

An Individual-based Model for Reviewing Marine Reserves in the Light of Fisheries-induced Evolution in Mobility and Size at Maturation

Tanja Miethe¹

York Centre for Complex Systems Analysis,
University of York, PO Box 373, YO10 5YW, UK.
tanja.miethe@googlemail.com

Jon Pitchford¹

York Centre for Complex Systems Analysis,
University of York, PO Box 373, YO10 5YW, UK.

Calvin Dytham¹

Vegetationsökologie and Naturschutz,
Universität Potsdam, 14469 Potsdam, Germany.

Miethe, T., J. Pitchford, and C. Dytham. 2009. An individual-based model for reviewing marine reserves in the light of fisheries-induced evolution in mobility and size at maturation. *J. Northw. Atl. Fish. Sci.*, 41: 151–162. doi:10.2960/J.v41.m624

Abstract

Size-selective fishing mortality may induce evolutionary changes to smaller size at maturation in fish stocks. Marine reserves can be a useful management tool dealing with the ecological and evolutionary effects of fisheries. We examine the effect of size-selective harvesting and the implementation of marine reserves on the evolution of size at maturation using individual-based models. The mobility of individual fish is included as an evolving trait to account for possible behavioural changes in dispersal patterns. The evolutionary change in maturation size can be prevented inside the reserve, leading to higher abundance there. The results show the benefit of reserves on yield, especially at intermediate movement probability. Reserve implementation may cause mobility of individuals to decrease, increasing the possibility of local adaptation in maturation strategy. Evolutionary changes in mobility through marine reserve implementation increase the protection from evolution to small maturation size within the reserve, but may lead to overestimation of yield benefits due to reduced spill-over.

Keywords: dispersal, IBM, open population, protected area, stage-structured model

Introduction

The effect of commercial fisheries on fish stocks and marine ecosystems is a mounting concern (Pauly *et al.*, 2005). Besides imposing a major source of mortality, fisheries are often size-selective, targeting large individuals. The number of large fish in a population is an important determinant of the reproductive potential of fish stocks, because large fish are usually more fecund and produce eggs of higher quality (Marteinsdottir and Begg,

2002; Berkeley *et al.*, 2004a; Ottersen *et al.*, 2006). In addition to demographic effects on fish stocks, the selective removal of larger individuals reduces their relative contribution of offspring to the population. This selection pressure may induce evolutionary changes in life history traits such as age and size at maturation, which could decrease reproductive potential and sustainability of fish stocks (Law and Grey, 1989; Olsen *et al.*, 2004). Also non-selective fishing mortality may induce shifts to smaller size and younger age at maturation because it

¹ Additional address: Department of Biology, University of York, PO Box 373 YO10 5YW, UK

also includes mortality of large individuals (Heino and Kaitala, 1999; Conover, 2000; Heino and Godø, 2002). Higher mortality primarily on juveniles and small-sized individuals leads to a selection pressure in the opposite direction (Reznick, 1996; Conover and Munch, 2002; Edeline *et al.*, 2007). In contrast to non-selective mortality, strong size selectivity has a high potential to induce an evolutionary change. Decreases in size at maturation have been observed in stocks of Atlantic cod (*Gadus morhua*), North Sea plaice (*Pleuronectes platessa*), and Newfoundland American plaice (*Hippoglossoides platessoides*) (Grift *et al.*, 2003; Barot *et al.*, 2004; Barot *et al.*, 2005). Although conclusive genetic evidence for fisheries-induced change is lacking, studies support considerations of evolutionary effects in fisheries management (Jørgensen *et al.*, 2007; Kuparinen and Merilä, 2007; Browman *et al.*, 2008). Protection of young and small fish has been an important issue in fish stock management but there is growing awareness that sustainability of fish stocks requires the reduction of mortality on old and large individuals without increasing the mortality of small fish (Birkeland and Dayton, 2005; Law, 2007).

Marine reserves can help to improve habitat, maintain genetic diversity, buffer against stochastic recruitment failure, and increase yield for overexploited species through spill-over (Apostolaki *et al.*, 2002; Gell and Roberts, 2003; Perez-Ruzafa *et al.*, 2006; Pitchford *et al.*, 2007). Within reserves old and large individuals reach higher abundance than outside (Berkeley *et al.*, 2004b). Marine reserves have also been theoretically analyzed as a management tool to guard against evolutionary changes in size at maturation (Baskett *et al.*, 2005). The ecological and evolutionary effect of a reserve has been shown to depend on the dispersal abilities of fish which leads to a net transfer of individuals from the reserve to the fishery (Baskett *et al.*, 2005; Gerber *et al.*, 2005). In these studies, movement rates were assumed to be constant, but behavioural changes in mobility may also influence the long term effects of a reserve. It has been suggested that a reserve changes the selection pressure on movement rates by increasing the fitness of less mobile individuals inside the marine reserve (Travis and Dytham, 1998; Botsford *et al.*, 2003; Baskett *et al.*, 2007).

In this paper we combine the evolutionary analysis of size at maturation and mobility. Evolution in these traits has previously been considered only separately in the context of selective fishing and marine reserve implementation. We address the question of how evolution in one trait may affect evolution in the other. We also explore how this could affect yield, information that allows fisheries managers to form more realistic expectations on the effects of marine reserve implementation. We aim to

further enhance evolutionarily-enlightened management preparing for short as well as long term changes through fisheries and marine reserve implementation (Ashley *et al.*, 2003). First we investigate the evolution in mobility and maturation size separately, because size-selective fishing mortality and reserve implementation affects either trait. We then continue with a scenario combining the evolution in two traits and go on to consider different reserve sizes.

Models

Our models are based on an age-structured model for a single population by Gårdmark *et al.* (2003), that describes the evolutionary effect of size-selective fishing. For analytical tractability the model of Gårdmark *et al.* (2003) was deterministic and considered only a single evolving trait: the probability to mature small. In contrast, this study develops a simple, spatially structured, stochastic individual-based model (IBM). We include two traits subject to variability, mutation and selection: i) the probability γ to mature at small size and ii) the probability m to move at each annual time step.

The population is divided into two subpopulations: one fully protected by a marine reserve, and the other fished. The model set-up is illustrated in Fig. 1. Parameters and trait values are listed and explained in Table 1. Juveniles of class 1 grow to small size after one year. Depending on their inherited trait γ , they may enter either class 2 (with probability γ), to mature to adulthood and reproduce at a small size at age 2, or enter class 3 (with probability $1 - \gamma$) to remain immature but then maturing a time step later at large size when they enter class 4 at age 3. If individuals of class 2 survive for two additional time steps then they may also grow to large size and enter class 4 with probability p . Large fish have higher fecundity (f_4) than small fish (f_2) such that maturation at large size is favoured in the absence of fishing mortality. Due to size selectivity of fishing, large individuals are subject to higher fishing mortality. For simplicity, we focus on harvesting the large individuals at rate h and set the harvest rate on other size classes to zero. Reproduction occurs locally within each subpopulation with larvae not being transported into the other subpopulation (Cowen *et al.*, 2000). Juvenile survival is assumed to be negatively density-dependent (Myers and Cadigan, 1993; Cushing and Horwood, 1994). Local density is limited at the juvenile stage using a capacity-related parameter k , which is scaled by the size of the respective subpopulation.

The subpopulations are connected through movement of individuals (m) at small and large size irrespective of maturity status (class 2 to 4). The individual

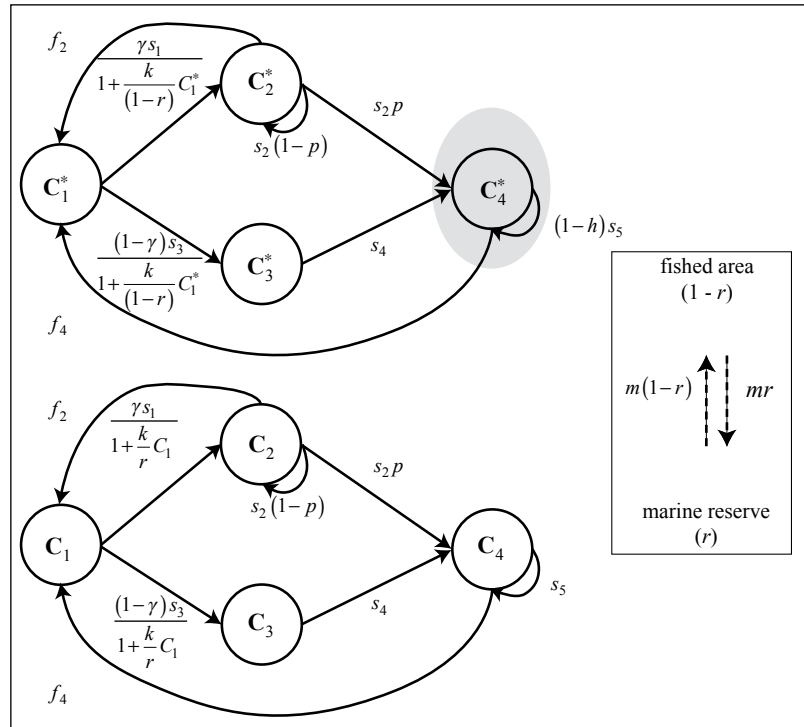


Fig. 1. Metapopulation model used for the simulations. Individuals mature to become adults at either the small size (C_2) or the large size (C_4). In one subpopulation (*, upper flow diagram) large individuals of class 4 are fished, the other subpopulation (lower flow diagram) is protected by a reserve. Connectivity is included through export of individuals of class C_2 , C_3 , and C_4 . Individual movement probability (m) is multiplied by the size of the respective destination area, r or $(1-r)$.

TABLE 1. Parameters and state variables with default values are listed and explained as used for simulations and illustrations.

Parameter or state variable	Values	Meaning
$C_{1,2,3,4}$		Class: 1-juveniles, 2-small size (mature), 3-small size (immature), 4-large size (mature)
$C^*_{1,2,3,4}$		As above, except class 4 individuals are fished
$s_{1,2,3,4,5}$	0.8	Survival probability from natural mortality per time step
p	0.2	Probability of small maturing individuals to grow to large size (age > 4)
k	0.0005	Factor scaling density dependence
$1-h$	0-1.0	Survival probability of large adults from fishing mortality per time step
f_2	5	Fecundity at small size, number of offspring per individual per time step
f_4	15	Fecundity at large size, number of offspring per individual per time step
γ	0-1.0	Probability to mature at small size
m	0-1.0	Probability of a large adult to move per time step
r	0, 0.125, 0.25, 0.5	Proportion of total area protected by marine reserve
mr		Probability of a large adult to move from fished to reserve area
$m(1-r)$		Probability of a large adult to move from marine reserve to fished area
M	0.1, 0.025	Mutation rate per generation

movement probability per time step ($0 \leq m \leq 1$) is scaled by the relative size of the destination area by multiplying m with either r (for fish moving from fishery to reserve) or $(1 - r)$ (movements from reserve to fishery), where r represents the fraction of the total space allocated to the reserve. This means that the larger the reserve the less likely an individual to move from the reserve into the fished area and vice versa. This leads to an exchange of individuals between fished and protected populations (Fig. 1) and follows the approach used by Baskett *et al.* (2007). Here, the evolving trait, movement probability, can be considered as an unconditional strategy (McPeck and Holt, 1992). Also we assume that fish within an age class must survive natural mortality before being harvested. Changing the order of events, such that harvesting occurs before survival of natural mortality, increases yield because a larger fraction enters the fishery. However, the results of abundance and the evolutionary effects are qualitatively the same because total mortality of the individuals remains unchanged. In reality natural mortality may affect individuals throughout the year, while the fishery is often seasonal. Our choice of event order does not overestimate yield and also does not qualitatively affect the population dynamics, as individuals have to survive both sources of mortality before the next reproductive event.

In the model, reproduction occurs asexually at the beginning of each year. A more realistic model with sexual reproduction would require more detailed knowledge of the effects of size-dependent distribution of mature individuals, sexual selection, and genetic recombination. Our modelling approach including asexual reproduction leads to offspring inheriting their movement behaviour and maturation strategy from one parent. The trait value is drawn randomly from a continuous uniform distribution with limits 0.1 and -0.1 around the parental strategy (Dytham, 2003). A mutation rate of $M = 0.1$ per generation ensures genetic diversity in offspring to avoid clonal offspring in this asexual model and allows for mutations in traits in the standard meaning. A reduction of the mutation probability and the mutation size in our model do not change the qualitative results and the speed of evolutionary changes. Maximum and minimum values for the evolving traits are set to 0 and 1. At the start of the simulation the initial population, 10 000 individuals, has a uniform distribution in the evolving traits. Depending on the reserve size and harvest rate, populations comprise a total of 40 000 to 100 000 individuals after 200 time steps. Individual fish are tracked by size class, location, maturation size strategy and movement strategy.

The model was implemented in C++. Simulations were run for 200 annual time steps and replicated five

times. Increasing the simulation time to 400 time steps does not significantly change the results, confirming that equilibrium is reached already after 200 time steps. We present results for an evolving trait as the mean of juveniles at the end of a simulation run; standard deviation is calculated from the replicated simulation runs. Results are illustrated by comparison to a fishery without implementation of a reserve. Yield is given as the absolute number of large adults of class 4 caught at the respective harvest rate h . The results in yield can also be interpreted qualitatively in terms of biomass because individuals of class 4 are assumed to have equal size and biomass. In section 3.1, we analyse a scenario with evolution in maturation size alone, at different constant movement rates. We then briefly explain the results of the scenario where only movement is included as an evolving trait and maturation size is held constant (section 3.2). In the subsequent simulations summarized in section 3.3, both the probability to mature at small size and the probability to move between the areas are used as evolving traits. For the results presented in sections 3.1–3.3 the two areas (fishery and reserve) are assumed to have the same size $r = 0.5$. In section 3.4, we consider reserves covering different fractions of the total area. We relate the evolution in the traits to the yield for the different evolutionary scenarios. In the last part of our analysis, in section 3.5, the effects of different starting values and lower mutation rates on the evolutionary results are explained.

Results

Evolution of size at maturation at constant movement probability

Our results indicate that the reserve effect differs depending on the mobility of individuals. In Fig. 2, yield and the mean values in the evolving trait within and outside the reserve are illustrated. For comparison, the results without reserve are plotted as a control; these are equivalent for different movement rates because in the homogeneous population movement is a neutral trait. If there is no movement ($m = 0$), the two subpopulations develop independently. In the fished subpopulation, a switch from small to large maturation size is induced at the same harvest rate as in the control scenario without reserve (Fig. 2a). With increasing harvest on large adults, the fitness of individuals with small maturation size increases, and the yield of large individuals is reduced accordingly (Fig. 2a, b). The reserve population is not affected by fishing mortality. From this it follows that the yield halves for the same harvest rate, because only half the area is available to the fishery (Fig. 2b). Mean values of the evolving trait γ never reach the extreme trait values of zero or one. Therefore even at strong selection

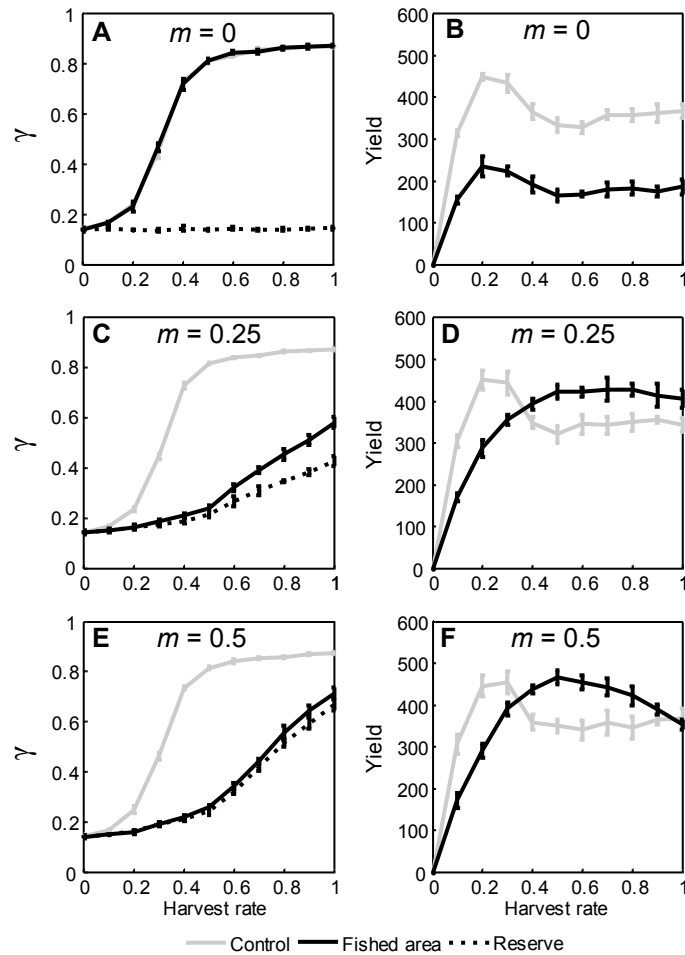


Fig. 2. Results modelling the evolution of the probability to mature small (γ , **A**, **C**, **E**) and yield (**B**, **D**, **F**) for different harvest rates in the fished (solid black) and marine reserve (dashed black) areas. Movement probability of large adults is constant: $m = 0$ (**A**, **B**), $m = 0.25$ (**C**, **D**) and $m = 0.5$ (**E**, **F**). For comparison, results without reserve are shown as control (grey), where both areas are fished. The controls for all three movement scenarios are equivalent. Reserve size: 50%. Means and standard deviation are plotted for five replicated simulations, including only juveniles of the population to calculate means of the evolving trait.

pressure, a few individuals, with $\gamma < 1$, may mature at large size. Decreasing mutation probability or maturation size leads to mean trait values closer to the extreme strategies but leaves the qualitative outcome unaffected. The mean γ of 0.5 at $h = 0.3$ corresponds to a uniform distribution in the trait values of juveniles; all maturation strategies have equal fitness. At higher or lower harvest rates, strategies with higher probability of either small or large maturation size become more abundant and the distribution becomes unimodal and is skewed towards either $\gamma = 1$ or $\gamma = 0$, respectively.

At an individual movement probability of $m = 0.25$, large adults spill over from the reserve into the fished area and increase yield of adult-fish compared to the zero-movement case (Fig. 2d). The exchange of individuals across the reserve boundary decreases the selection pressure towards small maturation size in the fishery. The selection pressure is reduced and yield is ensured at all harvesting rates. The probability of small maturation size increases within the reserve (Fig. 2c). The two subpopulations differ in the mean γ of juveniles. Selection on maturation size takes place, but it occurs in opposite

directions within the two subpopulations. The trait values among juveniles at the end of the simulations show that an intermediate value in γ represents a bimodal distribution with higher frequencies of small and large-maturing individuals and slightly lower frequencies of intermediate trait values.

At movement probability of 0.5, individuals have a high probability of being in the fished or protected area in the next time step. The mean probability to mature small is similar in both areas (Fig. 2e). An intermediate mean value corresponds to a uniform distribution in the evolving trait among juveniles. The distributions of γ are similar in the two subpopulations. Yield declines as evolution to small maturation size is induced (Fig. 2f).

Overall, in the absence of evolution in movement, the results show that at low movement probability marine reserves can ensure both protection from evolutionary changes and high yield.

Evolution of movement at constant probability of small maturation size

With implementation of a marine reserve mobility decreases in both fishery and reserve but is lower within

the reserve (Fig. 3a, c). This evolutionary decrease in mobility is largest when all individuals mature at large size ($\gamma = 0$), because there is a strong selective advantage for large-maturing individuals to remain within the reserve. The decline in mean movement probability as harvest rate increases can be attributed to reduced abundances of individuals with high movement rates through fishing.

Yield in the fishery increases with increasing harvest rate (Fig. 3b, d). Results in yield depend on the probability to mature small. Yield is markedly reduced if all individuals mature small ($\gamma = 1$) because only a small number of fish grow to large size only after surviving two additional time steps (Fig. 3d). Results for intermediate values of γ (not shown) show a smooth transition between the results depicted for the extreme values of γ .

Evolution of size at maturation and movement probability

Without a reserve, fishing effort is the same everywhere, so location does not matter and there is little selection on movement (Fig. 4, control). Evolution to small maturation size is induced at low harvest rates (Fig. 4a). As anticipated, reserve implementation causes

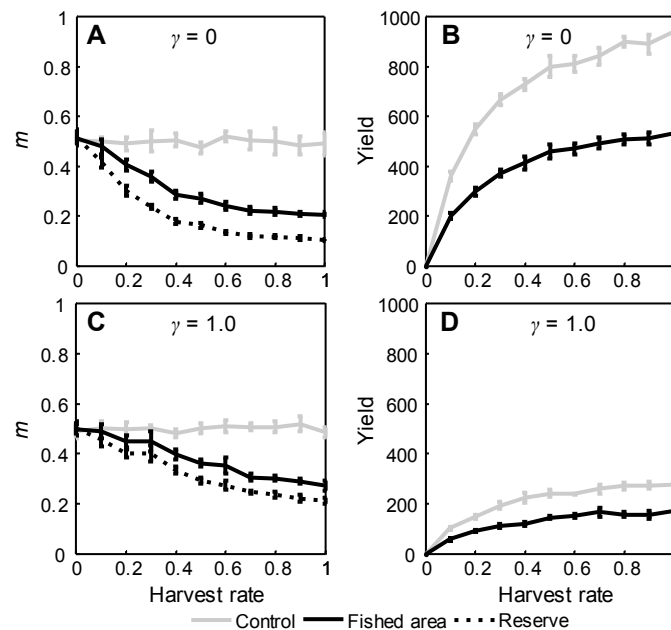


Fig. 3. Probability of movement (m , A, C), in the fished (solid black) and marine reserve area (dashed black), and yield (B, D) for different harvest rates. The probability to mature small is constant: $\gamma = 0$ (A, B) and $\gamma = 1.0$ (C, D). For comparison, results without reserve are shown as control (grey). Reserve size: 50%. Means and standard deviation are plotted for five replicated simulations, including only juveniles of the population to calculate means of the evolving trait.

the movement probability to decrease inside the reserve with increasing fishing effort (Fig. 4b). The movement probability also decreases in the fishery, but to a smaller extent. In the fished population evolution towards small maturation size is induced similar to the scenario with constant high movement probability (Fig. 2e). In contrast, the population within the reserve is relatively protected from fishing pressure and individuals mature at large size. At low and high harvest rates yield is lower than in the scenario without marine reserve (Fig. 4c) and lower than expected at intermediate to high movement probabilities without consideration of evolutionary changes in mobility (Fig. 2d, f). In other words, the combination of evolution in life history and movement parameters can lead to a scenario where reserves provide protection from evolution to smaller sizes at maturation, but without necessarily causing a concomitant increase in yield.

The effect of reserve size

In Fig. 5, the results are shown for the two evolving traits for smaller reserve sizes ($r = 0.125$, $r = 0.25$, compared to $r = 0.5$ in Fig. 4). For clarity, we show only mean values for the entire population. Larger reserves increase the protection from evolutionary change to small maturation size (Fig. 5a). A reserve causes the mobility to decrease (Fig. 5b), and a small reserve leads to evolution of higher overall mobility than those in a larger reserve where a higher fraction of the population inhabits the protected area (*cf.* Fig. 4b). Within a smaller reserve fewer individuals are protected, resulting in a higher selection pressure towards small maturation size and less selection pressure on movement probability.

Yield decreases as small maturation size is induced. Compared to a fully fished population (control) reserves of larger size ($r = 0.5$) result in lower yield for all har-

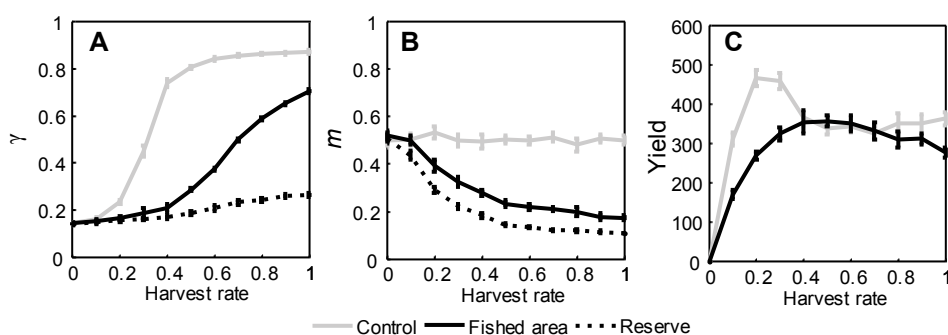


Fig. 4. The probability to mature small (γ , **A**) and the probability to move (m , **B**), in the fished (solid black) and marine reserve area (dashed black), and their effect on yield (**C**). For comparison results without marine reserves are plotted (grey). Reserve size: 50%. Means and standard deviation are plotted for five replicated simulations, including only juveniles to calculate means of the evolving traits.

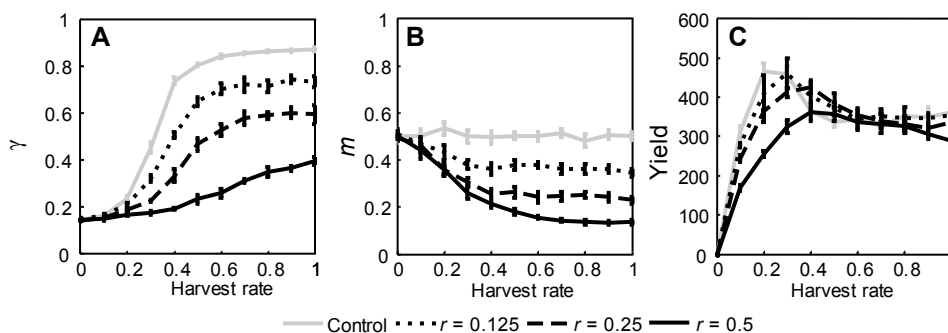


Fig. 5. Varying the reserve size affects the evolutionary outcome. Results for small maturation size (γ , **A**), probability of movement (m , **B**) and yield (**C**), are summarized for the entire population. No reserve (control, grey), 12.5% (dotted black), 25% (dashed black) and 50% (solid black) protected area. The mean and standard deviation of the evolving traits are plotted for five replicated simulations including only juveniles for the calculations.

vest rates because less area is available to the fishery and because the mobility of fish decreases thereby limiting the spill-over from the reserve into the fished area (Fig. 5c). A smaller reserve ($r = 0.125$) ensures yield at high harvesting rates due to higher spill-over.

Alternative starting values and mutation rates

In all previous simulations individuals had a uniform distribution in their trait values at the start of the simulation resulting in a mean of 0.5 for γ and m . Using specific starting values for the evolving traits, which are the same for all individuals, leads to qualitatively similar results. After 200 time steps at maximum harvest rate $h = 1.0$, mean of γ reaches values around 0.87 without reserve and 0.4 with a reserve protecting 50% of the population (Fig. 6a, b; cf. Fig 5a). The speed of evolution depends on the difference between starting values and the favoured trait value in the respective scenario. At maximum harvest rate without reserve, a population with mean $\gamma = 0.2$ evolves at a speed of around 0.4%

annually towards higher probability of small maturation size (Fig. 6a). In comparison starting at $\gamma = 0.5$ the evolutionary change occurs at around 0.2% annually.

A reduction in mutation rate does not affect the speed of evolution if trait values are uniformly distributed at the start of a simulation. With the use of distinct starting values, a reduction of mutation probability and size lowers the speed of evolutionary change in the trait values. A mutation rate $M = 0.1$ and starting value of $\gamma = 0.2$ result in an evolutionary change of 0.4% per year at maximum harvest rate without a reserve (Fig. 6a). At a mutation rate of $M = 0.025$, using a mutation probability of 0.5 and a mutation size of 0.05, the evolutionary change occurs at 0.15% per year for the same harvest scenario (Fig. 6c). At reduced mutation rate 500 time steps are required to reach evolutionary equilibrium (not shown). Reserve implementation may lead to a recovery in maturation size from $\gamma = 0.8$ at a rate 0.2% per year towards lower probabilities of small maturation size (Fig. 6b). At a reduced mutation rate a reserve, protecting 50%

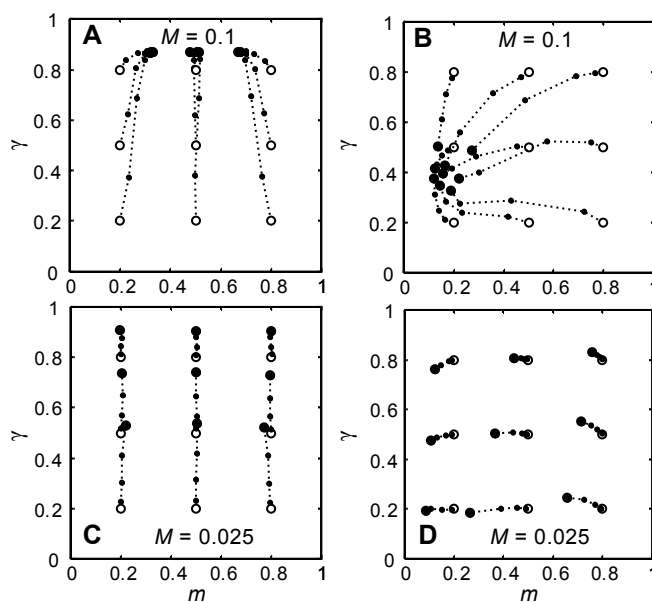


Fig. 6. Evolution of probability to mature small (γ) and probability to move over time (m) at maximum harvest rate ($h = 1$) for no reserve (control, A, C) and 50% reserve (B, D) for different mutation rates: $M = 0.1$ (A, B) and $M = 0.025$ (C, D). Mean values for five replicated simulations of juvenile trait values are plotted at the start of the simulation (open circles), after 50, 100, 150 time steps (small black circle), and after 200 time steps (large black circle), connected by evolutionary trajectories (dotted line).

of the population, may not lead to any recovery in γ after more than 200 time steps, while evolutionary changes towards lower mobility occur (Fig. 6b, d).

Discussion

Evolution of size at maturation

In agreement with previous studies, harvesting the largest individuals favours small maturation size (Law and Grey, 1989). Gårdmark *et al.* (2003) used the adaptive dynamics approach for an evolutionary analysis of an age-structured population model where a population is assumed to be homogenous in the trait value, and ecological and evolutionary timescales are separated. In their study evolutionary dynamics follow a bang-bang control with abrupt switch between the evolutionarily stable strategies $\gamma = 0$ and $\gamma = 1$, leading to a homogeneous population with either delayed maturation or early maturation. In this study we used an individual-based model for the analysis, and find variability in strategies within a subpopulation as well as between subpopulations. The fitness of a life history strategy is determined by the harvest rate in the fished area. This directly translates into frequencies of different life history strategies present in a population, causing a more gradual shift in the mean trait value of juveniles in the subpopulations from predominantly large maturation size to small maturation size with increasing harvest rate (Fig. 2a). The rate of evolutionary change in our model of 0.4% per year at maximum harvest rate for fish at initially large maturation size without protection by a reserve (Fig. 6a) is realistic compared to observation of changes in size at maturation around 1% per year for salmon and 0.35% per year for cod as summarized by Jørgensen *et al.* (2007).

With implementation of a reserve, subpopulations may differ in their mean trait values. Depending on fish mobility, individuals maturing at large size are more likely to be found within the reserve. Lenormand (2002) surmised that gene flow through dispersal counteracts local adaptation and we also find a higher degree of local adaptation at low movement rates. The evolutionary shift from large to small maturation size, which also determines yield, can be prevented to differing extents depending on the movement rates of individuals.

Ideally, reserves should protect fish stocks and enhance yield in adjacent fisheries. The chances of success for fulfilling these two objectives depends on movement rates, but in opposite directions (Rakitin and Kramer, 1996). Ecological analysis showed protection at low movement rates, while intermediate to high rates of adult movement benefit fisheries yield (Botsford *et al.*, 2003; Follesa *et al.*, 2007). The evolutionary analysis confirms

the conclusion for low movement rates; high ecological protection also includes evolutionary protection from changes to smaller maturation size. At high movement rates the degree of ecological protection of size at maturation decreases because more fish move across the boundary and enhance the fishery. The inclusion of an evolutionary analysis shows that the fishery may benefit to a smaller degree than expected from modelling without evolution as changes in maturation size affect reproductive potential, abundance, and consequently yield.

Evolution of movement

In a fishery without reserve, movement is almost a neutral trait, as predicted by Gadgil (1971), although there is weak selection for increased movement both to avoid competition with kin (Travis and Dytham, 1998), and because on average an individual spends more time in the more crowded patch and thereby benefits from movement to the less crowded patch (Travis and Dytham, 1999). Once the model includes a fishery and a reserve there is strong spatial heterogeneity. Movement will be favoured when leaving an area increases fitness, while low movement evolves if, on average, individuals move from a high fitness to a low fitness area. In our simulations we observed a reduction in mean movement rate as harvest rate increased because the fitness penalty for leaving the reserve is increasing. Individuals in the reserve have lower mean movement rates than individuals in the fishery. Within the reserve, individuals with high site fidelity have a higher fitness through protection from fishing and therefore increase in abundance, although they suffer from high density. Individuals with higher movement probability are penalized by entering the fished area and suffering from fishing mortality, although they benefit from the lower density. Individuals in the fishery also have low movement probabilities, although higher than in the reserve, because it is generally a sink population, continually augmented by individuals with relatively low movement rates spilling over from the reserve (Fig. 3). This intermediate movement rate allows fish to move across the boundary into the reserve and stay long enough to produce offspring. Maximum movement rates increase the probability of leaving the fishery, but also increase the probability of return in the next time step. This interpretation accords with Bull *et al.* (1987) where fitness was calculated with regard to multiple movement events, *i.e.* leaving and returning to a given patch.

Evolution of size at maturation and movement

Reduced mobility of fish within the reserve increases their fitness by avoidance of fishing mortality. As connectivity is reduced, evolution towards small maturation

size is induced only in the fished area and prevented within the reserve. The spatially heterogeneous habitat selects for reduced mobility, which in turn, supports local adaptation. This supports earlier studies suggesting that selection acts against individuals leaving favourable environments (Balkau and Feldman, 1973; Nosil *et al.*, 2005; Rocha *et al.*, 2005). The modelling results are the same whatever the starting values of movement used for the initial population. In reality there may be limits to evolutionary changes in movement. In the zero movement scenario (Fig. 2a), subpopulations may be geographically separated or connectivity may be restricted by migration costs which cause higher mortality for individuals leaving an area. In this case changing the fishing mortality on one subpopulation by implementation of a reserve will not affect movement probabilities; populations stay separate. On the other hand in populations with initially high mobility, movement may provide a sufficient contribution to fitness of individuals, such that increased spatial variability through implementation of a reserve may not necessarily cause the predicted decrease in mobility. The environment varies in space as well as time and so does fitness; movement modifies the conditions individuals and their offspring experience in a life time (McPeck and Holt, 1992). It has been shown that strong temporal variability (McPeck and Holt, 1992), demographic stochasticity (Travis and Dytham, 1998; Cadet *et al.*, 2003), disturbances, and succession processes (Olivieri *et al.*, 1995) favour higher mobility.

Fishing, especially using mobile fishing gear, is often highly destructive to habitat (Watling and Norse, 1998). Reserve implementation may increase habitat diversity and complexity leading to better protection of juvenile stages and more productive feeding grounds and thereby increase the carrying capacity of the reserve area (Halpern, 2003). Increased productivity of marine reserves is not considered in this study. It may lead to better protection against evolutionary changes and increase yield due to higher net export of individuals. But spill-over is then limited by evolution of mobility because improved habitat quality inside the reserve further increases the fitness gradient between the habitats, and selects for higher site fidelity. Also, fish may be able to sense the quality of the other habitat, which would favour accumulation of fish inside the reserve and reduce spill-over further until density-dependence limits overcrowding. We did not include any conditional movement, but predict that individuals would be strongly selected to leave crowded patches, as in Murrell *et al.* (2002).

Marine reserves can be an important management tool to prevent evolution to smaller maturation size. In accordance with the review by Kuparinen and Merilä

(2007), our study suggests that reduced genetic variability after intense exploitation, in our model lower mutation rate per generation, reduces the speed of recovery in size at maturation, if an evolutionary change already occurred (Fig. 6d). In comparison to the evolutionary speed of recovery in size at maturation, with implementation of a reserve a change in mobility of individuals may occur at a faster rate (Dytham and Travis, 2006).

General conclusions

This analysis shows the importance of deciding on the objectives of a reserve. There are trade-offs in the protection from evolutionary changes in mobility and size at maturation, protection of abundance, and improvement of yield. These factors can be weighed for the community and species concerned, and managed also with regard to reserve size and location. Evolutionary changes in mobility and maturation strategy may not always occur, or only one of the traits may be affected. This work enhances the understanding of the complex interactions in marine ecosystems, and moves towards the theory of marine reserve design requested by Botsford *et al.* (2003). We also emphasize that this general model may be used and applied to open populations in terrestrial ecosystems that are subject to size selective mortality. Recent publications show evolutionary concerns on selective hunting techniques also apply to terrestrial populations such as mouflon (Garel *et al.*, 2007), red deer (Proaktor *et al.*, 2007), and kangaroo (Tenhumberg *et al.*, 2004).

Acknowledgements

This research was supported by the European Marie Curie Research Training Network FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks), funded through the European Community's Sixth Framework Programme (Contract MRTN-CT-2004-005578). We would like to thank members of the FishACE network for their support. We are thankful to C. Roberts, M. Heino, C. West, and two anonymous reviewers for comments on earlier versions of the manuscript.

References

- APOSTOLAKI, P., E. J. MILNER-GULLAND, M. K. MCALISTER, and G. P. KIRKWOOD. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. *Can. J. Fish. Aquat. Sci.*, **59**: 405–415. doi:10.1139/f02-018
- ASHLEY, M. V., M. F. WILLSON, O. R. W. PERGAMS, D. J. O' DOWD, S. M. GENDE, and J. S. BROWN. 2003. Evolutionarily enlightened management. *Biol. Conserv.*, **111**: 115–123. doi:10.1016/S0006-3207(02)00279-3

- BALKAU, B. J., and M. W. FELDMAN. 1973. Selection for migration modification. *Genetics*, **74**: 171–174.
- BAROT, S., M. HEINO, L. O' BRIEN, and U. DIECKMANN. 2004. Long-term trend in the maturation reaction norm of two cod stocks. *Ecol. Appl.*, **14**: 1257–1271. doi:10.1890/03-5066
- BAROT, S., M. HEINO, M. J. MORGAN, and U. DIECKMANN. 2005. Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? *ICES J. Mar. Sci.*, **62**: 56–64. doi:10.1016/j.icesjms.2004.10.004
- BASKETT, M. L., S. A. LEVIN, S. D. GAINES, and J. DUSHOFF. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. *Ecol. Appl.*, **15**: 882–901. doi:10.1890/04-0723
- BASKETT, M. L., J. S. WEITZ, and S. A. LEVIN. 2007. The evolution of dispersal in reserve networks. *Am. Nat.*, **170**: 59–78. doi:10.1086/518184
- BERKELEY, S. A., C. CHAPMAN, and S. M. SOGARD. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**: 1258–1264. doi:10.1890/03-0706
- BERKELEY, S. A., M. A. HIXON, R. J. LARSON, and M. S. LOVE. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, **29**: 23–32. doi:10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2
- BIRKELAND, C., and P. K. DAYTON. 2005. The importance in fishery management of leaving the big ones. *Trends Ecol. Evol.*, **20**: 356–358. doi:10.1016/j.tree.2005.03.015
- BOTSFORD, L. W., F. MICHELI, and A. HASTINGS. 2003. Principles for the design of marine reserves. *Ecol. Appl.*, **13**: S25–S31. doi:10.1890/1051-0761(2003)013[0025:PFTDOM]2.0.CO;2
- BROWMAN, H. I., R. LAW, C. T. MARSHALL, A. KUPARINEN, J. MERILÄ, C. JØRGENSEN, K. ENBERG, E. S. DUNLOP, R. ARLINGHAUS, D. S. BOUKAL, K. BRANDER, B. ERNANDE, A. GÅRDMARK, F. JOHNSTON, S. MATSUMURA, H. PARDOE, K. RAAB, A. SILVA, A. VAINIKKA, U. DIECKMANN, M. HEINO, and A. D. RIJNSDORP. 2008. The role of fisheries-induced evolution. *Science*, **320**: 47–50. doi:10.1126/science.320.5872.47b
- BULL, J. J., C. THOMPSON, D. NG, and R. MOORE. 1987. A model for natural selection of genetic migration. *Am. Nat.*, **129**: 143–157. doi:10.1086/284626
- CADET, C., R. FERRIERE, J. A. J. METZ, and M. VAN BAALLEN. 2003. The evolution of dispersal under demographic stochasticity. *Am. Nat.*, **162**: 427–441. doi:10.1086/378213
- CONOVER, D. O. 2000. Darwinian fishery science. *Mar. Ecol. Prog. Ser.*, **208**: 303–307.
- CONOVER, D. O., and S. B. MUNCH. 2002. Sustaining fisheries yields over evolutionary time scales. *Science*, **297**: 94–96. doi:10.1126/science.1074085
- COWEN, R. K., K. M. MLWIZA, S. SPONAUGLE, C. B. PARIS, and D. B. OLSON. 2000. Connectivity of marine populations: Open or closed? *Science*, **287**: 857–859. doi:10.1126/science.287.5454.857
- CUSHING, D. H., and J. W. HORWOOD. 1994. The growth and death of fish larvae. *J. Plankton Res.*, **16**: 291–300. doi:10.1093/plankt/16.3.291
- DYTHAM, C. 2003. How landscapes affect the evolution of dispersal behaviour in reef fishes: results from an individual-based model. *J. Fish Biol.*, **63**: 213–225. doi:10.1111/j.1095-8649.2003.00231.x
- DYTHAM, C., and J. M. J. TRAVIS. 2006. Evolving dispersal and age at death. *Oikos*, **113**: 530–538. doi:10.1111/j.2006.0030-1299.14395.x
- EDELIN, E., S. M. CARLSON, L. C. STIGE, I. J. WINFIELD, J. M. FLETCHER, J. B. JAMES, T. O. HAUGEN, L. A. VØLLESTAD, and N. STENSETH. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proc. Nat. Acad. Sci. U. S. A.*, **104**: 15799–15804. doi:10.1073/pnas.0705908104
- FOLLESA, M. C., D. CUCCU, R. CANNAS, A. SABATINI, and A. CAU. 2007. Emigration and retention of *Palinurus elephas* (Fabricius, 1787) in a central western Mediterranean marine protected area. *Sci. Mar. (Barc.)*, **71**: 279–285. doi:10.3989/scimar.2007.71n2279
- GADGIL, M. 1971. Dispersal - Population consequences and evolution. *Ecology*, **52**: 253–261. doi:10.2307/1934583
- GÅRDMARK, A., U. DIECKMANN, and P. LUNDBERG. 2003. Life-history evolution in harvested populations: the role of natural predation. *Evol. Ecol. Res.*, **5**: 239–257.
- GAREL, M., J. M. CUGNASSE, D. MAILLARD, J. M. GAILLARD, A. J. M. HEWISON, and D. DUBRAY. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecol. Appl.*, **17**: 1607–1618. doi:10.1890/06-0898.1
- GELL, F. R., and C. M. ROBERTS. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.*, **18**: 448–455. doi:10.1016/S0169-5347(03)00189-7
- GERBER, L. R., S. S. HEPPELL, F. BALLANTYNE, and E. SALA. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. *Can. J. Fish. Aquat. Sci.*, **62**: 863–871. doi:10.1139/f05-046
- GRIFF, R. E., A. D. RIJNSDORP, S. BAROT, M. HEINO, and U. DIECKMANN. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar. Ecol. Prog. Ser.*, **257**: 247–257. doi:10.3354/meps257247
- HALPERN, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol. Appl.*, **13**: S117–S137. doi:10.1890/1051-0761(2003)013[0117:TOMRD]2.0.CO;2
- HEINO, M., and O. R. GODØ. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bull. Mar. Sci.*, **70**: 639–656.
- HEINO, M., and V. KAITALA. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *J. Evol. Biol.*, **12**: 423–429. doi:10.1046/j.1420-9101.1999.00044.x
- JØRGENSEN, C., K. ENBERG, E. S. DUNLOP, R. ARLINGHAUS, D. S. BOUKAL, K. BRANDER, B. ERNANDE, A. GÅRDMARK, F. JOHNSTON, S. MATSUMURA,

- H. PARDOE, K. RAAB, A. SILVA, A. VAINIKKA, U. DIECKMANN, M. HEINO, and A. D. RIJNSDORP. 2007. Ecology - Managing evolving fish stocks. *Science*, **318**: 1247–1248. doi:10.1126/science.1148089
- KUPARINEN, A., and J. MERILÄ. 2007. Detecting and managing fisheries-induced evolution. *Trends Ecol. Evol.*, **22**: 652–659.
- LAW, R., and D. R. GREY. 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.*, **3**: 343–359. doi:10.1007/BF02285264
- LAW, R. 2007. Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.*, **335**: 271–277. doi:10.3354/meps335271
- LENORMAND, T. 2002. Gene flow and the limits to natural selection. *Trends Ecol. Evol.*, **17**: 183–189. doi:10.1016/S0169-5347(02)02497-7
- MARTEINSDOTTIR, G., and G. A. BEGG. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.*, **235**: 235–256. doi:10.3354/meps235235
- MCPEEK, M. A., and R. D. HOLT. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.*, **140**: 1010–1027. doi:10.1086/285453
- MURRELL, D. J., J. M. J. TRAVIS, and C. DYTHAM. 2002. The evolution of dispersal distance in spatially-structured populations. *Oikos*, **97**: 229–236. doi:10.1034/j.1600-0706.2002.970209.x
- MYERS, R. A., and N. G. CADIGAN. 1993. Density-dependent juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.*, **50**: 1576–1590. doi:10.1139/f93-179
- NOSIL, P., T. H. VINES, and D. J. FUNK. 2005. Perspective: Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution*, **59**: 705–719.
- OLIVIERI, I., Y. MICHALAKIS, and P. H. GOUYON. 1995. Metapopulation genetics and the evolution of dispersal. *Am. Nat.*, **146**: 202–228. doi:10.1086/285795
- OLSEN, E. M., M. HEINO, G. R. LILLY, M. J. MORGAN, J. BRATTEY, B. ERNANDE, and U. DIECKMANN. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, **428**: 932–935. doi:10.1038/nature02430
- OTTERSEN, G., D. O. HJERMANN, and N. C. STENSETH. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fish. Oceanogr.*, **15**: 230–243. doi:10.1111/j.1365-2419.2006.00404.x
- PAULY, D., R. WATSON, and J. ALDER. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Phil. Trans. R. Soc. B*, **360**: 5–12. doi:10.1098/rstb.2004.1574
- PEREZ-RUZAFSA, A., M. GONZALEZ-WANGUEMERT, P. LENFANT, C. MARCOS, and J. A. GARCIA-CHAR-TON. 2006. Effects of fishing protection on the genetic structure of fish populations. *Biol. Conserv.*, **129**: 244–255. doi:10.1016/j.biocon.2005.10.040
- PITCHFORD, J. W., E. A. CODLING, and D. PSARRA. 2007. Uncertainty and sustainability in fisheries and the benefit of marine protected areas. *Ecol. Modelling*, **207**: 286–292. doi:10.1016/j.ecolmodel.2007.05.006
- PROAKTOR, G., T. COULSON, and E. J. MILNER-GUL-LAND. 2007. Evolutionary responses to harvesting in ungulates. *J. Anim. Ecol.*, **76**: 669–678. doi:10.1111/j.1365-2656.2007.01244.x
- RAKITIN, A., and D. L. KRAMER. 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.*, **131**: 97–113. doi:10.3354/meps131097
- REZNICK, D. 1996. Life history evolution in guppies: A model system for the empirical study of adaptation. *Neth. J. Zool.*, **46**: 172–190. doi:10.1163/156854295X00140
- ROCHA, L. A., D. R. ROBERTSON, J. ROMAN, and B. W. BOWEN. 2005. Ecological speciation in tropical reef fishes. *Proc. R. Soc. B*, **272**: 573–579.
- TENHUMBERG, B., A. J. TYRE, A. R. POPLE, and H. P. POSSINGHAM. 2004. Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting? *Ecology*, **85**: 2003–2017. doi:10.1890/03-4111
- TRAVIS, J. M. J., and C. DYTHAM. 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proc. R. Soc. B*, **265**: 17–23. doi:10.1098/rspb.1998.0258
1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. B*, **266**: 723–728. doi:10.1098/rspb.1999.0696
- WATLING, L., and E. A. NORSE. 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conserv. Biol.*, **12**: 1180–1197. doi:10.1046/j.1523-1739.1998.0120061180.x