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The Economics of reversing fisheries-induced evolution

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Fisheries typically consider short planning horizons that stand in contrast to long-term sustainability and biodiversity targets, especially when evolutionary time scales play a role. Many global fish stocks are exploited above sustainable levels, having caused fisheries-induced evolution towards smaller maturation sizes, lower growth rates, and lower economic values of individual fish. Here we couple economic decision-making with eco-evolutionary fish population dynamics to explore (1) the impact of alternative planning horizons in fisheries management on evolution and (2) the trade-off between profit and a set conservation target. We find that evolutionary decline is only reversed under century-long planning horizons. With more typical short-term planning, stock recovery in terms of biomass is achieved, but evolutionary decline continues. Setting genetic trait conservation targets only slightly reduced profits and the trade-off is further alleviated if the fishery can select for genotypes and thereby assist evolutionary reversal.

Global fisheries have severely impacted marine ecosystems, contributing to the decline of fish stocks, the degradation of marine habitats and the loss of biodiversity (*IPBES, 2019*). Beyond overall population decline, the intense fishing has lead to the truncation of age structure and caused evolutionary changes in important life-history traits (*Therkildsen et al., 2019, Heino et al., 2015*) that can have contrasting effects: earlier reproduction can increase stock resilience in the short-term but over time results in populations with smaller fish, a lower reproductive output (*Stige et al., 2017, Jørgensen and Holt, 2013, Barneche et al., 2018, Hixon et al., 2014*) and less value on the market (*Zimmermann and Heino, 2013*). Here we ask what it takes to bend the curve of evolutionary decline after decades of intensive exploitation, in light of potential trade-offs between economic profitability and conservation targets.

A key challenge is the mismatch between the timescales typical for economic decision making and for ecosystem dynamics, especially when it comes to evolutionary time scales (*Conover and Munch, 2002*). Firms usually plan for only a few years or decades (13–16 years, which is equivalent to a discount rate of 20-25% per year, if we define the planning horizon as the time it takes for the time discounted profit to fall below 5% of the current value). The corresponding planning horizon for public investments is longer, but the time until investments in nature conservation pay off may be very long as well. What is the appropriate planning horizon (or, equivalently, the appropriate discount rate) is a key question in sustainability economics (*Stern, 2007, Nordhaus, 2007, Weitzman, 2007*). For greenhouse gas mitigation, experts recommend planning horizons of around 150 years (discount rate of 2% per year) but many argue that it should be infinite (0% per year) (*Drupp et al., 2018*). For natural resource use, in the example of blue whales, the consequences of a mismatch between short-sighted profit-maximization vs. conservation have been pointed out long ago (*Clark, 1973a, Clark, 1973b*), and it has been debated to which extent commercial fisheries are prone to collapse under profit-maximizing behavior (*Grafton et al., 2007, Clark et al., 2010a, Grafton et al., 2010, Clark et al., 2010b*).

The dynamics of populations span time scales from individual life history (months or years) to population dynamics (years to decades) and evolutionary change (decades to centuries). Economic models of resource harvesting often ignore these complexities, although demography and trait composition are crucial for the productivity and resilience of a population, and their economic value (*Zimmermann and Heino, 2013*). Body size and genetic structure are directly affected by harvesting that truncates demography, triggers plastic responses and can induce evolutionary adaptation of wildlife populations (*Heino et al., 2015, Conover and Munch, 2002*) with detrimental effects for the sustainability and economic benefits of hunting (*Allendorf and Hard, 2009*) and fishing (*Jørgensen et al., 2007, Laugen et al., 2014*). Removing the large mature individuals leaves the small early maturing types to reproduce, favoring undesirable traits and inducing adverse selection that is antithetical to common practices in animal husbandry and breeding.

Beyond economic considerations of fisheries management, the United Nations' sustainable development goals (SDGs) and the Convention on Biological Diversity (CBD) Aichi targets require to reduce the pressure on biodiversity and ecosystems, and to safeguard genetic diversity (*CBD, 1992*), which implies the target to restore the genetic trait distribution in fish populations to more natural levels. The use-values of biodiversity and genotype conservation are difficult to quantify since they are delicately intertwined with resilience and ecosystem functioning (*mac, 2012*). The non-use values of genotypic states for society are also not quantified and therefore cannot be included accurately in a welfare function. Here we assume that recovering, to some extent, the genotypic state is an exogenously set conservation target.

We propose an economic-ecological fishery model (details in Supplement) that combines evolutionary population dynamics, structured by size and genotype (*Zimmermann and Jørgensen, 2015*), and hyper-allometric fecundity (*Barneche et al., 2018*) with an economic model of harvesting costs and consumers with preferences for consuming fish of different sizes (*Quaas et al., 2016, Quaas and Requate, 2013*). The resource manager optimizes time-dependent harvesting from the different size classes of fish such as to maximize the present value of profits for the given planning horizon. State-of-the art numerical optimization routines (*Byrd et al., 2006*) are used to find the optimal values for $\sim$ 66'066 ecological and economic variables. We apply the model to the North Sea Cod stock, which has been heavily exploited since the 1970s, leading to overfishing, declining stock sizes and a decline in the mean maturation size (Fig. 1). We used stock assessment data (*Alvestad et al., 2020, ICES, 2019*), size dependent price data (*BLE, 2019*) and profit margins (*Berkenhagen et al., 2021*) to calibrate the model; the calculated heritability of size at maturity $\mathtt{h}^2 = 0.17$ matches literature values (*Kolstad et al., 2006, Kristjánsson and Arnason,*).

Results

Our results show that profit-maximising fisheries management would typically reduce harvest and rebuild the stock to more productive levels than it has been in the past couple of decades (Fig. 1). Only for a very short planning horizon of much less than a decade, stock depletion, i.e. reducing the biomass further, would maximize profits (Fig. 2). With more far-sighted planning horizons (more than a few years, but less than centuries), the stock biomass is always rebuilt; yet evolutionary decline continues and the genetic trait distribution of the fish population is typically not rebuilt. For century-long planning horizons, it becomes economically optimal to also reverse the evolutionary decline, which takes much longer than the recovery of the stock biomass (Fig. 1). Reversing evolution is especially beneficial when the genetic distribution has strongly deteriorated towards small maturation sizes; as is the case for North Sea cod, where the maturation size was around 50.6cm in 2019.

Our analysis indicates a trade-off between evolutionary reversal and economic profitability. We quantify this trade-off as the Pareto frontier between a restoration target, namely to achieve a minimum mean maturation size by 2050 (or 2100), and the maximum profit that could be obtained until then given the conservation target, relative to the maximum profit without an explicit conservation target (Fig. 3). Confirming expectations, the trade-off is stronger if the target has to be reached early. A hypothetical harvesting technology that can select for genotypes in addition to size classes assists evolutionary reversal, and higher conservation targets can be reached faster and with less value lost (as shown in Fig. 3). While the perfect selection of genotypes is a theoretical consideration, some targeting is conceivable, as late or early maturing individuals may arrive at different times at the spawning grounds (*Jørgensen et al., 2008, Wieland et al., 2000*). Using stock-specific knowledge may therefore enable evolutionary enlightened harvest strategies that greatly reduce the trade-off between economic profitability and the conservation target of bending the curve of evolutionary decline.

Discussion

Our findings highlight that the planning horizon is key for the economic analysis of evolutionary overexploitation, adding a critical perspective to the existing literature that has not considered evolutionary recovery as a specific objective. Previous studies have focused on the optimal harvest strategy under evolutionary change, finding that the optimal harvesting strategies are more or less the same with or without considering evolution (*Eikeset et al., 2013, Zimmermann and Jørgensen, 2015*). The explanation is that evolution is not relevant on common economic timescales: biomass and, thus, harvest recovers within a few decades, whereas evolutionary recovery takes centuries, even with a fishing moratorium (Fig. 1).

Stakeholders and the society need to clearly define objectives and consider the trade-offs among them. Social welfare maximisation should consider non-use values and side benefits (or costs) of rebuilding a population (effects on other species and the ecosystem; resilience of the stock to e.g. climate change shocks), and include existence values of species. The CBD acknowledges an intrinsic value of biodiversity and genetic diversity, and therefore calls for preserving or restoring these natural features. Our analysis shows that conservation targets and sustainable development goals are unlikely to be achieved unless planning horizons are expanded beyond few decades, establishing intergenerational equity as a core objective of resource management.

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Competing interests

The authors declare that they have no competing interests.

Data and materials availability

The optimisation code will be available at Github

Supplementary materials

Mathematical model

Calibration, methods and software

Figs. S1 to S5

Tables S1 to S2

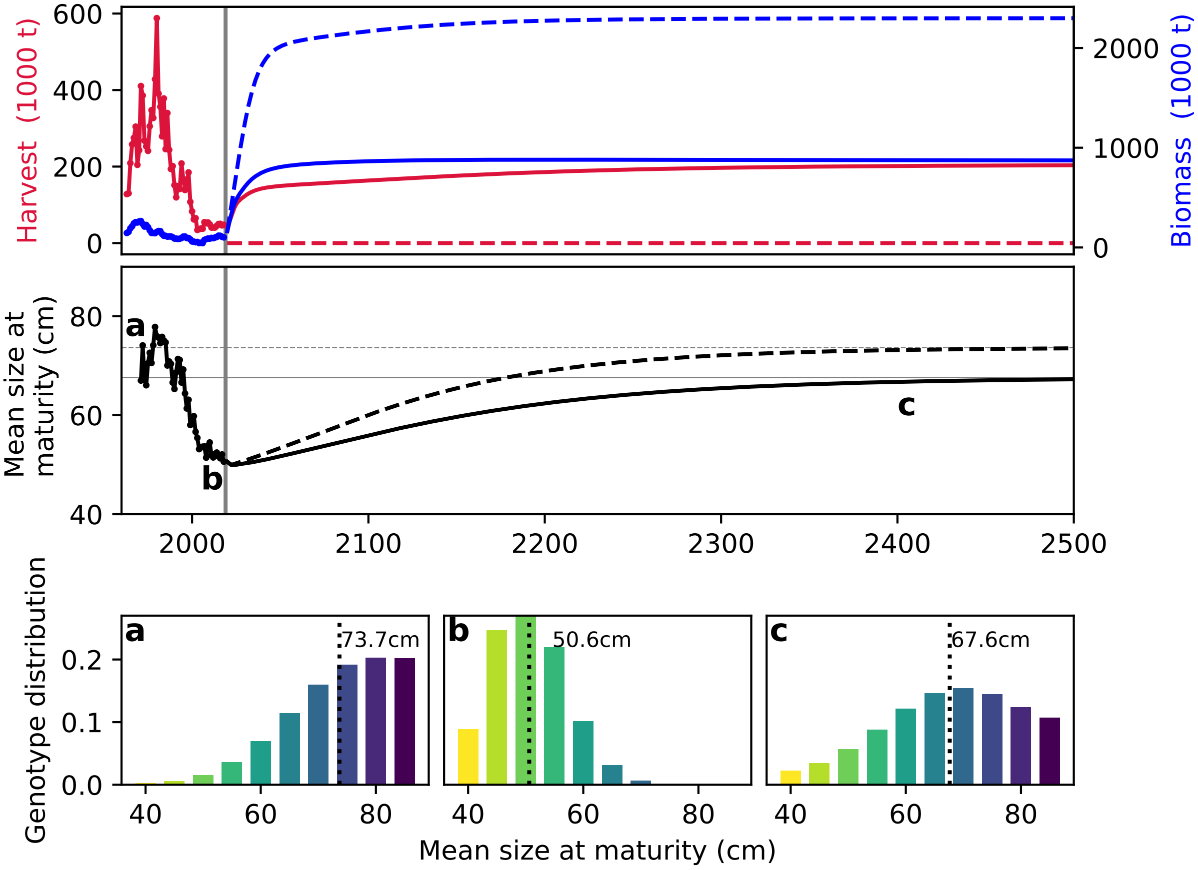

Figure 1: **Stock and maturation size decline and recovery over time**: Stock assessment data showing the decline in spawning stock biomass (right axis, blue) owing to large harvest quantities (left axis, red) and a substantial decline in the mean size at maturity until 2019 **(b)**. Optimisation results from 2019 onward, showing the recovery of spawning stock biomass, harvest and population-mean maturation length to the ecological-evolutionary-economic steady state **(c)** under management with infinite planning (0% discount rate, solid lines) and recovery to the ecological-evolutionary pristine state **(a)** if fishing is stopped altogether from 2020 (dashed lines).

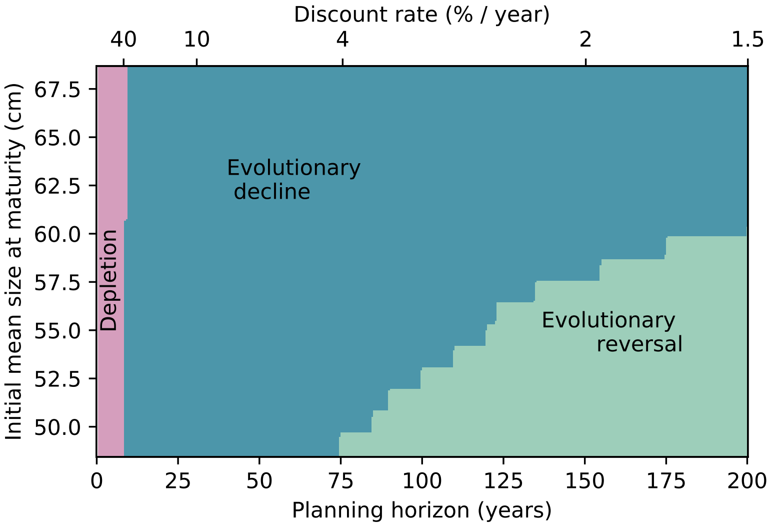

Figure 2: **Evolutionary decline and reversal**: Profit maximisation will result in three different categories of stock decline or recovery, depending on the planning horizon (or discount rate, horizontal axis) and the initial state of the population (vertical axis). Short-term profit maximisation results in further fisheries-induced evolutionary decline (blue). Stock depletion results only for extremely short planning horizons (pink). Far-sighted economic planning (low discounting) leads to evolutionary reversal (green). This is especially the case when the initial evolutionary state is strongly deteriorated. Stock depletion is classified as a decline in the spawning stock biomass (2019–2050); evolutionary reversal is defined as an increasing maturation length by the year 2050. The planning horizon is defined as the time it takes until the discounted profit falls below 5% of the current value.

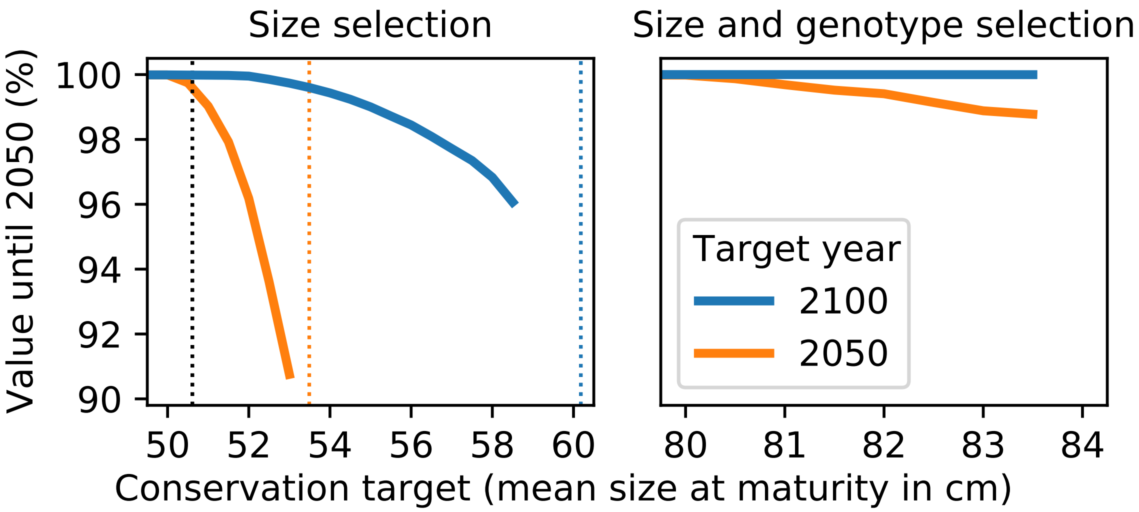

Figure 3: **Trade-off between economic profitability and evolutionary conservation**: A target for a minimal evolutionary state, i.e. mean maturation length, after 2050 (2100) reduces the economic profit of the fishery. Starting with a mean size at maturity of 50.6cm (dotted vertical line) the size selective fishery can only recover the mean size at maturity to a maximum of 53.5cm (60cm) [vertical lines], if fishing is stopped altogether. If genotype selection is possible evolution is assisted and much higher targets can be reached. The planning horizon is 150 years (2% discount rate per year).