



REPLY TO LE PAPE ET AL.:

Management is key to preventing marine extinctions

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Our report (1) examines factors that maintain the profitability of harvesting a population as it declines. Without management, this can incentivize harvesting to extinction (2). Le Pape et al. (3) note that humans have not yet caused many marine extinctions, and argue that harvesting fish populations to complete extinction should be difficult because of the high fecundity of these populations. This argument is intuitive, but the extinction mechanism we examine (1, 2) does not depend directly on the harvested species' fecundity. High fecundity might indirectly lessen this extinction threat in some cases, but the importance of management in preventing both past and future marine extinctions should not be underestimated.

Our theory (1) shows that harvesting a small population remains profitable as the population declines if "price flexibility" (f : the percentage increase in harvest price per 1% decrease in harvest) is greater than or equal to "catch flexibility" (β : the percentage increase in harvest cost per 1% decrease in abundance). Neither parameter depends on fecundity. However, if $f \geq \beta$ currently for a harvested population—seemingly the case for several marine populations (1)—extinction could still be avoided in three ways, as elucidated below. High fecundity might facilitate the first two, but the third—management intervention—is undoubtedly the safest bet.

First, price flexibility (f) could eventually become smaller than catch flexibility (β), eliminating the extinction-enabling incentive, before the population declined sufficiently to become doomed to extinction by demographic stochasticity (4) or Allee effects (5). In fish, high fecundity seems to reduce the prevalence of

Allee effects (6), but high recruitment variability and larval mortality can increase susceptibility to demographic threats, and fish populations' maximum growth rates are similar to those of terrestrial mammals (7).

Second, if recruitment is only density-dependent at low abundances (termed high "steepness" in fisheries), $f > \beta$ is more likely to result in alternative stable states, whereby unmanaged harvesting does not result in extinction as long as the population remains above a tipping-point abundance (see figure 1 in ref. 1). The reason is that high steepness makes catch—and consequently price—initially less sensitive to abundance declines (see figure 3.2 in ref. 8). High fecundity likely makes high steepness more common in fish than in terrestrial species. However, high steepness is unlikely to prevent extinction in populations that hyperaggregate, because harvest costs decrease as these populations decline.

Finally, management interventions can prevent extinction, even if incentives would have otherwise enabled it. Management interventions have been key to stabilizing many overharvested fish populations, including northern cod (9) and Atlantic bluefin tuna (10), mentioned by Le Pape et al. (3). Whereas high fecundity might have eventually saved these populations from complete extinction, there is danger in assuming that certain species are unkillable. This danger is illustrated well by the case of the passenger pigeon, a once-abundant species that few thought could be driven extinct until it was (11). We agree with Le Pape et al. (3) that preventing fish population depletions is important regardless of whether or not complete extinction is possible.

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2 Courchamp F, et al. (2006) Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biol* 4:e415.

3 Le Pape O, Bonhommeau S, Nieblas A-E, Fromentin J-M (2017) Overfishing causes frequent fish population collapses but rare extinctions. *Proc Natl Acad Sci USA* 114:E6274.

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The authors declare no conflict of interest.

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