark. South of Møre there is little documentation of the exact position of the spawning grounds, and the localities are also here somewhat subjectively assigned to areas likely to promote a northbound drift route. These spawning grounds are named after their respective counties, derived from the Norwegian fisheries statistics (Anon. 1866-1976), and constitute, from north to south; Sogn, Hordaland, Rogaland and Vest-Agder (Fig 1).

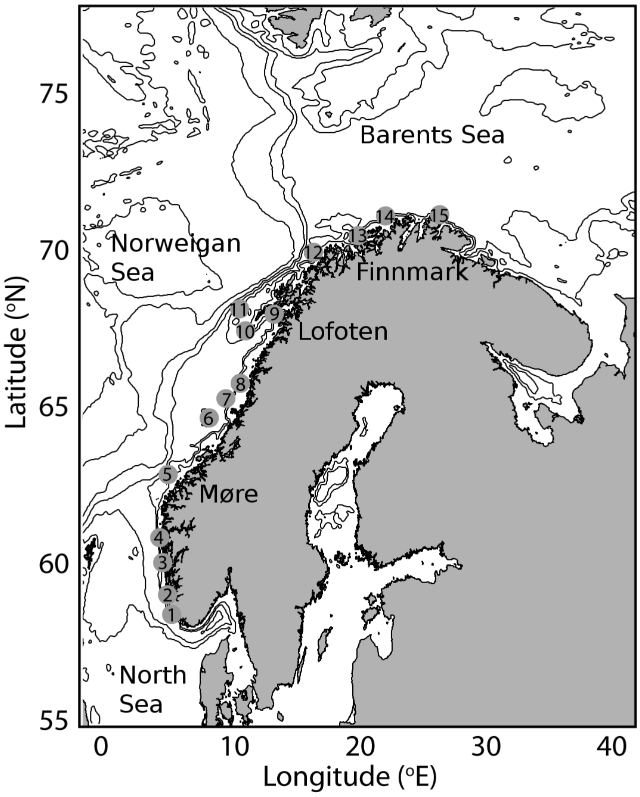

Figure 1. Location of spawning grounds along the Norwegian coast, from south to north; 1) Vest-Agder, 2) Rogaland, 3) Hordaland, 4) Sogn, 5) Buagrunnen (Møre), 6) Yttergrunnen, 7) Vikna, 8) Vega, 9) Vestfjorden, 10) Røstbanken, 11) Moskenesgrunnen, 12) Malangsgrunnen, 13) Breivikbotn (West-Finnmark), 14) Central-Finnmark, and 15) East-Finnmark.

The particles (eggs and larvae), are released in batches of 300 per spawning ground every third day from the beginning of March through April to analyse seasonality, and for each year from 1989 to 2008 in order to capture inter-annual variation. A total of ca. 100.000 particles are released each year. All particles are tracked until September 1st using a Lagrangian particle-tracking model (Ådlandsvik and Sundby 1994), where also particle depth and temperature exposure is recorded. Note that particles are released in equal numbers at all spawning grounds, and do not attempt to replicate spawning ground distribution for the years 1989 to 2008. The subsequent larval drift and final distribution in the Barents Sea for the different years is used to estimate potential inter-annual variation, not the actual distribution for those years.

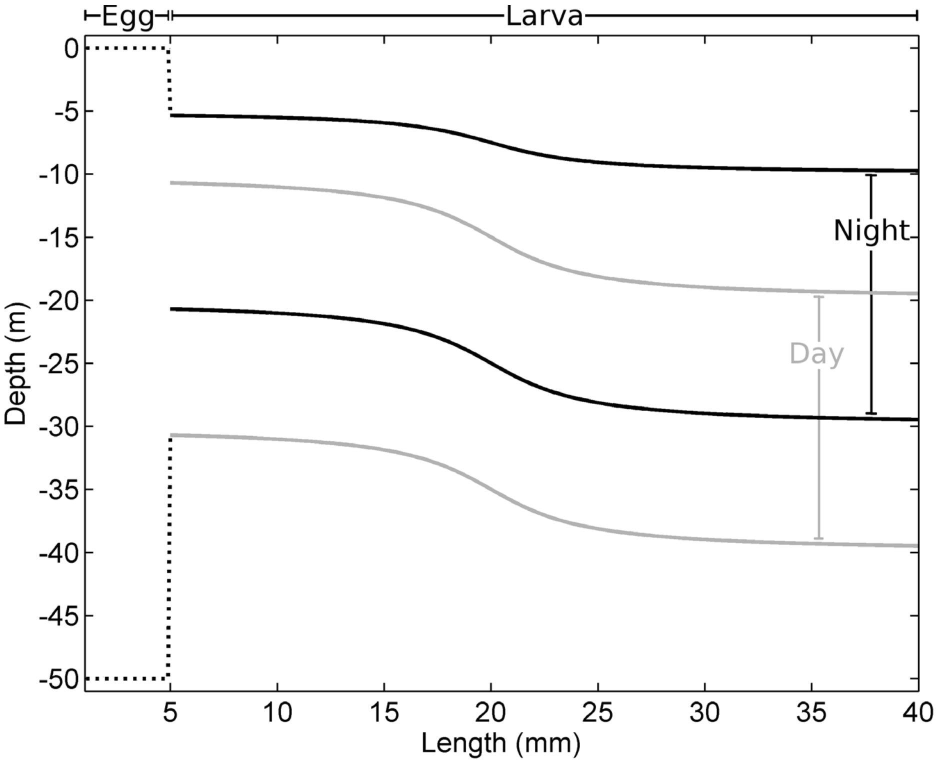

Figure 2. Depth boundaries during egg stage (black dotted line), and for day (grey line) and night (black line) during larval stage, as a function of larval length. From larval length, upper and lower depth boundaries are set for day and night in concurrence with a size dependent depth distribution found in Vikebø et al (2007). Night is defined as light levels < 1.0 μmol photons m^{-2} s^{-1}. Within the set depth boundaries, larvae move directionally up at night and down at day with at a speed of 0.1 body lengths (L) per time step (dt), where dt = 1 hour. In addition, there is also a random vertical movement at a speed of 0.33 body lengths (L) per time step (dt). In total, the vertical distance moved, dZ, within a time step (dt) is defined as $dZ/dt = \alpha \cdot 0.33L - 0.1L$, during the day, and $dZ/dt = \alpha \cdot 0.33L + 0.1L$, during night, where α is a behavioural variable defined as random number between -1 and 1.

GROWTH, SURVIVAL AND VERTICAL BEHAVIOUR

Larval growth is calculated as a function of temperature, through the empirical relationship found for Atlantic cod by Folkvord (2005), and presented as standard growth rate (SGR, d^{-1}). All individuals are initialized with the same length of 5 mm, corresponding to a dry weight of 0.093 mg, according to the length-weight relationship derived for Atlantic cod (Folkvord 2005). To calculate spatial and temporal variation in survival probability to a given size (the stage-duration hypothesis of survival), we use an estimated daily mortality rate for Atlantic cod larvae found by Sundby et al (1989), $M = 0.2\ d^{-1}$. Both temperature dependent growth and subsequent survival was estimated up to a larval length of 18 mm, as this is the maximum size to which the utilized growth model remains valid.

Opdal et al. (2008) use fixed egg and larval depths to reduce the number of variables associated with different drift routes, temperature exposure and related growth. They suggest that differences between spawning grounds are persistent throughout the water column. A more realistic scenario includes vertical movement due to altered egg buoyancy, as well as larval vertical behaviour. Here, egg buoyancy, and consequently its vertical movement, is calculated as a function of egg density, ocean temperature, salinity and turbulence (Thygesen and Ådlandsvik 2007). After the egg stage, which is set to last 22 days (e.g. Iversen and Danielssen 1984), the larva exhibit a diel vertical migration pattern, with increasing depth and range with larval length (i.e. Lough and Potter 1993). From larval length, we set upper and lower depth boundaries for day and night in concurrence with a size dependent depth distribution found in Vikebø et al (2007). Within the set depth boundaries the larva moves directionally up or down depending on night or day respectively, in addition to a random vertical movement component relative to body length (see Fig 2).

RESULTS

First we explore the average inter-annual drift patterns for particles released from the different spawning grounds, and how they lead to differences in the final distributions in the Barents Sea. Secondly, we show how these various patterns invoke large variations in the larval temperature exposure and temperature-dependent growth potential. Finally, we illustrate how this may affect survival probability between the relevant spawning grounds.

DRIFT PATTERNS AND DISTRIBUTIONS IN THE BARENTS SEA

Buoyant eggs, which later become vertically mobile larvae, are released from 15 different spawning grounds (Fig 1), and experience various drift patterns depending on spawning ground, year and season. The 20 year mean distribution of larvae on September 1st (1989 – 2008) is shown in figure 3, where spawning grounds are aggregated into three main components; a southern (grounds 1, 2, 3 and 4), an intermediate (grounds 5, 6, 7, 8, 9, 10 and 11) and a northern (grounds 12, 13, 14 and 15). The most striking differences are that most eggs and larvae released at the southern spawning grounds distribute closer to the coast with limited densities in the eastern parts of the Barents Sea. There is also a fraction experiencing a south-eastern drift, away from the southern Norwegian coast, topographically steered by the

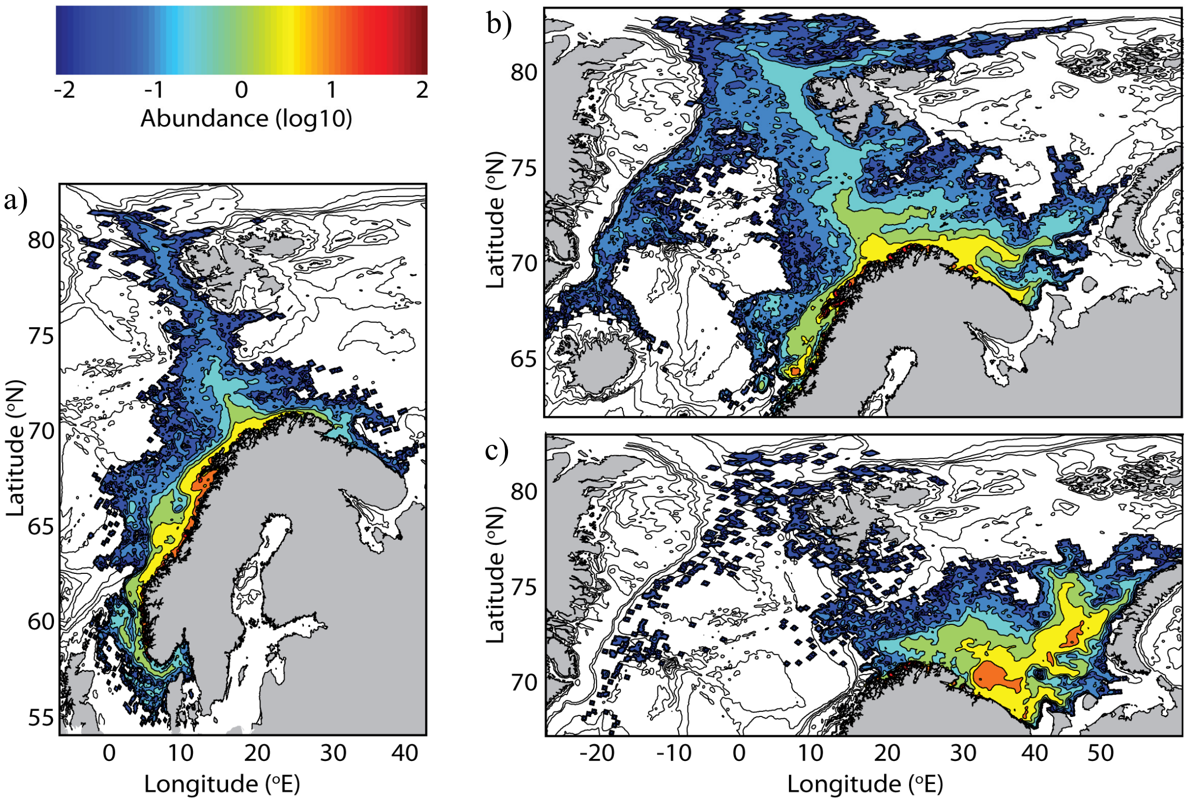

Figure 3. Aggregated mean larval distributions (1989-2008) on September 1st from spawning grounds a) 1, 2, 3 and 4, b) 5, 6, 7, 8, 9, 10 and 11, and c) 12, 13, 14 and 15 (see Fig 1). Colours denote the log10 transformed abundance (number of individuals) per cell (4 by 4 km).

Norskerenna. Larvae from the northern spawning grounds are almost exclusively distributed along the Finnmark coastline and into the eastern Barents Sea, whilst larvae from intermediate grounds have a strong component ending up in the western Barents Sea. A tendency of southbound drift west of Svalbard is also apparent. Overall, there are large inter-annual variations in the distribution pattern of larvae from all spawning grounds, such as for 1990 and 2008 (Fig 4). In 1990 larvae are

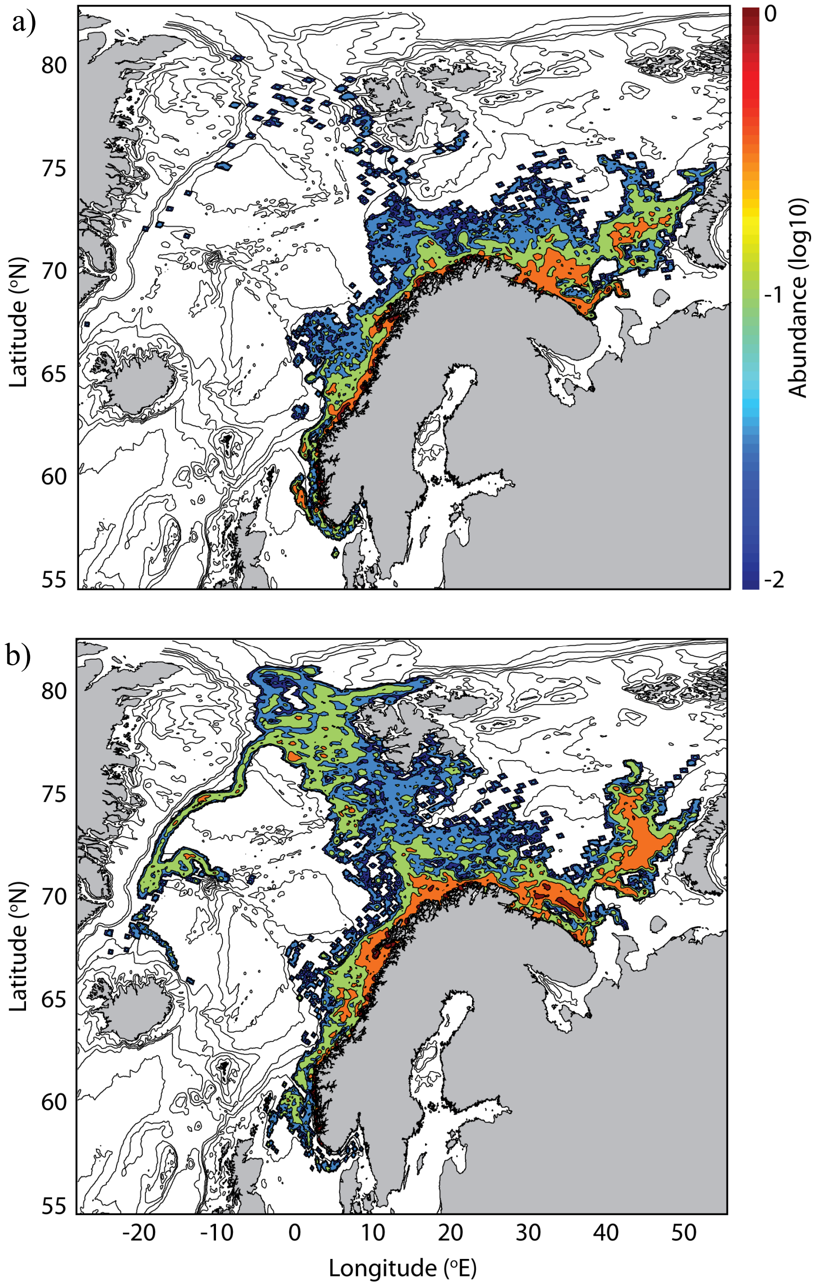

Figure 4. Example of inter-annual variations in larval distributions on September 1st in a) 1990 and b) 2008, for all spawning grounds. Colours denote the log10 transformed abundance (number of individuals) per cell (4 by 4 km).

primarily distributed in the eastern parts of the Barents Sea, while in 2008 there are also high densities west of Svalbard. A more detailed account of final distribution (September 1st.) is given in figure 5, where each of the four panels denote separate parts of the Barents Sea/Norwegian Sea area; the northwest (north of 70 °N and west of 30 °E), the northeast (north of 72 °N and east of 30 °E), the southwest (south of 70 °N and west of 30 °E), and the southeast (south of 72 °N and east of 30 °E). Here, it is evident that larvae released at the southern spawning grounds are for the most part distributed in the south-western section, whilst larvae from the northern spawning grounds are mainly in the south-eastern, but also some in the north-eastern section. Larvae from the intermediate grounds are more evenly distributed across the different

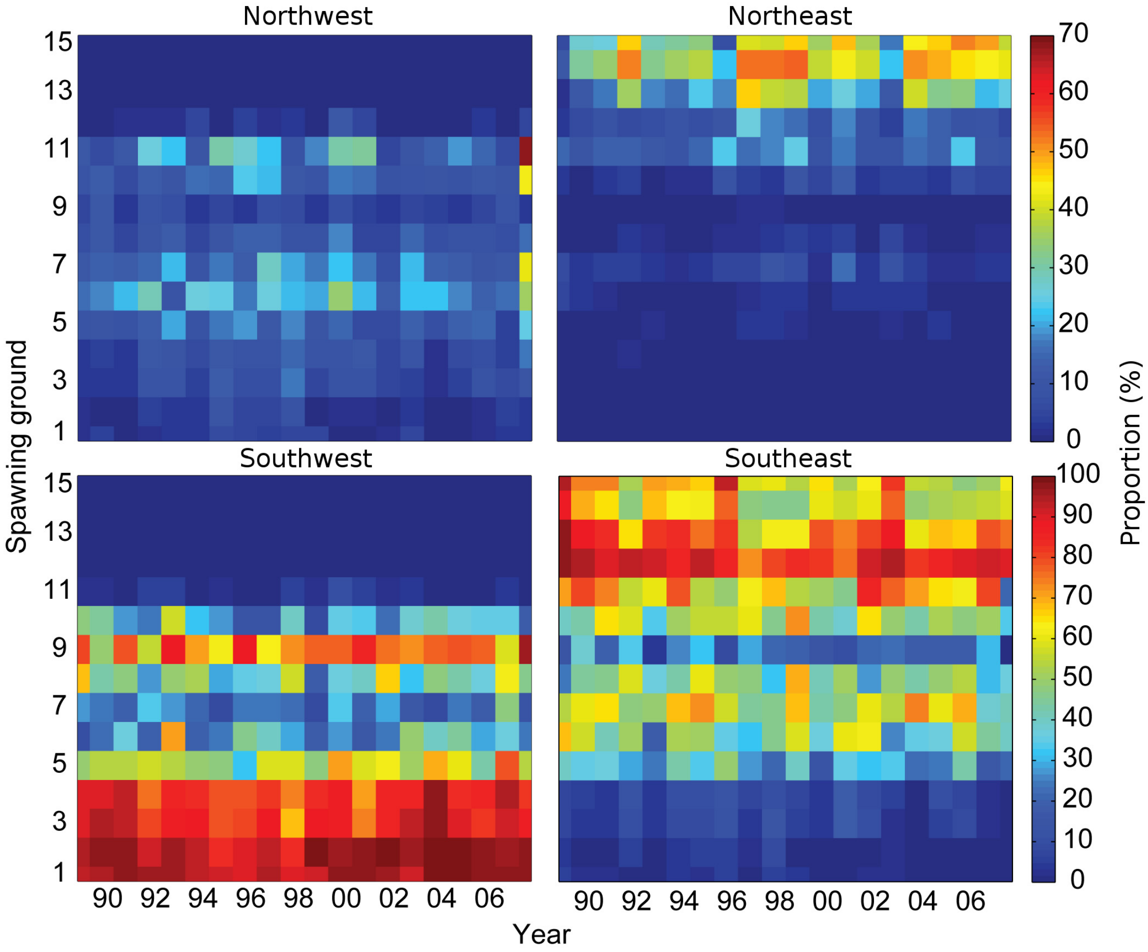

Figure 5. Larval distribution in the Barents Sea as a function of spawning ground and year. The Barents Sea is divided into four areas, *the northwest* (north of 70 °N and west of 30 °E), *the northeast* (north of 72 °N and east of 30 °E), *the southwest* (south of 70 °N and west of 30 °E), and *the southeast* (south of 72 °N and east of 30 °E). Colours denote the proportion (%) of individuals from each spawning ground, for each year.

sections, though a very small proportion distribute in the north-eastern section. There is some variation in distribution between years, but this does not contribute to any significant alterations of the general pattern.

TEMPERATURE EXPOSURE, GROWTH AND SURVIVAL

The various spawning grounds give rise to different larval drift patterns, with higher temperature exposures during the drift phase from more southerly spawning grounds (Fig 6a). Inter-annual variation is also apparent. Larvae from southern spawning grounds experience relatively low temperature exposures during a few years in the mid 1990s, whilst for larvae spawned further north, this colder period seems to last slightly longer.

Larval growth potential for the 60 first days after hatching (larval length < 18 mm), is calculated as a function of temperature (Folkvord 2005) (Fig 6b) Growth is generally faster for larvae spawned in the south (spawning grounds 1-6), but some years stand out with particularly high growth potential in the most southern grounds. There are also some years where larvae from the most southern spawning ground actually experience relatively lower temperatures than larvae from more northbound spawning grounds. On average, larvae spawned in the south (spawning grounds 1-6) may grow at about twice the rate of their northbound counterparts (spawning grounds 7-15). The cumulated survival probability up to a larval length of 18 mm, is calculated for

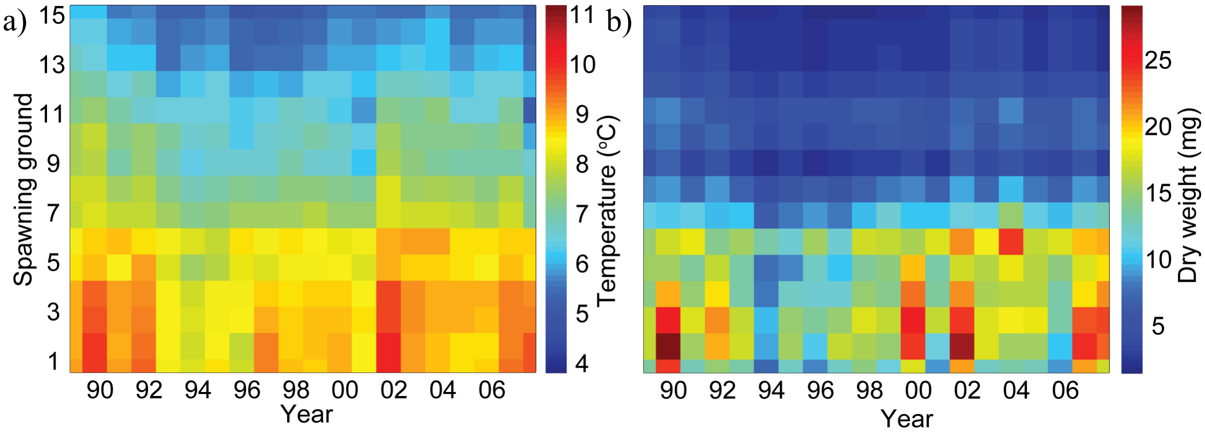

Figure 6. a) Mean temperature conditions of all individuals integrated from spawning until September 1st as a function of year and spawning ground**.** b) Larval temperature dependent growth potential (Folkvord 2005), for the first 60 days after hatching (larval length < 18 mm), as a function of spawning ground and year.

all years and spawning grounds, given a fixed daily mortality rate (M = 0.2 d^{-1}; Sundby *et al.* 1989) and purely temperature-driven growth (Folkvord 2005) (Fig 7). Larvae spawned in the south will under these assumptions experience an overall lower mortality, with three to four orders of magnitude higher survival probability in the most southern areas compared to the most northern. There is also inter-annual variation in survival, though less pronounced compared to the geographical trend

DISCUSSION

We show that historically important spawning grounds may harbour significant fitness benefits in terms of increased temperature conditions, larval growth potential and survival, compared to the more northern, contemporary, spawning grounds. The relationship between spawning ground location and larval fitness, indicate that spawning ground distribution might not be a simple function of climatic variation, but could also bee seen as a trade off between migration cost and offspring survival (Jørgensen et al. 2008).

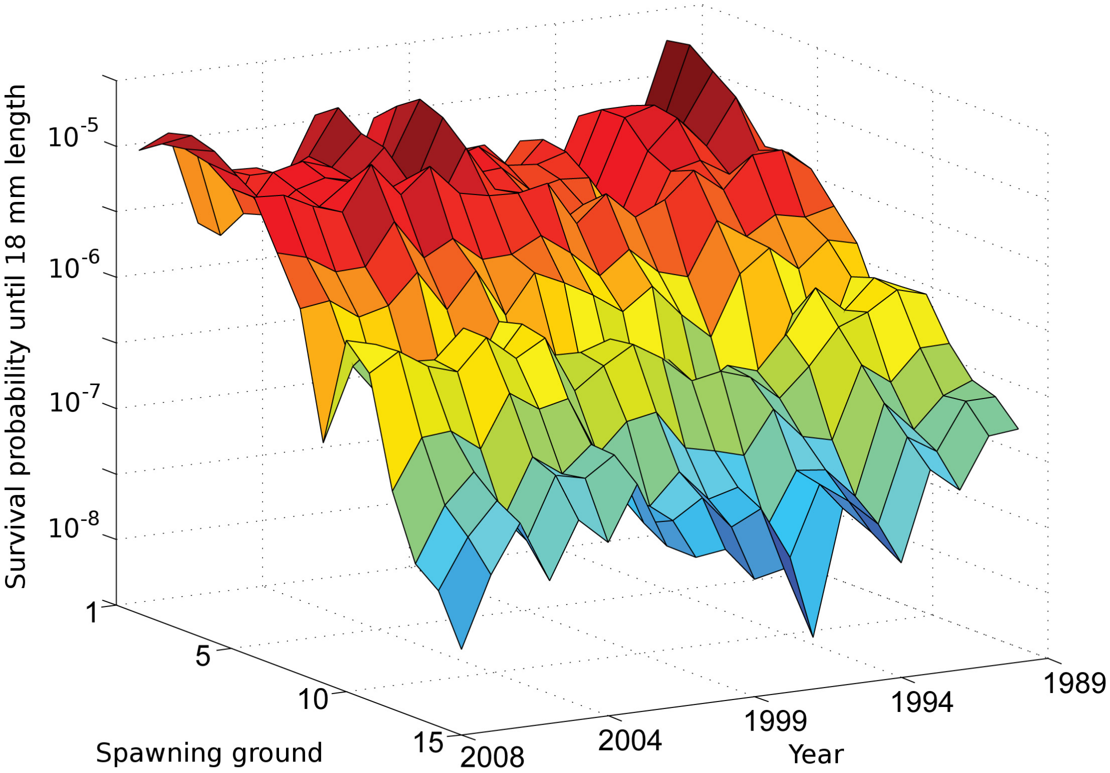

Figure 7. Survival probability as a function of spawning ground and year. The cumulative survival probability up to 18 mm length is calculated from a fixed daily mortality rate (M = 0.2 d^{-1}; Sundby *et al.* 1989) and purely temperature-driven growth (Folkvord 2005).

OCEAN MODEL AND LARVAL DRIFT PATTERNS

Several modelling studies have performed particle tracking from both single (Ådlandsvik and Sundby 1994, Vikebø et al. 2010) and multiple (Vikebø et al. 2005, Vikebø et al. 2007, Opdal et al. 2008) spawning grounds along the Norwegian coast. These studies have been limited to only a few years of forcing data, and constrained by model domain, only covering the northern half of the Norwegian coastline. In this study simulations covered 20 years of forcing data, making it possible to capture significant temperature variability, and study the effects of relatively warm and cold periods on drift and temperature exposure during early life of fish. The model performed well in reproducing observed inter-annual ocean temperatures along the Norwegian coast, both from offshore transects (Vikebø *et al.* 2010), and from stationary temperature recordings along the coast (Pers. com., Øystein Skarseth, Institute of Marine Research, Bergen; http://www.imr.no/forskning/forskningsdata/-stasjoner). The inclusion of egg buoyancy and larval vertical positioning also contributed to a more realistic scenario, even though the main findings do not differ significantly from those of Opdal et al (2008) using fixed larval depths. However, variations in vertical behaviour have been shown to influence drift patterns and larval distributions (Fiksen et al. 2007, Vikebø et al. 2007, Johansen et al. 2009).

Drift patterns from the spawning grounds are generally northbound towards the Barents Sea, even from the most southern spawning grounds, suggesting that larvae from these grounds could also recruit to the NA cod population in the Barents Sea (Bergstad *et al.* 1987). However, the most southern areas also experience some dispersion east and south towards the Swedish coast, away from the Barents Sea. This could indicate that the southern spawning areas selected in the model are not representative of the actual spawning grounds, or that these areas propose a real risk in terms of reduced recruitment to the NA cod stock. Compared to earlier modelling studies of larval drift (Vikebø et al. 2007, Opdal et al. 2008), particles are in this model distributed somewhat closer to the coast. We believe that some larval retention in local fjord systems is a plausible phenomenon, but this might be overestimated in the simulations. However, larvae ending up in various fjords do not necessarily mean a recruitment- or fitness loss, as individuals might continue northbound migration at a later life stage.

When simulating the larval distributions in the Barents Sea, we observe that larval drift routes diverge in a northern and a north-eastern component at about 70 °N, over the Tromsøflaket. This divergence area has long been known to have significant impact on larval distributions (Bjørke and Sundby 1984), and that individual behaviour has a great influence on whether the larva ends up in the eastern or western parts of the Barents Sea (Fiksen et al. 2007, Vikebø et al. 2007). We also note that some of the larvae spawned at the intermediate spawning grounds end up in western parts of the Nordic Seas (e.g. Fig 3b). These larvae are transported westwards by recirculated Atlantic Water in the Fram-Strait located between Svalbard and Greenland. In our case, it is reasonable to assume that in the field, these larvae might settle to the bottom before they are transported southwards along the East Greenland Current, and perhaps already on the west coast of Svalbard. Otherwise, they may be considered lost, possibly due to starvation.

OFFSPRING SURVIVAL AND SPAWNING GROUND DISTRIBUTION

The search for critical factors that govern stock recruitment and abundance has long traditions in fisheries research. From the early works of Hjort (1914), being the first to link environment to stock recruitment, environmental and climatic variability has been the foremost influential factor used to explain recruitment in a range of fisheries such as the Baltic Sea sprat (MacKenzie and Koster 2004), the North Sea herring (Axenrot and Hansson 2003), the North Sea cod (O'Brien et al. 2000, Beaugrand et al. 2003), the Pacific sardine (Jacobson and MacCall 1995), the northern cod (deYoung and Rose 1993), and also the NA cod (Ellertsen et al. 1989, Ottersen and Loeng 2000, Godø 2003). Increased offspring survival due to the presence of favourable environmental cues, climate driven or not, unify the mentioned studies. In our model, prey and predator abundances are unaccounted for as environmental factors, since little is known about their spatial and temporal distribution along the Norwegian continental shelf (but see primary production model by Skogen *et al.* 2007). Taking ocean temperature as a coarse proxy for environmental variation, we calculate larval temperature-dependent growth and the cumulative survival up to 18 mm length. We find that the latitudinal effects on survival, by far outweigh the inter-annual climatic influence, suggesting that location of spawning grounds could be more important than climatic variability in determining the ambient environmental conditions of the recruiting age-class. Similar results were also found by Opdal et al. (2008), but the effect becomes much stronger when the full range of spawning grounds are included. It is important to note that while we have assumed the same constant mortality rate ($M = 0.2\ d^{-1}$; Sundby *et al.* 1989) for larvae spawned at all spawning grounds, there is evidence that mortality in early life stages of fish can be temperature-dependent, with increasing mortality with temperature (Houde 1989). This effect would reduce larval survival from the southern spawning grounds. However, studies have also shown that early life mortality decrease with size (Folkvord and Hunter 1986, McGurk 1986, Bailey and Houde 1989), in which case, larvae spawned in the south would experience relatively higher survival probabilities.

In addition to temporal changes in environmental conditions, many species also experience changes in spatial distribution caused by both climatic variability (e.g. deYoung and Rose 1993, Perry et al. 2005, Sundby and Nakken 2008), and intensive harvest (e.g. Dragesund et al. 1997, Opdal 2010). Jørgensen et al (2008) suggest that a size selective trawl fishery in the Barents Sea has truncated the size distribution of the stock, and lowered the age at maturation through fisheries-induced evolution. They hypothesise that large late-maturing fish, and fish in good condition, would have optimal spawning locations further south, compared to small early maturing fish, and fish in poorer condition. Opdal (2010) show that before the onset of the Barents Sea trawl fishery in the 1920s, the NA cod's spawning grounds were distributed along the entire west coast of Norway, and that a northbound shift was evident after. The fitness benefits of southern spawning proposed here, suggests that intensive harvest and fisheries induced evolution, leading to truncated and northbound spawning ground distribution, could potentially have greater impact on larval survival compared to climatic fluctuations. Truncation of spawning ground distribution could also increase offspring vulnerability to climatic changes, strengthening the link between climate and recruitment (Ottersen *et al.* 2006).

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