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Marine reserves and the evolutionary effects of fishing on size at maturation

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Size-selective fishing may induce rapid evolutionary changes in life-history traits such as size at maturation. A major concern is that these changes will reduce population biomass and detrimentally affect yield and recruitment. While marine reserves have been proposed as a tool for fisheries management, their evolutionary implications have as yet attracted little scrutiny. Here we use a simple model to investigate whether marine reserves can be expected to mitigate the evolutionary impacts of fishing on maturation size. We analyze the adaptive dynamics of size at maturation based on a stage-structured population model including size-selective fishing and marine reserves with different retention rates. As has been shown before, imposing higher fishing mortality on the largest individuals promotes an evolutionary change towards smaller maturation size. We find that, in our model, protecting part of a fish stock using a marine reserve can prevent such fisheries-induced evolution. We demonstrate that this protection critically depends on the type and extent of movement between the reserve and the fished area. Specifically, while the frequent movement of large adults increases catches of large adult fish outside a marine reserve, it also reduces the reserve's effectiveness in preventing fisheries-induced evolution. By contrast, when the exchange between protected and fished areas occurs through juvenile export alone, a marine reserve can effectively prevent evolution towards smaller maturation size, but does so at the expense of reducing the yield of large adult fish. We conclude that differences in the movement behaviour of successive life stages have to be considered for marine reserves to help making fisheries to be more evolutionarily sustainable.

Keywords: connectivity, fitness, life history evolution, metapopulation, size-structured model, spill-over

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1 Introduction

Commercial fisheries have caused declines in fish stocks and catches around the world (e.g., Hilborn *et al.*, 2003; Pauly *et al.*, 2005; Pauly, 2008). Besides reduction of abundances, fishing truncates the age and size structure of populations (e.g., Jackson *et al.*, 2001; Berkeley *et al.*, 2004b; Ottersen *et al.*, 2006). The removal of old and large adults decreases the reproductive potential of fish stocks and thereby their ability to withstand and recover from overexploitation (Begg and Marteinsdottir, 2003; Aubone, 2004a; Law, 2007). In particular, large females contribute disproportionately to recruitment, due to their production of higher numbers of eggs that are also larger and of better quality (Marteinsdottir and Steinarsson, 1998; Vallin and Nissling, 2000; Berkeley *et al.*, 2004a; Carr and Kaufman, 2009). Juvenescence in fish stocks was found to contribute to increased variability in stock dynamics and abundance (Anderson *et al.*, 2008).

In addition to demographic effects, fishing may induce evolutionary changes in life-history traits, which may decrease a population's reproductive potential, resilience, and sustainable yield (e.g., Law and Grey, 1989; Heino and Godø, 2002; Walsh *et al.*, 2006). Evolution towards maturation at smaller sizes and younger ages has been inferred for wild fish stocks by estimating probabilistic maturation reaction norms (Heino *et al.*, 2002b; Dieckmann and Heino, 2007; Heino and Dieckmann, 2008) for North Sea plaice *Pleuronectes platessa* (Grift *et al.*, 2003; Grift *et al.*, 2007), North Sea sole *Solea solea* (Mollet *et al.*, 2007), Newfoundland American plaice *Hippoglossoides platessoides* (Barot *et al.*, 2005), and stocks of Atlantic cod *Gadus morhua* (Heino *et al.*, 2002a, c; Barot *et al.*, 2004; Olsen *et al.*, 2004; Olsen *et al.*, 2005). According to life-history theory, the reproductive value of age classes decreases with survival probability so that elevated mortality favours reproduction early in life (Michod, 1979). It has also been shown experimentally that when large individuals are harvested, populations evolve towards smaller body size, whereas harvesting small fish induces evolution towards larger body size (Reznick *et al.*, 1990; Conover and Munch, 2002; Conover *et al.*, 2005).

There are additional circumstances that may contribute to the observed changes in size at maturation in fish stocks. For example, as population density decreases in exploited stocks, more food becomes available to the remaining fish, so that their growth rate increases. This may imply that they mature earlier, as a phenotypically plastic response to the altered growth conditions (Trippel, 1995). On the other hand, life-history theory predicts that maturation should be postponed when resource levels increase, because the payoff of future reproduction then also increases. Although conclusive genetic evidence for fisheries-induced evolutionary changes is lacking, studies support considerations of evolutionary effects (Jørgensen *et al.*, 2007; Kuparinen and Merilä, 2007; Browman *et al.*, 2008; Hutchings and Fraser, 2008; Jørgensen *et al.*, 2008; Kuparinen and Merilä, 2008). Independent of other environmental factors that also influence the size at maturation in wild stocks, size-selective fishing represents an evolutionary force that should be considered and managed in accordance with the precautionary principle (Lauck *et al.*, 1998; Ashley *et al.*, 2003).

The classical tools of fisheries management include catch quotas, as well as restrictions on landing sizes, gears, and number of vessels. These measures can be inadequate to release stocks from fishing pressure under conditions of poor enforcement, discard of bycatch, misreporting, and illegal landings (Roberts, 2000). It has been pointed out that scientific advice on total allowable catches has been repeatedly ignored, causing fish stocks to remain overexploited (Cardinale and Svedäng, 2008). As fish stocks decline, more selective fishing-gear technology is often likely to be used (Madsen, 2007), which may aggravate the demographic, ecological, and evolutionary implications of fishing.

Marine reserves have been suggested as an alternative management tool in support of a precautionary approach to the protection of marine diversity, aquatic habitat, and fish stocks (Roberts, 1997; Apostolaki *et al.*, 2002; Aubone, 2004b). The prohibition of fishing in marine reserves may help to rebuild fish stocks and their age structure by allowing individuals to survive longer and grow larger (Berkeley *et al.*, 2004b). Examples such as the Apo Island reserve in the Philippines (Russ *et al.*, 2004; Abesamis and Russ, 2005) and the Merritt Island National Wildlife Refuge in Florida (Roberts *et al.*, 2001) demonstrate that marine reserves can benefit both fish stocks and adjacent local fisheries. Besides positive effects of marine reserves in the tropics, benefits have also been demonstrated in temperate regions. A number of small reserves in the Mediterranean Sea had positive effects on population structure and density, with the greatest effect on large-bodied and target species (García-Charton *et al.*, 2008); these reserves also resulted in the spill-over of fish from protected to fished areas (Goñi *et al.*, 2008; Harmelin-Vivien *et al.*, 2008).

Different processes affect the spatial connectivity of protected and fished areas, and therefore influence the effects of marine reserves. These processes include larval dispersal, juvenile and adult mobility, as well as movement of fishers (Botsford *et al.*, 2009). In particular the dispersal abilities of fish determine whether there is a net export of individuals from the marine reserve to the fished area (Baskett *et al.*, 2005; Gerber *et al.*, 2005). Home ranges of fish may vary within and among species (Kramer and Chapman, 1999; Chateau and Wantiez, 2009). Le Quesne and Codling (2009) describe the differential effects of larval dispersal and adult mobility and conclude that reserves were more efficient for sedentary stocks with dispersing larvae. The effects of marine reserves have been analyzed to determine their optimal size and level of fragmentation, and to assess their impacts on abundance, catches, age structure, spatial structure and species interactions (Gerber *et al.*, 2003; Pelletier and Mahévas, 2005; Costello and Polasky, 2008). Marine reserves were found to be especially useful for the management of late-maturing and long-lived species (Kaplan, 2009).

Few studies to date have taken into account the evolutionary implications of marine reserves for changes in life-history traits. Models based on quantitative genetics theory have been used to examine the effects of marine reserves on the evolution of life-history traits and to explore how marine reserves may benefit fisheries yields and protect stocks against evolution towards early maturation (Trexler and Travis, 2000; Ratner and Lande, 2001; Baskett *et al.*, 2005; Dunlop *et al.*, 2009a). In the individual-based models by Baskett *et al.* (2005) and Dunlop *et al.* (2009a), genotype and phenotype dynamics were coupled, resulting in complex models that are analytically intractable.

In this paper, we instead explore the evolutionary implications of marine reserves using relatively simple deterministic population models with a small number of parameters. We combine the simple difference-equation model studied by Gårdmark *et al.* (2003) of an age-structured harvested population with a metapopulation model applied by Pitchford *et al.* (2007). Our models describe, in a simple form, basic life-history processes of growth, maturation, reproduction, mortality, and movement with a stage-specific dimension (Metcalf and Pavard, 2007). Through a reduction of detail, we develop a comprehensible model that facilitates the analysis. On this basis, we investigate whether marine reserves can prevent the evolution of maturation size in response to size-selective fishing. In particular, we compare different stage-dependent movement scenarios, such as juvenile export and adult spill-over, to elucidate the expected efficacy of differently sized marine reserves in terms of ensuring evolutionary protection and providing yield for adjacent fisheries.

2 Model description

2.1 Single-population model

Gårdmark *et al.* (2003) analyzed an age-structured population model in discrete time, which we here transform into a stage-structured model with a size-based interpretation. The deterministic model comprises four difference equations representing the dynamics of a population with three size classes and two alternative life histories (Equations 1a to 1d; Figure 1). Time steps are interpreted as annual. We distinguish two adult classes, 2 and 4. Depending on the probability γ to mature at small size, after one year juveniles of class 1 can either enter the mature class 2, with fecundity f_2, or spend a year being immature in class 3 before maturing at large size and entering class 4, with fecundity $f_4 > f_2$. Although in reality fish grow indeterminately, in our simple model fish stop growing after reaching maturity. Individuals of class 2 therefore do not grow to class 4 (for an extension see Appendix B). The survival probabilities, s_1 to s_4, describe the fractions of a class surviving to the next year. The description so far implies that juveniles remain in class 1 for a year before potentially spending several years as adults, maturing at the age of 2 or 3 years in the reproductive classes 2 or 4, respectively. Fishing mortality is size-dependent and differs between intermediate-sized fish in class 2 or 3 experiencing a harvest proportion of $h_{2,3}$, and large fish in class 4 experiencing a harvest proportion of h_4. Density-dependent survival is considered at the juvenile stage in class 1 (Myers and Cadigan, 1993; Cushing and Horwood, 1994), with a parameter m determining the strength of density dependence, so that m^{-1} measures the density of juveniles at which the natural survival probability is halved (Gårdmark *et al.*, 2003). Parameters, their descriptions, and their default values for the numerical illustrations are summarized in Table 1.

The dynamics of the population densities N_1 to N_4 are given by

$$N_1(t+1) = f_2N_2(t) + f_4N_4(t), \tag{1a}$$

$$N_2(t+1) = \frac{\gamma s_1 N_1(t)}{1+mN_1(t)} + s_2(1-h_{2,3})N_2(t), \tag{1b}$$

$$N_3(t+1) = \frac{(1-\gamma)s_1 N_1(t)}{1+mN_1(t)}, \tag{1c}$$

$$N_4(t+1) = s_3(1-h_{2,3})N_3(t) + s_4(1-h_4)N_4(t). \tag{1d}$$

The corresponding equilibrium equations can be solved analytically to obtain the equilibrium densities ($N_1^*, N_2^*, N_3^*, N_4^*$),

$$N_1^* = \frac{1}{m}\left[\frac{(1-\gamma)f_4 s_1 s_3(1-h_{2,3})}{1-s_4(1-h_4)} + \frac{\gamma f_2 s_1}{1-s_2(1-h_{2,3})}\right] - \frac{1}{m}, \tag{2a}$$

$$N_2^* = \frac{N_1^* \gamma s_1}{(1+mN_1^*)(1-s_2(1-h_{2,3}))}, \tag{2b}$$

$$N_3^* = \frac{N_1^*(1-\gamma)s_1}{(1+mN_1^*)}, \tag{2c}$$

$$N_4^* = \frac{N_1^*(1-\gamma)s_1 s_3(1-h_2)}{(1+mN_1^*)(1-s_4(1-h_4))}. \tag{2d}$$

Provided $0 \le N_1^* < \infty$, which includes all biologically relevant cases, there exists a unique non-trivial equilibrium. This equilibrium is locally stable, because the dominant eigenvalue λ_J of the respective Jacobian matrix J of Equations (1) has an absolute value that is smaller than 1 (Kot, 2001). This can be confirmed analytically by deriving the characteristic equation of J evaluated at the local equilibrium and finding λ_J as the zero of a linear Taylor approximation around the threshold $\lambda_J = 1$.

2.2 Marine-reserve model

We extend the single-population model described above to a metapopulation model by linking two identical populations. This mimics a situation in which a fished area is combined with a marine reserve (Gerber *et al.*, 2005; Pitchford *et al.*, 2007). In the first part of our analysis below, we assume the fished area and the marine reserve to be of equal size ($r = 0.5$). We then go on to consider different fractions of area protected by a marine reserve. For this extension, the metapopulation model is modified by scaling the movement probability of individuals in each area to be proportional to the relative size of the destination area (Figure 2). The two populations are connected by individual movement, either through juvenile export with movement probability d_1 or through large-adult spill-over with movement probability d_4. Below we show the results of these two movement scenarios. Movement of individuals of the intermediate size classes 2 and 3 produces intermediate results.

Population 1, with densities N_{11} to N_{14}, is exposed to the size-selective harvest proportion h_4 in size class 4,

$$N_{11}(t+1) = (1-d_1)\left[f_2 N_{12}(t) + f_4 N_{14}(t)\right] + d_1\left[f_2 N_{22}(t) + f_4 N_{24}(t)\right], \tag{3a}$$

$$N_{12}(t+1) = \frac{\gamma s_1 N_{11}(t)}{1+m_1 N_{11}(t)} + s_2 N_{12}(t), \tag{3b}$$

$$N_{13}(t+1) = \frac{(1-\gamma)s_1 N_{11}(t)}{1+m_1 N_{11}(t)}, \tag{3c}$$

$$N_{14}(t+1) = (1-d_4)\left[s_3 N_{13}(t) + s_4(1-h_4)N_{14}(t)\right] + d_4\left[s_3 N_{23}(t) + s_4 N_{24}(t)\right]. \tag{3d}$$

Equations for the densities N_{21} to N_{24} in population 2, which is protected by the marine reserve, are analogous and are derived from the equations above by setting $h_4 = 0$ and exchanging d_1 and d_4 with $(1-d_1)$ and $(1-d_4)$, respectively. In both populations of the marine-reserve model, the harvest proportion $h_{2,3}$ of small individuals is set to 0 to allow focusing on the evolutionary effects of harvesting large fish. The stage-dependent fecundities and survival probabilities for each size class are equal in both areas, while the density-dependent survival of juveniles depends separately on their density in each population, and the factor m^{-1} in each area is scaled by the area's relative size.

2.3 Evolutionary analysis

The life-history trait γ evolves in our models and measures the probability that an individual starts reproduction at small size (this is analogous to the corresponding parameter for age at maturation used by Gårdmark *et al.*, 2003). Small-maturing individuals are assumed to have invested in early reproduction rather than in further growth; they gain neither the higher fecundity of large individuals, nor do they suffer from the fishing mortality h_4. We use adaptive dynamics theory (Metz *et al.*, 1992; Dieckmann and Law, 1996; Metz *et al.*, 1996; Dieckmann, 1997; Geritz *et al.*, 1997; Geritz *et al.*, 1998; Meszéna *et al.*, 2001; Diekmann, 2004) to determine the outcomes of evolution in γ, and thus in size at maturation. This approach assumes a separation of timescales for the ecological and evolutionary dynamics, with population dynamics getting sufficiently close to equilibrium during successive invasions of variant phenotypes favoured by selection. Evolutionary outcomes can thus be inferred from assessing the eventual fate of a rare variant γ' trying to invade in an environment determined by the resident population with phenotype γ. The fitness $w(\gamma',\gamma)$ of the variant, and thus its potential for such invasion, is given by its geometric growth factor $\lambda(\gamma',\gamma)$ (Metz *et al.*, 1992). The selection pressure towards small maturation size is then calculated as

$$\left.\frac{dw(\gamma)}{d\gamma}\right|_{\gamma'=\gamma} = \lim_{\gamma'\to\gamma}\frac{w(\gamma',\gamma)-w(\gamma,\gamma)}{\gamma'-\gamma} = \lim_{\gamma'\to\gamma}\frac{|\lambda(\gamma',\gamma)|-1}{\gamma'-\gamma}. \qquad (4)$$

3 Results

3.1 Single-population model

To establish a baseline for our evolutionary analysis of the marine-reserve model, we start by summarizing salient results for the single-population model. In this model, the geometric growth factor $\lambda(\gamma',\gamma)$ of a rare variant phenotype γ' in a resident population with phenotype γ can be calculated analytically as the dominant eigenvalue (in terms of absolute values) of the variant's population projection (or Leslie) matrix $L(\gamma',\gamma)$,

$$L(\gamma',\gamma)=\begin{bmatrix} 0 & f_2 & 0 & f_4 \\ \dfrac{\gamma' s_1}{1+mN_1^*(\gamma)} & s_2(1-h_{2,3}) & 0 & 0 \\ \dfrac{(1-\gamma')s_1}{1+mN_1^*(\gamma)} & 0 & 0 & 0 \\ 0 & 0 & s_3(1-h_{2,3}) & s_4(1-h_4) \end{bmatrix}, \qquad (5)$$

$$\lambda(\gamma',\gamma)=\frac{1}{1+mN_1^*(\gamma)}\left[\frac{f_2 s_1}{1-s_2(1-h_{2,3})}\gamma'+\frac{f_4 s_1 s_3(1-h_{2,3})}{1-s_4(1-h_4)}(1-\gamma')\right]. \qquad (6)$$

The environment for the variant's invasion is defined by the resident population, with the variant's density-dependent survival being a function of the equilibrium number of juveniles $N_1^*(\gamma)$ of the resident population. The variant can only invade if $\lambda(\gamma',\gamma)>1$. Under this condition, the variant population on average grows in density and can eventually replace the previous resident population (Geritz *et al.*, 2002).

We find that the evolutionary dynamics of the single-population model exhibit frequency-independent selection and follow an optimization principle. This can be inferred from the fact that $N_1^*(\gamma)$ is the only term in Equation (6) through which the resident's phenotype γ influences the variant's geometric growth factor $\lambda(\gamma',\gamma)$ (Heino *et al.*, 1998). Moreover, following the selection pressure in Equation (4), the single population gradually evolves either to maturation at large size ($\gamma=0$) or to maturation at small size ($\gamma=1$). The latter happens if the following inequality is fulfilled,

$$\frac{f_2 s_1}{1-s_2(1-h_{2,3})}>\frac{f_4 s_1 s_3(1-h_{2,3})}{1-s_4(1-h_4)}. \qquad (7)$$

Also, when this equality is fulfilled (not fulfilled), the outcome $\gamma=1$ ($\gamma=0$) is globally evolutionarily stable.

We can interpret the left-hand side and the right-hand side of this inequality, respectively, as the lifetime reproductive success resulting from maturation at small size ($\gamma=1$) and at large size ($\gamma=0$). Since the right-hand side decreases as h_4 increases, increased harvesting of large adult individuals favours maturation at small size. In contrast, the harvest proportion $h_{2,3}$ in the intermediate size range appears twice in the inequality, decreasing reproductive output at large as well as at small size. Fishing intermediately sized fish alone may favour maturation at large size or small size as detailed in Appendix A.

For the evolutionary analysis of the marine-reserve model, we focus on analyzing the effect of the harvest proportion h_4, because fishing of the large adult individuals induces a stronger selection pressure than fishing of intermediate-sized adult individuals, and because fisheries-induced evolution towards smaller maturation size is a widely observed empirical phenomenon (e.g., Rijnsdorp, 1993; Trippel, 1995; Olsen *et al.*, 2004).

3.2 Marine-reserve model: large-adult spill-over

The effect of marine reserves on the evolution of size at maturation was analyzed with the help of the marine-reserve model, consisting of eight equations with an 8×8 population projection matrix $L_{MR}(\gamma', \gamma)$ for the variant. The marine-reserve model shows richer evolutionary dynamics than the single-population model. In particular, the evolutionary dynamics no longer follow an optimization principle. Instead, frequency-dependent selection may lead to a stable dimorphism. We start our analysis by focusing on the effects of large-adult spill-over, measured by d_4, in the absence of juvenile export, $d_1 = 0$.

Without movement, $d_1 = d_4 = 0$, the two populations in the protected and fished areas are uncoupled, and therefore evolve independently. The matrix $L_{MR}(\gamma', \gamma)$ becomes reducible, and its dominant eigenvalue describes the variant's local geometric growth factor in only one area, with evolutionary dynamics as described by the single-population model for that area. Two resident phenotypes may then coexist, each being adapted separately to the ecological conditions in one of the two areas.

With movement, $d_4 > 0$, small phenotypic steps result in gradual evolution towards one of the extreme maturation strategies. Figure 3A shows how gradual evolution towards maturation at small size switches to evolution towards maturation at large size in dependence on the movement probability d_4 of large adults and on the harvest proportion h_4 of large adults.

The grey area in Figure 3B shows, in contrast, the conditions under which non-gradual evolution through large phenotypic steps can lead to the coexistence $\gamma = 0$ and $\gamma = 1$. Increasing large-adult spill-over diminishes the range of harvest proportions h_4 over which the two extreme maturation strategies can coexist.

3.3 Marine-reserve model: alternative movement scenarios

Figures 4A and 4B show how the selection pressure towards small maturation size depends on the harvest proportion of large adults when movement between the protected and fished areas occurs either through juvenile export (Figure 4A) or through large-adult spill-over (Figure 4B). The selection pressure is positive whenever the fitness of a variant phenotype with a higher probability to mature at small size exceeds the fitness of the resident phenotype (Equation 4). For comparison, the selection pressure that applies in the absence of a marine reserve is also shown (grey line).

In our numerical example, a marine reserve with juvenile export alone altogether prevents an evolutionary switch to small maturation size, even when the harvest proportion of large adults is maximal (Figure 4A). In contrast a marine reserve with large-adult spill-over prevents such an evolutionary switch only when the harvest proportion of large adults is low or the movement probability of large adults is low (Figure 4B). Less movement of large adults leads to lower fishing mortality of large adults, which reduces the selection pressures towards small maturation size, and therefore shifts the critical harvest proportion to higher values $(d_4 = 0.6)$, or even prevents the evolutionary switch to small maturation size altogether $(d_4 = 0.2)$.

We can understand these results as follows. Juvenile fish in class 1 have only one year during which they can move through juvenile export, whereas large-maturing adults can move through large-adult spill-over during several years they remain alive in class 4. Therefore, over the years large-adult spill-over causes a larger proportion of each cohort to move outside the marine reserve. This lower retention of the marine reserve results in a higher exposure of fish to size-selective fishing and thus explains why marine reserves with juvenile export are more effective in mitigating fisheries-induced maturation evolution than marine reserves with large-adult spill-over. Movement of large adults occurs later in life, after the annual harvest event on large adults of class 4, and as such should exert a smaller selection pressure than juvenile export if all individuals die after spending one year in class 4. However, survival in class 4 for more than a year increases the probability of individuals to be subject to size-selective fishing mortality, which intensifies the selection pressure.

3.4 Marine-reserve model: effects on yield

To complement Figures 4A and 4B showing how marine reserves weaken the selection pressure towards maturation at small size in dependence on different movement scenarios the corresponding effects on yield are illustrated in Figures 4C and 4D. As expected, the figures show that catches of large adults collapse whenever the evolutionary switch to small maturation size is induced. Juvenile export altogether prevents this switch, so that catches of large adults are ensured at all harvest proportions (Figure 4C). When movement occurs through large-adult spill-over, yield of large adults is ensured at low movement probabilities, by preventing the evolutionary switch, while at higher movement probabilities the catch collapses (Figure 4D). With decreasing large-adult spill-over, the implementation of a marine reserve increases the harvest proportion at which yield is maximized. In comparison to a fully fished stock, marine reserves thus lead to reduced catches only at low harvest proportions. When harvest proportions are higher, the marine reserve dramatically improves catches, by preventing the collapse of catch otherwise resulting from the evolutionary switch to small maturation size.

We also considered the effects of redistributed fishing effort. When a marine reserve is established, fishing may intensify in the areas that are still fished to make up for reductions in the accessible area and catches. We therefore assume that, for a reserve covering 50% of the total area, fishing effort doubles on the remaining fishing ground. Under the (typically unrealistically high) maximum large-adult movement probability $d_4 = 1.0$, evolutionary outcomes and yields are then equivalent with and without the marine reserve. However, when large-adult spill-over is smaller than this maximum (assuming realistic values), with reserve implementation the evolutionary switch occurs at higher harvest proportions. The lower large-adult spill-over then reduces yield despite the assumption of redistributed fishing effort.

3.5 Marine-reserve model: reserve size

In the numerical illustrations shown so far, fished and protected areas are equal. Figure 5A shows how the critical harvest proportion h_4^* of large adults at which the evolutionary switch occurs depends on reserve size r. We see that the implementation of a marine reserve ($r > 0$) shifts this evolutionary switch to higher harvest proportions. If the reserve is large enough, evolution towards small maturation size can be prevented altogether. The critical reserve size needed to prevent the evolutionary switch for any harvest proportion differs for the different movement scenarios. In general, populations with high movement probabilities require larger reserves to achieve such protection. For all movement probabilities, a population with large-adult spill-over requires a larger reserve than a population with juvenile export. If movement occurs only through juvenile export at low probability, implementation of a small reserve (in our numerical example, requiring no more than 10% of the total area) will suffice to achieve evolutionary protection. Larger reserves will be needed to protect populations with large-adult spill-over or with more juvenile export. Such other movement scenarios necessitate intermediate-sized reserves, here at between 20% and 40% of the total area.

To analyze the effect of reserve size on yields, we investigated catch per unit effort $\mathrm{CPUE} = \mathrm{Y} / \mathrm{h}_4$, defined as the ratio between yield Y and harvest proportion h_4 (Gulland, 1969). For this, we focused on the CPUE right above the critical harvest proportion, $\mathrm{CPUE}^* = \lim_{\mathrm{h}_4 \to \mathrm{h}_4^*} \frac{\mathrm{Y}}{\mathrm{h}_4}$, with $\mathrm{h}_4^* = 1$ when $\mathrm{h}_4 = 1$ does not induce an evolutionary switch to small maturation size. If intensive harvesting induces an evolutionary switch to small maturation size, the yield Y of large adult fish, as well as CPUE, will be zero, implying $\mathrm{CPUE}^* = 0$ for $\mathrm{h}_4^* < 1$. On the other hand, if no evolutionary switch is induced, $\mathrm{CPUE}^* > 0$ for $\mathrm{h}_4^* = 1$. Since CPUE rises above CPUE^* for $\mathrm{h}_4 < \mathrm{h}_4^*$, CPUE^* describes a worst-case scenario. Figure 5B illustrates, for different movement scenarios, that CPUE^* attains its maximum once the critical reserve size is reached that prevents evolution to smaller maturation size. The figure also shows that implementing a reserve larger than the critical size will be less profitable, by reducing CPUE^* relative to its maximum.

4 Discussion

Here we have examined the effects of marine reserves on maturation evolution by analyzing selection pressures on the probability that individuals mature at small size in stage-structured populations exposed to size-selective fishing. We have shown that an evolutionary switch from large to small maturation size induced by intensive fishing on large adults can be prevented by marine reserves of sufficient size. We have also demonstrated how the critical harvest proportion at which the shift occurs depends on alternative movement scenarios, including large-adult spill-over and juvenile export. While marine reserves with juvenile export better protect against fisheries-induced maturation evolution, marine reserves with large-adult spill-over can better sustain yields of large adults. To maximize catch per unit effort, intermediate harvest proportions must be combined with marine reserves exceeding a critical size.

4.1 Single-population model

The single-population model described in section 2.1 results in density-dependent but frequency-independent selection, so that the resultant evolutionary dynamics follow an optimization principle (Heino *et al.*, 1998). Our evolutionary analysis of this model (Inequality 7) shows that size-selective fishing can cause an evolutionary switch from maturation at large size to maturation at small size. This is in agreement with the results for an age-structured model reported by Gårdmark *et al.* (2003), where a high harvest proportion of the oldest individuals induced an evolutionary switch from late maturation to early maturation.

Our results show that the propensity for such an evolutionary switch depends on relative, rather than on absolute values of the parameters characterizing the harvested species and its harvest regime (Equation 7). This means that even species suffering from relatively low fishing mortality can undergo an evolutionary switch towards small maturation size when their relative fecundities, natural mortalities, and the size-selectivity of harvesting make them vulnerable to fishing. On the other hand, if, for example, the gain in fecundity with size is only small, or if the survival of small individuals is disproportionately low, an evolutionary switch to small maturation size may not occur.

In the numerical example using the default parameter values listed in Table 1, the evolutionary switch from large to small maturation size occurs at a harvest proportion of $h_4 = 0.35$. Notice that it is possible to choose parameters that favour the survival and fecundity of the large-maturing individuals in class 4 to an extent that Inequality 7 is never fulfilled. For instance, using the same survival probabilities as before, but for $f_4 \geq 32$, even very high harvest proportions will not induce the evolutionary switch to small maturation size. Naturally, default parameter values used for illustrating the results were chosen to be plausible. For example, the annual probability of natural survival was chosen to equal 0.8 (Guénette and Pitcher, 1999). The harvest proportion can vary considerably depending on the commercial value of the fished species, and proportions have been estimated to rise as high as 0.96 in some heavily exploited populations (Willis and Millar, 2005).

4.2 Marine-reserve model

The evolutionary switch to small maturation size can be prevented by reducing the harvest proportion of large adults below a critical value, since this weakens the corresponding selection pressure. As it is often difficult to estimate fishing mortalities accurately and to enforce corresponding limits the implementation of a marine reserve may offer an alternative for reliably reducing fishing mortalities. While the implementation of a marine reserve eliminates harvesting on part of a population, it also leads to increased spatial heterogeneity in the selection pressures caused by fishing. As illustrated in Figure 3, this may give rise to an evolutionarily stable dimorphism in size at maturation, especially when movement between the protected and fished areas is low. Limited movement and strong differences in selective pressures operating in each area, in conjunction with suitable frequency dependence promotes the stability of such a dimorphism (Meszéna *et al.*, 1997; Heino *et al.*, 1998; Kisdi and Geritz, 1999; Fox *et al.*, 2001). This potential for dimorphism has important practical consequences, since it enables a population of large-maturing phenotypes to be successfully invaded by small-maturing phenotypes, which will usually imply a potentially unexpected transition in population composition. For organisms with sexual reproduction, a maturation dimorphism might of course be gradually eroded by interbreeding among maturation strategies, unless such interbreeding is limited by some form of assortative mating (Kisdi and Geritz, 1999).

High movement probabilities between protected and fished areas increase catches outside the reserve and may strengthen the evolutionary pressure towards small maturation size (Figure 4). In addition, we have demonstrated that the evolutionary effects of a marine reserve depend on the stage-specific movement of individuals. Compared with juvenile export, large-adult spill-over from the marine reserve to the fished area causes higher selection pressures on maturation size and therefore reduces the reserve-based protection from evolution to small maturation size. Juvenile export, in contrast, keeps selection pressures lower but does not lead to an increasing yield of large adults outside the reserve as the juvenile movement becomes more frequent (Figure 4). This underscores that managing fisheries-induced maturation evolution through marine reserves requires not only accounting for the differential movement probabilities of a fished species as a whole, but, more specifically, must be informed also by how such movement is distributed across the species' life-history stages.

It should be noted that despite the optimistic message conveyed by Figure 4A, a marine reserve with juvenile export alone may still fail to protect a fished population from an evolutionary switch to small maturation size at high harvest proportions. For example, it is possible to choose parameters, such as $f_2 = 5$ and $f_4 < 10$, that lower the difference in lifetime reproductive success between the two extreme maturation strategies and strengthen the selection pressure on size at maturation to an extent that the evolutionary switch to small maturation size occurs even for marine reserves with juvenile export alone, provided harvest proportions are sufficiently high.

If we consider the redistribution of fishing effort from the marine reserve to the fished area, the harvest proportion in the fished area doubles with reserve implementation when the two areas have identical size (Guénette and Pitcher, 1999; Baskett *et al.*, 2005). At maximum movement probability, the evolutionary switch from large to small maturation size then occurs at exactly $h_4 = 0.7$, which is also twice the harvest proportion in the fished area without redistribution of fishing effort. Recognizing that the harvest proportion in the total area is half of that in the fished area after the implementation of a marine reserve, the resulting selection pressures in the single-population model are then equal to those in the marine-reserve model with maximum large-adult spill-over (Figure 4B). At maximum large-adult spill-over and redistributed fishing effort, marine reserve implementation does not affect fisheries-induced changes in maturation size. But the degree of protection against fisheries-induced evolution is likely to be higher with implementation of a marine reserve at lower movement probabilities. Nevertheless, additional habitat disturbances resulting from the redistribution of fishing effort may have undesirable effects (Dinmore *et al.*, 2003; Greenstreet *et al.*, 2009).

4.3 Model limitations

We highlight that our model includes several simplifying assumptions, some of which may be relaxed without significantly changing the results. For example, individuals in class 2 may also grow to large size and attain higher fecundity of large individuals. This will favour the small-maturing life-history strategy, which, relative to the large-maturing strategy, then has an extra reproductive event at age 2. This reduces the costs of maturation at small size for fecundity later in life so that the evolutionary switch from large to small maturation size can be expected at lower harvest proportions. Similarly, if individuals in class 3 are allowed to take more than one extra year to mature, their reproductive output is reduced relative to that of the small-maturing life-history strategy. As demonstrated in Appendix B, both of these extensions favour the small-maturing life-history strategy. This shows that, by leaving out these possible extensions, our simple model does not overestimate the selection pressures towards small maturation size that result from size-selective fishing.

Our models predict an evolutionary switch in the size at maturation, resulting in a collapse of catches of large adults as their harvest proportion is increased beyond a critical value. In natural systems, the pace of this collapse will depend on how long it takes the evolving population to adapt its maturation strategy from large-maturing to small-maturing. Even though the selection pressure on the maturation strategy changes abruptly at the critical harvest proportion, it will typically take populations many generations to exhibit the full selection response to such an altered selection pressure. To describe such gradual selection response accurately, one would need to account for genetic variability among individuals with different maturation strategies (Baskett *et al.*, 2005; Codling, 2008; Dunlop *et al.*, 2007; Dunlop *et al.*, 2009a; Dunlop *et al.*, 2009b; Enberg *et al.*, 2009; Miethe *et al.*, 2009; Okamoto *et al.*, 2009).

Also stochastic effects and uncertainty may greatly affect results and are likely to increase the importance of marine reserves for the management of fish stocks and fisheries (Mangel, 2000; Gerber *et al.*, 2003; Pitchford *et al.*, 2007; Codling, 2008). Acknowledging the uncertainty in fishing mortality, implementing marine reserves can serve as a precautionary strategy even if harvest proportions are assumed to be below critical values predicted by deterministic models (Lauck *et al.*, 1998). Similarly, evolutionary dynamics may be affected by demographic and environmental stochasticity. In particular, environmental stochasticity has been found to favour delayed maturation, especially in semelparous organisms (Koons *et al.*, 2008).

The movement of fish tends to exhibit richer dynamics and detail than accounted for in our study. Our model treats movement as a simple diffusive process. As one example of a complication encountered in nature, movement that is correlated among individuals was found to lead to greater dispersal distances (Codling, 2008). These may in turn imply a higher degree of population connectivity, which could affect evolutionary outcomes in our model by decreasing the evolutionary protection provided by marine reserves. In our model, both reproduction and movement occur once per year. Le Quesne and Codling (2009) point out that this may be unrealistic. While reproduction is often a seasonal event, movement tends to occur continuously throughout the year. If movement occurs more than once per year, the movement probabilities in our model must be interpreted as effective annual movement probabilities, integrating over multiple movements.

Recruitment depends on the abundance or biomass of spawning stock (Myers and Barrowman, 1996). There are different ways to model stock-recruitment relationships. We use a nonlinear density-dependent recruitment function of Beverton-Holt type (Gårdmark *et al.*, 2003). This relationship implies a consistently high mean recruitment when the spawning stock is large. In contrast, stock-recruitment functions of Ricker type, also commonly used in fisheries models, describe dome-shaped relationships with negative effects of density dependence increasing as the spawning stock becomes larger (Needle, 2002). As in our model the density-dependent survival of juveniles of class 1 affects small-maturing and large-maturing phenotypes equally, the shape of the stock-recruitment function has no impact on the evolutionary outcomes. Nevertheless, different relationships need to be taken into account when fitting a model to data. Beverton-Holt stock-recruitment models assume an increase in recruitment per spawner as a stock's density decreases, which may lead to overestimating a stock's carrying capacity (Barrowman and Myers, 2000).

Another important simplification made in our study results from its focus on a single species. The resultant model is easily understood, straightforward, and may still help achieving some ecosystem objectives (Mace, 2004). While fisheries management based on multi-species models is desirable, such models are still very difficult to design and parameterise. It has actually been suggested that the lack of political will to implement scientific advice is more important for understanding failing fisheries management than the traditional focus on single-species approaches (Cardinale and Svedäng, 2008).

4.4 Stage-dependent mobility and reserve size

Ecological effects of juvenile movement were observed in marine reserves on the Australian Great Barrier Reef reserves, where the abundance of sedentary coral-reef fish increased inside the reserve because dispersal in these fish occurs only at the larval stage; no adult spill-over was observed (Williamson *et al.*, 2004). For obvious reasons, adult spill-over has a stronger positive effect on the yield of adult fish. This is in agreement with a study by Le Quesne and Codling (2009), who found that adult spill-over has a greater potential to improve yield than juvenile export. Strong positive effects of adult spill-over on yield were observed where the protected and fished areas feature the same habitat and adult fish are mobile (Russ *et al.*, 2003). As shown above, however, the protection afforded by a marine reserve with adult-spill-over from evolution towards small maturation size is weaker. Adult spill-over directly increases the number of large-maturing adults reaching the fished area and suffering from size-selective mortality.

We have shown that juvenile export alone, or low to moderate large-adult spill-over between the protected and fished areas, prevent an evolutionary switch to small maturation size (Figures 4A and 4B). This finding gains extra significance when considering how the implementation of a marine reserve may result in selection for shorter dispersal distances. This gradually decreases the movement out of the reserve and thereby diminishes the reserve's beneficial effect on yield (Botsford *et al.*, 2001; Baskett *et al.*, 2007). Modelling the joint evolution of size at maturation and mobility Miethe *et al.* (2009) confirm the gradual reduction of large-adult spill-over through selection for lower dispersal within the marine reserve.

We verified that movement of only intermediately sized individuals leads to results that lie between the two extreme scenarios of juvenile export and large-adult spill-over analyzed above. Moreover, movement of several size classes leads to a higher connectivity between the protected and the fished area; this reduces the scope for a stable dimorphism of maturation strategies and also lessens the evolutionary protection provided by the marine reserve.

In the study by Baskett *et al.* (2005), reserve size did not affect evolutionary outcomes when movement was low; whereas high movement resulted in decreased protection from maturation evolution. We show that reserve size affects populations with low as well as high movement probability but in different ways (Figures 5A and 5B). Movement processes at different life stages differ in the net transfer rates of harvestable large adults. For stocks with mainly juvenile export or with very low fishing mortality, we recommend small reserves, while populations with high adult movement that suffer from high exploitation require large reserves. The effects of a marine reserve increase with its size and with the time since its implementation (Botsford *et al.*, 2003; Claudet *et al.*, 2008; Le Quesne and Codling, 2009).

For the management of mixed fisheries that include species with different movement and other life-history characteristics, one reserve size will not be optimal for of those species (Sale *et al.*, 2005). We recommend adapting the degree of protection, and thus the size of the considered marine reserve, to the most vulnerable fished species, where a species' vulnerability should be defined in terms of its sensitivity to the demographic and evolutionary effects of harvesting. While such an approach may lead to the implementation of a large reserve reducing the catch per unit effort of other species, it respects the precautionary approach and will buffer the fished community against uncertainty, not the least against uncertainty with regard to choosing the most appropriate reserve size. Furthermore, for preventing evolutionary changes towards small maturation size it may be effective to combine the implementation of a reserve with a reduction of fishing mortality outside of the reserve.

4.5 Marine reserves as a management tool

Use of natural home ranges as reserve boundaries reduces spill-over and increases the resultant protection (Chapman and Kramer, 2000; Topping *et al.*, 2005). A network of protected areas on spawning and nursery grounds of haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* off the east coast of Iceland helped to increase haddock abundance and mean size without affecting species richness and composition (Jaworski *et al.*, 2006). Nevertheless, the positive effects were quickly reversed after reopening of the temporary closure. Although marine reserves were generally found to be efficient as management tools (Halpern, 2003), there are also examples of unsuccessful reserve implementation. The "plaice box" was set up to protect undersized fish on the nursery grounds of North Sea plaice *Pleuronectes platessa* (Pastoors *et al.*, 2000). The observed reduction of juvenile density within this reserve was attributed to changes in the spatial distribution of North Sea plaice and possibly also to deteriorating feeding conditions through reduced abundance of small invertebrates resulting from diminished trawling (Hiddink *et al.*, 2008). A protected area in a haddock nursery ground on the Scotian Shelf, Canada, failed to protect juveniles, but benefited haddock adults as well as other local fish stocks of American plaice *Hippoglossoides americanus* and winter flounder *Pseudopleuronectes americanus* (Frank *et al.*, 2000).

In our models, we specifically analyzed a sedentary population with a marine no-take reserve. The effect of protection afforded by a marine reserve may indeed be critically affected by the occurrence of seasonal spawning migrations and ontogenetic habitat shifts (Horwood *et al.*, 1998; Dunlop *et al.*, 2009a; West *et al.*, 2009). Kelly *et al.* (2006) found that seasonal protection of spawning grounds, in the context of the recovery plan for Atlantic cod in the Irish Sea, did not succeed, probably because some fisheries were still allowed in the area, causing cod bycatch, increased fishing effort outside the protected area, and data uncertainty. Reversal of evolutionary changes in life-history traits is expected to be a slow process, although lab experiments show that reversal is possible (Law and Grey, 1989; Law, 2000; Swain *et al.*, 2007; Conover *et al.*, 2009; Enberg *et al.*, 2009). After the collapse of Canadian cod, a fishing moratorium was declared that so far did little for demographic recovery (Hutchings and Reynolds, 2004) or evolutionary recovery (Olsen *et al.*, 2004; Olsen *et al.*, 2005). Currently, only a small fraction of the sea has been set aside for protection, and long-term protection is rare. Therefore, evolutionary effects of marine-reserve implementation have not been documented to date.

Part of a reserve's benefit in terms of enhanced yield may accrue through improved habitat quality inside the reserve, which supports larger populations and increases spill-over. Lundberg *et al.* (1999) used habitat-selection theory based on the ideal free distribution to show that differences in habitat quality between a marine reserve and a fished area lead to increased catches, especially at high movement. This is important in situations in which fishing activity deteriorates the habitat. Gårdmark *et al.* (2006) showed that marine reserves do not increase yield when density-dependent growth inside the reserve limits yield outside the reserve, despite movement between the areas. Their model, however, did not account for the potential prevention of evolutionary changes towards smaller maturation size through the implementation of a marine reserve.

Our model describes a life cycle with three size classes, a mean life expectancy of about 7 years, and an age at maturation of about 3 years in the absence of fishing. Life expectancy and age at maturation decrease as harvesting increases resulting in the life history of a relatively short-lived species. Baskett *et al.* (2005) found similar patterns in the modelled effects of marine reserves on evolutionary outcomes for species with different life histories, while pointing out that evolutionary protection is lower for long-lived species exhibiting high movement and facing strong selection. The model by Dunlop *et al.* (2009a) confirmed the potential of marine reserves to mitigate the evolutionary impacts of fishing on several life-history traits, while pointing out that for the effective protection of fish stocks with spawning migrations, the reserve must be located in the stock's feeding grounds, rather than its spawning grounds. Together, the results presented here and in the two aforementioned studies cover a range of different life histories, indicating the robustness of the concordant findings.

An evolutionary switch from large-maturing to small-maturing phenotypes as reported above has also been found when an evolving population's size structure is described continuously, instead of in terms of discrete size classes (Taborsky *et al.*, 2003; Gårdmark and Dieckmann, 2006). Such a switch may occur repeatedly within a larger spectrum of size classes when fecundity and fishing mortality increase with size. As the largest adults disappear in the wake of such a switch, fisheries then may shift their targeted size range, exploiting the next-largest size class in an effort to maintain yield. This could result in an analogous evolutionary switch in that size class. As these evolutionary switches cascade through the relevant size classes, the stock is sent on an ecological and evolutionary death spiral, resulting in smaller sizes and lower abundances until collapse occurs. This conceivable scenario is the evolutionary counterpart of the well-known phenomenon of "fishing down the food web" (Pauly *et al.*, 1998) and may affect species as well as entire communities.

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References

Abesamis, R. A. and Russ, G. R. 2005. Density-dependent spill-over from a marine reserve: long-term evidence. Ecological Applications, 15: 1798-1812.

Anderson, C. N. K., Hsieh, C. H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M. and Sugihara, G. 2008. Why fishing magnifies fluctuations in fish abundance. Nature, 452: 835-839.

Apostolaki, P., Milner-Gulland, E. J., McAllister, M. K. and Kirkwood, G. P. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. Canadian Journal of Fisheries and Aquatic Sciences, 59: 405-415.

Ashley, M. V., Willson, M. F., Pergams, O. R. W., O'Dowd, D. J., Gende, S. M. and Brown, J. S. 2003. Evolutionarily enlightened management. Biological Conservation, 111: 115-123.

Aubone, A. 2004a. Loss of stability owing to a stable age structure skewed toward juveniles. Ecological Modelling, 175: 55-64.

Aubone, A. 2004b. Threshold for sustainable exploitation of an age-structured fishery stock. Ecological Modelling, 173: 95-107.

Barot, S., Heino, M., Morgan, M. J. and Dieckmann, U. 2005. Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? ICES Journal of Marine Science, 62: 56-64.

Barot, S., Heino, M., O'Brien, L. and Dieckmann, U. 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications, 14: 1257-1271.

Barrowman, N. J. and Myers, R. A. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences, 57: 665-676.

Baskett, M. L., Levin, S. A., Gaines, S. D. and Dushoff, J. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. Ecological Applications, 15: 882-901.

Baskett, M. L., Weitz, J. S. and Levin, S. A. 2007. The evolution of dispersal in reserve networks. American Naturalist, 170: 59-78.

Begg, G. A. and Marteinsdottir, G. 2003. Spatial partitioning of relative fishing mortality and spawning stock biomass of Icelandic cod. Fisheries Research, 59: 343-362.

Berkeley, S. A., Chapman, C. and Sogard, S. M. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology, 85: 1258-1264.

Berkeley, S. A., Hixon, M. A., Larson, R. J. and Love, M. S. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries, 29: 23-32.

Botsford, L. W., Brumbaugh, D. R., Grimes, C., Kellner, J. B., Largier, J., O'Farrell, M. R., Ralston, S., Soulanille, E. and Wespestad, V. 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Reviews in Fish Biology and Fisheries, 19: 69-95.

Botsford, L. W., Hastings, A. and Gaines, S. D. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters, 4: 144-150.

Botsford, L. W., Micheli, F. and Hastings, A. 2003. Principles for the design of marine reserves. Ecological Applications, 13: S25-S31.

Browman, H. I., Law, R. and Marshall, C. T. 2008. The role of fisheries-induced evolution – Letter. Science, 320: 47-50.

Cardinale, M. and Svedäng, H. 2008. Mismanagement of fisheries: policy or science? Fisheries Research, 93: 244-247.

Carr, J. P. and Kaufman, L. 2009. Estimating the importance of maternal age, size, and spawning experience to recruitment of Atlantic cod (*Gadus morhua*). Biological Conservation, 142: 477-487.

Chapman, M. R. and Kramer, D. L. 2000. Movements of fishes within and among fringing coral reefs in Barbados. Environmental Biology of Fishes, 57: 11-24.

Chateau, O. and Wantiez, L. 2009. Movement patterns of four coral reef fish species in a fragmented habitat in New Caledonia: implications for the design of marine protected area networks. ICES Journal of Marine Science, 66: 50-55.

Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J. A., Pérez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J. M., Dimech, M., Falcon, J. M., Guala, I., Milazzo, M., Sanchez-Meca, J., Somerfield, P. J., Stobart, B., Vandeperre, F., Valle, C. and Planes, S. 2008. Marine reserves: size and age do matter. Ecology Letters, 11: 481-489.

Codling, E. A. 2008. Individual-based movement behaviour in a simple marine reserve-fishery system: why predictive models should be handled with care. Hydrobiologia, 606: 55-61.

Conover, D. O., Arnott, S. A., Walsh, M. R. and Munch, S. B. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 730-737.

Conover, D. O. and Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. Science, 297: 94-96.

Conover, D. O., Munch, S. B. and Arnott, S. A. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. Proceedings of the Royal Society B - Biological Sciences, doi: 10.1098/rspb.2009.0003.

Costello, C. and Polasky, S. 2008. Optimal harvesting of stochastic spatial resources. Journal of Environmental Economics and Management, 56: 1-18.

Cushing, D. H. and Horwood, J. W. 1994. The growth and death of fish larvae. Journal of Plankton Research, 16: 291-300.

Dieckmann, U. 1997. Can adaptive dynamics invade? Trends in Ecology and Evolution, 12: 128-131.

Dieckmann, U. and Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Marine Ecology Progress Series, 335: 253-269.

Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of Mathematical Biology, 34: 579-612.

Diekmann, O. 2004. A beginner's guide to adaptive dynamics. *In* Mathematical Modelling of Population Dynamics, 63, pp. 47-86. Banach Center Publications, Warszawa.

Dinmore, T. A., Duplisea, D. E., Rackham, B. D., Maxwell, D. L. and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. ICES Journal of Marine Science, 60: 371-380.

Dunlop, E. S., Baskett, M. L., Heino, M. and Dieckmann, U. 2009a. Propensity of marine reserves to reduce the evolutionary impacts of fishing in a migratory species. Evolutionary Applications, in press.

Dunlop, E. S., Heino, M. and Dieckmann, U. 2009b. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications, in press.

Dunlop, E. S., Shuter, B. J. and Dieckmann, U. 2007. The demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model of the smallmouth bass. Transactions of the American Fisheries Society, 136: 749-765.

Enberg, K., Dunlop, E. S., Jørgensen, C., Heino, M. and Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications, in press.

Fox, C. W., Roff, D. A. and Fairbairn, D. J. (eds.) 2001. Evolutionary Ecology: Concepts and Case Studies. Oxford University Press, New York. 424 pp.

Frank, K. T., Shackell, N. L. and Simon, J. E. 2000. An evaluation of the Emerald/Western Bank juvenile haddock closed area. ICES Journal of Marine Science, 57: 1023-1034.

García-Charton, J. A., Pérez-Ruzafa, A., Marcos, C., Claudet, J., Badalamenti, F., Benedetti-Cecchi, L., Falcon, J. M., Milazzo, M., Schembri, P. J., Stobart, B., Vandeperre, F., Brito, A., Chemello, R., Dimech, M., Domenici, P., Guala, I., Le Diréach, L., Maggi, E. and Planes, S. 2008. Effectiveness of European Atlanto-Mediterranean MPAs: do they accomplish the expected effects on populations, communities and ecosystems? Journal for Nature Conservation, 16: 193-221.

Gårdmark, A. and Dieckmann, U. 2006. Disparate maturation adaptations to size-dependent mortality. Proceedings of the Royal Society B – Biological Sciences, 273: 2185-2192.

Gårdmark, A., Dieckmann, U. and Lundberg, P. 2003. Life-history evolution in harvested populations: the role of natural predation. Evolutionary Ecology Research, 5: 239-257.

Gårdmark, A., Jonzén, N. and Mangel, M. 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. Journal of Applied Ecology, 43: 61-69.

Gerber, L. R., Botsford, L. W., Hastings, A., Possingham, H. P., Gaines, S. D., Palumbi, S. R. and Andelman, S. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications, 13: S47-S64.

Gerber, L. R., Heppell, S. S., Ballantyne, F. and Sala, E. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. Canadian Journal of Fisheries and Aquatic Sciences, 62: 863-871.

Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A. and Parvinen, K. 2002. Invasion dynamics and attractor inheritance. Journal of Mathematical Biology, 44: 548-560.

Geritz, S. A. H., Kisdi, É., Meszéna, G. and Metz, J. A. J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology, 12: 35-57.

Geritz, S. A. H., Metz, J. A. J., Kisdi, É. and Meszéna, G. 1997. Dynamics of adaptation and evolutionary branching. Physical Review Letters, 78: 2024-2027.

Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., Polti, S., Cadiou, G., Valle, C., Lenfant, P., Bonhomme, P., Perez-Ruzafa, A., Sanchez-Lizaso, J. L., Garcia-Charton, J. A., Bernard, G., Stelzenmuller, V. and Planes, S. 2008. Spill-over from six western Mediterranean marine protected areas: evidence from artisanal fisheries. Marine Ecology Progress Series, 366: 159-174.

Greenstreet, S. P. R., Fraser, H. M. and Piet, G. J. 2009. Using MPAs to address regional-scale ecological objectives in the North Sea: modelling the effects of fishing effort displacement. ICES Journal of Marine Science, 66: 90-100.

Grift, R. E., Heino, M., Rijnsdorp, A. D., Kraak, S. B. M. and Dieckmann, U. 2007. Three-dimensional maturation reaction norms for North Sea plaice. Marine Ecology Progress Series, 334: 213-224.

Grift, R. E., Rijnsdorp, A. D., Barot, S., Heino, M. and Dieckmann, U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology Progress Series, 257: 247-257.

Guénette, S. and Pitcher, T. J. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. Fisheries Research, 39: 295-303.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications, 13: S117-S137.

Harmelin-Vivien, M., Le Diréach, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J. A., Ody, D., Pérez-Ruzafa, A., Reñones, O., Sanchez-Jerez, P. and Valle, C. 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spill-over? Biological Conservation, 141: 1829-1839.

Heino, M. and Dieckmann, U. 2008. Detecting fisheries-induced life-history evolution: an overview of the reaction-norm approach. Bulletin of Marine Science, 83: 69-93.

Heino, M., Dieckmann, U. and Godø, O. R. 2002a. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science, 59: 562-575.

Heino, M., Dieckmann, U. and Godø, O. R. 2002b. Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669-678.

Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science, 70: 639-656.

Heino, M. Dieckmann, U. and Godø, O. R. 2002c. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. ICES CM, 2002/Y: 14.

Heino, M., Metz, J. A. J. and Kaitala, V. 1998. The enigma of frequency-dependent selection. Trends in Ecology and Evolution, 13: 367-370.

Hiddink, J. G., Rijnsdorp, A. D. and Piet, G. 2008. Can bottom trawling disturbance increase food production for a commercial fish species? Canadian Journal of Fisheries and Aquatic Sciences, 65: 1393-1401.

Hilborn, R., Branch, T. A., Ernst, B., Magnussson, A., Minte-Vera, C. V., Scheuerell, M. D. and Valero, J. L. 2003. State of the world's fisheries. Annual Review of Environment and Resources, 28: 359-399.

Horwood, J. W., Nichols, J. H. and Milligan, S. 1998. Evaluation of closed areas for fish stock conservation. Journal of Applied Ecology, 35: 893-903.

Hutchings, J. A. and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology, 17: 294-313.

Hutchings, J. A. and Reynolds, J. D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. Bioscience, 54: 297-309.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjørndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629-638.

Jaworski, A., Solmundsson, J. and Ragnarsson, S. A. 2006. The effect of area closures on the demersal fish community off the east coast of Iceland. ICES Journal of Marine Science, 63: 897-911.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M. and Rijnsdorp, A. D. 2007. Managing evolving fish stocks. Science, 318: 1247-1248.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M. and Rijnsdorp, A. D. 2008. The role of fisheries-induced evolution – Response. Science, 320: 48-50.

Kaplan, D. M. 2009. Fish life histories and marine protected areas: an odd couple? Marine Ecology Progress Series, 377: 213-225.

Kelly, C. J., Codling, E. A. and Rogan, E. 2006. The Irish Sea cod recovery plan: some lessons learned. ICES Journal of Marine Science, 63: 600-610.

Kisdi, É. and Geritz, S. A. H. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. Evolution, 53: 993-1008.

Koons, D. N., Metcalf, C. J. E. and Tuljapurkar, S. 2008. Evolution of delayed reproduction in uncertain environments: a life-history perspective. American Naturalist, 172: 797-805.

Kot, M. 2001. Elements of Mathematical Ecology. University Press, Cambridge. 453 pp.

Kramer, D. L. and Chapman, M. R. 1999. Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes, 55: 65-79.

Kuparinen, A. and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology and Evolution, 22: 652-659.

Kuparinen, A. and Merilä, J. 2008. The role of fisheries-induced evolution - Letter. Science, 320: 47-48.

Lauck, T., Clark, C. W., Mangel, M. and Munro, G. R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications, 8: S72-S78.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659-668.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Marine Ecology Progress Series, 335: 271-277.

Law, R. and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology, 3: 343-359.

Le Quesne, W. J. F. and Codling, E. A. 2009. Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. ICES Journal of Marine Science, 66: 122-131.

Lundberg, P. and Jonzén, N. 1999. Spatial population dynamics and the design of marine reserves. Ecology Letters, 2: 129-134.

Mace, P. M. 2004. In defence of fisheries scientists, single-species models and other scapegoats: confronting the real problems. Marine Ecology Progress Series, 274: 285-291.

Madsen, N. 2007. Selectivity of fishing gears used in the Baltic Sea cod fishery. Reviews in Fish Biology and Fisheries, 17: 517-544.

Mangel, M. 2000. Irreducible uncertainties, sustainable fisheries and marine reserves. Evolutionary Ecology Research, 2: 547-557.

Marteinsdottir, G. and Steinarsson, A. 1998. Maternal influence on the size and viability of Icelandic cod (*Gadus morhua)* eggs and larvae. Journal of Fish Biology, 52: 1241-1258.

Meszéna, G., Czibula, I. and Geritz, S. A. H. 1997. Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. Journal of Biological Systems, 5: 265-284.

Meszéna, G., Kisdi, É., Dieckmann, U., Geritz, S. A. H. and Metz, J. A. J. 2001. Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. Selection 2, 193-210.

Metcalf, C. J. E. and Pavard, S. 2007. Why evolutionary biologists should be demographers. Trends In Ecology & Evolution, 22: 205-212.

Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A. and van Heerwaarden, J. S. 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. *In* Stochastic and Spatial Structures of Dynamical Systems, pp. 183-231. KNAW Verhandelingen, North Holland, Amsterdam.

Metz, J. A. J., Nisbet, R. M. and Geritz, S. A. H. 1992. How should we define fitness for general ecological scenarios? Trends in Ecology and Evolution, 7: 198-202.

Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. American Naturalist, 113: 531-550.

Miethe, T., Pitchford, J. and Dytham, C. 2009. An individual-based model for reviewing marine reserves in the light of fisheries-induced evolution in mobility and size at maturation. Journal of Northwest Atlantic Fisheries Science, 41: 151-162.

Mollet, F. M., Kraak, S. B. M. and Rijnsdorp, A. D. 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. Marine Ecology Progress Series, 351: 189-199.

Myers, R. A. and Barrowman, N. J. 1996. Is fish recruitment related to spawner abundance? Fishery Bulletin, 94: 707-724.

Myers, R. A. and Cadigan, N. G. 1993. Density-dependent juvenile mortality in marine demersal fish. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1576-1590.

Needle, C. L. 2002. Recruitment models: diagnosis and prognosis. Reviews in Fish Biology and Fisheries, 11: 95-111.

Okamoto, K. W., Whitlock, R., Magnan, P. and Dieckmann, U. 2009. Mitigating fisheries-induced evolution in lacustrine brook charr (*Salvelinus fontinalis*) in southern Quebec, Canada. Evolutionary Applications, in press.

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B. and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature, 428: 932-935.

Olsen, E. M., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J. and Dieckmann, U. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 811-823.

Ottersen, G., Hjermann, D. O. and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fisheries Oceanography, 15: 230-243.

Pastoors, M. A., Rijnsdorp, A. D. and Van Beek, F. A. 2000. Effects of a partially closed area in the North Sea ("plaice box") on stock development of plaice. ICES Journal of Marine Science, 57: 1014-1022.

Pauly, D. 2008. Global fisheries: a brief review. Journal of Biological Research-Thessaloniki, 9: 3-9.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres, F. 1998. Fishing down marine food webs. Science, 279: 860-863.

Pauly, D., Watson, R. and Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society B – Biological Sciences, 360: 5-12.

Pelletier, D. and Mahévas, S. 2005. Spatially explicit fisheries simulation models for policy evaluation. Fish and Fisheries, 6: 307-349.

Pitchford, J. W., Codling, E. A. and Psarra, D. 2007. Uncertainty and sustainability in fisheries and the benefit of marine protected areas. Ecological Modelling, 207: 286-292.

Ratner, S. and Lande, R. 2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. Ecology, 82: 3093-3104.

Reznick, D. A., Bryga, H. and Endler, J. A. 1990. Experimentally induced life-history evolution in a natural-population. Nature, 346: 357-359.

Rijnsdorp, A. D. 1993. Fisheries as a large-scale experiment on life-history evolution – disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea Plaice, *Pleuronectes platessa L.* Oecologia, 96: 391-401.

Roberts, C. M. 1997. Ecological advice for the global fisheries crisis. Trends in Ecology and Evolution, 12: 35-38.

Roberts, C. M. 2000. Why does fisheries management so often fail? *In* Science and Environmental Decision-making, pp. 170-192. Addison Wesley Longman, Harlow.

Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P. and Goodridge, R. 2001. Effects of marine reserves on adjacent fisheries. Science, 294: 1920-1923.

Russ, G. R., Alcala, A. C. and Maypa, A. P. 2003. Spill-over from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. Marine Ecology Progress Series, 264: 15-20.

Russ, G. R., Alcala, A. C., Maypa, A. P., Calumpong, H. P. and White, A. T. 2004. Marine reserve benefits local fisheries. Ecological Applications, 14: 597-606.

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., Polunin, N. V. C., Russ, G. R., Sadovy, Y. J. and Steneck, R. S. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology & Evolution, 20: 74-80.

Swain, D. P., Sinclair, A. F. and Hanson, J. M. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B – Biological Sciences, 274: 1015-1022.

Taborsky, B., Dieckmann, U. and Heino, M. 2003. Unexpected discontinuities in life-history evolution under size-dependent mortality. Proceedings of the Royal Society of London Series B – Biological Sciences, 270: 713-721.

Topping, D. T., Lowe, C. G. and Caselle, J. E. 2005. Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. Marine Biology, 147: 301-311.

Trexler, J. C. and Travis, J. 2000. Can marine protected areas restore and conserve stock attributes of reef fishes? Bulletin of Marine Science, 66: 853-873.

Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience, 45: 759-771.

Vallin, L. and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua* – implications for stock structure effects on recruitment. Fisheries Research, 49: 21-37.

Walsh, M. R., Munch, S. B., Chiba, S. and Conover, D. O. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters, 9: 142-148.

West, C. D., Dytham, C., Righton, D. and Pitchford, J. W. 2009. Preventing overexploitation of migratory fish stocks: the efficacy of marine protected areas in a stochastic environment. ICES Journal of Marine Science, doi:10.1093/icesjms/fsp1159.

Williamson, D. H., Russ, G. R. and Ayling, A. M. 2004. No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. Environmental Conservation, 31: 149-159.

Willis, T. J. and Millar, R. B. 2005. Using marine reserves to estimate fishing mortality. Ecology Letters, 8: 47-52.

Appendices

Appendix A: Harvesting the intermediate size classes

The evolutionary switch from large to small maturation size occurs when Inequality (7) becomes fulfilled. Rearranging that inequality and defining a function F leads to an equivalent condition for the evolution of small maturation size,

$$F = \frac{f_2}{1 - s_2(1 - h_{2,3})} - \frac{f_4 s_3 (1 - h_{2,3})}{1 - s_4(1 - h_4)} > 0, \qquad \text{(A1)}$$

with the switch from large to small maturation size happening at $F = 0$. To predict the evolutionary effect of increasing $h_{2,3}$, we determine the slope of F with respect to $h_{2,3}$,

$$\frac{\partial F}{\partial h_{2,3}} = -\frac{f_2 s_2}{(1 - s_2(1 - h_{2,3}))^2} + \frac{f_4 s_3}{1 - s_4(1 - h_4)}. \qquad \text{(A2)}$$

Using the fact that $F = 0$ at the evolutionary switch point allows this expression to be simplified (at the switch point) to

$$\frac{\partial F}{\partial h_{2,3}} = \frac{f_4 s_3 (1 - 2 s_2 (1 - h_{2,3}))}{(1 - s_4(1 - h_4))(1 - s_2(1 - h_{2,3}))}. \qquad \text{(A3)}$$

Since both factors in the right-hand side's denominator are strictly positive, $\partial F / \partial h_{2,3}$ is positive if and only if

$$s_2(1 - h_{2,3}) < \frac{1}{2}. \qquad \text{(A4)}$$

Under this condition, increasing $h_{2,3}$ close to the switch point causes F to increase and therefore inequality (A1) to be fulfilled. Thus, when Inequality (A4) is satisfied, harvesting more strongly on the intermediate size classes favors maturation at small size. Conversely, when Inequality (A4) is not satisfied, increasing $h_{2,3}$ favors maturation at large size.

Harvesting only mature intermediate-sized fish ($h_2 > 0$ with $h_3 = 0$) always favors maturation at large size. Such a harvest regime can occur if immature fish stay in feeding grounds and move to strongly fished spawning grounds only when they reach maturity, as observed, e.g., for migratory cod (Begg and Marteinsdottir, 2003).

Appendix B: Extensions of the single-population model

In Equations (3a) to (3d), it is assumed that individuals maturing at large size grow directly from class 3 to class 4. Instead, they could be allowed to remain more than one year in class 3 by introducing an annual probability p for an individual to remain in class 3 before entering class 4. Furthermore, many fish exhibit indeterminate growth, so individuals maturing at small size could be allowed to grow to large size by introducing an annual probability q for an individual to remain in class 2 before entering class 4. These parameters are assumed to be set at $p = 0$ and $q = 1$ in the models we describe in Section 2, but these restrictions can be relaxed.

Analysis of this more general model is analogous to that leading to Inequality (7), and reveals that for $p > 0$ and $q < 1$ evolution favors maturation at small size when

$$G = \frac{1}{1-qs_2(1-h_{2,3})}\left(f_2 s_1 + \frac{f_4 s_1 s_2 (1-h_{2,3})(1-q)}{1-s_4(1-h_4)}\right) - \frac{f_4 s_1 s_3 (1-h_{2,3})(1-p)}{(1-s_4(1-h_4))(1-ps_3(1-h_{2,3}))} > 0, \tag{A5}$$

with the switch from large to small maturation size happening at $G = 0$. As in Appendix A, we can predict the evolutionary effects of allowing $p > 0$ and $q < 1$ by examining the corresponding partial derivatives of G close to the evolutionary switch point. Differentiating G with respect to p gives

$$\frac{\partial G}{\partial p} = \frac{f_4 s_1 s_3 (1-h_{2,3})(1-s_3(1-h_{2,3}))}{(1-s_4(1-h_4))(1-ps_3(1-h_{2,3}))^2} > 0. \tag{A6}$$

Since this partial derivative is strictly positive, the arguments in Appendix A enable us to conclude that allowing $p > 0$ makes evolution at small maturation size more likely. The evolutionary conclusions of the simpler model based on Equations (3a) to (3d) are therefore conservative in this respect.

Differentiating G with respect to q gives

$$\frac{\partial G}{\partial q} = -(1-h_{2,3}) s_1 s_2 \frac{f_4(1-s_2(1-h_{2,3})) - f_2(1-s_4(1-h_4))}{(1-s_4(1-h_4))(1-qs_2(1-h_{2,3}))^2} < 0. \tag{A7}$$

Since $(1-h_{2,3})s_1 s_2$ and both factors in the right-hand side's denominator are strictly positive, $\partial G/\partial q$ is negative if and only if

$$\frac{f_2}{1-s_2(1-h_{2,3})} < \frac{f_4}{1-s_4(1-h_4)}. \tag{A8}$$

Using the fact that $F = 0$ at the evolutionary switch point (Appendix A, Equation A1) allows this inequality to be simplified (at the switch point) to

$$\frac{f_4 s_3(1-h_{2,3})}{1-s_4(1-h_4)} < \frac{f_4}{1-s_4(1-h_4)} \tag{A9}$$

and hence to $s_3(1-h_{2,3})<1$, which is true. We can thus conclude that decreasing q from $q=1$ increases G, so that allowing $q<1$ favors (at least close to the switch point) maturation at small size. Again the evolutionary conclusions based on Equations (3a) to (3d) are conservative in this respect.

In summary, increasing p (allowing individuals to spend more than one year in class 3) and decreasing q (allowing individuals to move from class 2 to class 4) both cause the evolutionary switch from large to small maturation size to occur at lower harvest proportions. This implies that the simpler model we analyze in the main text does not overestimate fisheries-induced maturation evolution. Numerical results show that the effects of p and q in the marine-reserve model are analogous to their effects in the single-population model.

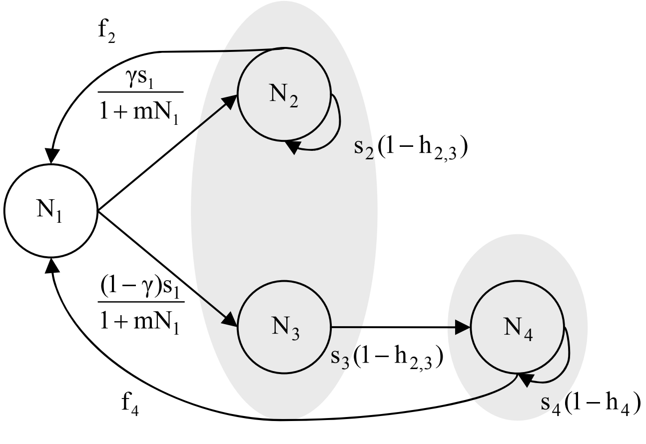

Figure 1

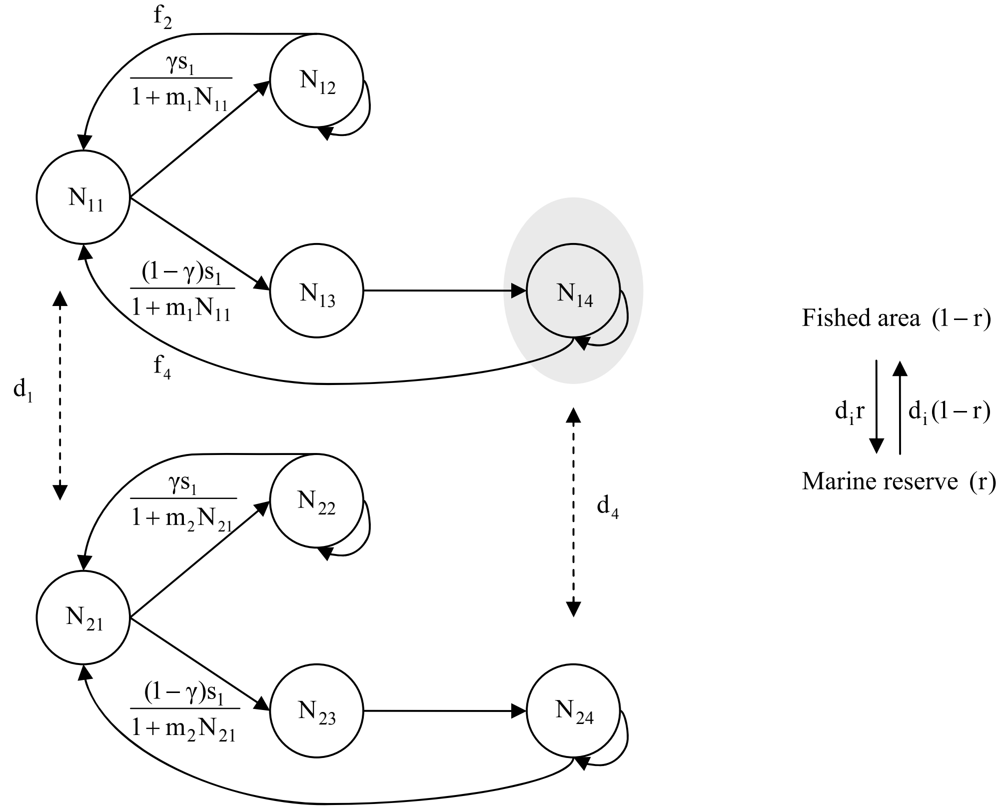

Figure 2

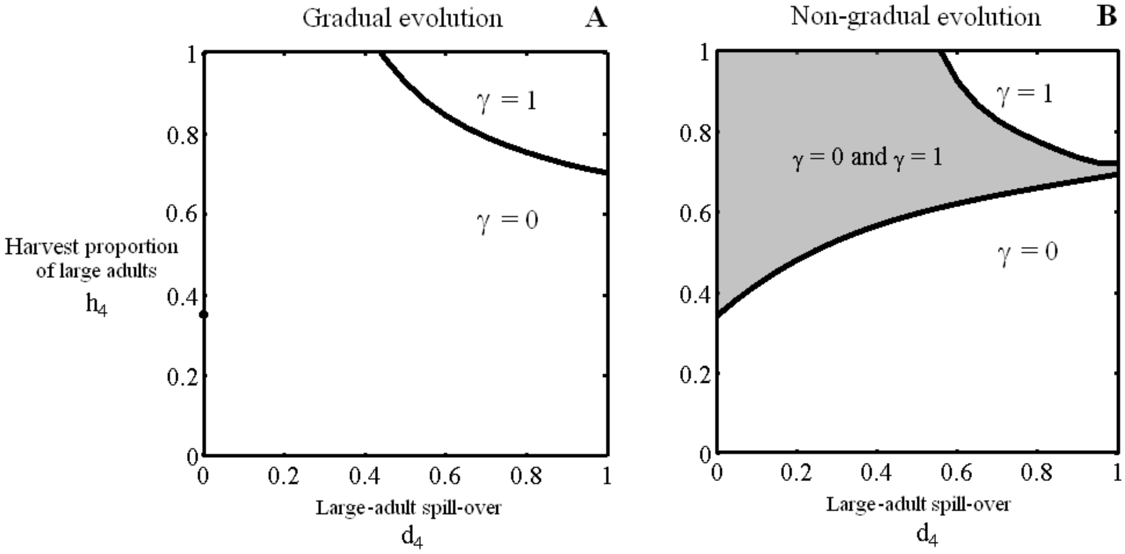

Figure 3

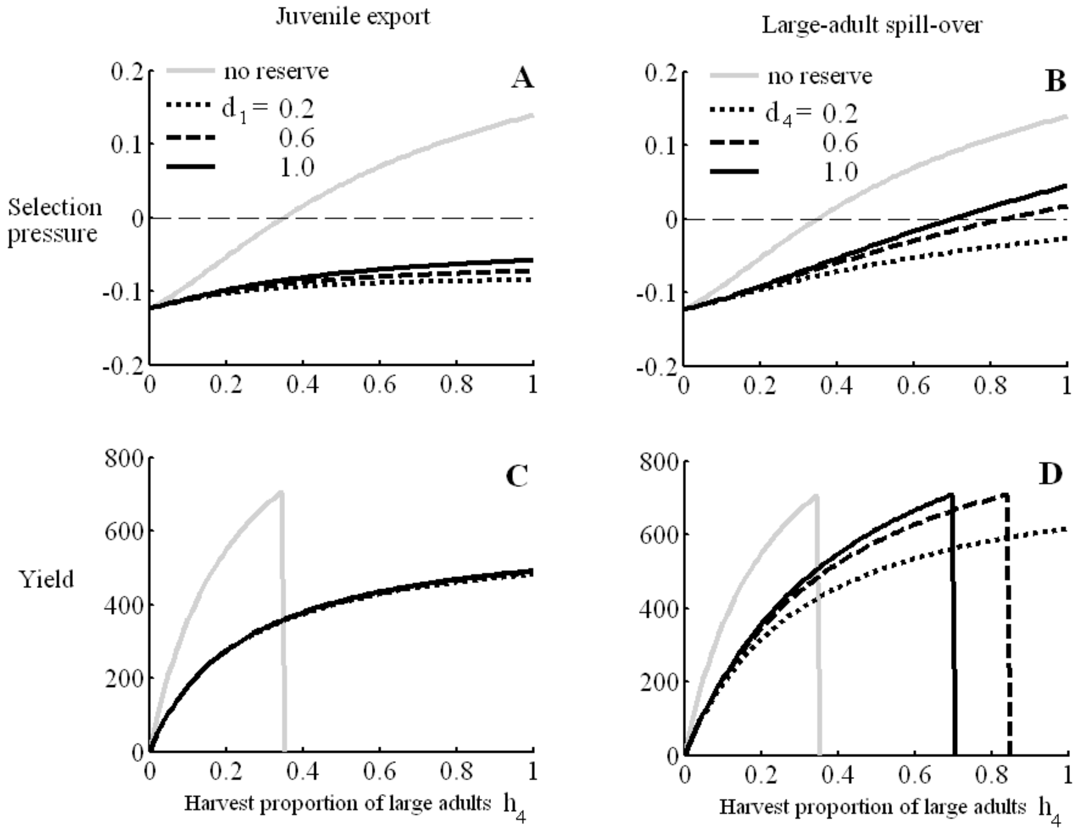

Figure 4

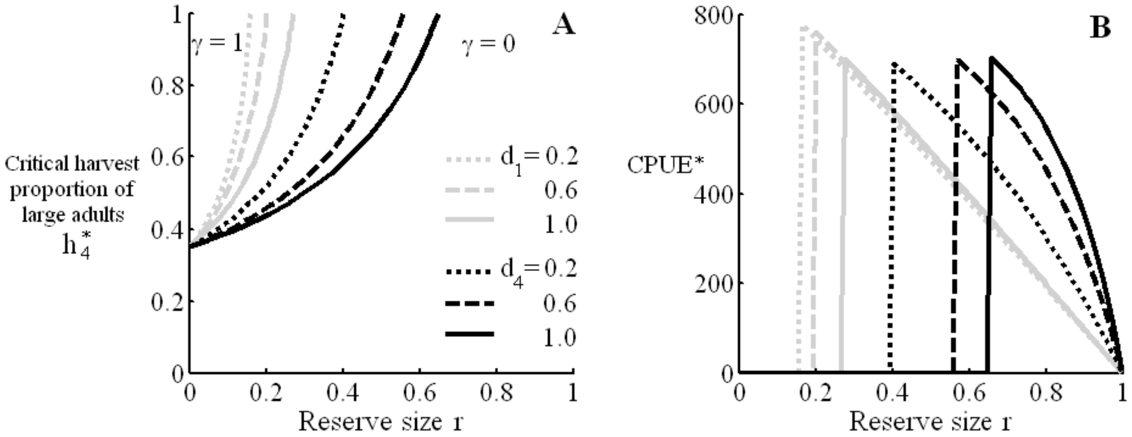

Figure 5

Captions

Table 1. Parameters, their description, and their default values used for the numerical illustrations.

Figure 1. Schematic illustration of single-population model. Fish are born into class 1 (small juveniles) where they experience density-dependent survival. They then grow to class 2 (small adults) with probability γ, or to class 3 (large juveniles) with probability $(1-\gamma)$. Fish maturing at small size start reproduction in class 4, while fish maturing at large size do not start reproduction until they reach class 4 (large adults). The evolving trait γ thus describes the probability of fish to mature at small size. Due to size-selective fishing, harvest proportions $h_{2,3}$ and h_4 can differ between intermediate-sized and large-sized fish, respectively. The harvested classes are indicated by shading.

Figure 2. Schematic illustration of marine-reserve model. Populations inhabit two areas; one is harvested (above) and while the other is protected by a marine reserve (below). Only large adults in the harvested area are subject to fishing in accordance with the harvest proportion h_4. Movement between the two areas can occur in class 1 (juvenile export with movement probability d_1) or in class 4 (large-adult spill-over with movement probability d_4). The per capita movement probabilities are scaled with the relative size of the destination area, r for the marine reserve and $(1-r)$ for the harvested area. Other details as described in the caption of Figure 1.

Figure 3. Evolutionary outcomes of maturation evolution in the marine-reserve model in dependence on the movement probability d_4 of large adults and on the harvest proportion h_4 of large adults. **A)** Gradual evolution through successive invasion of variant phenotypes that slightly differ from resident phenotypes. When movement probabilities or harvest proportions are low, the population evolves towards maturation at large size ($\gamma = 0$). When movement probabilities and harvest proportions are high, the population evolves towards maturation at small size ($\gamma = 1$). The continuous line depicts the bifurcation points at which the switch between the two evolutionary outcomes occurs. **B)** Non-gradual evolution through the successive invasion of variant phenotypes that arbitrarily differ from resident phenotypes. The shaded area indicates the

conditions under which the two extreme maturation strategies $\gamma = 0$ and $\gamma = 1$ can coexist. Outside the shaded area, the evolutionary outcomes are monomorphic ($\gamma = 0$ below or $\gamma = 1$ above the shaded area).

Figure 4. Selection pressure at $\gamma = 0.5$ and yield at evolutionary outcome in dependence on movement probabilities d_1 or d_4 and on the harvest proportion h_4 of large adults. $d_1 > 0$ describes juvenile export (left column), while $d_4 > 0$ describes large-adult spill-over (right column). For comparison, the results in absence of a marine reserve are shown in grey. **A), B)** Selection pressure at $\gamma = 0.5$ as given in Equation (4). When the selection pressure is negative, selection favors the decrease of γ towards 0, resulting in maturation at large size. When the selection pressure is positive, selection favors the increase of γ towards 1, resulting in maturation at small size. The critical harvest rate at which the sign of the selection pressure changes is the same for different values of γ . **C), D)** Yield at the evolutionary outcome $\gamma = 0$ (negative selection pressure) or $\gamma = 1$ (positive selection pressure).

Figure 5. Critical harvest proportion and catch per unit effort in dependence on movement probabilities d_1 or d_4 and on the reserve size r . $d_1 > 0$ describes juvenile export (grey curves), while $d_4 > 0$ describes large-adult spill-over (black curves). **A)** Critical harvest proportion h_4^* at which the switch from large to small maturation size occurs. **B)** Catch per unit effort $CPUE^*$ right above the critical harvest proportion h_4^*. Catches of large adults collapse to 0 whenever harvesting induces an evolutionary switch to small maturation size.

Table 1.

Parameter	Description	Default value
f_2	Per capita annual fecundity at intermediate size	5
f_4	Per capita annual fecundity at large size	15
s_1, s_2, s_3, s_4	Per capita annual survival probabilities in classes 1 to 4	0.8
$h_{2,3}$	Per capita annual harvest proportion of intermediate-sized	0

	individuals	
h_4	Per capita annual harvest proportion of large adults	[0, 1]
d_1, d_4	Per capita annual movement probability in class 1 or 4	[0, 1]
r	Fraction of total area protected by a marine reserve	[0, 1]
m	Factor to scale strength of density-dependent juvenile survival	0.001
m_1	Factor to scale strength of density-dependent juvenile survival in fished area	$\frac{m}{1-r}$
m_2	Factor to scale strength of density-dependent juvenile survival in marine reserve	$\frac{m}{r}$