Throwing down a genomic gauntlet on fisheries-induced evolution

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Beginning with studies on crypsis and camouflage, the hypothesis that predators can generate evolutionary change in their prey has a long and rich history (1). Few predators, however, rival humans in their potential to generate selection responses and concomitant phenotypic change on contemporary timescales. In the 1930s, J. B. S. Haldane (2) mused that fishing would be an ideal candidate for such "observable evolution" within a human lifetime, proceeding "with extreme and abnormal speed." However, it was not until the late 1970s that research on fisheries-induced evolution (FIE) gained a substantive scientific foothold, beginning with thought-provoking work on Canadian whitefish (*Coregonus clupeaformis*) (3) and Pacific salmon (*Oncorhynchus* spp.) (4).

Backed by the logical premise that high fishing mortality (selective or not) can generate evolution in heritable traits, a great deal of research on FIE has been empirically fueled by the reductions in age (and often size) at maturity routinely observed in heavily fished natural populations (5). Laboratory studies have repeatedly found that highly intense selection (e.g., 75 to 90% mortality per generation), imposed by age- and size-based culling of obligatorily semelparous experimental populations, can alter life histories and gene frequencies (6–8). These experiments stimulated a slew of mathematical models that have predicted undesirable consequences of FIE—altered life histories, reduced recovery potential, lowered per capita population growth (*r*), decreased sustainable yields—against a backdrop of FIE-induced genetic change that might prove difficult or impossible to reverse (9, 10). Calls for evolutionarily enlightened management have ensued (11, 12).

Despite a theoretically strong conceptual basis, evidence of genetic change unequivocally attributable to wild-capture fisheries has been elusive (10, 13). Among the top five threats to biodiversity, evidence for genetic trait change is strongest for studies of pollution and weakest for studies of overexploitation (and

habitat change) (14). Determining whether phenotypic change in declining populations is the result of evolution, as opposed to other influences on growth, survival, and fitness, or gene flow from adjacent populations, has proven challenging (5, 9, 10, 13, 15).

A recent paper in PNAS (16) threatens to pierce a 21st-century narrative that FIE has been broadly and negatively implicated in effecting phenotype change in exploited fish populations (9–11). Pinsky et al. (16) examine two geographically distinct populations ("stocks" in management parlance) of Atlantic cod (*Gadus morhua*) to test for evidence of genomic change before and after fishery-induced population collapses: northern cod (southeastern Labrador to Newfoundland's Grand Banks) and northeast Arctic cod (northern coastal Norway and the Barents Sea). Historical and contemporary tissues (northern cod: 1940, 2013; northeast Arctic cod: 1907, 2011, 2014), collected from the same locations over time (Twillingate, Canada; Lofoten, Norway), provided sufficient DNA to detect 346,290 single-nucleotide polymorphisms (SNPs) in 113 individuals.

These cod stocks are strong candidates for exploring temporal shifts in gene frequencies and genetic variation resulting from FIE. Both experienced decades of overfishing, population biomass declining by 90% or more over roughly 30-y periods, and both exhibited considerable phenotypic change in life history, reflected by 30 to 35% (2 to 3 y) reductions in age at maturity (10, 16). However, Pinsky et al.'s analyses of whole-genome sequence data yielded no evidence of unusually strong shifts in allele frequencies over time (16). Large genomic changes were absent. Distinct signals of strong selective sweeps over time, anywhere in the genome, were lacking. There was no evidence of a substantive loss of genetic diversity. Effective population sizes remain high (~10,000 to 36,000). In short, there was little evidence of outlier loci suggestive of rapid evolution.

On the other side of the ledger, the authors acknowledge that their methods and sample sizes could

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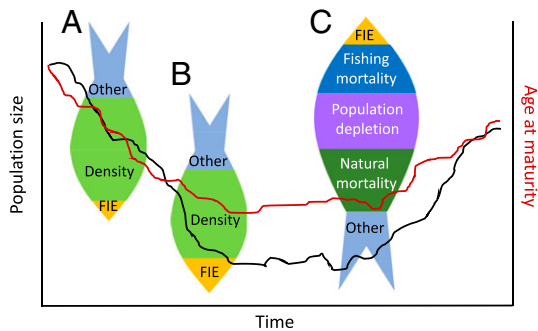Author contributions: J.A.H. and A.K. wrote the paper.

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Fig. 1. Commercial fisheries are often associated with reductions in population size (black line) and age at maturity (red line); subsequent recovery to former values can simultaneously occur in both variables. (*A*) When populations are at the beginning of a declining trajectory, the proportional influence of fisheries-induced evolution (FIE) on phenotypic changes in traits, such as age at maturity, may be small relative to density and other factors (such as sexual selection, temperature, climate, predation). (*B*) The influence of FIE on phenotypic change might increase as population size becomes increasingly small (19). (*C*) The importance of FIE to recovery appears to be secondary compared to the influence of reduced fishing mortality, magnitude of the initial population depletion, natural mortality, and other factors, such as those described in *A* (10).

not entirely discount the possibility that subtle, low-intensity selection in response to fishing (or other directionally selective agents) could have occurred through undetectable gene-frequency changes across many loci. Because of technical challenges, parts of the genome—the most highly repetitive regions—could not be genotyped. A few outlier loci were observed, predominantly single SNPs. However, Pinsky et al. advise caution in interpreting these as reflecting selection because of the high risk of false positives associated with multiple selection tests, a lack of congruent changes among adjacent loci in the genome, and the observation that these outliers were associated with significantly lower-quality genotype calls.

Pinsky et al.'s research does not negate the hypothesis that northern cod and northeast Arctic cod have been subjected to FIE. However, it does indicate that genomic traces of FIE in these stocks are not prominent. The clear implication is that other factors have been considerably more important in driving phenotypic change in these populations than evolution (17). This conclusion harkens back to circumspection offered by the first paper on FIE that "selection of this sort may only rarely be capable of determining the direction of change in population parameters, that is, that [fisheries-induced] selection is only rarely capable of producing an effect larger than and opposed to that associated with density-dependent compensation" (3).

There is an emerging realization that FIE might generally be of less importance to population demography and life history than

previously believed, particularly in light of the overarching influence of density. As populations decline under prolonged fishing pressure, reduced competition for resources leads to faster rates of individual growth, which lead *ceteris paribus* to earlier maturity (Fig. 1 *A* and *B*) (9, 10). In terms of recovery, FIE appears to be of secondary importance when compared with overfishing, magnitude of depletion, and natural mortality (Fig. 1*C*) (10, 18).

The PNAS study (16) provides genomically based support for this conclusion, meaning that the proportional contribution of fisheries-induced selection to phenotypic change in natural populations may often be small. This conclusion would be consistent with some studies in the terrestrial realm. Phenotypic changes in horn length of a Canadian population of bighorn sheep (*Ovis canadensis*), a species hypothesized to be subject to hunting-induced evolution, are driven primarily by density (26.5% of the variation) and secondarily by genetic change (8.8%); 62% of the phenotypic variation is unexplained (19). The threefold difference in the contribution of density to phenotypic shifts in horn length, relative to that of evolution, may well be considerably greater in fish populations, given the higher sensitivity of ectotherms to environmental change. There is also the consideration that natural and sexual selection can act on age and size at maturity in a manner opposite to changes favored by FIE, making the latter difficult to detect.

That said, a small influence of FIE on phenotypes need not mean an insignificant influence. Fisheries-induced selection might synergistically contribute to, if not magnify, the effects of other factors known to affect population demography. There might be interactions between FIE and density (20), such that evolution and its relative importance to life histories and density-dependent changes in r are not manifest until declining populations become small (Fig. 1*B*). It is when populations are small that they have increased probability of experiencing a decline in r with declining population size, i.e., Allee effects. Also, the smaller a population, the greater its susceptibility to environmental, demographic, and genetic stochasticity.

The metaphorical gauntlet laid down by Pinsky et al. should serve as a stimulus for greater circumspection in FIE research: a reset, a refocus, if not a rethink. One could begin by addressing questions pertaining to the subset of depleted populations for which the implications of FIE are likely to be magnified because of their synergistic interactions with correlates of productivity, resilience, and yield. Such efforts might serve to clarify the relative importance of FIE to the viability and recovery of exploited populations.

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