A long evolutionary reach for fishing nets

Earlier maturation of Atlantic salmon is linked to indirect effects of fisheries on its prey

By Nina Overgaard Therkildsen[1] and
Malin L. Pinsky[2]

[1]Department of Natural Resources and the Environment, Cornell University, Ithaca, NY, USA. nt246@cornell.edu
[2]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA.

Adaptive evolution is not just the stuff of geological history books—it is an ongoing process across ecosystems and can occur on a year-to-year time scale. However, in a world rapidly changing as the result of human activity, it can be challenging to differentiate which changes result from evolution rather than other mechanisms (*1*). On page 420 of this issue, Czorlich *et al*. (*2*) reveal a fascinating example that suggests that commercial fishing drove rapid evolutionary change in an Atlantic salmon population over the past 40 years. Their findings are surprising in two ways—that fishing for salmon drove evolution in the opposite direction from what one would typically expect, and that salmon evolution also was affected by fishing for other species in the ecosystem.

The potential for fishing to drive abnormally fast evolution has been recognized for at least 80 years (*3*), yet conclusive evidence for these effects has remained elusive. The underlying logic is that fisheries often substantially increase adult mortality for harvested populations, creating a fitness benefit for reproduction at earlier ages and smaller sizes. If variation in maturation has a genetic basis, the added mortality from fishing can drive evolution. Laboratory experiments have demonstrated rapid fisheries-induced evolution causing widespread impacts across the fish genome (*4*, *5*), and many wild populations of fish today indeed mature at earlier ages and at smaller sizes compared to decades ago (*6*). Putting lab and field data together, however, has been a major challenge. Atlantic cod, for example, has been a classic putative example of fisheries-induced evolution, yet some of the most heavily fished populations have not revealed clear genomic signals of adaptive evolution (*7*).

Czorlich *et al*. provide some of the strongest evidence to date linking fishing to changes in the genetic composition and maturation of a wild population. They studied Atlantic salmon, which are born in fresh water, migrate to the ocean to grow and then return to their birthplace once they are mature and ready to spawn. There is substantial variation in the time salmon spend at sea, both within and across populations, and many populations now mature and return to spawn at an earlier age (*8*).

In previous studies, researchers had identified a single gene—the *vestigial-like family member 3* (*vgll3*) gene—that has a large effect on salmon maturation timing (*9*). By analyzing the DNA collected from scales of 1319 salmon captured between 1975 and 2014 from the Tenojoki population in the Teno River located at the Finland-Norway border (*10*), researchers also uncovered that a shift toward earlier maturation over this period coincided with an 18% increase in the frequency of a *vgll3* variant linked with early maturation (*10*). To identify the drivers behind this change, Czorlich *et al*. compared interannual fluctuations in the frequency of early- and late-maturing genetic variants with historical data on environmental, eco- logical, and fishing-related factors. They revealed that temporal genetic changes were associated with fishing, consistent with fisheries-induced evolution, but in surprising ways. Rather than selecting for earlier maturation, as typically expected, salmon fishing in the Teno River had selected for later maturation. This result highlights the subtle context dependence of evolution. In this case, it appears to have emerged because the main fishing method in this river primarily captures smaller, younger fish and leaves older, larger fish to spawn.

Perhaps even more surprising, another major factor that strongly correlated with the genetic changes in salmon was the population size of a small marine fish called capelin. During their ocean development, salmon grow in part by feeding upon capelin. But capelin have experienced marked population booms and busts over the last few decades, in large part because of capelin fishing. Capelin appear to influence salmon evolution through the at-sea survival of salmon, which is lower when fewer capelin are present. With lower survival, early- rather than late-maturing salmon are especially likely to return to their natal population and pass their genes on to the next generation, increasing the number of early-maturing salmon. Thus, capelin fisheries affected not just their target species, but had cascading evolutionary effects else- where in the ecosystem. In an interesting coincidence, the capelin are caught partly as feed for farmed Atlantic salmon, revealing distant and unexpected impacts of fish farming. These ripple effects from fisheries and aquaculture have been widely appreciated for ecological processes, but Czorlich *et al.* show a rare example of evolutionary impacts beyond the targeted species.

The distinct large-effect gene region that accounts for 40% of the variation in Atlantic salmon maturation timing made it feasible for Czorlich *et al.* to track adaptive evolution at the genetic level. Large-effect loci have also been discovered in other fish species—e.g., affecting the migration timing in Pacific salmonids (*11*) and the growth rate in Atlantic silversides (*5*)—but not all traits are like this. Many growth and maturation traits are expected to be highly polygenic— that is, influenced by small effects from hundreds of different genes (*12*). Changes in traits with such genomic architectures will be more difficult to detect.

Another key to Czorlich *et al.*'s discovery was the detailed series of annual allele frequency estimates from the Tenojoki population that allowed the testing of environmental associations not just based on long-term change, but with year-to-year fluctuations. The inference from Czorlich *et al.* remains correlational and does not provide definitive evidence of causation, but the high temporal resolution provides great power to test as- sociations, highlighting the value of comprehensive historical collections.

Despite the clarity of the Tenojoki salmon example, many questions remain. For in- stance, the evolutionary result does not ap- pear immediately generalizable to other salmon populations. Despite exposure to some of the same fisheries and capelin inter- actions, a different Teno River salmon population does not show the same evolutionary change toward earlier maturation, perhaps because the effects of *vgll3* on maturation are mediated by other, as-yet-unknown genes (*10*). The broader genomic footprint of fishing also remains an important and open question, because the study only examined a couple hundred of the roughly 3 billion positions in the salmon genome.

Whether and how human activities drive rapid evolutionary change, such as how they influence ecosystems beyond the directly affected species, remains a vital research topic. Evolutionary impacts may be wide- spread but poorly recognized because they have been hidden from view. A key question will be whether evolutionary impacts can be predicted, perhaps with better knowledge of genomic architecture. Answering these questions is not just an academic exercise. The effects of fisheries-induced evolution can include lower population productivity and greater population instability, and can be difficult to reverse (*6*). The first step toward mitigating their negative impacts will be understanding when and where they occur.

REFERENCES AND NOTES

F. Pelletier, D. W. Coltman, *BMC Biol.* 16, 7 (2018).
Y. Czorlich *et al.*, *Science* 376, 420 (2022).
J. B. S. Haldane, *Am. Nat.* 71, 337 (1937).
S. Uusi-Heikkilä, T. Sävilammi, E. Leder, R. Arlinghaus, C.
R. Primmer, *Mol. Ecol.* 26, 3954 (2017).
N. O. Therkildsen *et al.*, *Science* 365, 487 (2019).
M. Heino, B. Diaz Pauli, U. Dieckmann, *Annu. Rev. Ecol. Evol. Syst.* 46, 461 (2015).
M. L. Pinsky *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* 118, e2025453118 (2021).
J. Erkinaro *et al.*, *Can. J. Fish. Aquat. Sci.* 76, 42 (2019).
N. J. Barson *et al.*, *Nature* 528, 405 (2015).
Y. Czorlich, T. Aykanat, J. Erkinaro, P. Orell, C. R. Primmer,
Nat. Ecol. Evol. 2, 1800 (2018).
N. F. Thompson *et al.*, *Science* 370, 609 (2020).
N. H. Barton, P. D. Keightley, *Nat. Rev. Genet.* 3, 11 (2002).

ACKNOWLEDGMENTS

N.O.T. acknowledges funding from NSF OCE-1756316. M.L.P. acknowledges funding from NSF OISE-1743711 and serves as an Oceana science adviser.