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Contrasting evolutionary and ecological management objectives in the context of sustainable harvesting

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ABSTRACT

Background: Harvesting of large, old fish can induce evolutionary changes in fish life histories (e.g. reduce age and size at maturation). Although reducing phenotypic selectivity of fishing can minimize the evolutionary impacts of fishing, this can lead to overfishing of immature individuals. The fishing strategy that aims to secure sufficient recruitment for the next generation, and thus targets solely the adult proportion of the population, is called the 'spawn-at-least-once' policy. However, this strategy conflicts with the attempt to avoid fisheries-induced evolution.

Questions: What are the ecological and evolutionary impacts of the prevailing hake fishing strategy that can be characterized by low phenotypic selectivity, compared with a strategy that uses a spawn-at-least-once policy? How do these two fishing strategies contribute to the sustainability of hake fisheries from both the ecological and evolutionary perspectives?

Methods: We address the questions using a case study, the European hake fishery. We simulate the eco-evolutionary dynamics of European hake populations under two alternative fishing strategies. The simulation approach is individual-based and describes individual life histories through von Bertalanffy growth curves and life-history invariants. We implemented the two strategies through two alternative fishing selectivity curves: (1) a low selectivity strategy estimated from current European hake fishing, which targets equally both immature and mature individuals, and (2) a spawn-at-least-once strategy of selectivity, which targets mature individuals.

Key assumptions: Growth histories and vulnerability to fishing do not depend on the sex of an individual. Reproductive success depends on female body size. Mature individuals have higher natural mortality owing to the survival costs of reproduction. The model does not incorporate any differences between geographical areas or any behavioural adaptations that may vary among fish.

Conclusions: The two fishing strategies showed opposite responses at the population and phenotypic levels. The spawn-at-least-once policy resulted in life-history evolution towards earlier maturation and smaller adult body size, but the population abundance remained high. In contrast, the prevailing low-selective fisheries strategy led to large reductions in population abundance but no evolutionary changes in life histories.

Keywords: age at maturation, European hake, fisheries-induced evolution, fishing, spawn-at-least-once.

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INTRODUCTION

Fishing is one the most intensive anthropogenic disturbances introduced into marine ecosystems (Law, 2000; Dieckmann and Heino, 2007). While historically fisheries have simply aimed to maximize short-term yields (Larkin, 1977; Vasilakopoulos *et al*., 2011), nowadays more attention is paid to the long-term sustainability of fisheries, so that harvested populations might provide catches also in the future. Population renewal ability is directly linked to successful reproduction and, to promote this, a 'spawn-at-least-once' policy is now widely applied in the management of numerous fish species (Vasilakopoulos *et al*., 2011). The objective of a spawn-at-least-once policy is to preserve the immature fish, such that they can reproduce before being caught, and thus contribute to the following generations (Murua *et al*., 2010; Vasilakopoulos *et al*., 2011; Garcia *et al*., 2012). Although a spawn-at-least-once policy positively affects population abundance and resilience to fishing in the short term (Vasilakopoulos *et al*., 2011), it does not necessarily consider any long-term effects of fishing, such as fisheries-induced evolution (Law, 2000; Kuparinen and Merilä, 2007).

Given that fishing often intensively targets large, old individuals and given that fish life-history traits are at least to some extent heritable, spawn-at-least-once fishing is likely to cause evolutionary changes in life histories towards earlier maturation at smaller body size and reduced adult body size (Law, 2000; Jørgensen *et al*., 2007). Phenotypic trends have been documented in numerous commercially harvested fish stocks that support the view that fisheries-induced evolution might be common in many exploited fish populations (Sharpe and Hendry, 2009; Audzijonyte *et al*., 2013). Fisheries-induced evolution is problematic from both fisheries and conservation perspectives, as it can decrease catches (Heino and Godø, 2002; Laugen *et al*., 2014) and reduce population recovery ability while increasing fluctuations in population abundance (Anderson *et al*., 2008; Enberg *et al*., 2009). Therefore, it has been suggested that the evolutionary consequences of fishing should be accounted for in fisheries management and that fishing strategies should be designed to minimize the evolutionary impacts of fishing (Jørgensen *et al*., 2007; Laugen *et al*., 2014). However, although reducing the phenotypic selectivity of fishing would best mitigate fisheries-induced evolution (Garcia *et al*., 2012; Laugen *et al*., 2014), this would conflict with the principles of traditional fisheries management (i.e. the spawn-at-least-once policy) and with the protection of immature individuals (Myers and Mertz, 1998).

The European hake (*Merluccius merluccius* L., 1758) is a gadiform bottom-dweller (Casey and Pereiro, 1995). It is commercially important to the countries of the northeast Atlantic shelf, the Mediterranean Sea, and the Black Sea (Ragonese, 2009; ICES, 2012). Hake has experienced drastic declines in numbers (ICES, 2005, 2012) and, simultaneously, reductions in body size associated with fishing mortality trends; these were documented in the Bay of Biscay and on the Galician coast between 1980 and 2004 (Dominguez-Petit *et al*., 2007). Current hake fishing practices largely do not select between immature and mature fish (Jusufovski, 2013; Santiago Cerviño, personal communication) and should therefore minimize evolutionary pressures associated with fishing because they do not employ a spawn-at-least-once policy. Here, we use hake as the study system to: (1) investigate the ecological and evolutionary impacts of the two contrasting management strategies with the objective of either minimizing fisheries-induced evolution or protecting immature fish, and (2) evaluate how they contribute to the common goal of the sustainability of fishing. To this end, we simulate eco-evolutionary hake population dynamics under two opposing fishing strategies: the current non-selective strategy (which should minimize fisheries-induced evolution) and, in contrast, a strategy based on a spawn-at-least-once policy.

METHODS

To investigate evolutionary changes in hake phenotypes associated with alternative fishing strategies, we use an individual-based simulation model that incorporates the key ecological and evolutionary processes that drive the dynamics of a fish population. The model is described extensively elsewhere (Kuparinen *et al.*, 2011, 2014; Kuparinen and Hutchings, 2012), thus in the following we briefly outline its main features and focus on its parameterization for the European hake.

Simulation approach

The individual fish growth trajectories are described by the von Bertalanffy (1938) growth curve, where the length at age t is given by $L(t)$:

$$L_\infty - (L_\infty - L_0)\mathrm{e}^{-Kt}, \tag{1}$$

where L_∞ denotes the asymptotic length, K is an intrinsic growth rate, and L_0 is the length of the fish at $t = 0$. We define the life histories of individuals by their von Bertalanffy growth trajectories and consider them heritable. As quantitative traits are generally coded by a large number of loci with small additive effects (Roff, 2002), we describe fish genotypes through 10 diploid loci with two alleles in each, coded by 0 or 1 (Kuparinen *et al.*, 2011). The alleles are inherited from parents and transferred to the offspring through classical Mendelian inheritance. The sum of the allele values ranges between 0 and 20 (hereafter called the genetic trait value) and represents the genetic basis of an individual life history. Defined as such, we transfer the genetic trait value into the phenotype after the addition of an appropriate amount of phenotypic variation to yield realistic heritabilities of 0.2–0.3 (Mousseau and Roff, 1987). We translate the genetic trait value into L_∞ and predict the value of K through the strong negative correlation between K and L_∞. We assume an individual is sexually mature when its body size has reached a fixed proportion of L_∞ (see 'Model parameterization').

We implement density dependence of growth, which varies the progress of an individual along its von Bertalanffy growth trajectory. In practice, the annual process from year 1 to year $t + 1$ is given by $L(t + \Delta t)$, which ranges between 0 and 1 and is given by:

$$\Delta t = e^{15 - 17.6 \times c}(1 + e^{15 - 17.6 \times c}) - 1. \tag{2}$$

The instantaneous mortality rate consists of the overall natural mortality (M) and the survival cost of reproduction (Bell, 1980), which is applied only to the mature individuals. Both of these mortality rates are set to be equal in males and females. We use a Bernoulli trial to decide on the fate of the individual at every time step.

For each reproduction event, we randomly assign a mature male to a mature female. Egg production depends on the weight of the female, and the survival of juveniles is determined by a baseline juvenile mortality rate and a density-dependent effect (modelled similar to Δt above). They both equally contribute to the overall juvenile survival. We define genotypes of the juveniles as described above and the sex of a juvenile is determined through a Bernoulli trial ($P = 0.5$).

Model parameterization

We introduce a dataset of 64 individual-based growth trajectories of the European hake. The dataset represents a compilation of growth parameters across Mediterranean fishing grounds to provide a general overview of the species traits (for details, see Ragonese *et al.*, 2012). However, in practice, most of the data we used for model parameterization originated from studies of the Southern hake stock. For the sake of normality, we model a log-transformation of K through a linear regression to obtain the final model: $\log(K) = 0.511 - 0.005 \times L_\infty$ (Table 1). Hence, in the simulations we linearly translate the sum of the allele values (and phenotypic variation about it) into the value of L_∞ based on the observed range of L_∞ (Table 1) and then we predict the value of K through the above regression. We set the same value of L_0 for each individual, which we determine based on the above growth parameter data. The threshold for maturation (RL) is set to $0.51 \times L_\infty$, which is an average value pulled from the $L_{\mathrm{mat}}/L_\infty$ ratios for hake.

For the estimation of egg production, we used the available data on recruitment and spawning stock biomass. The amount of eggs produced is calculated by the equation: eggs = RPS × weight. Here, RPS is the mean number of recruits per kilogram of spawning stock biomass (recruit-per-spawner; derived from the database); and the weight of the female is calculated as $\text{weight} = 0.00000513 \times \text{length}^{3.074}$ (ICES, 2012). Survival of the eggs up to the age of 2 years is determined by average rates of natural mortality of 0–2-year-old fish obtained from the ICES (2012) and the number of surviving eggs is drawn from an appropriate binomial distribution. The maximum lifespan of the individual is set to 20 years of age (www.fao.org; www.fishbase.org).

Simulation design

We ran the simulations with two contrasting fishing selectivity scenarios and compared the evolutionary and ecological impacts of fishing (Fig. 1). The first selectivity scenario describes the prevailing hake fishing practice and is set to best estimate the asymptotic trend of fish removal by a cross-section of the most common fishing tools in hake fisheries. The second scenario describes the spawn-at-least-once fishing policy. In both scenarios, fishing selectivity is modelled as $s = e^{a+b\times L} \times (1 + e^{a+b\times L})^{-1}$. For the prevailing fishing scenario, we chose parameters a and b with length at 50% retention (L_{50}) on the basis of current hake

Table 1. Parameters and the chosen values reflecting the biological characteristics of the European hake

Parameter	Value
Standard deviation of K	0.126
Range of L_∞	70–120 cm
L_0	2.5 cm
RL	0.51
Max. life span of individual	20 years
a	−7.6
b	0.38
F	0.15

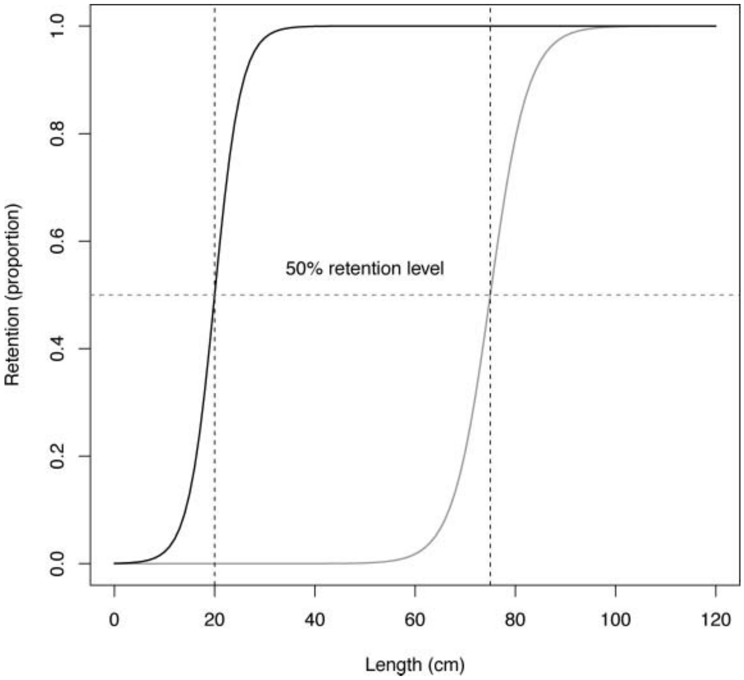

Fig. 1. The probability of retention by the fishing gear shown as a function of hake body size. The selective curves depict the two scenarios tested: current fishing scenario (black line) and a spawn-at-least-once scenario (grey line). The 50% retention level (horizontal dashed line) is set at 20 cm and 75 cm length (L_{50}; vertical dashed lines) for the current fishing and the spawn-at-least-once scenario, respectively.

stock estimation practices (Fig. 1; and Santiago Cerviño, personal communication). For the spawn-at-least-once policy, we chose values of *a* and *b* such that the L_{50} was set to 75 cm, at which length both sexes are mature (www.fishbase.org; www.fao.org; Cerviño *et al.*, 2013). Each simulation is initialized with a population of 2000 individuals, which corresponds to ~1500 kg. Population carrying capacity is set to 5000 kg. In each simulation run, we allowed the population to grow, achieve equilibrium, and adapt evolutionarily during the first 2000 years. After the adaptation period, the population undergoes a period of fishing for 100 years followed by 400 years of recovery.

Overall fishing mortality (*F*) is based on the current level of fishing pressure experienced by hake. We kept *F* the same for both fishing selectivity scenarios. At every simulation time step, we monitored the ecological parameters and life-history traits. The monitored traits included population biomass, recruitment, asymptotic length, and age at maturation. We simulated each scenario with 10 independent replicates. We performed all simulation runs and graphical analyses in R v.2.15.2 (R Development Core Team, 2012).

RESULTS

Under the current fishing practice, the introduction of fishing decreased population biomass drastically, so that by the end of the fishing period it had declined to ≈4% of carrying capacity. In contrast, the spawn-at-least-once scenario revealed a lower impact on the

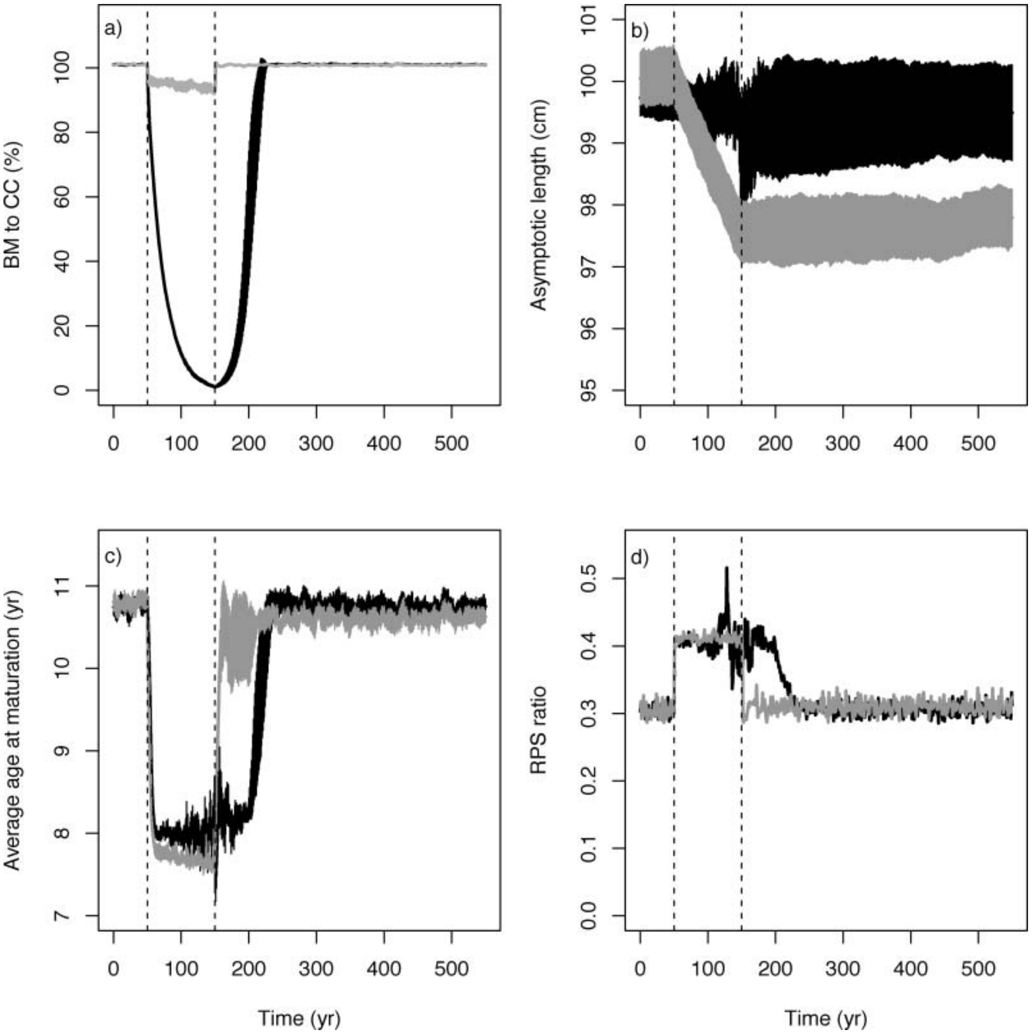

Fig. 2. The impact of the current fishing scenario (black) and spawn-at-least-once scenario (grey) at the population and phenotype level. The two different scenarios are shown as averages with 95% confidence intervals denoted by vertical lines. The panels show the following parameters: (a) population biomass with respect to carrying capacity ratio (BM to CC); (b) asymptotic length (L_∞); (c) age at maturation; and (d) recruit-per-spawner ratio (RPS). The x-axes represent the last 550 years of the total 2500 years of simulation. Vertical dashed lines divide the simulation time into pre-fishing (first 50 years), fishing (from 50 to 150 years), and post-fishing period (from 150 to 550 years).

population biomass: the population reached a new equilibrium biomass at about 95% of carrying capacity (Fig. 2a). The magnitude of temporal variability in population biomass was also less in the spawn-at-least-once scenario versus the prevailing selectivity scenario. After the relaxation of fishing, the spawn-at-least-once scenario showed a rapid increase to the pre-fishing level, while the current fishing scenario exhibited a slower and gradual recovery to the same pre-fishing level of population biomass.

In contrast to its minimal ecological effects, the spawn-at-least-once scenario induced evolutionary changes in asymptotic body length. The asymptotic length declined by ~2.5 cm, whereas the prevailing fishing scenario caused virtually no changes in the asymptotic length (Fig. 2b). In the case of the spawn-at-least-once scenario, the asymptotic body size did not recover after the cessation of fishing but maintained the same level throughout the recovery period, reflecting a permanent change in the population's genetic composition.

In both selectivity scenarios, the fishing pressure decreased the average age at maturation by ~3 years (Fig. 2c). As fishing ceased, the age at maturation recovered quickly under the spawn-at-least-once scenario, but remained at a slightly lower level compared with its pre-fishing state. In the case of the prevailing fishing scenario, the recovery was slower, but the age at maturation did reach its pre-fishing level.

The impacts of the two selectivity scenarios on population productivity were assessed through the recruit-per-spawner (RPS; number of recruits divided by mature biomass) ratio (Fig. 2d). The RPS showed higher temporal fluctuation under the prevailing fishing scenario, whereas under the spawn-at-least-once scenario it remained on the same level throughout the fishing period. After the removal of the fishing pressure, under the prevailing fishing scenario the RPS decreased gradually to its pre-fishing level. However, under the spawn-at-least-once scenario, the RPS returned to the pre-fishing level immediately.

DISCUSSION

Our results demonstrate that the avoidance of fisheries-induced evolution can lead to ecologically unsustainable fishing, whereas a fishing strategy that causes evolutionary changes in fish life histories can still be ecologically sustainable. These patterns arise from the differences in size-dependent fishing mortality: in the studied hake fishery, current fishing practices remove individuals of different sizes evenly, whereas a spawn-at-least-once strategy selectively targets large individuals. The latter then creates evolutionary pressure towards earlier maturation and smaller adult body sizes (Fig. 2b). From an ecological perspective, however, equal removal of different sized individuals erodes a population's reproductive capacity, as many individuals die before they manage to reproduce (Fig. 2a). In contrast, targeted removal of mature individuals ensures reproduction prior to individuals being killed by fishing. While lower selectivity appears essential to avoiding evolutionary changes in phenotypes, and therefore preserves adaptive genotypic diversity, it enhances the risk of a population collapse. Therefore, a fishing strategy that focuses solely on mitigating evolution cannot be considered a sustainable fishing strategy *per se*.

As in any modelling study, in the present study we made a number of assumptions that need to be addressed: (1) growth rate did not depend on sex; (2) relative egg production depended solely on female body size; and (3) no geographical characteristics or behavioural adaptations were considered. But it is well known that hake growth differs between the sexes, which then influences individual growth trajectories, especially after sexual maturation (Cerviño, 2014). Therefore, the effects of fishing documented here using a simplified, non-sex-specific model are likely to be conservative. In reality, fishing could also alter the sex ratio of a hake population and lead to larger changes in population productivity and fluctuations about it. Similarly, in reality, egg production likely depends on female age, in addition to body size (Venturelli *et al.*, 2009). This feature might affect our projections for fisheries-induced evolution, as the fitness benefits of large, old spawners can be higher than those we consider here. Specifically, evolutionary decreases in adult body size and age at maturation might remain smaller than those projected here, further supporting the importance of the ecological impacts of fishing as compared with fisheries-induced evolution. Hake stocks are well known to differ in many biological characteristics (Casey and Pereiro, 1995; ICES, 2012), but the objective of the present study was to explore hake as a general study system (at the species level) and, to this end and for the sake of model transparency and tractability, we parameterized the model by averaging data across different geographic regions. Consequently, our results cannot be used to predict how one specific hake population would react to fishing; obviously, this depends not only on population-specific characteristics, but also on ecosystem impacts such as predation pressure and prey availability.

In terms of the sustainability of fisheries, ecological impacts of fishing are a major concern for the demography and dynamic stability of the populations. On that view, the risks associated with fisheries-induced evolution might be a cost worth paying to avoid the risk of population collapse. However, such ecologically minded fisheries management, characterized by highly size-dependent selectivity (i.e. a spawn-at-least-once policy), might nonetheless affect yields in the long run: fisheries-induced evolution might reduce fish body size and population equilibrium (Enberg *et al.*, 2009; Kuparinen and Hutchings, 2012) and thereby reduce catch biomasses. Apart from direct biomass reductions, decreasing fish size can also lower the economic value of the catch (Garcia *et al.*, 2012; Laugen *et al.*, 2014). Furthermore, although reducing fishing mortality and allowing a depleted population to rebuild might mitigate short-term ecological impacts of fishing, the reversibility of fisheries-induced evolution is less obvious. Evolutionary changes can be very slow or even impossible to reverse, as natural selection can be much weaker than that induced by fishing (Heino and Godø, 2002; Garcia *et al.*, 2012). Ultimately, evolutionary changes in life-history traits can lead to loss of adaptive genetic diversity and thereby adversely affect population resilience to environmental changes (Enberg *et al.*, 2009; Kuparinen and Hutchings, 2012).

Ecologically and evolutionarily sustainable harvesting requires much more complex considerations than those surrounding yields and phenotypic selectivity rules in current day management (Garcia *et al.*, 2012). In the light of the present study, it is clear that sustainability cannot be achieved either by solely preserving the immature fish or by avoiding proportionally higher fishing pressure among bigger and older individuals. The confusion largely arising from mixed priorities and differing time-scales is important. Are the immediate ecological impacts of fishing worse than fisheries-induced evolution together with its potentially far-reaching consequences? The present study suggests that the immediate ecological impacts threatening the very persistence of the population are an obvious concern and so avoidance of population extinction should be the key priority of fisheries management. Nonetheless, this objective can simultaneously support the avoidance of fisheries-induced evolution. Hutchings (2009) showed that both the adverse ecological impacts of fishing and fisheries-induced evolution can be best avoided by simply reducing the overall fishing mortality. This view is qualitatively similar to the principles of balanced harvesting, where the overall mortality is proportional to the overall ecosystem productivity and it is evenly scattered across the body-size spectrum in the ecosystem, to avoid over-exploitation of certain species and phenotypes (Law *et al.*, 2012; Jacobsen *et al.*, 2013).

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