

# Evolutionary impacts of fishing: overfishing's 'Darwinian debt'

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*F1000 Biology Reports* 2009, 1:43 (doi:10.3410/BI-43)

The electronic version of this article is the complete one and can be found at: <http://F1000.com/Reports/Biology/content/1/43>

## Abstract

Human harvesting of fish results in far greater mortality than natural causes, with enormous potential to affect the phenotypic traits of fish populations, even after exploitation stops. Central to understanding these effects is the untangling of the genetic versus environmental components of phenotypic response. Evolutionary consequences of harvesting must be incorporated into conservation and management strategies.

## Introduction and context

Harvesting by humans is widely recognized to exert significant evolutionary changes in wild populations [1,2]. Rates of phenotypic change in harvested populations can exceed those in their 'natural' counterparts by as much as 300% [3]. Because of the significant depletion in many of the world's fisheries [4], there is now considerable interest in fisheries-induced evolution (FIE) [5-8] from both an evolutionary [9] and a conservation [5] perspective. Fisheries have been associated with a plethora of phenotypic changes in wild fish populations [9-11], manifested in changes in growth [12,13], reproduction [14,15], morphology [16], physiology and behaviour [17,18], and life history traits such as size and age at maturation [13,19-24]. Modelling studies have also predicted fisheries-induced changes in both life history traits [25] and spawning migration strategy [26]. The evolution of traits that genetically covary with those under direct selection can also influence the rate of evolution occurring by exploitation alone [27]. FIE has even been invoked to explain vulnerability to recreational fishing [28,29].

Despite the weight of evidence for phenotypic change induced by fishing, it is generally accepted that unequivocal empirical evidence of underlying genetic change resulting from fishing is lacking [9,30], though tantalizing experimental evidence is highly suggestive [17,31].

The crux of the problem is that changes in fish density and the environment can act to drive phenotypic plasticity in the absence of any genetic response attributable to selection [32,33]. However, there is also widespread acceptance of the notion that fishing causes a change in the selective regime of wild stocks, so that evolutionary change should be inevitable [34]. The implications are far-reaching; seemingly minimal shifts in age at maturity (say from 6 to 4 years in Atlantic cod) can result in reduced annual population growth by up to 30%, and a doubling in the probability of negative population growth [35]. One of the most promising techniques for understanding the genetic contribution to phenotypic change is probabilistic reaction norms for maturation (PRNM) - the fish's probability of maturing as a function of its age and size [23,36,37].

## Major recent advances

Important recent work is helping to quantify selection responses to overfishing, where there has been a dearth of data [38]. The study of Atlantic cod from Canada's Southern Gulf of St Lawrence stands out for estimating selection from an exploited stock [13]. Sexual selection might also be involved in altering the rate of evolutionary change by fishing [39]. A logical question stems from this work - how much evolution is caused by natural selection and how much is harvest-induced? Are these opposing forces or do they work synergistically [40,41]?

Recent studies suggest that fisheries-induced selection acts against and tends to swamp natural selection, leading to changes in populations that may take a long time, if ever, to reverse [42].

In fact, rates of reversibility in 'evolutionary changes' due to FIE could be extremely low even after fishing pressure ceases [13,42], especially when there has been major depletion of fish stocks due to over-exploitation, resulting in lower heritable genetic variation. Such is not surprising in light of the fact that fishing can result in fish mortality far greater than natural mortality - by more than 400%, resulting in far greater selection differentials [43,44]. The phenomenon in which current levels of exploitation will require several years of evolutionary recovery has been termed by U Dieckmann as the 'Darwinian debt' [45], which will need to be paid by future generations. Earlier studies showed a reduction in the ability of populations to recover [46] so FIE might keep resilience of fish populations low for long periods [27]. However, a recent laboratory study demonstrated evolutionary reversibility, despite full recovery taking up to 12 generations in fish with an annual life cycle, (equivalent to 36-84 years in typical harvested fish that have generation times of 3-7 years) [31]. Decadal scales of recovery mean we still need to consider evolution in fisheries management [31].

### Future directions

One of the biggest challenges for proponents of the theory of FIE is to disentangle genetic changes from environmental changes - even PRNM do not yet have strong empirical support [7]. But does this matter? Only in the sense that evolutionary changes could take longer to recover from once fishing pressure is reduced, as now appears to be the case [31]. So another key question arises as to how quickly FIE occurs in fish stocks [7]. If it occurs on a scale of years to decades, then it is much more relevant to fisheries management than if it occurs on a centennial scale.

Because it is so widespread and potentially harmful, there is justified and increasing interest in FIE to be incorporated into ecosystem-based management of fisheries worldwide [5,47-49]. Some authors are even calling for the adoption of 'evolutionary impact assessments' [5]. Others have used FIE to stress the recent recommendation of keeping the larger fish around [7,8,50]. But it must also be stressed that effects of FIE are variable and, where they occur, might be managed effectively [51]. Experimental studies confirm recovery from FIE after selection regimes have been relaxed in the laboratory [31], supporting the notion that genetic diversity loss does not necessarily accompany FIE. Evolutionary

scientists will need to work more closely with managers to incorporate FIE into conservation management [52].

The consequences of FIE are many and daunting considering the importance of life history traits to population dynamics, biomass, demography and economic yield [5]. FIE may also lead to reduced productivity [12], lower maximum sustainable yields [12], slower rates of population growth, and lower probabilities of recovery [46]. As such, further research should focus on the demographic consequences of FIE over multiple temporal scales [8]. While the field is exciting and changing almost daily, we still have very little information of how species are affected by FIE, and the extent to which various traits are vulnerable.

### Abbreviations

FIE, fisheries-induced evolution; PRNM, probabilistic reaction norms for maturation.

### Competing interests

The author declares that he has no competing interests.

### Acknowledgements

Thanks to Christopher Brown (The Ecology Centre, University of Queensland and CSIRO Marine and Atmospheric Research) and three anonymous reviewers for their comments on the manuscript.

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