

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. Although marine reserves have been proposed as a tool for fisheries management, their evolutionary implications have as yet attracted little scrutiny. A simple model is used to investigate whether marine reserves can be expected to mitigate the evolutionary impacts of fishing on maturation size. The adaptive dynamics of size at maturation are analysed based on a stage-structured population model including size-selective fishing and marine reserves with different retention rates. As has been shown before, imposing greater fishing mortality on the largest individuals promotes an evolutionary change towards smaller maturation size. In the model, protecting part of a fish stock using a marine reserve can prevent such fisheries-induced evolution, and this protection critically depends on the type and extent of movement between the reserve and the fished area. Specifically, although 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. In contrast, when there is exchange between protected and fished areas 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. Differences in the movement behaviour of successive life stages need to be considered for marine reserves, to help make fisheries more sustainable evolutionarily.

Keywords: connectivity, fitness, life-history evolution, metapopulation, size-structured model, spillover.

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Introduction

Commercial fisheries have caused declines in fish stocks and catches around the world (Hilborn *et al.*, 2003; Pauly *et al.*, 2005; Pauly, 2008). Besides reducing abundance, fishing truncates the age and size structure of populations (Jackson *et al.*, 2001; Berkeley *et al.*, 2004b; Ottersen *et al.*, 2006). The removal of old, large adults decreases the reproductive potential of fish stocks and hence their ability to withstand and recover from overexploitation (Begg and Marteinsdottir, 2003; Aubone, 2004a; Law, 2007). In particular, large females contribute disproportionately to recruitment, owing to their production of more 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 contributes 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 (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, 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, 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 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 also increases. Although conclusive genetic evidence for fisheries-induced evolutionary changes is lacking, studies support considerations of evolutionary effects (Jørgensen *et al.*, 2007, 2008; Kuparinen and Merilä, 2007, 2008; Browman *et al.*, 2008; Hutchings and Fraser, 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, and restrictions on landing sizes, gears, and number of vessels. Such 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). Prohibiting fishing in marine reserves may help to rebuild fish stocks and their age structure by allowing individuals to survive longer and to 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 the 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 have 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 spillover 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, and the 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 are more efficient for sedentary stocks with dispersing larvae. The effects of marine reserves have been analysed 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 especially useful for managing late-maturing, 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 genetic 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 of Baskett *et al.* (2005) and Dunlop *et al.* (2009a), genotype and phenotype dynamics were coupled, resulting in complex models that are analytically intractable.

Here, we explore the evolutionary implications of marine reserves using relatively simple deterministic population models with a small number of parameters, combining the simple difference-equation model of an age-structured harvested population studied by Gårdmark *et al.* (2003) with a metapopulation model applied by Pitchford *et al.* (2007). The 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 reducing detail, we develop a comprehensible model that facilitates the analysis, and 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 spillover, to elucidate the expected efficacy of marine reserves of different size in terms of ensuring evolutionary protection and providing yield for adjacent fisheries.

Model description

Single-population model

Gårdmark *et al.* (2003) analysed 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)–(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 1-year juveniles of class 1 can either enter 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 fish of intermediate size 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.*,

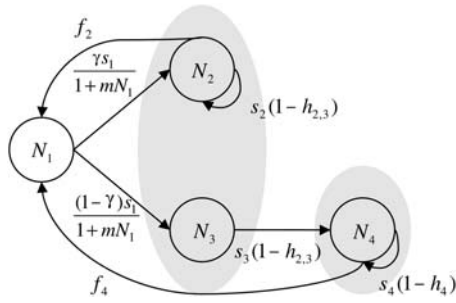


Figure 1. Schematic illustration of a single-population model. Fish are born into class 1 (small juveniles), where they experience density-dependent survival. They then grow to class 2 (small adults) with probability γ , or to class 3 (large juveniles) with probability $(1 - \gamma)$. Fish maturing at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

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

$$N_1(t + 1) = f_2 N_2(t) + f_4 N_4(t), \tag{1a}$$

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

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

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

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

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

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

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

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

Provided $0 \leq N_1^* < \infty$, 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 Equation (1) has an absolute value that is < 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 $\lambda_j = 1$.

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, 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 spillover 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:

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

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

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

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

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

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 1–4	0.8
$h_{2,3}$	Per capita annual harvest proportion of individuals of intermediate size	0
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 class 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 the fished area	$m / (1 - r)$
m_2	Factor to scale strength of density-dependent juvenile survival in a marine reserve	m / r

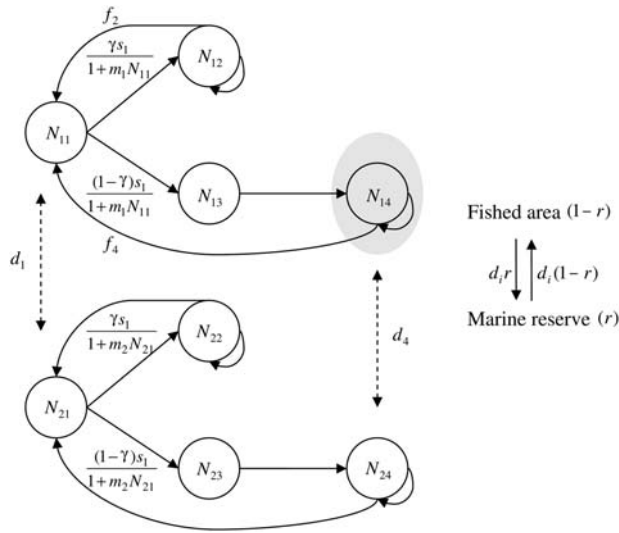


Figure 2. A schematic illustration of the marine-reserve model. Populations inhabit two areas: one is harvested (above) and the other is protected by a marine reserve (below). Only large adults in the harvested area are subject to fishing in accordance with the harvest proportion h_4 . Movement between the two areas can occur in class 1 (juvenile export with movement probability d_1) or 4 (spillover of large adults 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 are described in the caption of Figure 1.

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 focus on the evolutionary effects of harvesting large fish. The stage-dependent fecundities and survival probabilities for each size class are equal in both areas, whereas 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.

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, 1996; Dieckmann and Law, 1996; Dieckmann, 1997; Geritz *et al.*, 1997, 1998; Meszén *et al.*, 2001; Dieckmann, 2004) to determine the outcomes of evolution in γ , and hence in size at maturation. This approach assumes a separation of time-scales 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 therefore be inferred from assessing the eventual fate of a rare variant γ' trying to invade an environment determined by the resident population with phenotype γ . The fitness $w(\gamma', \gamma)$ of the

variant, and hence 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

$$\frac{dw(\gamma)}{d\gamma} \Big|_{\gamma'=\gamma} = \lim_{\gamma' \rightarrow \gamma} \frac{w(\gamma', \gamma) - w(\gamma, \gamma)}{\gamma' - \gamma} = \lim_{\gamma' \rightarrow \gamma} \frac{|\lambda(\gamma', \gamma)| - 1}{\gamma' - \gamma}. \quad (4)$$

Results

Single-population model

To establish a baseline for an evolutionary analysis of the marine-reserve model, we start by summarizing salient results for the single-population model. In that 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 $L(\gamma', \gamma)$:

$$L(\gamma', \gamma) = \begin{bmatrix} 0 & f_2 & 0 & f_4 \\ \frac{\gamma' s_1}{1+m_1 N_1^*(\gamma)} & s_2(1-h_{2,3}) & 0 & 0 \\ \frac{(1-\gamma') s_1}{1+m_1 N_1^*(\gamma)} & 0 & 0 & 0 \\ 0 & 0 & s_3(1-h_{2,3}) & s_4(1-h_4) \end{bmatrix}, \quad (5)$$

$$\lambda(\gamma', \gamma) = \frac{1}{1+m_1 N_1^*(\gamma)} \left[\frac{f_2 s_1}{1-s_2(1-h_{2,3})} \gamma' + \frac{f_4 s_1 s_3(1-h_{2,3})}{1-s_4(1-h_4)} (1-\gamma') \right]. \quad (6)$$

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 that condition, the variant population on average grows in density and can eventually replace the previous resident population (Geritz *et al.*, 2002).

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:

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

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

We can interpret the left and right side of this inequality, respectively, as the lifetime reproductive success resulting from maturation at small ($\gamma = 1$) and large sizes ($\gamma = 0$). As the right side decreases as h_4 increases, heavier 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 fish of intermediate size alone

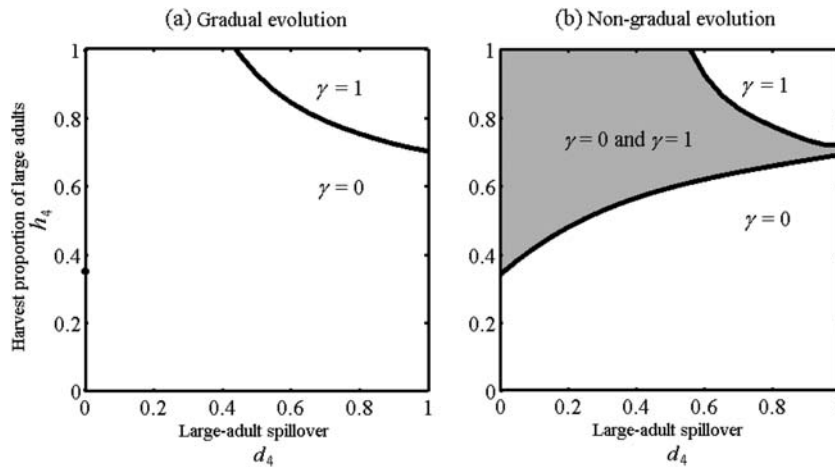


Figure 3. The evolutionary outcomes of maturation evolution in the marine-reserve model depend on the movement probability d_4 of large adults and on the harvest proportion h_4 of large adults. (a) Gradual evolution through successive invasion of variant phenotypes that slightly differ from resident ones. When movement probabilities or harvest proportions are low, the population evolves towards maturation at large size ($\gamma = 0$), but when they are high, the population evolves towards maturation at small size ($\gamma = 1$). The line depicts the bifurcation points at which there is a switch between the two evolutionary outcomes. (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).

may favour maturation at large or small size, as detailed in Appendix A.

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

Marine-reserve model: spillover of large adults

The effect of marine reserves on the evolution of size at maturation was analysed 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 stable dimorphism. The analysis is started by focusing on the effects of large-adult spillover, 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 they 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 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 and depends 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 of the strategies $\gamma = 0$ and $\gamma = 1$. Increasing the spillover of large adults diminishes the range of harvest proportions h_4 over which the two extreme maturation strategies can coexist.

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 there is movement between the protected and the fished areas through either juvenile export (Figure 4a) or spillover of large adults (Figure 4b). The selection pressure is positive whenever the fitness of a variant phenotype with a greater probability of maturing at small size exceeds that of the resident phenotype [Equation (4)]. For comparison, the selection pressure that applies in the absence of a marine reserve is also shown (the grey line).

In the numerical example, a marine reserve with juvenile export alone 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 spillover of large adults 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 on large adults, which reduces the selection pressures towards small maturation size, so it 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 understand these results as follows. Juvenile fish in class 1 have only 1 year during which they can move through juvenile export, whereas large-maturing adults can move through the spillover of large adults during the several years they remain alive in class 4. Therefore, over the years, the spillover of large adults

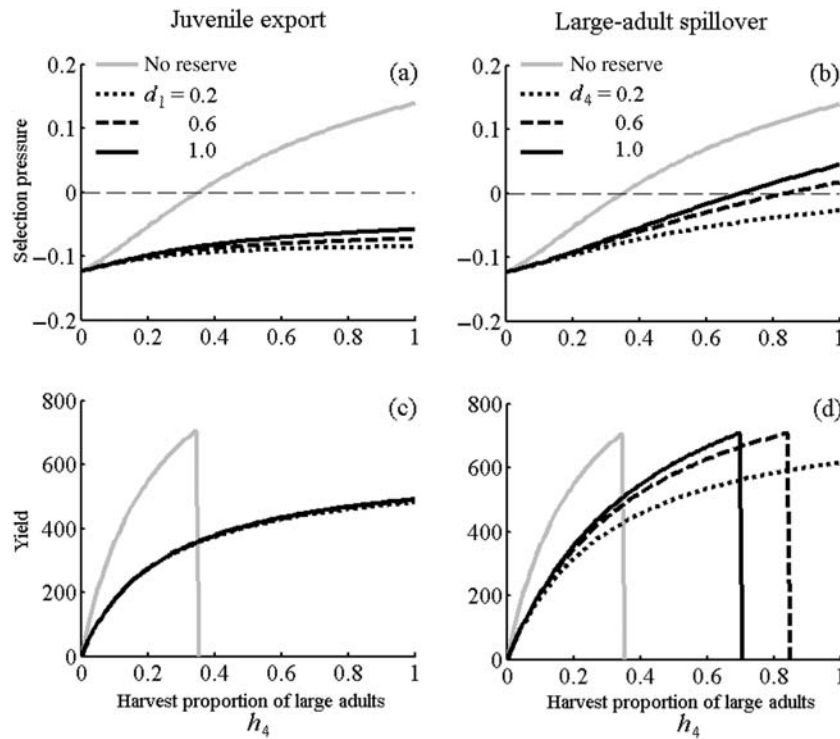


Figure 4. Selection pressure at $\gamma = 0.5$ and yield at evolutionary outcomes depending on movement probabilities d_1 or d_4 and on the harvest proportion h_4 of large adults. $d_1 > 0$ describes juvenile export (a and c), whereas $d_4 > 0$ describes the spillover of large adults (b and d). For comparison, the results in the absence of a marine reserve are shown in grey. (a and b) Selection pressure at $\gamma = 0.5$ as given in Equation (4). When the selection pressure is negative, selection favours the decrease of γ towards zero, resulting in maturation at large size. When the selection pressure is positive, selection favours 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 and d) Yield at the evolutionary outcome $\gamma = 0$ (negative selection pressure) or $\gamma = 1$ (positive selection pressure).

causes a greater proportion of each cohort to move outside the marine reserve. This lesser retention in the marine reserve results in greater exposure of the fish to size-selective fishing and hence explains why marine reserves with juvenile export are more effective in mitigating fisheries-induced maturation evolution than marine reserves with spillover of large adults. Movement of large adults takes place later in life, after the annual harvest of large adults of class 4, and as such should exert a smaller selection pressure than juvenile export if all individuals die after spending 1 year in class 4. However, survival in class 4 for >1 year increases the probability of individuals being subjected to size-selective fishing mortality, which intensifies the selection pressure.

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 depending on different movement scenarios, the corresponding effects on yield are illustrated in Figures 4c and 4d. As expected, catches of large adults collapse whenever the evolutionary switch to small maturation size is induced. Juvenile export alone prevents this switch, and catches of large adults are ensured at all harvest proportions (Figure 4c). When movement is through the spillover of large adults, the yield of large adults is ensured at low movement probabilities, by preventing the evolutionary switch, whereas at greater movement probabilities the catch collapses (Figure 4d). With decreasing spillover of large adults, the implementation of a marine reserve increases the harvest proportion at which yield

is maximized. Compared with a fully fished stock, marine reserves therefore 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 catches 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 assumed 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 equivalent with and without the marine reserve. However, when the spillover of large adults is smaller than this maximum (assuming realistic values), with reserve implementation the evolutionary switch is at higher harvest proportions. Less spillover of large adults then reduces the yield, despite the assumption of redistributed fishing effort.

Marine-reserve model: reserve size

In the numerical illustrations shown so far, fished and protected areas are of equal size. 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

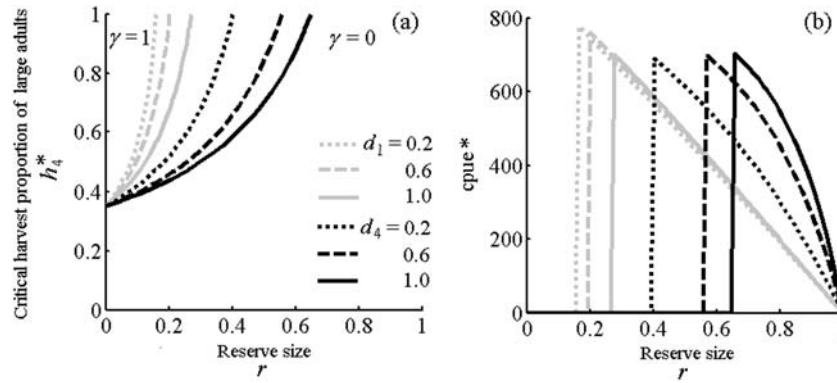


Figure 5. Critical harvest proportion and cpue depends on movement probabilities d_1 or d_4 and on the reserve size r . $d \geq 0$ describes juvenile export (grey curves), and $d_4 > 0$ describes the spillover of large adults (black curves). (a) The critical harvest proportion h_4^* at which there is a switch from large to small maturation size. (b) Catch per unit effort cpue* right above the critical harvest proportion h_4^* . The catches of large adults collapse to zero whenever harvesting induces an evolutionary switch to small maturation size.

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 spillover of large adults requires a larger reserve than a population with juvenile export. If movement is 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 spillover of large adults or with greater juvenile export. Such other movement scenarios necessitate the creation of reserves of intermediate size, here between 20 and 40% of the total area.

To analyse the effect of reserve size on yields, we investigated catch per unit effort cpue = Y/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, $\text{cpue}^* = \lim_{h_4 \rightarrow h_4^*} (Y/h_4)$, with $h_4^* = 1$ when $h_4 = 1$ 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 $\text{cpue}^* = 0$ for $h_4^* < 1$. On the other hand, if no evolutionary switch is induced, $\text{cpue}^* > 0$ for $h_4^* = 1$. As the cpue rises above cpue^* for $h_4 < h_4^*$, cpue^* describes a worst-case scenario. Figure 5b illustrates, for different movement scenarios, that cpue^* peaks once the critical reserve size that prevents evolution to smaller maturation size is reached. It also shows that implementing a reserve larger than the critical size will be less profitable, by reducing cpue^* relative to its maximum.

Discussion

We have examined the effects of marine reserves on maturation evolution by analysing selection pressures on the probability that individuals mature at small size in stage-structured populations exposed to size-selective fishing. An evolutionary switch from large to small maturation size is induced by intensive fishing on large adults but can be prevented by marine reserves of sufficient size. We also demonstrated how the critical harvest proportion at which the shift occurs depends on alternative movement scenarios, including spillover of large adults and juvenile export.

Although marine reserves with juvenile export better protect against fisheries-induced maturation evolution, marine reserves with spillover of large adults can better sustain the yields of large adults. To maximize cpue, intermediate harvest proportions need to be combined with marine reserves exceeding a critical size.

Single-population model

The single-population model described results in density-dependent but frequency-independent selection, so 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 agrees 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 to early maturation.

Our results show that the propensity for such an evolutionary switch depends on relative, rather than 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. If, for example, the gain in fecundity with size is only small, or if the survival of small individuals is disproportionately high, an evolutionary switch to small maturation size may happen.

In the numerical example using the default parameter values listed in Table 1, the evolutionary switch from large to small maturation size was at a harvest proportion of $h_4 = 0.35$. Note 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, the default parameter values used for illustrating the results were chosen to be plausible. For example, the annual probability of natural survival was chosen as 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).

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, because 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 reducing fishing mortalities reliably. Although 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 the fished areas is low. Limited movement and strong differences in selective pressures operating in each area, in conjunction with suitable frequency-dependence, promote the stability of such a dimorphism (Meszena *et al.*, 1997; Heino *et al.*, 1998; Kisdi and Geritz, 1999; Fox *et al.*, 2001). This potential for dimorphism has important practical consequences, because it allows 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 the protected and the fished areas increase catches outside the reserve and may strengthen the evolutionary pressure towards small maturation size (Figure 4). In addition, it is clear that the evolutionary effects of a marine reserve depend on the stage-specific movement of individuals. Compared with juvenile export, the spillover of large adults from the marine reserve to the fished area causes greater selection pressure on maturation size and therefore reduces the reserve-based protection from evolution to small maturation size. Juvenile export, in contrast, keeps selection pressure lower, but it does not lead to an increased yield of large adults outside the reserve because juvenile movement becomes more frequent (Figure 4). This underscores the fact that managing fisheries-induced maturation evolution through marine reserves requires not only to account 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 life-history stages of the species concerned.

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 the 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 (Guenette and Pitcher, 1999; Baskett *et al.*, 2005). At maximum movement probability, the evolutionary switch from large to small maturation size is then at exactly $h_4 = 0.7$, which is also twice the harvest proportion in the fished area without redistributing fishing effort. Recognizing that the harvest proportion in the total area is half 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 spillover of large adults (Figure 4b). At maximum spillover of large adults and redistributed fishing effort, marine-reserve implementation does not affect fisheries-induced changes in maturation size. However, the extent of protection against fisheries-induced evolution is likely to be greater 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).

Model limitations

We stress 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 greater fecundity as 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, reducing the cost 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 these extensions favour the small-maturing life-history strategy. This shows that, by omitting 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 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- to small-maturing. Although 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 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; Dunlop *et al.*, 2007, 2009a, 2009b; Codling, 2008; Enberg *et al.*, 2009; Miete *et al.*, 2009; Okamoto *et al.*, 2009).

Also, stochastic effects and uncertainty may influence the 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 less than the 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 favours 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 leads 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) stress that this assumption may be unrealistic; reproduction is often seasonal, but movement tends to be continuous 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 non-linear density-dependent recruitment function of Beverton–Holt type (Gårdmark *et al.*, 2003). This relationship implies a consistently high mean value of recruitment when the spawning stock is large. In contrast, stock–recruitment functions of the 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- 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 the data. Beverton–Holt stock–recruitment models assume an increase in recruitment per spawner as a stock's density decreases, which may lead to an overestimate of 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 in achieving some ecosystem objectives (Mace, 2004). Although fisheries management based on multispecies models is desirable, such models are still difficult to design and to parameterize. 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).

Stage-dependent mobility and reserve size

The 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 was only at the larval stage; no spillover of adults took place (Williamson *et al.*, 2004). For obvious reasons, adult spillover has a stronger positive effect on the yield of adult fish, agreeing with the results of the study by Le Quesne and Codling (2009), who found that adult spillover has a greater potential to improve yield than juvenile export. Strong positive effects of adult spillover on yield were observed where the protected and fished areas featured 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

spillover from evolution towards small maturation size is weaker. Adult spillover 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 spillover of large adults between the protected and the fished areas, prevents an evolutionary switch to small maturation size (Figure 4a and b). 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, Miethé *et al.* (2009) confirmed the gradual reduction of spillover of large adults through selection for less dispersal within the marine reserve.

We have now verified that movement of only individuals of intermediate size leads to results that lie between the two extreme scenarios of juvenile export and spillover of large adults analysed above. Moreover, the movement of several size classes leads to greater connectivity between the protected and the fished area, reducing the scope for a stable dimorphism of maturation strategies and also lessening 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 limited, whereas extensive movement resulted in decreased protection from maturation evolution. We have shown that reserve size affects populations with low as well as high movement probability, but in different ways (Figure 5a and b). 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 believe that small reserves would be most effective, whereas populations with extensive adult movement that suffer from heavy 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 managing mixed fisheries that include species with different movement and other life-history characteristics, one reserve size will not be optimal for all those species (Sale *et al.*, 2005). We would propose therefore adapting the extent of protection, and hence the size of the marine reserve considered, to that of 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. Although such an approach may lead to the implementation of a large reserve, reducing the cpue of other species, it respects the precautionary approach and would buffer the fished community against uncertainty, not least against the uncertainty with regard to choosing the most appropriate reserve size. Moreover, to prevent evolutionary change towards small maturation size, it may be effective to combine the implementation of a reserve with a reduction of fishing mortality outside the reserve.

Marine reserves as a management tool

The use of natural home ranges as reserve boundaries reduces spillover 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 (*G. 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 after the temporary closure. Although marine reserves are generally efficient as management tools (Halpern, 2003), there are also examples of unsuccessful reserve implementation. The so-called “plaice box” was set up to protect undersized fish on the nursery grounds of North Sea plaice (*P. platessa*; Pastoors *et al.*, 2000). The observed reduction of juvenile density within this reserve was attributed to changes in the spatial distribution of plaice and possibly also to deteriorating feeding conditions through a 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 analysed 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; West *et al.*, 2009; Dunlop *et al.*, 2009a). Kelly *et al.* (2006) found that seasonally protecting spawning grounds, in the context of the recovery plan for Atlantic cod in the Irish Sea, failed to succeed in its objectives, probably because some fisheries were still allowed in the area, causing cod bycatch, increased fishing effort outside the protected area, and data uncertainty. A reversal of evolutionary changes in life-history traits is expected to be a slow process, although laboratory 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 has done little for demographic (Hutchings and Reynolds, 2004) or evolutionary recovery (Olsen *et al.*, 2004, 2005). Currently, just a small fraction of the sea has been set aside for protection, and long-term protection is rare. Therefore, the 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, supporting larger populations and increasing spillover. Lundberg and Jonzén (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 with extensive movement. This is important in situations in which fishing activity leads to deterioration in 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 ~7 years, and an age at maturation of ~3 years in the absence of fishing. Life expectancy and age-at-maturation decrease as harvesting increases, resulting in species being relatively short-lived. Baskett *et al.* (2005) found similar patterns in the modelled effects of marine reserves on evolutionary outcomes for species with different life histories, pointing out that evolutionary protection is less for long-lived species exhibiting extensive

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, and underscored the fact that for the effective protection of fish stocks with spawning migrations, the reserve must be located in the stock’s feeding 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- 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 take place 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 lesser abundances until collapse. This conceivable scenario is the evolutionary counterpart of the well-known phenomenon of fishing down the foodweb (Pauly *et al.*, 1998), and it may affect both species and entire communities.

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Appendix A

Harvesting the intermediate size classes

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

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

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 $h_{2,3}$:

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

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

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

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

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

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

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

Appendix B

Extensions of the single-population model

In Equations (3a)–(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. Moreover, 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 text, 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

favours maturation at small size when

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

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

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

As 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)–(3d) are therefore conservative in this respect.

Differentiating G with respect to q gives

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

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

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

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

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

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

In summary, increasing p (allowing individuals to spend more than 1 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 take place at lower harvest proportions. This implies that the simpler model we analyse in the 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.