

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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First, I would like to thank my main supervisor, Øyvind, for all your good advice, enthusiastic encouragement, and scientific insight. Your working capacity has always amazed me, and I still wonder how you find time for so much cycling and roller-skiing.

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Mikko, you are thanked for conceiving and getting funding for the project, and for including me in your group.

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Special thanks to Knut, for our numerous discussions, coffee drinking, and climbing trips. In you and Eivind, I have at least two friends who don't think it's weird to drink beer, listen to Motorpsycho vinyl, and discuss egg buoyancy, spawning migration and glacial sedimentation.

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,

A handwritten signature in black ink, appearing to read 'Anders Frugård Opdal'. The signature is fluid and cursive, with a large initial 'A' and 'O'.

Anders Frugård Opdal

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LIST OF PAPERS

PAPER I

Jørgensen, C, Dunlop, E, Opdal, A.F., and Fiksen, Ø. (2008)

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

PAPER II

Opdal, A.F., Vikebø, F.B., and Fiksen, Ø. (2008)

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

PAPER III

Opdal, A.F. (2010)

2010. Fisheries change spawning ground distribution of northeast Arctic cod. *Biology Letters* **6** (2): 261-264.

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*

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 Hylén 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.

D) SPAWNING AREA

”Det lange dunkle Spørgsmaal om, hvorfra Lofotskreien kommer, maa saaledes nu ved vor Expeditions Arbejder 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 Hysten 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 Hysten 1964, Garrod 1967, Nakken 1994, Godø 2003, Hjermmann 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 Hysten 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 predator-

detection 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 Hysten 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 (Toreisen 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 were 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 its 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 (Toreisen 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.

LITERATURE CITED

- Anon. 1866-1976. Norges Fiskerier. *in* D. o. Fisheries, editor. Norges offisielle statistik. Departementet for det Indre / Det Statistiske Centralbureau (from 1875), Oslo.
- Atkinson, D. B., G. A. Rose, E. F. Murphy, and C. A. Bishop. 1997. Distribution changes and abundance of northern cod (*Gadus morhua*), 1981-1993. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:132-138.
- Bailey, K. M. and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* **25**:1-83.
- Bailey, M. C., C. D. Maravelias, and E. J. Simmonds. 1998. Changes in the spatial distribution of autumn spawning herring (*Clupea harengus L.*) derived from annual acoustic surveys during the period 1984-1996. *ICES Journal of Marine Science* **55**:545-555.
- Begg, G. A. and G. Marteinsdottir. 2000. Spawning origins of pelagic juvenile cod *Gadus morhua* inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. *Marine Ecology-Progress Series* **202**:193-217.
- Block, B. A., S. L. H. Teo, A. Walli, A. Boustany, M. J. W. Stokesbury, C. J. Farwell, K. C. Weng, H. Dewar, and T. D. Williams. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**:1121-1127.
- Bogstad, B. 2009. Northeast Arctic cod. Page 185 *in* H. Gjøsæter, A. Dommasnes, T. Falkenhaus, M. Hauge, E. Johannesen, E. Olsen, and Ø. Skagseth, editors. *Havets ressurser og miljø 2009*. Institute of Marine Research, Bergen.
- Brander, K. 2010. Impacts of climate change on fisheries. *Journal of Marine Systems* **79**:389-402.
- Brickman, D., G. Marteinsdottir, K. Logemann, and I. H. Harms. 2007. Drift probabilities for Icelandic cod larvae. *ICES Journal of Marine Science* **64**:49-59.

-
- Buehler, D. M. and T. Piersma. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**:247-266.
- Clark, C. W. 2006. *The Worldwide Crisis in Fisheries*. Cambridge University Press, Cambridge.
- Clark, C. W. and M. Mangel. 2000. *Dynamic state variable models in ecology*. Oxford University Press, New York.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* **426**:655-658.
- Corkeron, P. J. and R. C. Connor. 1999. Why do baleen whales migrate? *Marine Mammal Science* **15**:1228-1245.
- Cushing, D. H. 1986. The migration of larval and juvenile fish from spawning ground to nursery ground. *Journal Du Conseil* **43**:43-49.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations - an update of the match mismatch hypothesis. *Advances in Marine Biology* **26**:249-293.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London.
- deYoung, B. and G. A. Rose. 1993. On recruitment and distribution of Atlantic cod (*Gadus-morhua*) off Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2729-2741.
- Dingle, H. 1996. *Migration: the biology of life on the move*. Oxford University Press, Oxford, UK.
- Dodson, J. J. 1997. Fish migration: an evolutionary perspective. Pages 10-36 *in* B. J. Godin, editor. *Behavioural Ecology of Teleost Fishes*. Oxford University Press, Oxford.

- Dragesund, O., A. Johannessen, and Ø. Ulltang. 1997. Variation in migration and abundance of Norwegian spring spawning herring (*Clupea harengus L.*). *Sarsia* **82**:97-105.
- Drinkwater, K. F. 2002. A review of the role of climate variability in the decline of northern cod. *Fisheries in a Changing Climate* **32**:113-129.
- Drinkwater, K. F., G. Beaugrand, M. Kaeriyama, S. Kim, G. Ottersen, R. I. Perry, H. O. Portner, J. J. Polovina, and A. Takasuka. 2010. On the processes linking climate to ecosystem changes. *Journal of Marine Systems* **79**:374-388.
- Edwards, M. and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**:881-884.
- Ernande, B., U. Dieckmann, and M. Heino. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**:415-423.
- FAO. 2008. Part 1: World review of fisheries and aquaculture. The state of world fisheries and aquaculture 2008:3-84.
- Fiksen, Ø., C. Jørgensen, T. Kristiansen, F. Vikebø, and G. Huse. 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Marine Ecology Progress Series* **347**:195-205.
- Fisher, R. A. 1930. *Genetical theory of natural selection*. Oxford University Press, Oxford, UK.
- Forseth, T., T. F. Næsje, B. Jonsson, and K. Harsaker. 1999. Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology* **68**:783-793.
- Fossum, P. and E. Moksness. 1993. A study of spring- and autumn-spawned herring (*Clupea harengus L.*) larvae in the Norwegian coastal current during spring 1990. *Fisheries Oceanography* **2**:73-81.
- Gade, G. 1894. *Temperaturmålinger i Lofoten 1891-1892 utgivet efter foranstaltning af Departementet for det Indre* The Norwegian Home Office, Christiania.

-
- Garrod, D. J. 1967. Population dynamics of Arcto-Norwegian cod. *Journal of the Fisheries Research Board of Canada* **24**:145-190.
- Godø, O. R. 2003. Fluctuation in stock properties of North-east Arctic cod related to long-term environmental changes. *Fish and Fisheries* **4**:121-137.
- Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Review: Marine ecology - Emerging marine diseases - Climate links and anthropogenic factors. *Science* **285**:1505-1510.
- Heath, M. R. and A. Gallego. 1998. Bio physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. *Fisheries Oceanography* **7**:110-125.
- Heino, M., U. Dieckmann, and O. R. Godø. 2002. Measuring probabilistic reaction norms for age and size at maturation. *Evolution* **56**:669-678.
- Hinckley, S., A. J. Hermann, and B. A. Megrey. 1996. Development of a spatially explicit, individual-based model of marine fish early life history. *Marine Ecology-Progress Series* **139**:47-68.
- Hinrichsen, H. H., C. Mollmann, R. Voss, F. W. Koster, and G. Kornilovs. 2002. Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:1858-1873.
- Hjermann, D. O., N. C. Stenseth, and G. Ottersen. 2004. The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:1747-1755.
- Hjort, J. 1895. Hydrografisk-biologiske studier over norske fiskerier A. W. Brøggers Bogtrykkeri, Christiania, Norway.
- Hjort, J. 1905. Norsk havfiske. Norges Fiskerier. John Griegs Bogtrykkeri, Bergen.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **20**:1-228.

- Houde, E. D. 2002. Mortality. *in* L. A. Fuiman and F. E. Werner, editors. Fishery science. The unique contributions of early life stages. Blackwell, Oxford.
- Houston, A. I. and J. M. McNamara. 1999. Models of adaptive behaviour. An approach based on state. Cambridge University Press, Cambridge.
- Husebø, A., A. Slotte, L. A. W. Clausen, and H. Mosegaard. 2005. Mixing of populations or year class twinning in Norwegian spring spawning herring? *Marine and Freshwater Research* **56**:763-772.
- Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:943-962.
- Hutchings, J. A. and R. A. Myers. 1994. What can be learned from the collapse of a renewable resource - Atlantic cod, *gadus-morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:2126-2146.
- Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. Gardmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp. 2007. Ecology: Managing Evolving Fish Stocks. *Science* **318**:1247-1248.
- Jørgensen, C., B. Ernande, Ø. Fiksen, and U. Dieckmann. 2006. The logic of skipped spawning in fish. *Canadian Journal of Fisheries and Aquatic Sciences* **63**:200-211.
- Jørgensen, C. and Ø. Fiksen. 2006. State-dependent energy allocation in cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **63**:186-199.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus-morhua L*). *Journal Du Conseil* **46**:235-248.
- Kjesbu, O. S., J. Klungsøyr, H. Kryvi, P. R. Witthames, and M. G. Walker. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus-morhua*) in relation to proximate body-composition. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:2333-2343.

-
- Kristiansen, T., C. Jorgensen, R. G. Lough, F. Vikebo, and O. Fiksen. 2009. Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod. *Behavioral Ecology* **20**:490-500.
- Kurita, Y., S. Meier, and O. S. Kjesbu. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. *Journal of Sea Research* **49**:203-219.
- Lack, D. 1947. The significance of clutch-size. *Ibis* **89**:302-352.
- Lack, D. 1950. The breeding seasons of European birds. *Ibis* **92**:288-316.
- Lasker, R. 1981. The role of stable ocean in larval fish survival and subsequent recruitment. Pages 80-87 in R. Lasker, editor. *Marine fish larvae. Morphology, ecology, and relation to fisheries*. University of Washington Press, Seattle, USA.
- Law, R. and D. R. Grey. 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology* **3**:343-359.
- MacArthur, R. H. 1972. *Geographical ecology. Patterns in the distribution of species*. Princeton University Press, New Jersey.
- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603.
- MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. University of Washington Press, Seattle.
- MacKenzie, B. R. and T. Kiørboe. 2000. Larval fish feeding and turbulence: A case for the downside. *Limnology and Oceanography* **45**:1-10.
- McNamara, J. M. and A. I. Houston. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**:301-319.
- Mehl, S. 2004. Abundance of spawning Northeast Arctic cod spring 2004. Pages 1-26 Report from the yearly Northeast Arctic cod survey (in Norwegian). Institute of Marine Research, Bergen.

- Michalsen, K., E. Johannesen, and L. Bogstad. 2008. Feeding of mature cod (*Gadus morhua*) on the spawning grounds in Lofoten. *ICES Journal of Marine Science* **65**:571-580.
- Mohn, H. and G. O. Sars. 1880. Fishes. Annelida. Spongiadae. Mollusca I (Buccinidae). Mollusca II. Grøndahl & Søn's Bogtrykkeri, Christiania, Norway.
- Mullon, C., P. Cury, and P. Penven. 2002. Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:910-922.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1996. Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology-Progress Series* **138**:293-308.
- Nakken, O. 1994. Causes of trends and fluctuations in the Arcto-Norwegian cod stock. *ICES marine science symposia* **198**:212-228.
- Neutel, A. M., J. A. P. Heesterbeek, and P. C. de Ruiter. 2002. Stability in real food webs: Weak links in long loops. *Science* **296**:1120-1123.
- Nøttestad, L., J. Giske, J. C. Holst, and G. Huse. 1999. A length-based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:26-34.
- O'Brien, C. M., C. J. Fox, B. Planque, and J. Casey. 2000. Fisheries - climate variability and North Sea cod. *Nature* **404**:142-142.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**:932-935.
- Otterlei, E., G. Nyhammer, A. Folkvord, and S. O. Stefansson. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:2099-2111.

-
- Ottersen, G., D. O. Hjernann, and N. C. Stenseth. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography* **15**:230-243.
- Ottersen, G., S. Kim, G. Huse, J. J. Polovina, and N. C. Stenseth. 2010. Major pathways by which climate may force marine fish populations. *Journal of Marine Systems* **79**:343-360.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. *Science* **279**:860-863.
- Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* **418**:689-695.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* **308**:1912-1915.
- Reznick, D. N. and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112**:183-198.
- Rollefsen, G. 1933. The otoliths of the cod. *Fiskeridirektoratets Skrifter* **4**:18 pp.
- Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:1553-1557.
- Rose, G. A. 2005. On distributional responses of North Atlantic fish to climate change. Pages 1360-1374.
- Rose, G. A., B. A. Atkinson, J. Baird, C. A. Bishop, and D. W. Kulka. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980-1992. *Cod and Climate Change - Proceedings of a Symposium* **198**:542-552.
- Rose, G. A., B. deYoung, D. W. Kulka, S. V. Goddard, and G. L. Fletcher. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:644-663.

- Sars, G. O. 1866. Om Vintertorskens Forplantning. Christiania, Norway.
- Sinclair, A. F. and S. A. Murawski. 1997. Why have groundfish stocks declined? Northwest Atlantic groundfish: Perspectives on a fishery collapse:71-93.
- Sinclair, M. and T. D. Iles. 1989. Population regulation and speciation in the oceans. *Journal Du Conseil* **45**:165-175.
- Slotte, A. and O. Fiksen. 2000. State-dependent spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology* **56**:138-162.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Sund, O. 1933. The cod and the sea. Directory of fisheries, Bergen.
- Sundby, S. and O. Nakken. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science* **65**:953-962.
- Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, UK.
- Sættersdal, G. and A. Hylen. 1964. The decline of the skrei fisheries. Reports on Norwegian Fishery and Marine Investigations **13**:58-69.
- Thesen, E. 2007-2009. DNA typing av torsk ved bruk av PCR metode. Fiskeridirektoratet region Nordland, Fiskerikontoret i Svolvær, Svolvær.
- Toresen, R. and O. J. Østvedt. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries* **1**:231-256.
- Varpe, Ø. and Ø. Fiksen. 2010. Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. *Ecology* **91**:311-318.
- Varpe, Ø., Ø. Fiksen, and A. Slotte. 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* **146**:443-451.
- Varpe, Ø., C. Jørgensen, G. A. Tarling, and Ø. Fiksen. 2007. Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos* **116**:1331-1342.

-
- Varpe, Ø., C. Jørgensen, G. A. Tarling, and Ø. Fiksen. 2009. The adaptive value of energy storage and capital breeding in seasonal environments. *Oikos* **118**:363-370.
- Verhulst, S. and J. M. Tinbergen. 1991. Experimental-evidence for a causal relationship between timing and success of reproduction in the great tit *Parus-major*. *Journal of Animal Ecology* **60**:269-282.
- Vikebø, F. B., Å. Husebø, A. Slotte, E. K. Stenevik, and V. S. Lien. 2010. Effect of hatching date, vertical distribution, and interannual variation in physical forcing on northward displacement and temperature conditions of Norwegian spring-spawning herring larvae. *ICES Journal of Marine Science* **67**:000-000.
- Vikebø, F. B., C. Jørgensen, T. Kristiansen, and Ø. Fiksen. 2007. Drift, growth and survival of larval Northeast Arctic cod with simple rules of behaviour. *Marine Ecology Progress Series* **347**:207-219.
- Vikebø, F. B., S. Sundby, B. Ådlandsvik, and Ø. Fiksen. 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Journal of Marine Science* **62**:1375-1386.
- Visser, M. E. and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences* **272**:2561-2569.
- Williams, G. C. 1966. Natural selection costs of reproduction and a refinement of Lack's principle. *American Naturalist* **100**:687-690.
- Worm, B., R. Hilborn, J. K. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, A. M. Parma, D. Ricard, A. A. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding Global Fisheries. *Science* **325**:578-585.
- Ådlandsvik, B. and S. Sundby. 1994. Modelling the transport of cod larvae from the Lofoten area. *ICES marine science symposia* **198**:379-392.

