LETTER

Overfishing causes frequent fish population collapses but rare extinctions

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Burgess et al.'s report in PNAS, "Range contraction enables harvesting to extinction" (1), provides a highly valuable perspective on the consequences of species range contractions that maintain local densities of declining populations. The authors suggest that this density-dependent contraction maintains local harvesting yields and economic incentives that enable depleted natural populations of both marine and terrestrial species to be harvested until collapse and extinction. Burgess et al.'s approach, combining modeling and empirical review, covers a large spectrum of species with convincing results.

However, although the direct link between overharvesting and high risk of extinction is well verified for terrestrial species (2, 3), humans have caused few complete extinctions in the sea (4, 5). Overfishing causes frequent population collapses, with fishing reducing population levels by several orders of magnitude. Marine fish populations can remain at these very low levels of biomass and contracted species ranges for years to decades without recovery (6). This is especially verified for schooling pelagic fish (7), as demonstrated by Burgess et al (1).

However, these collapses rarely lead to extinctions, as illustrated by the northern cod and Atlantic and southern bluefin tuna, also mentioned in Burgess et al. (1). The low level of extinction of marine fish is driven by their specific demographic strategy. Indeed, the life strategy of most marine fish species is characterized by high fecundity, the production and release of large amounts of eggs into the marine environment, and lack of parental care. This strategy leads to high mortality in early life stages, high variability in abundance, and survival-to-maturity rates as low as 1:100,000 (8) [compared with mammals and birds, who have few offspring (<20) per reproductive event but lower mortality rates (9)]. However, this life strategy also results in a much lower probability of population extinction, as only a few female marine fish can potentially generate millions of juvenile fish.

We fully agree with Burgess et al. (1) that mitigation of overexploitation threats merits greater attention for marine fish, as for other species. Avoiding marine fish collapse, with lasting dramatic population decrease and range contraction, is of primary interest, even if risks of extinction are low. The world's conservation problem is not only species extinction, but rather the precarious state of populations where only few remnants remain of once widespread species (6), with large consequences at the ecosystem scale.

1 Burgess MG, et al. (2017) Range contraction enables harvesting to extinction. *Proc Natl Acad Sci USA* 114:3945–3950.
2 Benítez-López A, et al. (2017) The impact of hunting on tropical mammal and bird populations. *Science* 356:180–183.
3 Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) Human impacts. The unique ecology of human predators. *Science* 349:858–860.
4 McCauley DJ, et al. (2015) Marine defaunation: Animal loss in the global ocean. *Science* 347:1255641.
5 Dulvy NK, et al. (2003) Extinction vulnerability in marine populations. *Fish Fish* 4:25–64.
6 Briggs JC (2014) Fauna in decline: Beyond extinction. *Science* 346:820.
7 Essington TE, et al. (2015) Fishing amplifies forage fish population collapses. *Proc Natl Acad Sci USA* 112:6648–6652.
8 Le Pape O, Bonhommeau S (2015) The food limitation hypothesis for juvenile marine fish. *Fish Fish* 16:373–398.
9 Cury PM, Fromentin J-M, Figuet S, Bonhommeau S (2014) Resolving Hjort's dilemma: How is recruitment related to spawning stock biomass in marine fish? *Oceanogr* 27:42–47.

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