

Fisheries-induced Evolution in Northeast Arctic Cod

Anne Maria Eikeset

*Centre for Ecological and Evolutionary Synthesis,
Department of Biology, University of Oslo, Norway*

Goal

To calibrate and apply an individual-based, eco-genetic model to study fisheries-induced evolution in Northeast Arctic cod.

Background and motivation

The Northeast Arctic (NEA) cod stock is currently the world's largest stock of Atlantic cod (*Gadus morhua*), and sustains both large open-ocean trawling fisheries (mainly from Norway and Russia) as well as fishing with conventional gear on the Norwegian coast (Nakken 1998). The fisheries can change the cod's age and size at maturation in two ways: first, by reducing the stock's biomass, which leads to faster individual growth (Heino and Godø 2002) and thereby to earlier maturation through phenotypic plasticity, and secondly, by altering the selective pressures so that the stock evolves towards maturing at a smaller size and younger age through a shift in its maturation reaction norm (Heino et al. 2002a; Barot et al. 2004; Olsen et al. 2004). As a result, NEA cod's median age at maturity has decreased from >10 years in the 1940s to 6-7 years in the 1980s and 1990s (Godø 2000), probably as a result of both the aforementioned processes. In addition, temperature variability has influenced the individual growth of NEA cod in the past (Godø 2000), and is expected to be further shaped by global climate change in the future (Brander 1994; Brander 1995). These changes in maturation dynamics influence various components of the cod-fishing fleet differently: for example, open-sea trawlers capturing young and small cod will be affected differently from conventional fishing boats targeting mature cod.

Besides being economically important, NEA cod is ecologically important because it is the main fish predator of the Barents Sea (Bogstad et al. 2000). By the age of 3-4 years, NEA cod consume large amounts of post-larval capelin (*Mallotus villosus*) and follow the spawning migration of capelin to the coasts of Northern Norway and Northwest Russia in spring (Hjermann et al. 2004a; Hjermann et al. 2004b). At maturation, NEA cod migrate from the Barents Sea to spawn along the Norwegian coast in March-May (Bergstad et al. 1987). The eggs and larvae are carried by currents into the southern Barents Sea and south and west of Svalbard. The immature cod make seasonal migrations whose extent increases with age (Hjermann et al. 2004b). Length growth has been found to be influenced by the abundance of capelin (Bogstad and Mehl 1997).

To fully understand the impacts of fishing on the life-history traits of a population, it is important to distinguish between plastic and genetic responses (Rijnsdorp 1993). One method of disentangling plastic from genetic responses is to examine trends in a maturation reaction norm. A reaction norm describes the range of phenotypes produced by a genotype under different environmental conditions (e.g., Roff 1992). Previous work has shown that mortality can influence growth and maturation in several fish populations (Reznick et al. 1996; Conover and Munch 2002). As growth rates may vary plastically in response to the environment, age and size at maturation

may also vary with growth rates in a plastic way. Within a population, this range of growth rates and the subsequent range in size and age at maturation determine the observable maturation reaction norm (Stearns and Koella 1986). Hence, a reaction norm for age and size at maturation illustrates the maturation schedule of a genotype under different growth conditions. Extending the original deterministic notion of maturation reaction norms (Stearns and Koella 1986), probabilistic maturation reaction norms are defined by the probability that immature individuals at a given age and size will mature during a given time interval (Heino et al. 2002b).

Commercial fishing can be size-selective because larger members of a stock are often targeted and removed by the fishery (Law 2000). Size-selective fishing mortality can act on the ages and sizes at maturation and cause the maturation reaction norm of a population to shift away from its original position. Such a shift may be genetic because the reaction norm itself is genetically determined (Olsen et al. 2004). Alternatively, fishing may alter the somatic growth rates of a population through its impact on population density, thereby shifting the ages and sizes at maturation along the reaction norm. Such a response is plastic because the ages and sizes at maturation are shifting in direct response to changing growth rates (Heino and Godø 2002). Several recent studies have shown that shifts in maturation reaction norms can be rapid (Grift et al. 2003; Barot et al. 2004; Olsen et al. 2004). Therefore, estimating maturation reaction norms can help disentangling plastic and evolutionary changes in the age and size at maturation (Heino et al. 2002b). This is important from a management perspective, as genetic changes are bound to be more difficult to reverse (Law 2000). Genetic changes in life-history traits thus give rise to concerns (Olsen et al. 2004) – in particular, since the consequences of fishery-induced evolution can result in lower sustainable yields (Law 2000; Conover and Munch 2002) and reduced stock stability (Ottersen et al. 2005). Relaxing the fisheries-induced selection pressures may halt the rapid evolution of key life-history traits in harvested populations, and is thus an important target for the management of fisheries-induced evolutionary change.

In this project, my aim is to study the effects of commercial fishing on the evolution of maturation, individual growth rate, and reproductive investment by using an individual-based eco-genetic model (Dunlop et al. 2005b). As mentioned previously, fishing is expected to cause a downward shift in the maturation reaction norm towards younger ages and smaller sizes at maturation (Heino et al. 2002a; Olsen et al. 2004). Fishing may also cause evolution of individual growth rate. For example, experimental harvest of Atlantic silversides resulted in rapid evolution of slower growth rates, since slower-growing individuals were more likely to escape size-selective harvest before reaching maturity (Conover and Munch 2002). However, fast-growing individuals may suffer a survival cost because they forage more actively and thereby are exposed to predators and fishing gear (Heino and Godø 2002). Harvest may also influence patterns of reproductive investment. High mortality selects for greater reproductive investment (Reznick and Ghalambor 2005), but greater investment into reproduction may also incur a cost. Furthermore, fishing is expected to alter traits affecting behavior and morphology (Heino and Godø 2002), but such effects are beyond the scope of this study.

An individual-based modeling approach will be chosen for this study because it allows an intuitive merging of genetics and demography, both of which are important in the context of fishing-induced change (i.e., Chambers 1993; Jager 2001; Dunlop et al. 2005b;). An individual-based approach also allows for modeling maturation as probabilistic, which is likely more realistic given the inherent stochasticity of the

maturation process (Heino et al. 2002b).

Time permitting, an important extension of the individual-based model will be to consider the effects of climate fluctuations and climate change. This is in light of the large changes in the Barents Sea climate predicted to occur towards the middle of the 21st century.

Fishery-induced life-history changes may alter the economic conditions of the cod fisheries and lead to changes in the fleet's structure and allocation; this in turn may either contribute towards enhancing or diminishing the ongoing changes. Optimal management strategies will be affected. As far as we know, this topic has not been treated in the bio-economic literature on NEA cod. Time permitting, this project will therefore aim at incorporating the fishery's effect on the evolving traits into a bio-economic model, in order to quantify the long-term cost of overfishing. I will study how the costs and benefits of different fishing strategies may change by using an existing, semi-spatial bio-economic model in which both the state (effort and allocation) of the fishing fleet, as well as the state of the cod stock, are dynamic variables, mutually affecting each other.

Research questions

I will use an individual-based model to predict how fishing influences the evolution of growth, reproduction, and maturation of NEA cod. The considered evolving traits include the immature somatic growth rate (i.e., the fraction of energy devoted to growth prior to maturation), the reproductive investment (i.e., the gonado-somatic index), and parameters describing the maturation reaction norm of NEA cod. A previously developed individual-based model by Dunlop et al. (2005) focused on evolution of the maturation reaction norm alone. Research suggests that other traits such as growth (Conover and Munch 2002) and reproductive investment (e.g., Roff 1992) might also be affected by fisheries-induced evolution. In addition to characterizing the magnitude and rate of fisheries-induced evolution in NEA cod, we plan to evaluate how different management strategies alter the evolutionary response. We also plan to assess the impact of the modeled evolutionary changes on yield and recovery potential. Finally, by introducing environmental fluctuations into the model, we may evaluate the impact of the evolutionary changes on stock stability.

Time permitting, I will enhance the developed model by adding a bio-economic component or by interfacing it with an existing bio-economic model. Also the effects of climate change may be examined.

Methods and work plan

I will use an individual-based model to examine the evolution of five quantitative traits: intercept of the maturation reaction norm, angle of the maturation reaction norm, width of the maturation reaction norm, gonado-somatic index, and fraction of energy devoted to growth prior to maturation. This model will be expanded from the existing model by Dunlop et al. (2005) and specifically parameterized for the NEA cod. The model will be run on yearly time steps with the processes of maturation, reproduction, growth, and mortality occurring on an annual basis. Growth will be assumed as density-dependent and linear prior to maturation. Following maturation, a component of the available energy will be devoted to reproduction. Maturation status will be based on an individual's probabilistic maturation reaction norm, and reproduction will occur randomly between pairs of mature individuals. The evolving traits will be passed on to offspring in dependence on the two parental trait values using a normal recombination kernel. Mortality of newborns will be determined

through a Beverton-Holt stock-recruitment function (Hjermann et al. in prep.). In all simulations, a constant level of age and/or size-specific natural mortality will be applied. A tradeoff between juvenile growth rate and survival will also be included. Realistic fishing mortality rates will be applied and their effect on the evolution of traits will be examined. The model will also include the effects of temperature on recruitment and length growth.

The individual-based model will be parameterized from existing data on NEA cod. When parameterizing the model, I will take into account important sources of varying natural mortality in NEA cod: climate-linked mortality at the larval stage (Sundby 2000) and cannibalism (linked to the abundance of capelin) for 1-3 year old cod (Hjermann et al. 2004a; ICES 2004). I will use data on length, weight, maturation, and abundance collected from research surveys in the Barents Sea (the cod's feeding grounds) and in the Lofoten region (the cod's spawning grounds) conducted by the Institute of Marine Research (Bergen) and by the Polar Research Institute of Marine Fisheries and Oceanography (Murmansk), available from the ICES report of 2004. Several existing laboratory studies, mesocosm studies, and field studies on growth and maturation (Suthers and Sundby 1993, 1996; Svasand et al. 1996; Suthers et al. 1999; Clemmesen et al. 2003; Godø 2003; van der Meeren and Moksness 2003) will also be considered.

The first steps in examining the parameterized model will focus on viable management strategies that reduce or slow potential fisheries-induced evolution. Preliminary re-search suggests that increasing the minimum size limit or implementing protective slot limits will significantly slow down evolution of the maturation reaction norm (Dunlop et al. 2005a).

The final stage of the project will be to assess the economic impacts of fisheries-induced evolution. I will use the results from the individual-based eco-genetic model and include estimates on maturation and individual growth as parameters in an existing bio-economic model for the NEA cod in the Barents Sea, developed at the Centre of Ecological and Evolutionary Synthesis (Oslo). On this basis, I can study how management strategies might change in light of the economic analyses. The fishery is modeled from the perspective of a resource manager who is interested in comparing the effects of different fishing strategies on the overall utilization of the stock. The manager has two main controls: total amount of effort and (ii) age selectivity of harvest, that is where and how effort is expended, with respect to impacts on different age classes. The spatial distribution of effort has an age selective effect where fish of different sizes are located in different regions: Older fish migrate to spawn in the Lofoten area, while younger fish remain in the Barents Sea or along the coast of northern Norway. During the summer, younger fish are also typically located further east and north in the Barents Sea. The combination of gear type and spatial distribution of effort determines the overall extent to which fish of different age groups are targeted. The economic model has no fleet structure, and cost and income are driven by fishing effort. Given different fishing strategies, the model can estimate cost and income. The first (and simplest) option is to use results from the evolutionary model as input to the bio-economic model, to analyze how profit and optimal fishing strategy are affected by changes in the cod's life-history parameters. The second option is to link the eco-genetic model to the bio-economic model, so that for every year in the simulation the output from the eco-genetic model (e.g., length at maturation) is used as input to the economic model, whose output (e.g., fishing mortality as a function of length) is used, in turn, as input for the eco-genetic model.

Relevance and link to ADN's research plan

This project aims to model the evolutionary effects of fishing in NEA cod and thus directly links to ADN's research focus on Fisheries-Induced Adaptive Change.

Expected output and publications

This work is intended for publication as a co-authored paper in an international scientific journal, and is expected to be integrated as a chapter into my PhD thesis.

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