

Density-dependent body growth reduces the potential of marine reserves to enhance yields

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Summary

1. Some models of marine no-take reserves predict that reserves can enhance fishery yield. However, empirical evidence of this remains inconclusive. One reason for this may be the disregard for density-dependent body growth in most models. Density-dependent body growth links the number and size of individuals, and thus could influence the biomass of fishery yield.
2. We developed an age- and size-structured model of an exploited population and analysed the effect of implementing a no-take reserve of varying size.
3. Protecting part of a population from exploitation in a no-take reserve results in a rapid build-up of biomass inside the reserve because of increased survival. However, when body growth is density-dependent it also results in reduced length at a given age within the no-take reserve because of crowding effects. This prediction is backed up by empirical observations.
4. If there is export of individuals (here larvae) from the no-take reserve, length at a given age will also decrease in the fished part of the population outside the reserve. An increase in the number of exploitable individuals thus results in decreased individual body mass. The positive effect of larval drift on fished population size and catch numbers will therefore rarely translate into an increase in equilibrium yield biomass.
5. *Synthesis and applications.* When body growth is density-dependent, implementation of no-take reserves affects the body size of both protected and exploitable individuals. Although reserves can have several benefits besides increasing yields, our study shows that, if density-dependent somatic effects are important, a general increase in yield biomass cannot be expected. In populations with density-dependent body growth, reserves are more likely to decrease yield biomass unless the population is severely overexploited. Analyses of the efficiency of marine reserves as a means of enhancing the yield of fisheries need to account for ecological processes, and density-dependent body growth is likely to be key.

Key-words: fishery management, larval drift, marine protected areas, population dynamics, size at age, size-structured model, somatic growth

Journal of Applied Ecology (2006) **43**, 61–69
doi: 10.1111/j.1365-2664.2005.01104.x

Introduction

Marine reserves are increasingly used to manage human use of dwindling marine resources (Murray *et al.* 1999;

National Research Council 2001; Ormerod 2003). Reserves (or no-take areas) are often implemented to protect biodiversity, exploited populations and their habitats (Gray 1997). The conservation benefits of no-take areas are well established: they allow populations and their truncated age- and size-structure to rebuild inside the reserve (Halpern 2003; Willis, Miller & Babcock 2003) and they protect habitats from structurally damaging fishing methods (Guénette, Lauck & Clark

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1998). As a consequence, implementation of no-take reserves increases the species biomass inside the reserve (Mosqueira *et al.* 2000; Sánchez Lizaso *et al.* 2000; Halpern 2003) and the average size of individuals therein (Sánchez Lizaso *et al.* 2000; Halpern 2003).

Another suggested benefit of reserves is to sustain or increase fishery yield (Murray *et al.* 1999; National Research Council 2001), but such benefits to fisheries of reserves are ambiguous. It has been suggested that reserves increase the fishable population by net drift of larvae or spillover of adults out of the reserves, thereby enhancing fishery yield (Gell & Roberts 2003) in spite of reducing the total fishing area. Earlier models of marine reserves predicted that no-take areas will increase yield in this way whenever the population is overexploited, i.e. fished at any intensity beyond that which maximizes yield (Quinn, Wing & Botsford 1993; Man, Law & Polunin 1995; Guénette & Pitcher 1999; Sladek Nowlis & Roberts 1999; Mangel 2000a; Pezzey, Robert & Urdal 2000). However, empirical support for these predictions is scarce (Gell & Roberts 2003). Roberts *et al.* (2001) reported an increase in total catch following reserve establishment in a severely over-exploited Caribbean reef fishery, but their results are contested (Hilborn 2002; Tupper 2002; Wickstrom 2002). To our knowledge, the only other example of reserves increasing total yield is in the scallop fishery at Georges Bank (Murawski *et al.* 2000). In contrast, studies of other reserves in coral reefs off the coast of Kenya (McClanahan & Mangi 2000) and in the Philippines (Maypa *et al.* 2002) have shown decreased or sustained total yield. One potential reason for this lack of correspondence between predictions and data is that marine reserve models have neglected a crucial ecological process, namely density-dependent body growth.

Density-dependent body growth links the number and the size of individuals; factors affecting population density also, indirectly, affect individual body size. For example, no-take areas cause spatial variation in mortality and may therefore affect both the density and size of exploitable individuals. Such changes in body size may, in turn, have consequences for population density and dynamics, as both fecundity and mortality patterns often depend on body size (Werner & Gilliam 1984; Roff 1992). The size of individuals caught is also important in a fishery, both because larger fish usually render a higher price per weight (Clark 1976; Gillis, Pikitch & Peterman 1995) and because the relevant measure of harvest is yield biomass, a function of the number and size of caught individuals. Body growth has been shown to be density-dependent in several exploited marine species (Booth 1995; Defeo 1998; Lorenzen & Enberg) and to be an important regulation mechanism in those populations (Lorenzen & Enberg 2002). Until now, however, the link between density-dependent body growth and the effect of marine reserves on fisheries has been unexplored.

Several studies have highlighted the importance of other density-dependent processes for the efficacy of

marine reserves (reviewed in Sánchez Lizaso *et al.* 2000). For example, Hastings & Botsford (1999) showed that, when there is density-dependent larval settlement and survival, reserves result in yield equal to that obtained using traditional effort control, but when density-dependence involves the density of adults, reserves instead decrease yield. Similarly, St Mary *et al.* (2000) showed that in populations with separate juvenile and adult habitats, reserves in juvenile habitats increased yield if density affected the reproductive rate but not if it affected maturation rate. A general prediction of models incorporating density-dependent recruitment (through larval mortality or settlement) is that reserves increase yield in overexploited populations (Gerber *et al.* 2003). However, because of the interplay between population density and individual size, density-dependent body growth might lead to different predictions of the effect of no-take reserves than density-dependent survival or recruitment. For example, reserves may not only affect population structure but individual characteristics, and the effect of reserves on yield biomass is not necessarily the same as the effect on the number of individuals caught.

In this study we used an age- and size-structured model to investigate the consequences of density-dependent body growth on the dynamics of exploited fish species managed by no-take reserves. We show that when a reserve is created, the build-up of biomass inside it results in a reduction in growth as a consequence of density-dependence. As a result, length at a given age decreases inside the reserve compared with in fished areas, which has also been observed in empirical studies (Fabrizio, Dorazio & Schram 2001; Béne & Tewfik 2003). Further, larval drift from the reserve increases the abundance of the fished part of the population but, as a consequence, also reduces the length at a given age among exploitable individuals. Consequently, yield biomass decreases, even though catch numbers and population size increase, and this holds for a wide range of reserve sizes and exploitation levels.

Model

We developed a simple age- and size-structured model based on cohorts of individuals of the same age and length at a given age. We thus assumed that there was pulse reproduction at the beginning of the year and that individuals born at the same time (i.e. within the same cohort) could be treated as identical with respect to somatic growth patterns, mortality risk and rate of reproduction. Let $N_{a,i,t}$ be the number of individuals of age a in area i at time t and $L_{a,i,t}$ their length. We assume that individuals grow according to a von Bertalanffy growth equation, such that their length from one year to the next is:

$$L_{a,i,t+1} = L_{\infty}(1 - e^{-k}) + L_{a-1,i,t}e^{-k} \quad \text{eqn 1a}$$

where L_{∞} is the asymptotic length and k is the von Bertalanffy growth rate (Beverton 1992) determining

how fast L_∞ is attained. We use a small enough k to allow the exponential to be Taylor approximated:

$$L_{a,i,t+1} = L_{a-1,i,t} + k(L_\infty - L_{a-1,i,t}) \quad \text{eqn 1b}$$

Individual mass is related to length by $W_{a,i,t} = \gamma L_{a,i,t}^3$, where γ is a constant conversion parameter. The population biomass in area i is thus $B_{i,t} = \sum_{a=1}^{\infty} N_{a,i,t} W_{a,i,t}$, i.e. the number of individuals of age a times their individual mass, summed over all ages.

When resources limit body growth, the increase in length is a function of competition for resources. If we assume that larger individuals use more resources and that resources are equally spread within the spatial distribution of the population, we can use the density of biomass as an approximation of the amount of competition. Theory predicts that resource limitation affects asymptotic length rather than growth rate (Beverton & Holt 1957; Walters & Post 1993), which also has empirical support (Beverton 1992; Lorenzen 1996; Shin & Rochet 1998). We therefore replace equation 1b with:

$$L_{a,i,t+1} = L_{a-1,i,t} + k(L_\infty - \alpha X_{i,t} - L_{a-1,i,t}) \quad \text{eqn 2}$$

where $X_{i,t}$ is the density of biomass in area i at time t (i.e. $X_{i,t} = B_{i,t} A_i^{-1}$, biomass $B_{i,t}$ divided by the size A_i of area i) and α is a constant that determines the strength of the dependence on the density.

Individuals of age a survive to age $a + 1$ with a probability s_a , and mature individuals (aged $a \geq a_m$) reproduce. Fecundity is often size-dependent (Wootton 1990), so that recruitment is proportional to body mass. Total recruitment to the population in area i at time t can then be written as a function of length at a given age:

$$R_{i,t} = \sum_{a=a_m}^{\infty} \beta \gamma L_{a,i,t}^3 N_{a,i,t} \quad \text{eqn 3}$$

where β is the fecundity (number of larvae produced) per gram body mass.

FISHED AREAS AND NO-TAKE RESERVES

We assume that fishing removes a fraction f_a of the individuals of age a (constant effort scenario; notice that this, strictly speaking, only corresponds to constant effort if catchability is constant). We later change this assumption and apply fishing of all individuals above a threshold number E_a of individuals of age a (constant escapement scenario). We assume that the population is not fished throughout its spatial distribution, but only in a fraction $1 - p$ of its total distribution area. The population is thus divided into individuals, $N_{a,h,t}$, inhabiting the fished areas, and individuals, $N_{a,r,t}$, within the reserve fraction p of the total area. We further assume that the total area is $A_{tot} = 1$, and, hence, $A_r = p$ is the size of the reserve and $A_h = 1 - p$ the size of the fished area.

To investigate the potential fishery benefit of reserves as sources of larval production, we consider an exploited species that has sedentary adults and planktonic larvae (as in many invertebrates or reef fish species; Love, Yoklavich & Thorsteinson 2002; Grantham, Eckert & Shanks 2003). We allow a fraction l_r of the larvae produced in the reserve to drift to areas outside the reserve, and a fraction l_h to drift in the opposite direction. Larval drift is assumed to be independent of distance, but we later relax this assumption.

We further assume that the length L_1 of newly hatched larvae is independent of population density and area of birth. The population dynamics are then given by one equation for larvae and a set of similar equations for older individuals. With constant fishing effort these are:

$$\begin{cases} N_{1,h,t+1} = \sum_{a=a_m}^{\infty} ((1-l_h)\beta\gamma L_{a,h,t}^3 N_{a,h,t} + l_r\beta\gamma L_{a,r,t}^3 N_{a,r,t}) \\ N_{a+1,h,t+1} = s_a(1-f_a)N_{a,h,t} \end{cases} \quad a \geq 1 \quad \text{eqn 4a}$$

in the fished area, and

$$\begin{cases} N_{1,r,t+1} = \sum_{a=a_m}^{\infty} ((1-l_r)\beta\gamma L_{a,r,t}^3 N_{a,r,t} + l_h\beta\gamma L_{a,h,t}^3 N_{a,h,t}) \\ N_{a+1,r,t+1} = s_a N_{a,r,t} \end{cases} \quad a \geq 1 \quad \text{eqn 4b}$$

in the reserve, in addition to equation 2 describing the change in length at a given age of individuals in each area. Density of biomass is now $X_{r,t} = B_{h,t} p^{-1}$ in the reserve and $X_{h,t} = B_{h,t} (1-p)^{-1}$ in the fished area. Notice that the order of events during one season is: somatic growth, reproduction, larval drift, natural survival, fishing and census, so that yield (in biomass) is:

$$Y_{B,t} = \sum_{a=2}^{\infty} s_a f_a N_{a,h,t} \gamma L_{a,h,t}^3 \quad \text{eqn 5a}$$

$$Y_{B,t} = \sum_{a=2}^{\infty} s_a (N_{a,h,t} - E_a) \gamma L_{a,h,t}^3 \quad \text{eqn 5b}$$

for constant fishing effort and constant escapement, respectively, assuming that larvae (age group 1) are not fished. Notice that we assume that fishing effort outside the reserve will remain regulated, and that reserves do not replace this control of fishing effort but rather complement it. Thus, we evaluate the percentage change in equilibrium yield biomass, ΔY_B^* , and yield numbers, ΔY_N^* , obtained with a reserve compared to without a reserve, assuming that fishing effort is *not* reallocated when the reserve is created. Hence, the fraction f_a removed by fishing remains the same before and after a reserve is implemented.

We solved equations 2–5 numerically using 10 age groups, assuming that individuals older than 2 years reproduce ($a_m = 3$). The growth parameters used in Figs 1–4 are within a range corresponding to common

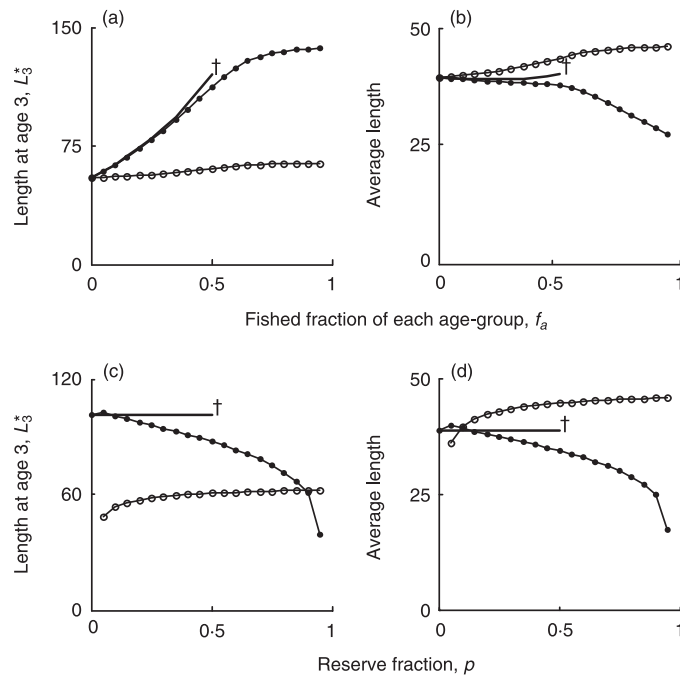


Fig. 1. Length at a given age $L_{a,i}$ and average length in the population at equilibrium vary with (a, b) fishing intensity f_a and (c, d) fraction p of the area set aside as a no-take reserve, when there is density-dependent body growth. In (a, c), length at a given age is illustrated by the length at age 3 years ($L_{3,i}^*$), the first-time reproducers. The effect is shown for an exploited population without a reserve (black line) and an exploited population outside (full circles) and inside (open circles) a no-take reserve. A dagger indicates when the exploited population goes extinct in the absence of reserves. Parameters used were $\alpha = 0.1 \text{ m}^2 \text{ g}^{-1}$, $\beta = 15 \text{ larvae g}^{-1}$, $\gamma = 10^{-7} \text{ g mm}^{-3}$, $f_1 = 0$, $k = 0.1 \text{ year}^{-1}$, $l_r = 0.3$, $l_n = 0.3$, $L_1 = 5 \text{ mm}$, $L_\infty = 500 \text{ mm}$, $s_{1-8} = 0.75$ and $s_9 = 0.0001$, and in (a, b) $p = 0.2$ and (c, d) $f_{2-9} = 0.4$.

fish species (e.g. plaice *Pleuronecta platessus* L.; Lorenzen & Enberg 2002) and we explore the effect of variation in growth parameters and larval drift in Appendix S1. As our focus is the benefit to fisheries of reserves rather than the effect of reserves on the persistence of populations, we assume a simple deterministic extinction process, with populations going extinct when there is less than one individual left. Density-dependent body growth may have a large effect on the population in the model because it is the only mechanism regulating population growth. Therefore we also analysed the effect of density-dependent body growth in a population with density-dependent *per capita* natural survival, by substituting s_a for $s'_a = s_a(1 + \rho X_{i,t})^{-1}$ (where ρ is the strength of density-dependence) in equations 4 and 5. However, there was no qualitative difference in the results from this model with two density-dependent processes, and we therefore used the simpler model described by equations 1–5 throughout the rest of the study.

Results

When body growth is density-dependent, individual growth rates increase when fishing reduces population density. The length at a given age in an exploited population thus increases with fishing pressure (Fig. 1a). In contrast, the average length in an exploited population decreases with fishing (Fig. 1b), because individuals do not survive long enough to reach old age and a large

body size. Correspondingly, protection from fishing in a no-take reserve results in a higher average length inside the reserve because of increased life spans (Fig. 1d). However, the higher density inside the reserve causes slower body growth and results in smaller length at a given age compared with the exploited part of the population (Fig. 1c).

This response of body growth to changes in density has several consequences for the way in which reserves affect yield through larval drift into fished areas. Most importantly, larval drift from the reserve increases the density outside the reserve, and therefore reduces individual body growth in the fished part of the population. As a result, length at a given age among exploitable individuals decreases (Fig. 1c). With larger reserves, more larvae will drift into fished areas, individual growth will be further reduced, and individuals caught outside the reserve will thus be smaller (Fig. 1c).

If the increase in population number in the fished areas as a result of larval drift from the no-take reserve does not compensate for (i) the un-exploitable part of the population inside the reserve and (ii) the decrease in length at a given age among exploitable individuals, yield measured in biomass will decrease when a reserve is created. For example, for the parameter values explored in Fig. 2, setting aside 20% of the total area as a no-take reserve only increases yield biomass if the population is severely overexploited, at fishing pressures close to those causing extinction in the absence of a reserve. No-take reserves of any size reduce yield

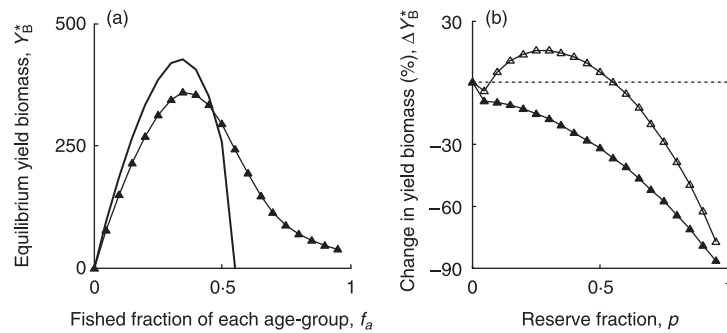


Fig. 2. (a) A no-take reserve only increases yield biomass outside of it in severely overexploited populations, but ensures population persistence and thus yield at fishing efforts at which the population otherwise would go extinct. Equilibrium yield biomass is shown in (a) for a population without a reserve (full line) and with a reserve covering 20% of the total population distribution (triangles). The proportional change in yield biomass is shown in (b) for a slightly overexploited population ($f_a = 0.4$, filled triangles) and for a severely overexploited population ($f_a = 0.5$, open triangles). Other parameters are as in Fig. 1.

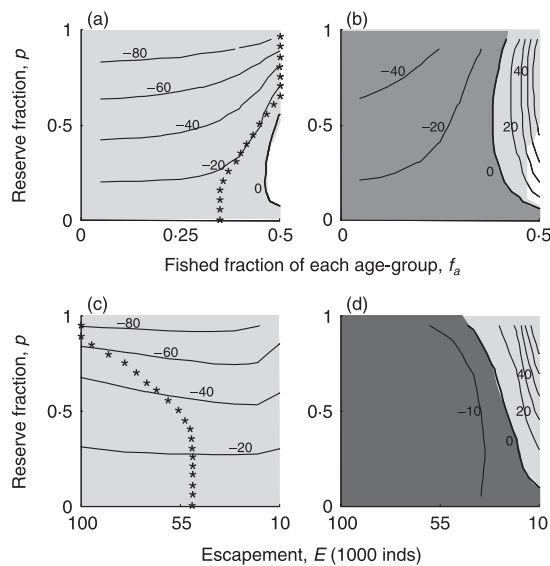


Fig. 3. (a, c) Equilibrium yield biomass decreases when a reserve is created for underexploited, optimally exploited and slightly overexploited populations, even though (b, d) yield numbers increase. The effect of creating a reserve covering a fraction p of the total population distribution on yield is shown as the change (%) in equilibrium yield biomass ΔY_B^* and yield numbers ΔY_N^* compared with the absence of reserve ($p = 0$), given as isoclines. Light grey areas indicate reserve fractions and fishing intensities (measured as fishing effort or escapement) for which $\Delta Y_B^* < 0$, and dark grey areas indicate $\Delta Y_N^* < 0$. Optimal fishing effort or escapement (maximizing ΔY_B^*) is indicated by stars. The effect of reserves is only shown for fishing intensities under which the population can persist in the absence of reserves. Notice that the x-axes in the lower panels are reversed, such that fishing intensity increases to the right in all panels. Parameters are in (a, b) $\alpha = 0.1$ and (c, d) $\alpha = 0.05$, otherwise as in Fig. 1.

biomass for most fishing pressures (Fig. 3). Even in overexploited populations (at fishing pressures above those that maximize yield biomass; Fig. 3a), in which establishment of a reserve increases both the number of individuals caught and the number of individuals in the fished areas (Fig. 3b), reserves decrease yield biomass.

Also, if fishing is done with constant escapement, yield biomass decreases in severely overexploited populations (Fig. 3c) when reserves can increase yield numbers (Fig. 3d).

The range of reserve sizes and fishing mortalities for which reserves decrease yield biomass changes with the strength of density-dependent growth (α) if mortality as a result of fishing is density-dependent (Fig. 4). This occurs, for example, under a constant escapement policy, when fishing reduces the population to a target population size. Reserves will then decrease yield for more reserve sizes and fishing intensities in populations with stronger density-dependence than in populations with weak density-dependence (Fig. 4). As fishing with constant effort incurs density-independent mortality, the parameter ranges of p and f_a for which reserves decrease yield is unaffected by α . Although the proportional change in equilibrium yield does not change, the absolute yield decreases with α .

Our results are robust to variation in larval dispersal. Variation in the fraction of larvae drifting out from the reserve does not alter our results qualitatively (see Appendix S1). For any level of larval drift, reserves always decrease equilibrium yield biomass in underexploited, optimally exploited and slightly overexploited populations. We also relaxed our assumption of distance-independent larval drift. When larval drift (and settlement) decreases with distance from reserve centre (see Appendix S1), yield losses are greater and occur for an even wider range of fishing mortalities and reserve sizes than when larval drift is independent of distance.

Discussion

We have shown that density-dependent body growth crucially alters the potential of no-take reserves to enhance fisheries, compared with predictions from models incorporating only density-dependent recruitment (reviewed in Gerber *et al.* 2003), because density-dependent body growth links population density to

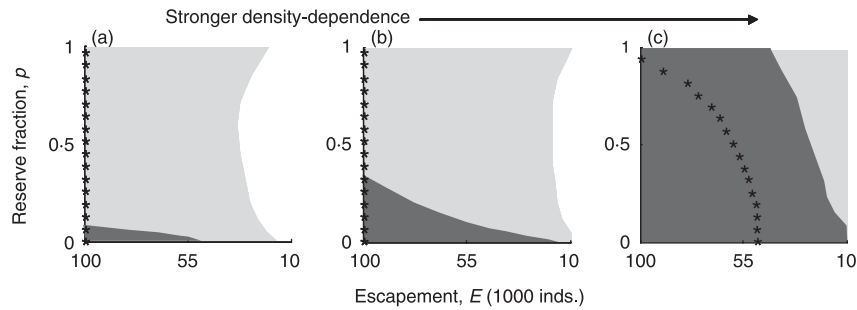


Fig. 4. The range of reserve sizes and fishing intensities for which a no-take reserve reduces equilibrium yield increases with the strength of density-dependence in body growth (α) when fishing is done using a constant escapement policy. Light grey indicates reserve fractions p and escapement levels E for which yield biomass decreases, dark grey indicates that yield in numbers also decreases, and stars indicate optimal escapement (which maximizes ΔY_B^*). Parameters are in (a) $\alpha = 0.05$, (b) $\alpha = 0.01$ and (c) $\alpha = 0.05$, otherwise as in Fig. 1.

individual size. Previous models generally predicted that if the population is overexploited, a no-take reserve increases yield by enhancing the population in fished areas through export of larvae or adults (Gerber *et al.* 2003). We show, however, that with density-dependent body growth an increased amount of larvae drifting into fished areas, which has been proposed as a goal of reserve design (Hastings & Botsford 2003), does not necessarily translate into increased yield biomass. Instead, the higher density as a result of larval input from a reserve decreases length at a given age in the fished population. Therefore, yield biomass decreases for an even wider range of fishing pressures (also above optimal levels) than catch numbers or the fished population size. In severely overexploited populations, however, small reserves can still increase yield biomass (and yield numbers), as in models of other density-dependent processes where fishing effort is supposed to be uncontrolled or reserves are assumed to replace effort control (Hastings & Botsford 1999; Gaines, Gaylord & Largier 2003).

There are several empirical observations of decreasing length at a given age following reserve establishment. It has been found in, for example, lake trout *Salvelinus namaycush* W. in Lake Superior (Fabrizio, Dorazio & Schram 2001) and queen conch *Strombus gigas* L. in the Caribbean (Béne & Tewfik 2003), observations that, until now, have not been explained by theories underlying the design of no-take areas. Our results also explain the mismatch between a general prediction from several previous models and data on yield effects of marine reserves. Although reserves have been shown to increase abundance and total recruitment in fished areas surrounding them (Tawake *et al.* 2001), to our knowledge only two studies have reported increased total catch biomass following reserve establishment: in a severely overexploited reef fishery in St Lucia in the Caribbean (Roberts *et al.* 2001; but see Hilborn 2002; Tupper 2002; Wickstrom 2002) and in the scallop fishery at Georges Bank (Murawski *et al.* 2000). We predict that for most fished populations, including overexploited ones, reserves will decrease

long-term annual yield biomass (Fig. 3a–c), a prediction supported by results from two other coral reef reserves (McClanahan & Mangi 2000; Maypa *et al.* 2002). In the case of severely overexploited populations (Figs 2 and 3a), such as in St Lucia, reserves may still increase yield biomass.

In our analyses we have made several simplifying assumptions, of which the most important are those of sedentary adults and unlimited settlement of larvae drifting out of the reserve. These assumptions are reasonable for species with larval dispersal but limited adult mobility, as in marine invertebrates and many reef fish species (Love, Yoklavich & Thorsteinson 2002), organismal groups that are both heavily exploited and contain several species known to exhibit density-dependent body growth (Booth 1995; Defeo 1998). Although models of marine reserves are often sensitive to patterns of larval dispersal (Botsford, Hastings & Gaines 2001) of which little is known empirically (Grantham, Eckert & Shanks 2003; Shanks, Grantham & Carr 2003), neither the proportion of larvae drifting out of the reserve nor a simple form of distance-dependent larval dispersal affected our results qualitatively. One caveat, however, is that for simplicity we did not assume any limit on how many larvae can settle in an area. Spatial limitation to settlement can occur in structure-dwelling invertebrates (Wahle & Steneck 1991) but may be less appropriate for invertebrates on soft substrates (Olafsson, Peterson & Ambrose 1994). Such a threshold would limit the density increase in the fished area caused by larval drift, and thus the extent, but not the quality, of its negative effects on length at a given age (and hence yield biomass) among exploitable individuals.

Density-dependent body growth has also been demonstrated in other important exploited species, such as herring and silver hake (Lorenzen & Enberg 2002). Our assumption of sedentary adults is not suitable for these species because they have seasonal adult migration. The qualitative results of a model with adult movement, however, are likely to be similar to what we present here, as body growth in our model depends on

total population density. Reserves will decrease length at a given age (and thus yield biomass) as long as reserves increase population density inside and outside reserves, independent of whether this is through larval drift or adult movement. Quantitative analyses of the extent of the effects we present, however, will require species- and fishery-specific assumptions, including fishermen behaviour and management practices in place.

For illustration, we have focused on only one effect (yield biomass) of decreased length at a given age that results when a reserve is implemented, but there are many other important consequences that warrant further analysis. For example, the smaller length at a given age in both the protected and exploited parts of the population can affect (i) the overall catchability of the population as a result of the practice of minimum mesh sizes; (ii) the economic value of the catch as smaller individuals generally render a lower price per weight (Clark 1976; Gillis, Pikitch & Peterman 1995); and (iii) the natural mortality patterns as both intra- and interspecific interactions are inherently size-dependent (Werner & Hall 1974; Gallego & Heath 1994; Vorburger & Ribí 1999). Thus, ignoring density-dependent body growth when designing no-take areas may underestimate reductions in the biomass and value of fishery yield and overestimate conservation benefits by overlooking effects on both body size and, subsequently, natural mortality.

There are many established benefits to fisheries of marine reserves that we did not study, such as reducing the risk of collapse of exploited populations (Mangel 2000a), buffering against biological and managerial uncertainties (Lauck *et al.* 1998) and decreasing the variability of catches (Mangel 2000b). We have shown, however, that even simple density-dependent body growth can drastically alter the predictions of the fishery benefit of reserves. Yield increases may still occur, in severely overexploited populations or in overexploited populations with density-independent body growth, but analyses of the potential for such benefits must account for processes specific for each system. We propose that, just as spatial population dynamics (such as habitat choice and source-sink dynamics) have recently been incorporated into the theory underlying the design of marine reserves (Lundberg & Jonzén 1999a,b; Tuck & Possingham 2000), so must processes linking population-level characteristics to individual traits. Attempts to deduce general principles for no-take reserves (Botsford, Micheli & Hastings 2003) can and must rest on fundamental ecological processes such as density-dependent body growth.

Acknowledgements

Thanks to Örjan Östman, Jörgen Ripa, Per Lundberg and Jonathan Chase and his laboratory for helpful comments on the manuscript, to Hugh Possingham, Rich Zabel and three anonymous referees for comments

on an earlier version of the manuscript, and to Teresa Ish and Steve Munch for general discussions. This work was financially supported by the Finnish Academy of Science's MaDaMe Programme (to A. Gårdmark); the Center of Excellence in Evolutionary Ecology at the Department of Biological and Environmental Science in University of Jyväskylä, and the Spatial Ecology Program at the Department of Ecology and Systematics in University of Helsinki (to N. Jonzén); and Lund University, which brought us together.

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Received 26 November 2004; final copy received 30 July 2005
Editor: Rob Freckleton

Supplementary material

The following supplementary material is available for this article online.

Appendix S1. Sensitivity analysis

Fig. S1. The effect of creating a no-take reserve on equilibrium yield biomass (% change compared to fishing the whole population)