

MARINE RESERVES EXPLOIT POPULATION STRUCTURE AND LIFE HISTORY IN POTENTIALLY IMPROVING FISHERIES YIELDS

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Abstract. The collapse of many of the world's fisheries has induced a reevaluation of existing fisheries management strategies. This has fueled interest in the establishment of networks of no-take marine reserves as an additional form of protection. Proponents of marine reserves have suggested that reserves can provide a number of advantages over other, more traditional, methods. However, concerns have also persisted that marine reserves will reduce overall catch. In a theoretical context, this concern has been only partially addressed by previous work suggesting that reserves can produce equivalent yields to those from traditional management, since this possibility is widely interpreted as a limiting case. However, an "equivalence-at-best" scenario is based on a highly simplified model construct that ignores all spatial pattern and size structure characterizing real populations. By contrast, when coupled effects of (1) spatial pattern in adult densities and larval dispersal, (2) population size structure, and (3) aspects of life history are considered in their most basic forms, model results suggest that reserve networks may have the potential to enhance fishery yields under a surprisingly large number of circumstances. Such enhancement is predicted to be greatest, and at times substantial, in species exhibiting postdispersal density dependence and that have relatively long-lived and sedentary adults, life history traits common to many harvested fishes and invertebrates. A goal of this study is to spark further theoretical attention and experimental testing on this unanticipated front.

Key words: fishery yield; harvesting; marine protected areas; spatially explicit; stage structure.

INTRODUCTION

Scientific interest in no-take marine reserves has increased enormously over the last decade (Willis et al. 2003), largely in response to a growing awareness of the declining state of many of the world's fisheries (Botsford et al. 1997, Pauly et al. 1998, 2002, Jackson et al. 2001, Myers and Worm 2003). Proponents of marine reserves emphasize that reserves can help to preserve critical habitat and trophic structure, reduce by-catch of untargeted species, maintain genetic diversity and integrity of fished populations, and insure against stochastic recruitment failure and management uncertainty (Plan Development Team 1990, Allison et al. 1998, Guenette et al. 1998, Hall 1998, Lauck et al. 1998, Hastings and Botsford 1999, Sladek Nowlis and Roberts 1999, Mangel 2000, Gell and Roberts 2003). However, despite these potential benefits, concerns persist that marine reserves will reduce overall catch, particularly in species that are not yet overfished (see review by Gerber et al. 2003).

This latter concern has been only partially addressed by previous theoretical work demonstrating that reserves can produce equivalent yields to those from traditional management (Hastings and Botsford 1999), since this possibility is typically interpreted as a limiting case. However, the equivalence argument is based on a simple, nonspatial construct where sedentary adults spawn into a common "larval pool" that redistributes young uniformly along an effectively infinite coast, and where recruitment and subsequent survival occurs without regard to the local density of individuals. Other analyses, in contrast, indicate that an optimal harvest strategy cannot be attained without establishing at least one reserve (Neubert 2003). More detailed modeling studies that consider additional features of natural populations also provide hints that reserves may at times increase yields, albeit mostly for fisheries that are already in an overexploited state (Lauck et al. 1998, Sladek Nowlis and Roberts 1999, Apostolaki et al. 2002).

To begin to tease apart these somewhat inconsistent theoretical projections, we present a model of intermediate detail that bridges between highly "strategic" baseline models (*sensu* Levins 1966; e.g., Hastings and

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Botsford 1999, Neubert 2003), and their more numerous, case-specific “tactical” counterparts (Polachek 1990, Russ et al. 1992, DeMartini 1993, Mann et al. 1995, Guenette and Pitcher 1999, Sladek Nowlis and Roberts 1999, Crowder et al. 2000, Mangel 2000, St. Mary et al. 2000, Stockhausen et al. 2000, Apostolaki et al. 2002, Gaines et al. 2003, Shirai and Harada 2003). This spatially explicit, population dynamic model includes sufficient complexity to examine a range of features characterizing a broad spectrum of fished species, yet still contains few enough parameters to enable a complete exploration and concise description of model behavior. Results reveal that there are important and fundamental connections among elements of population structure and life history that influence the potential yields that can be expected from the implementation of marine reserves. Here we focus on theoretical aspects of these connections, although we do cite a limited number of key reviews of empirical work as well.

METHODS

Spatially explicit larval dispersal

A fundamental trait of nearly all fished marine populations is that they possess a two-stage life cycle, one stage of which involves larval dispersal. Accounting for the spatial nature of this process is therefore likely to be critical in evaluating the potential performance of marine reserves, particularly given that reserves themselves are intrinsically spatial. Integro-difference models (Kot and Schaffer 1986) provide one effective means of accomplishing this task. A single-size-class version is given by

$$n_{t+1}(x) = \int_0^L n_t(y)\phi_n k(x, y) dy. \quad (1)$$

This expression tracks population density, $n_t(x)$, through successive increments of time, t , along a linear shoreline habitat of length L . The integral in Eq. 1 indicates that the population density at point x results from the summation of larval contributions from potential source sites throughout the shoreline habitat. The larval dispersal phase follows reproduction and occurs according to a Gaussian kernel, which quantifies the probability that a larva settling at point x originates from a small region centered on point y :

$$k(x, y) = \frac{1}{\sqrt{2\pi}d} \exp\left[-\frac{1}{2}\left(\frac{x-y}{d}\right)^2\right] \quad (2)$$

where d indicates the length scale of along-coast dispersion. Simulations of ocean mixing processes by Siegel et al. (2003) suggest that dispersal distributions averaged over population timescales will often closely approximate this form, although strongly advective flows can introduce asymmetry. We do not dwell on such cases of asymmetrical dispersal in this study, but acknowledge that they can have important population

consequences under some circumstances (Crowder et al. 2000, Gaylord and Gaines 2000, Gaines et al. 2003). The model also ignores adult movement and so is most relevant to species with relatively sedentary adults, although we return to this issue in the *Discussion*. The final term, ϕ_n , in Eq. 1 accounts for density-dependent processes, which are assumed to operate following either a traditional Beverton-Holt or Ricker formulation:

$$\phi_n = \frac{\exp(r)}{1 + [\exp(r) - 1]n_t} \quad (\text{Beverton-Holt}) \quad (3)$$

$$\phi_n = \exp[r(1 - n_t)] \quad (\text{Ricker}) \quad (4)$$

where r parameterizes the population growth rate such that Eqs. 3 and 4 produce similar rates of increase at low density. The population density term, n_t , in Eqs. 3 and 4 refers to either $n_t(y)$ or $n_t(x)$ and thereby accounts for either predispersal density dependence (e.g., due to density-dependent larval production) or postdispersal density dependence (e.g., due to density-dependent mortality during recruitment), respectively. Population density is scaled such that its equilibrium value would be 1 in the absence of fishing mortality and spatial structuring.

Population size structure, individual growth rate, and longevity

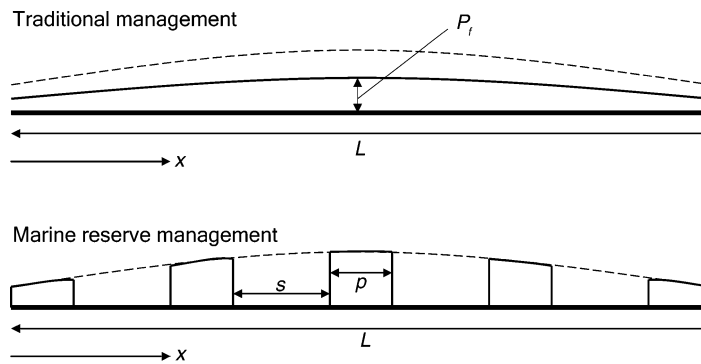
One of the more important effects of reserves is that older and larger, highly fecund, individuals often reach higher abundances within protected areas. This has been observed in both tropical and temperate fishes and invertebrates (Plan Development Team 1990, Polunin and Roberts 1993, Palsson 1998, Wallace 1998, Edgar and Barrett 1999, Paddock and Estes 2000, Halpern 2003). A beginning step towards accounting for such shifts in population size structure can be realized by adding a second size class to the model, yielding

$$n_{t+1}(x) = \sigma(1 - \gamma)n_t(x) + \int_0^L [n_t(y)\phi_n + N_t(y)\phi_N]k(x, y) dy \quad (5)$$

$$N_{t+1}(x) = \sigma\gamma n_t(x) + \sigma N_t(x). \quad (6)$$

Here, $n_t(x)$ and $N_t(x)$ are the densities at time t and location x of individuals in the first and second size classes, respectively. By analogy with Eqs. 3 or 4, density dependence operates as $\phi_n = f(r, M_t)$ and $\phi_N = f(R, M_t)$, where f represents either the Beverton-Holt or Ricker function, with n_t replaced by $M_t = n_t + N_t$ and r replaced in ϕ_N by $R = 2r$. The M_t adjustment accounts for the potential importance of both within- and among-cohort interactions in driving density dependence (Myers and Cadigan 1993, Myers 2001), while the R adjustment (where the doubling in population growth rate is quantitatively arbitrary and is generalized below) mimics the tendency of larger individuals to exhibit increased per-capita larval production (DeLacy et al.

FIG. 1. The two fishing strategies explored in this study. In approximating traditional quota- or effort-based management, a given fraction (P_f) of individuals at each shoreline location, x , within the habitat region, L , is protected, while the remaining fraction is fished. Areas outside L are assumed to be unsuitable for the species in question. In approximating management using marine reserves, a given fraction (again P_f) of the shoreline is set aside via one to multiple no-take reserve parcels of length p , separated by unregulated regions of length s where all individuals are fished. The dashed lines represent population densities just prior to fishing, and the solid lines represent densities following fishing. Both sketches are schematic only.



1964, Leaman and Beamish 1984, Love et al. 1990, Plan Development Team 1990, Hunter et al. 1992, Wallace 1998). As in the single-size-class situation, pre- and postdispersal density dependence are distinguished by using population densities either at the location of reproduction, $M_i(y)$, or the location of recruitment, $M_i(x)$, respectively. Individuals of the second size class are assumed to have W times the mass of those of the first size class, where W is set to 1.5 for most model runs. This value matches the average level of individual biomass increase observed in populations protected by reserves where larger size classes often persist more reliably (Polunin and Roberts 1993, Halpern 2003).

Two additional parameters in Eqs. 5 and 6 are used to account concisely for a range of individual (as opposed to population) growth rates and longevities (see also Neubert and Caswell 2000). The individual growth parameter, γ , dictates the rate at which individuals transfer from the first to the second size class, while σ specifies the size-independent natural survivorship rate. Eq. 5, therefore, states that the local population density of the smaller size class at time $t + 1$ is determined by both the rate at which surviving individuals shift out of the first size class into the second, and the rate of larval input by recruitment as progeny from both size classes are redistributed by dispersal over the habitat region. In the case of the larger size class (Eq. 6), its population density is set by the number of smaller individuals that enter the larger size class, and the survivorship of larger adults.

Fishing

In either the single- or the two-size-class situation, fishing is implemented during each time interval after dispersal but before the next bout of reproduction. Thus, fishing mortality begins when fish are roughly one year old. Fishing is also assumed to be regulated according to one of two methods: either via a strategy that approximates traditional quota-based or effort-based fisheries management, or via a network of one to several no-take reserves (Fig. 1). With the traditional management approach, a given fraction of individuals at each shoreline location is fished while the remaining

fraction, P_f , is protected. With the reserve management strategy, a given fraction (again P_f) of the shoreline is set aside and all individuals within it are protected, while the remainder outside reserves are fished without restriction. The lack of restriction provides the most challenging scenario for species persistence when reserves are employed as a management tool. In this second management case the overall reserve area is configured into one to multiple parcels, each of length p ($= P_f L / J$), where J is the number of parcels. If only a single reserve parcel is employed, it is placed in the center of the habitat. If multiple parcels are used, then they are distributed evenly over the habitat region such that the left edge of parcel j is located at

$$x_j = (j - 1)(p + s) \quad (j = 1, 2, \dots, J) \quad (7)$$

where the distance between parcels, s , equals $(L - Jp)/(J - 1)$. Maximal equilibrium yields resulting from each strategy are then expressed as fractions of the equilibrium standing biomass in the absence of spatial population structure, with individuals contributing to yields in proportion to their mass.

RESULTS

Single-size-class population

We begin by examining the single-size-class situation in order to better isolate effects of spatially structured population dynamics (both those of larvae and those of adults) from consequences of size structure and life history. Aside from a few cases with large r where the Ricker form of density dependence does not allow for an equilibrium solution, results are qualitatively identical using either the Beverton-Holt or Ricker forms; therefore only findings for the former are presented. Results indicate that yields peak at intermediate levels of protection, and increase as population growth rates rise (Fig. 2). In the case of traditional management, these yields are the same regardless of whether density dependence operates before or after dispersal. Yields with traditional management also decline slightly as the scale of dispersal (d) increases relative to the habitat length (L), since larger fractions of larvae are lost beyond the edges of the species'

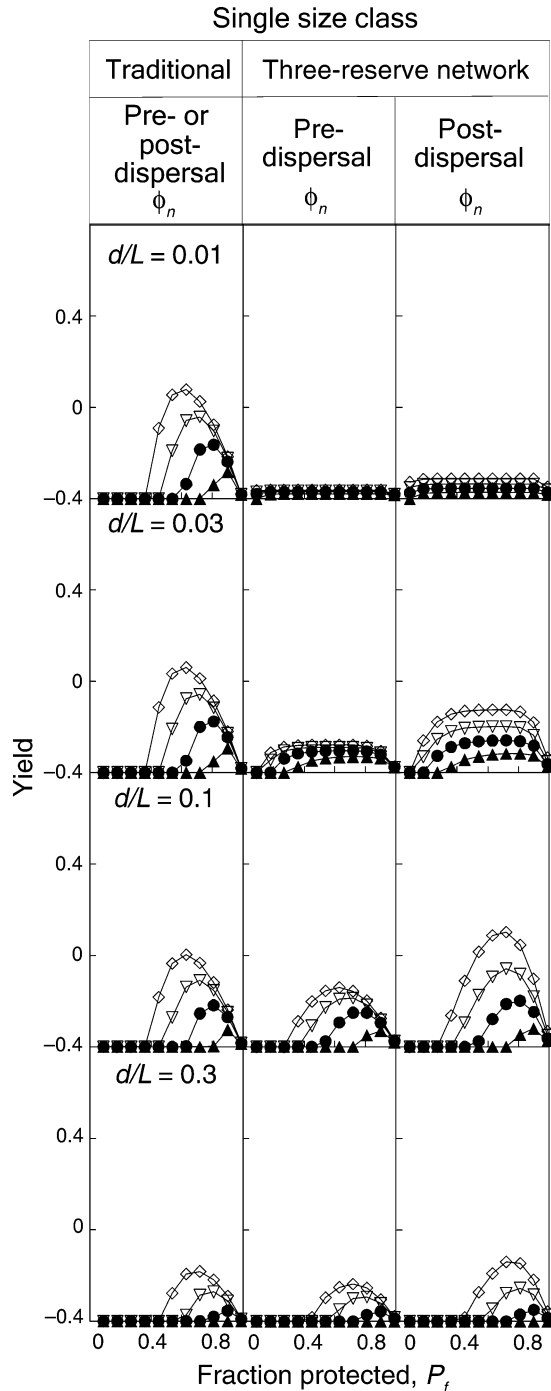


FIG. 2. Yields for a single-size-class population subjected to either traditional or reserve management, as a function of the level of fishery protection (P_f) and the relative scale of larval dispersal (d/L). Trends for several population growth rates are shown ($r = 0.25$ [solid triangles], 0.5 [solid circles], 0.75 [open triangles], 1 [open diamonds]). The fraction of shoreline protected by reserve management is assumed here to be split into three evenly distributed parcels. Unlike when traditional management is used, reserve yields depend on whether density dependence (ϕ_n) operates before or after dispersal. Yields are quantified as the mean fished biomass per length of shoreline relative to the equilibrium biomass per length of shoreline that would be present in the absence of fishing and spatial structuring.

range. This loss of larvae from the range edges (and the accompanying lack of larval delivery from such areas into border regions) is also what causes the decline in adult densities near the limits of the range (but see Sagarin and Gaines 2002). Such patterns support Neubert's (2003) observations regarding the importance of habitat boundaries. We display results for a range of dispersal scales both because different species can exhibit a spectrum of scales (Kinlan and Gaines 2003), and because precise estimates of dispersal distances are rarely known.

Yields using a marine reserve strategy applied to a single-size-class population differ from those for traditional management. Example trends for the case of a three-parcel reserve network are depicted in Fig. 2, although the majority of patterns hold true regardless of the number of parcels. In general, equilibrium yields with reserves are always lower with predispersal density dependence than with postdispersal density dependence. This is because high population densities inside reserves inhibit larval production, thereby reducing overall fishery yields. For the same reason, maximal yields for reserve-managed species with predispersal density dependence are always lower than those possible using traditional management, as has been suggested previously by Hastings and Botsford (1999). In the case of species with postdispersal density dependence, on the other hand, reserve management can elevate maximal yields. Given the three-parcel reserve situation shown in Fig. 1, the increase occurs only for species that produce longer dispersing larvae, and is rather modest. However, as is seen below, when elements of population size structure are considered, the increase can become pronounced.

Population size structure

Consequences of spatially explicit size structure within a population are shown in Fig. 3, which depicts the same model conditions as Fig. 2 except for a two-size-class population, in this case one with a fast-growing, long-lived, life history. Again results are qualitatively identical for both Ricker and Beverton-Holt forms of density dependence (the Ricker form is stable in the two-size-class case for all values of r used), so only findings for the Beverton-Holt form are shown. Two general trends emerge. The first is that differences between the maximal yields for reserve-managed species exhibiting pre- and postdispersal density dependence are magnified. Yields for reserve-managed species with predispersal density dependence are consistently low, while those for species with postdispersal density dependence can be far higher. This suggests that a management strategy relying wholly on reserves is unlikely to be appropriate for species possessing strong predispersal density dependence.

The second major trend observable in Fig. 3, however, is that the maximal yields for reserve-managed species with postdispersal density dependence can be

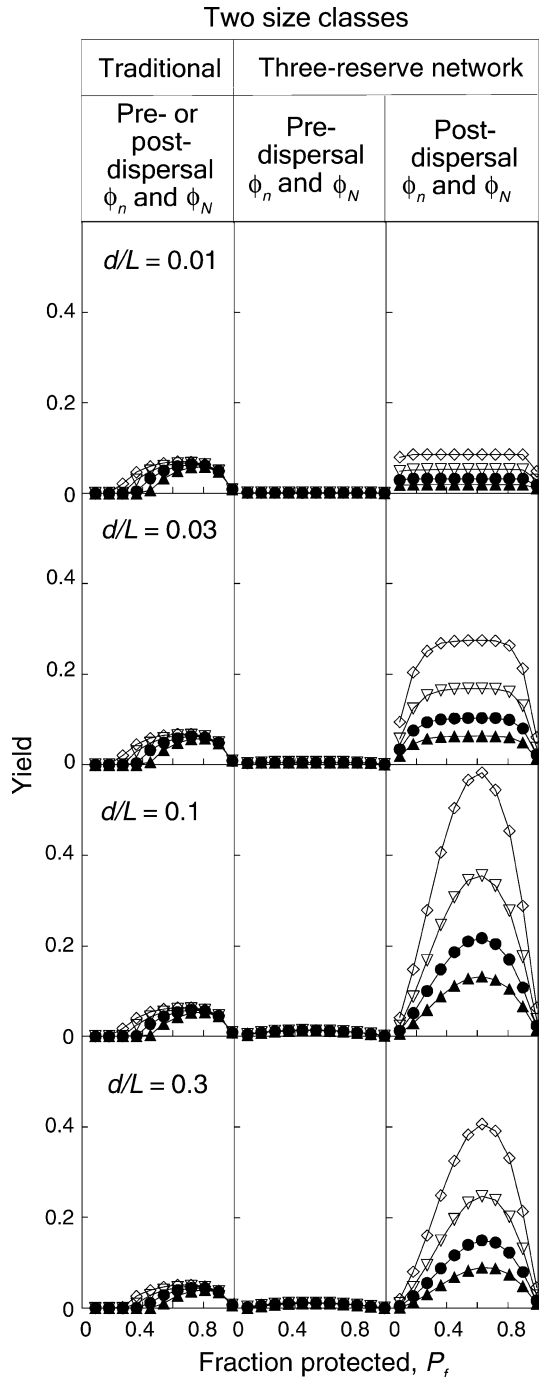


FIG. 3. Yields for a two-size-class population subjected to either traditional or reserve management, as a function of the level of fishery protection (P_f) and the relative scale of larval dispersal (d/L). Trends for several population growth rates for the first and second size classes (r and R , respectively) are displayed as multiple curves ($r = 0.25$ [solid triangles], 0.5 [solid circles], 0.75 [open triangles], 1 [open diamonds]; $R = 2r$ in this figure). The fraction of shoreline protected by reserve management is assumed here to be split into three evenly distributed parcels. Unlike when traditional management is used, reserve yields depend on whether density dependence (ϕ_n and ϕ_N) operates before or after dispersal. Results are for a long-lived, rapidly growing species (longevity, $\sigma = 0.9$; individual growth rate, $\gamma = 0.9$).

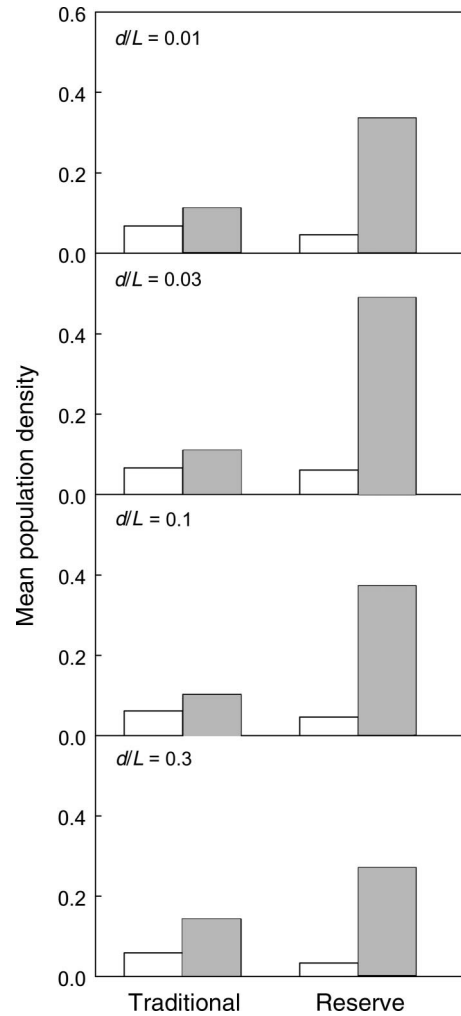


FIG. 4. Marine reserves produce a more right-skewed size distribution with greater numbers of large, highly fecund individuals than does traditional management. Mean population densities in each size class (small individuals, open bars; large individuals, solid bars), averaged over the full length of habitat (L), and normalized by the equilibrium population levels in the absence of fishing and spatial structure, are depicted for levels of fishery protection that maximize yields. Results are for a long-lived, rapidly growing species exhibiting post-dispersal density dependence ($\sigma = 0.9$, $\gamma = 0.9$, $r = 0.5$, $R = 1.0$). Reserve population densities are for a three-parcel network.

substantially higher than the peak yields achievable using traditional management. The higher yields derive in large part from marked shifts in population size structure that arise with reserves (Fig. 4). These shifts in size structure facilitate high levels of total larval production by maintaining larger, highly fecund individuals in the population. The simple effort or quota-based strategy examined in this study compresses a population's size distribution by layering harvest mortality onto natural mortality throughout the size distribution of reproductive adults, decreasing the probability that individuals will reach larger adult size class-

es. By contrast, the reserve strategy increases the longevity of protected subsets of individuals. This produces a more right-skewed size distribution with a relatively greater fraction of large individuals than is achievable using simple controls on average mortality. These right-skewed distributions approach the natural size distributions that would arise in the absence of fishing. Of course, right-skewed distributions can also be achieved by means of size-based auxiliary regulations in traditional management in some fisheries (e.g., where fishing techniques allow for slot fisheries that protect both small and large individuals). In this regard, achieving a true, globally optimal fisheries yield will require consideration of both traditional and reserve approaches. Marine reserves appear nonetheless to have the capacity to provide two general benefits for species that possess postdispersal density dependence: they maximize total larval production by protecting large, highly fecund individuals in high-density sites, while simultaneously minimizing density-dependent population losses in lower-density, harvested sites.

Number of reserve parcels

The model presented here also provides insight into what superficially appears to be an inherent trade-off associated with marine reserves. Yields for species with short-dispersing larvae (small d/L) managed using one or a few reserve parcels can be much lower than yields arising from traditional management (Figs. 2 and 3), despite the presence of higher mean population densities with reserves (Fig. 4). This inverse pattern derives from the inability of reserve-managed species with short-dispersing larvae to export enough larvae to replenish external populations. However, this potential trade-off across fished species is bypassed if the same overall protected fraction of coastline is divided into a greater number of smaller reserve parcels (Fig. 5). Given a sufficiently large number of parcels, maximal yields using reserves for species with postdispersal density dependence typically exceed yields using traditional management regardless of the scale of dispersal. That is, short distance dispersers benefit greatly from a larger number of smaller reserve parcels, while long distance dispersers do as well with many small parcels as they do with fewer large ones of the same total area. This means that management-related difficulties associated with estimating scales of dispersal become essentially irrelevant. In the case of longer-lived species, maximal yields using reserves composed of multiple parcels are predicted under some circumstances to exceed those using traditional management by nearly 60%. Such an advantage associated with increasing the number of reserve parcels may be related to the "chattering control" discussed by Neubert (2003), who showed that regions of rapidly alternating harvest and protection are intrinsic components of the optimal management strategy he explored.

Individual growth rate and longevity

The two-size-class population model employed in this study also demonstrates the role of life history in determining when marine reserves might improve or reduce yields in comparison with traditional management. Results depicted in Fig. 5 for species with postdispersal density dependence indicate that large increases in yields using reserves may be possible for long-lived species, regardless of the rate at which they grow. In contrast, increases in yields for short-lived species are routinely likely to be small even when a large number of reserve parcels are employed.

DISCUSSION

Our findings demonstrate that multiple-parcel reserve networks that protect a large fraction of the coastline may have the capacity to enhance peak yields in many species that have relatively sedentary adults and exhibit postdispersal density dependence. Such benefits are predicted to arise even with only two adult size classes and under the constraint of uniformly spaced reserves. Fisheries benefits could conceivably be greater if fecundity continues to increase with age and size, as it does in many marine species, or with a more optimal spatial configuration of reserves (Neubert 2003). Of perhaps equivalent relevance is the fact that many fished species possess life histories for which the increases in peak yields predicted by Fig. 5 may be possible. In particular, postdispersal density-dependent recruitment, often induced by competitive and predatory interactions or cannibalism, is pervasive and routinely strong in marine fishes as well as in some invertebrates (e.g., Caddy 1986, Caley et al. 1996, Myers 2001, Hixon and Webster 2002, Osenberg et al. 2002). Many temperate reef fishes, including Pacific rockfishes (which also happen to possess long life spans reaching decades; Love et al. 1990), may be especially appropriate examples (Carr and Syms, *in press*) and are the subject of much present attention in the United States. By contrast, the importance of predispersal density dependence is less well supported, particularly for exploited fishes (Rose et al. 2001). Furthermore, even though density-dependent larval production does occur in some harvested species (e.g., sea urchins and decapod crustaceans like crabs and lobsters; Caddy 1986, Levitan 1989, DeMartini et al. 2003), many organisms with predispersal density dependence also show elements of postdispersal density dependence (e.g., crabs can exhibit cannibalism in addition to density-dependent reproduction; Caddy 1986). Finally, as Quinn et al. (1993) note in the context of overexploited stocks, Allee effects in broadcast spawners like sea urchins or abalone mean that reserves can indirectly benefit yields by reducing extinction probabilities when species are at low population densities. This latter example is actually one that involves elements of positive density dependence, which serves as a reminder that the classic

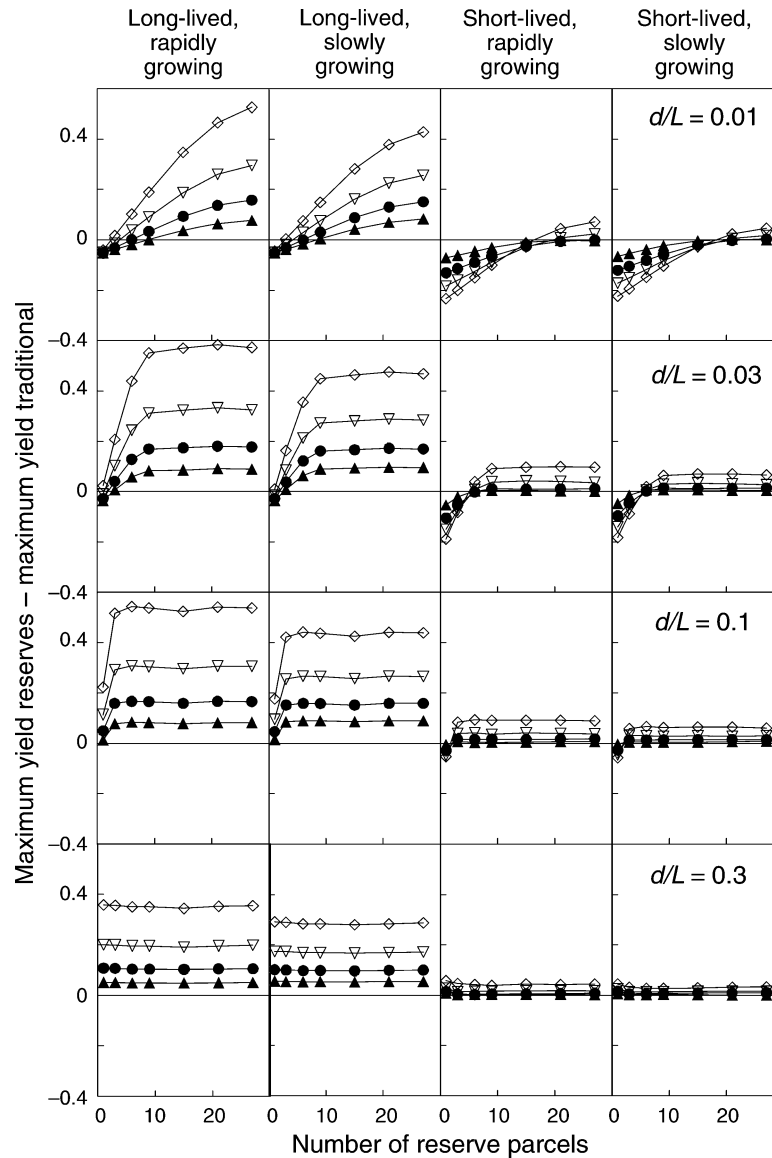


FIG. 5. Dividing a fixed protected fraction of coastline into a greater number of evenly distributed, smaller parcels connected by larval dispersal increases maximal yields. Results are expressed as the difference between the maximal yields using reserve management and the maximal yields using traditional management, as a function of the number of reserve parcels, the scale of larval dispersal (d/L), the population growth rates, r and R , and the longevities and individual growth rates for the species (long- or short-lived [$\sigma = 0.9$ or $\sigma = 0.1$, respectively]; rapidly or slowly growing [$\gamma = 0.9$ or $\gamma = 0.1$, respectively]). Density dependence operates postdispersal only. Symbols are as in Figs. 2 and 3.

formulations of density dependence used in this study (i.e., Ricker and Beverton-Holt) are simply two examples drawn from a range of possible alternatives.

This final point leads us to some further caveats and additional considerations. One important simplification of the model is that it implicitly assumes a shoreline with uniformly suitable habitat. In reality, areas that are potentially accessible to a species or community are located patchily in space and may differ in quality from site to site and over time. Such variation can alter amounts of larval production by one parcel relative to another, can change adult survivorship, growth, and

size relationships, and may modulate levels of connectivity among multiple reserve parcels (Carr and Reed 1993, Crowder et al. 2000, Shepherd and Litvak 2004). Certain regions may also be differentially important to the persistence of a species (as in spawning or nursery grounds). Habitat considerations extend offshore to the oceanographic environment to impact larvae as well. Although patterns of larval survivorship and transport are held constant in the model, in nature these processes are highly variable and can introduce considerable stochasticity into a species' population dynamics (Lewin 1986, Lenarz et al. 1995, Ralston and

Howard 1995, Miller and Sydeman 2004). Unfortunately, although such complexities are important and clearly have the capacity to alter predicted fishery yields (potentially seriously), generalizations regarding their effects depend on species-specific sensitivity to habitat characteristics and therefore fall outside the reach of our present approach.

An additional important simplification of the model, as already mentioned, is that it assumes adults are sedentary. If adults move across reserve boundaries, there can be a loss of reproductive biomass from protected areas (Sladek Nowlis and Roberts 1999), and thus a decline in a population's reproductive potential. Such is particularly the case if exiting individuals are harvested before they spawn even once. Although adults of many fished species have very limited home ranges (e.g., Griffiths and Wilke 2002, Lowe et al. 2003, Starr et al. 2004), recent data also suggest that individuals of what have been considered sessile species sometimes undergo fairly extensive "excursions" to other locations (Egli and Babcock 2004). This possibility has implications for model applicability in certain circumstances and suggests that a closer examination of the issue of adult movement is warranted.

Such a closer examination begins with the observation that a loss of adults from a reserve operates much like a loss of reproductive capacity from that reserve. This in turn suggests that negative consequences of adult movement can be mimicked in our model by a reduction in population growth rate, especially the value of R which is associated with larger individuals that would otherwise be differentially protected if they remained within a reserve (Fig. 4). We emphasize that this approach does not account for any harvest benefits of adult spillover, which presumably would arise as once-protected adults that have left reserves are caught by fishers, elevating their catch. In this sense the analysis is conservative.

As one might expect, the underlying effect of a reduced population growth rate is to reduce maximal yields. However, this effect is also intertwined with the relative magnitudes of the body masses of individuals in the two size classes (W). In general, the rate of increase in fecundity across size, relative to the rate of increase in body mass across size, plays a role in determining the yields that arise when using reserves. Steeper fecundity/body mass relationships facilitate better reserve performance. This issue has been almost entirely ignored in the marine reserve literature, but is addressed in Fig. 6, where the x - and y -axes are normalized to enable the collapse of results from a full spectrum of combinations of d/L , r , R , and W onto nearly coincident curves. Note that these plots assume postdispersal density dependence and a 27-parcel reserve network, which exploits the relative insensitivity of results to d/L when there are large numbers of parcels (Fig. 5). We have also relaxed the previously fixed

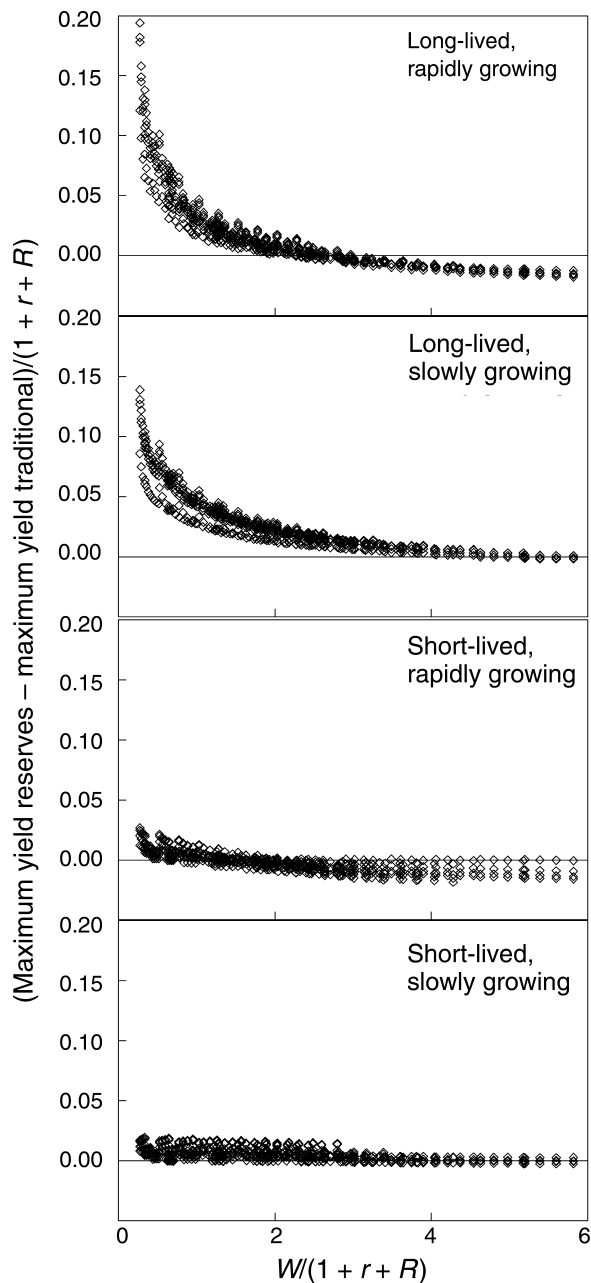


FIG. 6. Effects of varying the relationship between the rate of increase in body mass with size (W) and the rate of increase in fecundity with size (as indexed by the relative magnitudes of the population growth rates, R and r), which can also serve as a preliminary means of exploring consequences of adult movement. Longevities (σ) and individual growth rates (γ) are quantified as in Fig. 5. Among the parameters that are independently varied in this figure, r ranges from 0.25 to 1, R ranges from 0.3 to 2, and W ranges from 1.1 to 10. In calculating the maximal reserve yields, 27 parcels are assumed, which minimizes sensitivity to the scale of larval dispersal (d/L). This, together with the normalization $(1 + r + R)$, enables all points to be collapsed onto the common bands shown. Density dependence operates after dispersal.

relationship of $R = 2r$ to examine a broad range of relative population growth rates.

In interpreting Fig. 6, regions where the band of points falls above zero correspond to conditions where reserves are predicted to improve yields relative to traditional management. These results indicate that adult movement, which operates as a rightward shift in the panels of Fig. 6, reduces but need not eliminate the capacity of reserves to increase yields. Indeed, if a population begins with large enough growth rates, then a modest reduction in R due to adult movement will not result in a far enough rightward shift along the curves of Fig. 6 for y-axis values to drop below zero. Such modest declines in R may not be uncommon given that the highest yields using reserves occur when large fractions of the coast are set aside (Figs. 2 and 3), which means that even with rather high levels of adult movement, many individuals leaving their original reserve parcel may find their way to other parcels and thus retain some protection.

The results of Fig. 6 encompass a full spectrum of biologically relevant parameter values, including maximal annual reproductive rates (e^r and e^R) ranging from approximately 1.25 to 7.5, in accordance with estimates for fished populations worldwide (Myers 2001). In conjunction with values of W that range from 1.1 to 10, these numbers account effectively for the fecundity/body mass relationships reported for many fished species. For example, a typical egg production vs. body mass curve might show a 1.3 to 2.5-fold increase in the former, for a 1.5-fold increase in the latter, although size-specific production levels at least 10 times higher are possible (Delacy et al. 1964, Love et al. 1990, Plan Development Team 1990, Hunter et al. 1992). Such values (conservatively excluding the above extreme example of a 10-fold increase) correspond to a range of $W/(1 + r + R)$ of approximately 0.3–0.9, which for long-lived species falls well within the parameter space of Fig. 6 where reserves may enhance yields. This is still true even if some allowance for the effects of adult movement is made.

Conclusions

Most previous theoretical studies predict only modest, if any, potential improvements in yields using reserves, and only for fisheries that have been already overexploited (Gerber et al. 2003). Those studies that do imply reserve-induced enhancements in yields are also most commonly those that address consequences of uncertainty in recruitment and/or management (e.g., Sladek Nowlis and Roberts 1999, Mangel 2000). Although such issues of uncertainty are important, the capacity of marine reserves to reduce their detrimental impacts has been explored elsewhere (Lauck et al. 1998). As a consequence, we have instead focused our efforts on understanding interactions among several remaining elements of real populations that can affect reserve effectiveness.

We find that three interconnected factors are particularly fundamental to reserve function, even though most studies consider only one or two of them. First, it is clear that elevated reproductive capacity of larger individuals is important. Of the models that are not concerned primarily with uncertainty, at least two others besides ours predict potential improvements in yields even for stocks that are not overexploited (Sladek Nowlis and Roberts 1999, Apostolaki et al. 2002). Like ours, each of these models includes explicit mechanisms (i.e., size structure and reproduction/mass relationships) for appropriately representing increases in fecundity with size. Second, life history (e.g., the type of density dependence) has important effects, and these effects can interact with patterns of fecundity (e.g., through individual growth rates) in affecting outcomes of reserve implementation (Quinn et al. 1993, Hastings and Botsford 1999, St. Mary et al. 2000). Third, the functioning of marine reserves is inexorably tied to the spatial nature of larval dispersal. This is an important observation since the vast majority of marine reserve models account for dispersal, if at all, in a simplified, usually nonspatial fashion, most typically via a “larval pool” approximation (also implicit in standard stock-recruitment analyses), or via a metapopulation construct (e.g., Polachek 1990, Russ et al. 1992, DeMartini 1993, Mann et al. 1995, Guenette and Pitcher 1999, Crowder et al. 2000, Shirai and Harada 2003). However, without accounting for physically reasonable, spatially structured patterns of larval redistribution, levels of connectivity among subpopulations are potentially misrepresented. For example, in the case of larval pool models, self-recruitment to reserves may be underestimated, which can reduce predicted adult densities and thus lower the expected reproductive output from reserves. It is in fact possible that one reason that Sladek Nowlis and Roberts (1999) found only a modest increase in yields with reserves, while Apostolaki et al. (2002) predicted much greater increases, is that the former used a larval pool model while the latter incorporated a somewhat more structured form of organism redistribution. Such inclusion of spatial characteristics of dispersal may be even more critical in the face of strongly advective flows (Gaines et al. 2003).

The general model framework presented above has purposely ignored many details in order to effectively isolate interactions among key factors, and to enable exploration of the entire model parameter space. The use of this strategy is what has enabled the fundamental importance of size structure, life history traits, and spatial structure (in both adult pattern and larval dispersal) to be revealed and defined. Although at least one other study to our knowledge (Stockhausen et al. 2000) has also included the above three processes, their model incorporated a sufficiently large number of parameters that overarching trends are difficult to detect. As such, findings of the present study represent an explicit step

forward in understanding how marine reserves operate and the conditions under which they may have benefits.

This is not to imply that factors that remain unexplored in our modeling are not important. In addition to the issues of adult movement and habitat quality discussed above, most species also possess more than just two effective size classes, and, although preliminary examinations suggest that adding more classes does not strongly affect results, further attention is warranted on this topic. We have also made no attempt to examine the time course of a fishery's response to changes in management strategy. This should not be construed as an expectation that impacted fisheries will recover instantaneously if a more effective strategy is implemented; lags in the maximization of yield and cases where a preferred stable state cannot be reached from the current one will surely arise. We have additionally ignored economics, which can have striking consequences by layering other considerations (e.g., the cost of catching fish under different management scenarios) onto any potential gains in yields that reserves may bring (e.g., Smith and Wilen 2003). This may particularly be the case if traditional management and reserve methods are meshed to control harvest in ways that are more complex than those represented in our model. Further work coupling economics and fisher behavior with spatially explicit population models (including ones addressing species interactions; Micheli et al. 2004) and empirical field data is critical to testing and extending the results of the core construct presented here. Such future research will enable us to both understand better the potential benefits of marine reserves, as well as begin to place bounds (as noted by Rose and Cowan 2003) on what represents reasonable stakeholder expectations.

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