

decided orientation toward collaborative research ensures the widest possible dissemination of results obtained at IIASA and thus makes the best use of the resources IIASA offers. Moreover, serving as a central node within the adaptive dynamics research community is a critical element of ADN's agenda. This role gives ADN the credibility needed to offer guidance into uncharted scientific territory. Annual workshops on a variety of topical subjects (including spatial ecology, the evolution of infectious diseases, evolutionary conservation biology, speciation research, and fisheries management) strengthen ADN's scientific basis, broaden its scope, and ensure

wide visibility and critical discussion of novel findings. In the same vein, ADN staff serve as series editors for a newly established line of books published by Cambridge University Press: the *Cambridge Studies in Adaptive Dynamics*.

Over the past few years, ADN's innovative methodology has spread rapidly within the international research community. On this basis, the project leads the efforts that bring the resulting new insights to bear on pressing ecological and environmental problems.

For more information, see IIASA's ADN Web page [www.iiasa.ac.at/Research/ADN](http://www.iiasa.ac.at/Research/ADN).

## Shrinking Cod: Fishery-Induced Change in an Oceanic Stock

Fishing is a major source of food and other resources for humankind. Today most marine fish stocks are heavily exploited, and many are overexploited. Such intensive utilization has raised concerns about the sustainability of the modern fishing industry. Can the current level of catches be maintained in the long run, or are we running the risk that some stocks will collapse and the corresponding commercial fisheries will have to be closed?

In addition to having obvious effects on harvested species, fishing influences other, nontarget species. Those that utilize the target species as their own prey suffer, whereas those preyed upon by the target species or those that can feed on discarded fish benefit (Figure 1). These effects may cascade to other species in a food chain and can cause undesired impacts on biodiversity and ecosystem functioning.

Fisheries scientists and managers have increasingly begun to appreciate the diverse ecological implications of marine exploitation. However, they have not yet widely acknowledged that fishing can exert strong selective pressures on exploited stocks and may thus change their genetic composition. One particular type of selection arises as a direct consequence of elevated mortality. When fishing pressure increases, it becomes increasingly likely that a fish that matures late will be caught before

it has a chance to spawn. Such a fish leaves no descendants. Intensive fishing is therefore expected to select for an earlier age at first spawning. Such a change has a problematic consequence for the fishing industry: because a fish's growth slows after maturation, the average size of the fish decreases and with it the commercial value. These effects should be strongest, and especially evident, in fish with traditionally late maturation, such as cod, halibut, and many other large, bottom-dwelling fish species.

In collaboration with the Institute of Marine Research in Bergen, Norway, IIASA's Adaptive Dynamics Network (ADN) project has screened the largest cod stock of the Northeast Atlantic, the Northeast Arctic cod (*Gadus morhua*), for the occurrence of fishery-induced adaptive changes. In terms of productivity, these fish constitute one of the most important stocks in northern Europe. The Northeast Arctic cod is particularly well suited for such an analysis. The primary reason is the availability of detailed long-term data sets that document the cod's properties over the course of the 20th century. Moreover, this stock has experienced a well-documented change in harvesting pattern that is expected to make any adaptations induced by fishing practices particularly obvious.

The Northeast Arctic cod feeds in the Barents Sea. From there, mature fish undertake an annual migration to the spawning grounds near the Lofoten Islands off the Norwegian coast (Figure 2). The cod congregate in the spawning grounds in early spring, presenting an easy target for fishermen; estimates place mortality at between 20 and 30 percent of the spawning fish. The



Figure 1: The kittiwake is one of the winners in the expansion of trawling fisheries. Kittiwakes regularly follow fishing vessels far offshore, feeding on discarded fish.

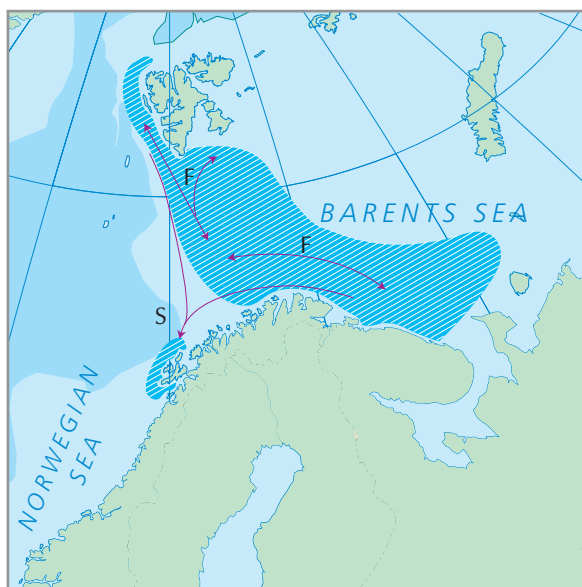


Figure 2: Spawning and feeding ranges of the Northeast Arctic cod.

highly productive spawner fishery at the Lofoten Islands has a very long history of exploitation: the first record of this fishery is found in *Egil's Saga*, which dates back to the 9th century.

Historically, the Northeast Arctic cod has matured late, with a mean age at first spawning of about 10 years. Scientists believe that the centuries of fairly intensive exploitation at the spawning grounds have been partially responsible for this late maturation. When faced with a high risk of being caught at the spawning



Figure 3: Large female cod from the beginning of the 20th century, weighing 30 kilograms. Cod of this size are no longer found. Photograph by Anders Beer Wilse, courtesy of the Norsk Folkemuseum, Oslo, Norway.

grounds and low levels of mortality at the feeding grounds, fish that delayed their maturation had an advantage. This allowed them to stay at the feeding grounds until a later age, and thus to grow to a larger size before arriving at the spawning grounds, where the risk of being caught was high. Because a cod's fecundity strongly depends on its size, delayed maturation paid off in terms of increased numbers of offspring expected (Figure 3).

However, the pattern of exploitation has changed drastically since the early 20th century. The development of

modern motor-powered trawler fishing in the late 1920s enabled offshore fishing at the feeding grounds in the Barents Sea. In fact, since the Second World War, most fishing effort has concentrated on the Barents Sea, with annual mortality often exceeding 40 percent of the fish population. A key factor here is that, as opposed to the spawner fishery, the feeder fishery is unselective with regard to maturation status. The current fishing mortality is actually so high that only a small fraction of fish survive to maturity; consequently, the current catch consists mostly of tiny, immature fish (Figure 4). Under the new exploitation regime, earlier maturation has therefore become advantageous.

Thus, the Northeast Arctic cod has undergone a change from a harvesting pattern that should favor late maturation to a pattern favoring early maturation. This hypothesis is in agreement with observations that show a clear trend toward earlier maturation of the Northeast Arctic cod, with a decrease of about three years in the mean age at first spawning from the 1940s until today (Figure 5). Because age at first spawning is a heritable characteristic, the data seem to support the hypothesis that the Northeast Arctic cod has responded evolutionarily to the altered exploitation regime.

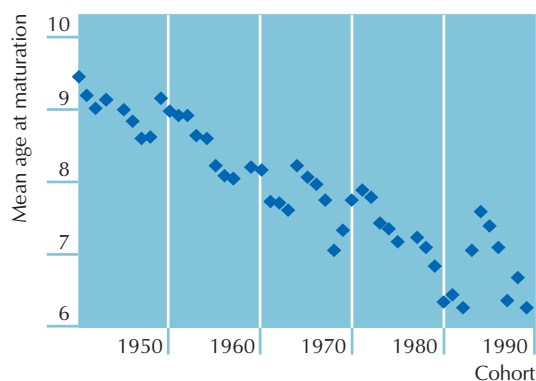


Figure 5: Decrease in the mean age at first spawning in the Northeast Arctic cod.

An alternative hypothesis, however, attributes this shift to environmental changes and does not imply an altered genetic composition of the stock. The reasoning is that as a result of intensive exploitation, the stock biomass has declined from an estimated 4.2 million tons right after the Second World War to below 1 million tons in the 1990s. This decline in biomass has resulted in better feeding conditions for those fish that remain; consequently, the growth rate of juvenile cod has increased. It is a common observation that fish mature at earlier ages if growth conditions improve; therefore, increased growth rates resulting from fishing

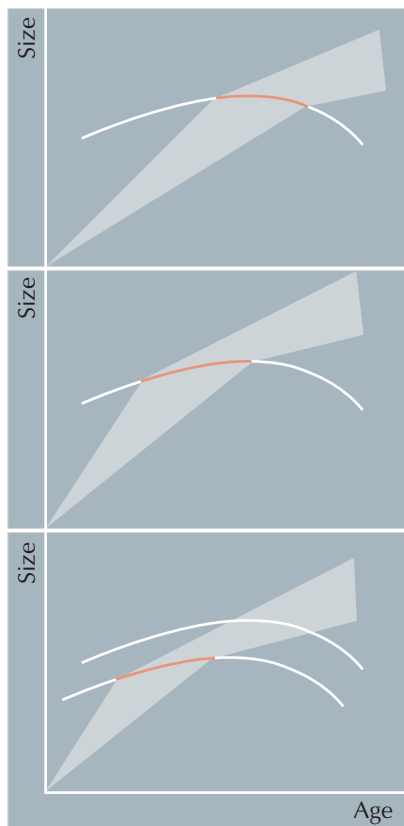


Figure 4: Catch from a survey haul, consisting mostly of cod.

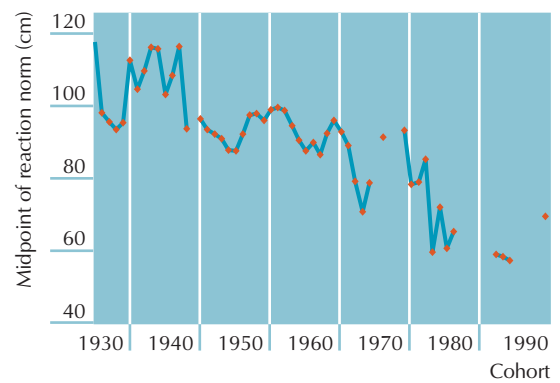
could also explain the observed decline in the age at first spawning.

Is it possible to distinguish between the two hypotheses for explaining the observed changes in age at first spawning? The answer is yes. IIASA's ADN project has disentangled the effects of changed growth conditions from those of genetic change by investigating changes in a compound trait known as the reaction norm of maturity, which relates age to size at first spawning. Analysis of this trait has allowed ADN to remove from the data most of the effects of varying growth rates (Figure 6). The residual variation in the maturation data investigated is then likely to have resulted from genetic effects.

After developing the necessary statistical methodology, ADN researchers studied the reaction norms for a data set of the Northeast Arctic cod collected by the Institute of Marine Research in Bergen. The data include information about cohorts from 1923 onward, thus covering the period during which the responses to the exploitation pattern should become manifest. The results show a



**Figure 6:** Reaction-norm analysis reveals whether change in maturation results only from improved growth conditions (change from top to middle) or must be attributed to genetic change (from top to bottom). In these graphs, individuals are considered mature at the point where their growth trajectory passes through the reaction norm curve; the shaded regions give the range of growth trajectories in the population.



**Figure 7:** Change in the midpoint of the reaction norm at age eight for the cohorts 1925–1990. The midpoint gives the length of fish at which probability of maturation is 50 percent.

continual decline in the reaction norm for age and size at maturity (Figure 7). In other words, present-day cod mature at a much younger age and smaller size than their ancestors at the beginning of the 20th century would have done when faced with similar growing conditions. This conclusion supports the hypothesis that exploitation pressures have caused changes in the genetic composition of the Northeast Arctic cod; thus the observed life-history changes cannot be fully explained only by the ability of fish to show plastic responses to improved feeding conditions.

Why should we care about genetic changes in fish stocks? First, and most important, changes in traits such as age at first spawning influence the productivity of the stock. When maturation takes place earlier, we can expect the sustainable yield from a stock to decline. Second, the average size of fish is expected to decrease, further diminishing the market value of catches. Third, if the observed changes in maturation have a genetic component—as now seems to be the case—the deterioration in yield will not easily be reversed, even if the fishing industry takes steps to alter harvesting patterns. Genetic recovery occurs much more slowly than ecological recovery. It is therefore in the interest of fisheries managers to prevent unwanted genetic changes as early as possible.

It is not yet known how many fish stocks have been strongly affected by fishing practices or how many are currently under threat of genetic change. At any rate, however, the precautionary principle in fisheries, as highlighted in United Nations declarations and in agreements about biodiversity, mandates increased awareness of this issue. ADN's fisheries research provides crucial evidence for policymakers concerned with ecology and with the world's food supply.

For more information, see IIASA's ADN Web page [www.iiasa.ac.at/Research/ADN/Fisheries.html](http://www.iiasa.ac.at/Research/ADN/Fisheries.html).