INCLUDING SPECIES INTERACTIONS IN THE DESIGN AND EVALUATION OF MARINE RESERVES: SOME INSIGHTS FROM A PREDATOR-PREY MODEL

Fiorenza Micheli, Priyanga Amarasekare,
Jordi Bascompte, and Leah R. Gerber

ABSTRACT

Conservation of marine species through fisheries management and no-take marine reserves have focused primarily on single species, but such protection may influence the target species' predators, prey, competitors, or mutualists. Conversely, successful protection may depend on responses of these other species. Empirical data and previous theory indicate that fisheries status and life-history attributes strongly influence species' responses to protection. Both direct effects and indirect effects of protection (through species interactions) have been documented. A predator-prey model depicting the dynamics of two species in a two-patch habitat (a no-take reserve and a fished area) revealed conditions under which the predator and prey may decline after reserve establishment. Not surprisingly, model results suggest that management scenarios and life-history traits leading to high predator population growth are more likely to produce prey declines following reserve establishment. Interestingly, trade-offs between enhancing predator and enhancing prey occurred at low fishing intensities regardless of the prey and predator life-history traits. At high fishing rates, reserve establishment generally outweighed predation effects and resulted in increased abundance of both predator and prey. Simple spatial models can help determine the range of possible responses of interacting species to protection and can yield some general insights for their management.

Marine reserves, portions of the coastline or ocean set aside and protected from fishing and other human uses, have recently received much attention as a means of conserving marine biodiversity and restoring depleted fish stocks (Bohnsack, 1996; Palumbi, 2001). One of the advantages of marine reserves over traditional fishery management is that reserves protect not only target species but also habitat, nontarget species, and the suite of biotic interactions within the protected area (Roberts and Polunin, 1993; Agardy, 1997; National Research Council, 2001). Although this multispecies focus of reserves is frequently discussed, few empirical or theoretical studies have addressed effects of protection on species interactions explicitly. A majority of empirical studies of marine reserves have compared abundance, biomass, or diversity of multispecies assemblages in reserves and unprotected areas or in single areas before and after the establishment of reserves (Boersma and Parrish, 1999; Halpern, 2003). In contrast, few studies have focused on the effects of reserves on ecological processes and interactions underlying community structure and function (Boersma and Parrish, 1999; but see Castilla, 1999; Shears and Babcock, 2002; Fanshawe et al., 2003, and references therein).

The bulk of the theory on marine reserves focuses on population dynamics from a single-species perspective (Gerber et al., 2003). Several investigators have evaluated multispecies issues indirectly by comparing effects of reserves on species with different life-history characteristics (e.g., DeMartini, 1993; Attwood and Bennett, 1995; Sladek Nowlis and Roberts, 1999), but their models do not explicitly include species interactions. A review of existing models pertaining to marine reserves (Gerber et al., 2003) found only one modeling approach that focused explicitly on multispecies interactions

(Walters et al., 1997, 1999; Walters, 2000). These investigators use spatially explicit Ecosim models (Ecospace) to estimate changes in biomass after reserve establishment on the basis of trophic interactions. A key general prediction of Ecospace models is that prey densities tend to be low where predator densities are high, such as within protected areas. Moreover, potential benefits of reserves can be counteracted by high movement rates and by concentration of fishing effort along the reserve edges, which can create prey gradients that attract predators outward from the reserve (Walters et al., 1999). This general model suggests that dispersal, trophic responses, and spatial fishing-effort responses are all likely to reduce the efficacy of small marine reserves (Walters, 2000).

The establishment of no-take marine reserves can influence populations of multiple species and the structure of whole communities through a suite of direct and indirect effects. Species may respond differently to protection depending on the intensity of exploitation they are subject to outside the reserve and prior to its establishment, their life-history characteristics, and their larval, juvenile, and adult dispersal ability (Gerber et al., 2002). Meta-analyses of studies of fish assemblages from marine reserves revealed that differential responses of fish families and species to marine reserve establishment were correlated with whether taxa were fishery targets, with body size, and with trophic level (Mosqueira et al., 2000; Micheli et al., in press). Fisher and Frank (2002) analyzed 31-yr time series of abundances of over 70 fish species within an area closed to fishing and an adjacent reference area on the Scotian Shelf, Canada. Fish community compositions were significantly different before and after the implementation of the fishing closure, and several species contributed to driving these differences. A preliminary review of life-history attributes for 16 species in this data set indicated that these different trajectories may be related to dispersal ability of the species (Fisher and Frank, 2002).

Protection can also influence species indirectly, through its effects on habitat and species interactions. For example, the establishment of a marine reserve designed to protect a particular species may influence that species' predators, prey, competitors, or mutualists. Indirect effects of predation on community structure, including trophic cascades, have been documented extensively in the marine environment (Pace et al., 1999; Pinnegar et al., 2000), and such interactions can influence all types of communities and can occur as a result of protection in marine reserves (Pace et al., 1999; Pinnegar et al., 2000). The question remains, however, of what combinations of species traits, environmental conditions, and human interventions are more likely to lead to counterintuitive effects of protection, including species declines and losses following the establishment of no-take reserves.

As a hypothetical example of how trophic interactions occurring within marine reserves can lead to counterintuitive effects of protection, let us consider two fish species with distinct dispersal abilities; species A has limited dispersal, and species B is highly mobile. The establishment of a reserve might be followed by an increase in abundance and a shift to larger size within the reserve for species A, but not for species B if the size of the reserve does not encompass the spatial extent of its movements and individuals are thus lost from the reserve. If species A and B do not interact, differential responses of species A and B to decreased fishing intensity within the reserve might have been accurately predicted on the basis of information about the life history and dispersal range of each species independently. If species B is prey to species A, however, its populations may undergo further decline because of increased predation intensity within the reserve. In addition, species A may also decline, with some time lag, because of feedback between the two species through the predator functional and numerical responses. Thus, the nonlin-

earity introduced by complex biotic interactions may lead to outcomes that are radically different from expectations about reserve management based on single species.

Counterintuitive population declines following the establishment of marine reserves may pose trade-offs between the primary conservation and management goals of specific reserves. Many pairs of species valued by fisheries are known to be linked through trophic interactions—e.g., abalone and lobsters; shellfish and crabs, cephalopods and carangid fishes—where successful enhancement of one species or trophic level might result in declines and losses of other valuable or threatened species. For example, sea otters in coastal marine communities of the Pacific Northwest control invertebrate herbivore populations, increasing productivity and pathways through the food web and the structural complexity in the system (Estes et al., 1998), but they prey so heavily on abalone that fewer abalone may be present in reserves with sea otters than in areas where abalone are fished but sea otters are absent (Fanshawe et al., 2003).

Conservation and management of multispecies assemblages requires better understanding of and greater predictive ability about how protection may directly and indirectly influence different species under different reserve configurations and environmental conditions. In the study reported here, we used a simple two-patch predator-prey model to examine the combined effects of reserve size and fishing intensity outside reserves on the population dynamics and long-term persistence of a prey and a predator characterized by different life histories and dispersal abilities. This simple heuristic model does not capture all the biological complexities of any two-species system, let alone of assemblages of multiple interacting species, but conceptually simple models can yield qualitative rules for the design and evaluation of reserves that can apply to a broad set of situations and can generate hypotheses to be tested empirically. In addition, these general models can represent an important first step in identifying the key variables and processes to be included in more complex and biologically realistic models.

Our approach was to build a two-patch predator-prey model that incorporates two types of parameters. The first set of parameters includes life-history characteristics such as prey growth rate, predator attack rate, and larval dispersal. The second includes management criteria, such as the fishing rates on prey and predators outside the reserve and the fraction of the total area allocated to the reserve.

We used this model to explore the implications of marine reserves from the perspective of consumer-resource interactions. In particular, we asked how consumer-resource dynamics vary with (1) the life history and dispersal characteristics of the species, (2) reserve size, and (3) fishing intensity outside the reserve. Our goal was to develop simple predictions about what combinations of these parameters may, in theory, lead to counterintuitive results of reserve establishment, such as decline or loss of one or both species linked though trophic interactions.

The Model

To determine how marine reserves might influence consumer-resource interactions, we used a coupled predator-prey model in which the prey and the predator had different dispersal abilities (see, e.g., Reeve, 1988). This model builds on a single-species model to determine what combinations of life-history parameters, reserve size, and fishing intensity are likely to lead to population persistence and/or increased fishery yields (Gerber et al., 2002). We used a discrete time model of a population with nonoverlapping generations (May, 1974; Hassell, 1978) because it captures the seasonal, pulsed reproduction

characteristic of many marine species better than do models assuming continuous reproduction. This model applies explicitly to nonoverlapping generations for any population whose dynamics can be approximated as a discrete recursion (Levin and Goodyear, 1980; Ludwig and Walters, 1981; Ludwig, 1998). The approximation for overlapping generations and age-structured populations is best if the population is at a stable age distribution.

In our model, the total predator and prey population was divided into two areas, the reserve and the unprotected area, where fishing removed fixed fractions of the prey and predator populations (Fig. 1). For example, the reserve might be a portion of the coastline that was set aside as a refuge and the unprotected area the surrounding coastline that was open to fishing. In contrast to patchy terrestrial environments, no distinct matrix separates suitable from unsuitable habitat. Under this scenario, the reserve and the unprotected area are separated by a boundary that is permeable to dispersing planktonic larvae but not to adults.

Using the results of Gerber et al. (2002) as a starting point, we used our model to ask how including a species interaction might alter predictions about population responses to protection from the single species model. Their systematic exploration of results from 5120 different parameter combinations indicated that exploitation rate and population growth rate were the most important parameters for predicting population responses to reserve establishment. We examined joint effects of varying reserve size and fishing regime on the dynamics of species characterized by different dispersal ability and linked through a predator-prey interaction. We used two measures of the species' responses to protection: (1) the ratio between abundances before and after reserve establishment and (2) the ratio of the densities of each species inside and outside the reserve. The choice of these response variables was based on the type of data generally collected in empirical studies, i.e. either abundance or biomass of species or groups of species within reserve and at "reference," fished locations or before and after the establishment of a reserve (Halpern, 2003).

We considered the situation in which the prey species was sedentary and the predator species had a dispersing stage. An example of a predator-prey system with these characteristics is the abalone-lobster-sheephead interaction in the eastern Pacific Ocean. These species support important fisheries along the coasts of California. Most abalone (*Haliotis* spp.) stocks have been severely depleted by overfishing. Much effort is devoted to conservation and replenishment of abalone stocks, including establishment of harvest refugia and transplanting of individuals into depleted areas (Tegner, 1993). Abalones are sedentary as adults and have short-lived larvae (5–9 d) with limited dispersal ability (Tegner, 1993). One strategy for promoting abalone recovery is the aggregation of broodstock within closed marine protected areas (Tegner, 1993). Increased aggregation is desirable because the species exhibits poor fertilization success at low densities (Babcock and Keesing, 1999) and limited larval dispersal. A suite of predators prey upon abalones in southern California, including the spiny lobster (*Panulirus interruptus*) and sheephead (*Semicossyphus pulcher*) (Tegner and Butler, 1985). Both lobsters and sheephead produce larvae that spend several weeks in the plankton and disperse over distances of hundreds of kilometers (Cowen, 1985; Pringle, 1986). Lobster, and possibly sheephead, adults are sedentary relative to the distances potentially traveled by their larvae.

We assumed that predator dispersal occurred in the larval stage and that adults were sedentary. The predators searched randomly for prey and exhibited a linear functional response, providing mathematical tractability at the cost of abstracting the biological
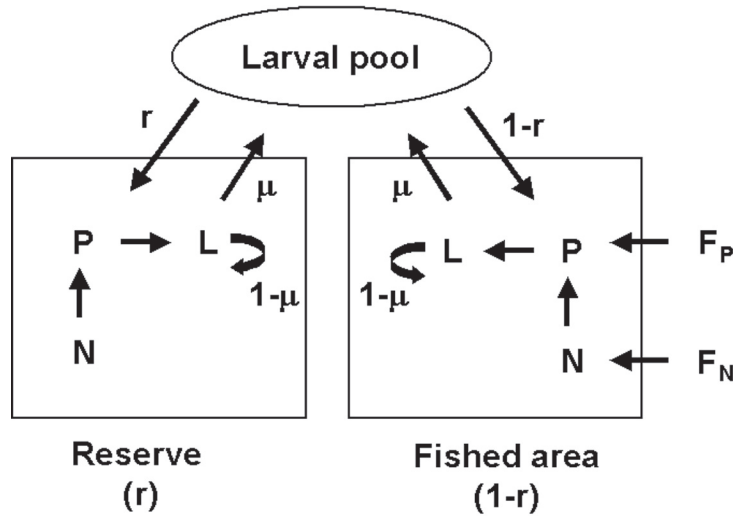
Figure 1. Schematic representation of the two-patch predator-prey model. A fraction r of the habitat is included within a no-take reserve, whereas fractions F of both the prey and the predator are fished in a fraction $1 - r$ of the habitat. The prey (N) does not have a dispersing stage. A fraction μ of the predator (P) larvae (L) leaves each patch to join a common larval pool. A fraction r of the larvae in the common larval pool recruits to the no-take reserve, and a fraction $1 - r$ to the fished area.

details of how the predator's attack rate depends on prey density (see Discussion). We describe prey dynamics using the Ricker model (Ricker, 1954). The Ricker formulation of self-limitation is frequently used in single-species fishery models (Ricker, 1977). Ricker-type models are common in the fisheries literature because they are simple to work with yet generally capture the most important features of fish population dynamics (Levin and Goodyear, 1980; Ludwig and Walters, 1981; Ludwig, 1998; Mangel, 1998).

We considered larval dispersal to be diffusive (random) rather than directed. A fraction μ of predator larvae dispersed from the reserve and the unprotected area to a common pool, whereas a fraction $1 - \mu$ remained within each area (Fig. 1). From this mixed larval pool, a fraction r recruited to the reserve and a fraction $1 - r$ recruited to the unprotected area. Larvae inside and outside the reserve matured into adults with a survival probability s. Prey and predators were fished outside the reserve. A fraction F_N of the prey individuals that escaped predation was fished, and a fraction F_P of the surviving adult predators was fished. Thus, fishing creates an additional source of mortality for predators and prey that live outside the reserve.

Predator-prey dynamics inside (reserve, R) and outside (unprotected, U) the reserve were described by

$$N_R(t+1) = N_R(t)\exp\left[\lambda\left(1 - \frac{N_R(t)}{rK}\right) - aP_R(t)\right]$$

$$L_R(t+h) = \alpha N_R(t)\left[1 - \exp(-aP_R(t))\right]$$

$$P_R(t+1) = s\left[(1-\mu)L_R(t+h) + r\mu\left(L_R(t+h) + L_U(t+h)\right)\right]$$

$$\text{(1)}$$

$$N_U(t+1) = \left\{ N_U(t)\exp\left[\lambda\left(1 - \frac{N_U(t)}{(1-r)K}\right) - aP_U(t)\right]\right\}(1 - F_N)$$

$$L_U(t+h) = \alpha N_U(t)\left[1 - \exp(-aP_U(t))\right]$$

$$P_U(t+1) = \left\{ s\left[(1-\mu)L_U(t+h) + (1-r)\mu\left(L_R(t+h) + L_U(t+h)\right)\right]\right\}(1 - F_P)$$

$$\text{(2)}$$

where $N_R(t)$ and $N_U(t)$ are the prey densities at time t, $L_R(t + h)$ and $L_U(t + h)$ the larval predator densities, and $P_R(t)$ and $P_U(t)$ the adult predator densities in the reserve and in the unprotected area respectively. For the predator species, each time step in the model was divided into two intervals, a larval phase from t to $t + h$ and an adult phase from $t + h$ to $t + 1$. The parameters λ and K are the prey growth rate and the prey carrying capacity respectively. The parameter r represents the fraction of the total area that was allocated to the reserve. We established a link between life-history parameters and reserve size by expressing r as the fraction of the prey carrying capacity for the whole environment that was contained within the reserve. Parameters a, s, and α represent the predator attack rate, the predator larval survivorship, and the number of predator larvae produced per prey eaten, respectively. Quantities F_N and F_P are the fractions of prey and predators fished in the area outside the reserve.

We can nondimensionalize the model by using the following scaling relationships:

$$N'_R = \frac{N_R}{K}, L'_R = \frac{L_R}{\alpha K}, P'_R = \frac{P_R}{\alpha sK}, N'_U = \frac{N_U}{K}, L'_U = \frac{L_U}{\alpha K}, P'_U = \frac{P_U}{\alpha sK}, d = a\alpha sK$$

Substituting these relationships into equations (1) and (2) and dropping the primes lead to the nondimensional system:

$$N_R(t+1) = N_R(t)\exp\left[\lambda\left(1 - \frac{N_R(t)}{r}\right) - aP_R(t)\right]$$

$$L_R(t+h) = N_R(t)\left[1 - \exp(-aP_R(t))\right]$$

$$P_R(t+1) = s\left[(1-\mu)L_R(t+h) + r\mu\left(L_R(t+h) + L_U(t+h)\right)\right]$$

$$\text{(3)}$$

$$N_U(t+1) = \left\{ N_U(t)\exp\left[\lambda\left(1 - \frac{N_U(t)}{(1-r)}\right) - aP_U(t)\right]\right\}(1 - F_N)$$

$$L_U(t+h) = N_U(t)\left[1 - \exp(-aP_U(t))\right]$$

$$P_U(t+1) = \left\{\left[(1-\mu)L_U(t+h) + (1-r)\mu\left(L_R(t+h) + L_U(t+h)\right)\right]\right\}(1 - F_P)$$

$$\text{(4)}$$

The nondimensional parameter a is a composite of the predator attack rate a, predator conversion efficiency α, predator larval survivorship s, and prey carrying capacity K. The prey density N is expressed as a fraction of the prey carrying capacity K, i.e., $N = [0,1]$. Similarly, the predator larval density is expressed as a fraction of the prey carrying capacity scaled by the predator efficiency and adult predator density. Therefore, if $\alpha \leq$

1 then $L = [0,1]$; otherwise $L = [0, L]$ where $L > 1$. Adult predator density is expressed as a fraction of the prey carrying capacity scaled by the predator efficiency and larval survivorship. Larval survivorship s is always < 1; therefore $P = [0,1]$. The nondimensionalization provides us with a model that retains only the key life history (λ, a, and μ) and management parameters (r, F_N, F_P). This simplification allows us to explore the influence of life-history traits and different management measures, separately and in combination, on the long-term dynamics of the predator-prey system.

To investigate the role of each life-history parameter in determining the predator and prey population responses to combinations of reserve size and fishing intensities, we changed one parameter value at a time while keeping the others constant at $\lambda = 1.5$, $a = 2.5$, and $\mu = 0.50$. The parameter values we examined were 0.5, 1, and 1.5 for λ; 2, 2.5, 3, and 4 for a; and 0.05, 0.50, and 0.95 for μ. Larger values of λ and a lead to cycles and chaos, whereas smaller values lead to the extinction of one or both species. The fraction of habitat set aside as a no-take reserve started at 0.1 and was increased to 0.9 in steps of 0.1. Fishing rates were set at 0.15, 0.45, and 0.75, for both the predator and the prey. For each parameter combination, we obtained the stationary values for the prey and predator total population size when the entire population was subject to fishing and after a fraction r of the population was not fished. In an additional set of simulations, the effects of reserve establishment were quantified by calculation of the ratios between the predator and prey densities inside and outside the reserve (i.e., their population size divided by the fraction allocated to the two patches, r for the reserve and $1 - r$ outside the reserve). Ratios between stationary abundances before and after reserve establishment or inside and outside the reserve equal to 1 indicate that setting aside a fraction of the population did not affect total abundances or relative densities under that particular fishing rate.

RESULTS

Responses of predator-prey dynamics to variation in reserve size and fishing intensity were complex but revealed two general points: (1) management measures that result in increased abundances for one species may be detrimental for other species, and (2) the occurrence of detrimental effects of protection depends on combinations of both life-history (e.g., prey and predator growth rate, attack and dispersal rates of predator) and management parameters (e.g., reserve size, fishing intensity). Therefore, species declines in any predator-prey system are likely to occur only for particular combinations of reserve configuration and fishing intensity in areas surrounding reserves.

At low fishing rates ($F_N = F_P = 0.15$), allocating increasing fractions of the habitat to the no-take reserve has opposite effects on the prey and predator responses for all combinations of life-history parameters (Figs. 2,3,4, panels A,B). In all cases, reserve establishment increases only prey abundances when less than half of the habitat is included in the reserve. Even at the lowest fishing intensities, the predator requires large fractions allocated to the reserve to overcome the detrimental effects of fishing. When the reserve is sufficiently large to increase the predator population size, however, predators control prey abundances, and protection results in no change, at low predator attack rates (Fig. 3A), or lower population sizes for the prey in all other cases (Figs. 2A,B,3B,4A,B).

At high fishing rates, reserve establishment results in higher abundances for both species under some parameter combinations. In particular, benefits to both species occur at $F_N = F_P = 0.45$ when a large fraction of the habitat is allocated to the reserve and predator population size is controlled by either low prey growth rates (Fig. 2C) or low predator
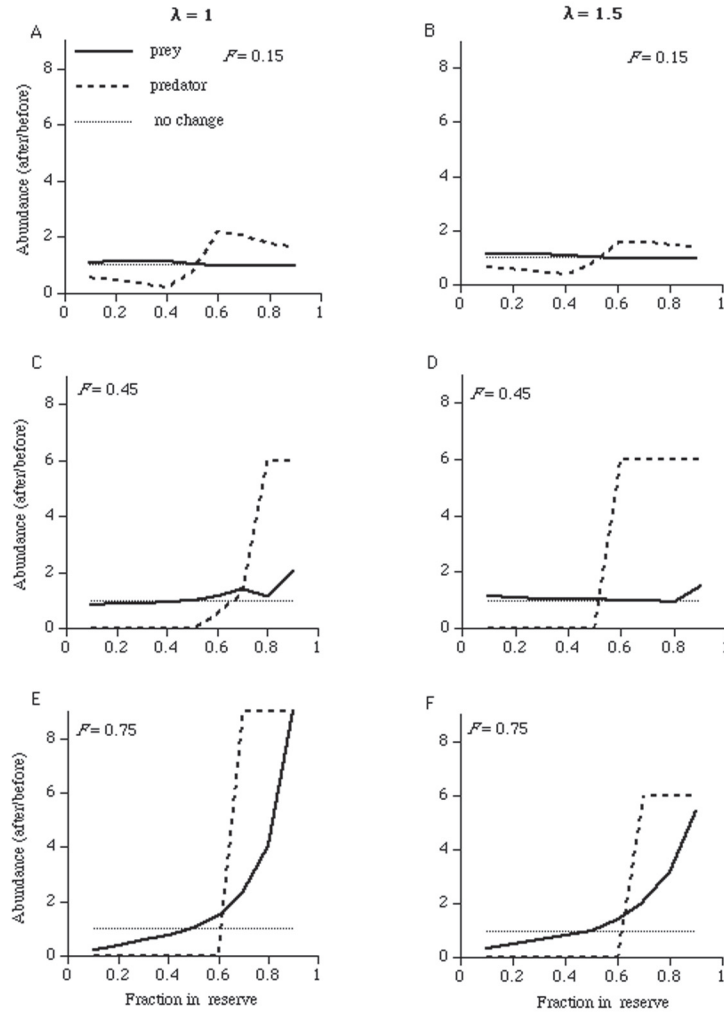
Figure 2. Effects of reserve size and fishing rates on prey and predator populations for different values of the prey population growth rate ($\lambda = 1$, panels A,C,E; $\lambda = 1.5$, panels B,D,F). Effects of protection were quantified as the ratio between total population abundances (sums of populations in the reserve and the fished area) after and before the reserve establishment. Abundance ratios are plotted as a function of the fraction of the total area within the reserve (r) for fishing rates (F) set at 0.15 (A,B), 0.45 (C,D), and 0.75 (E,F). Other parameters are $a = 2.5$ and $\mu = 0.5$.

attack rates and conversion efficiency (Fig. 3C). In addition, high predator larval dispersal has a similar effect through depletion of the common larval pool (Fig. 4C). Results for the lowest prey growth rate ($\lambda = 0.5$) are qualitatively similar to those for $\lambda = 1$ and are not reported. In contrast, traits favoring large predator population sizes—large prey growth rates (Fig. 2D), large predator attack rates and conversion efficiency (Fig. 3D), and low larval dispersal (Fig. 4D)—result in prey declines even at large reserve sizes. Results for the highest predator attack rate and conversion efficiency ($a = 4$) are qualitatively similar to those for $a = 3$ and are not reported.
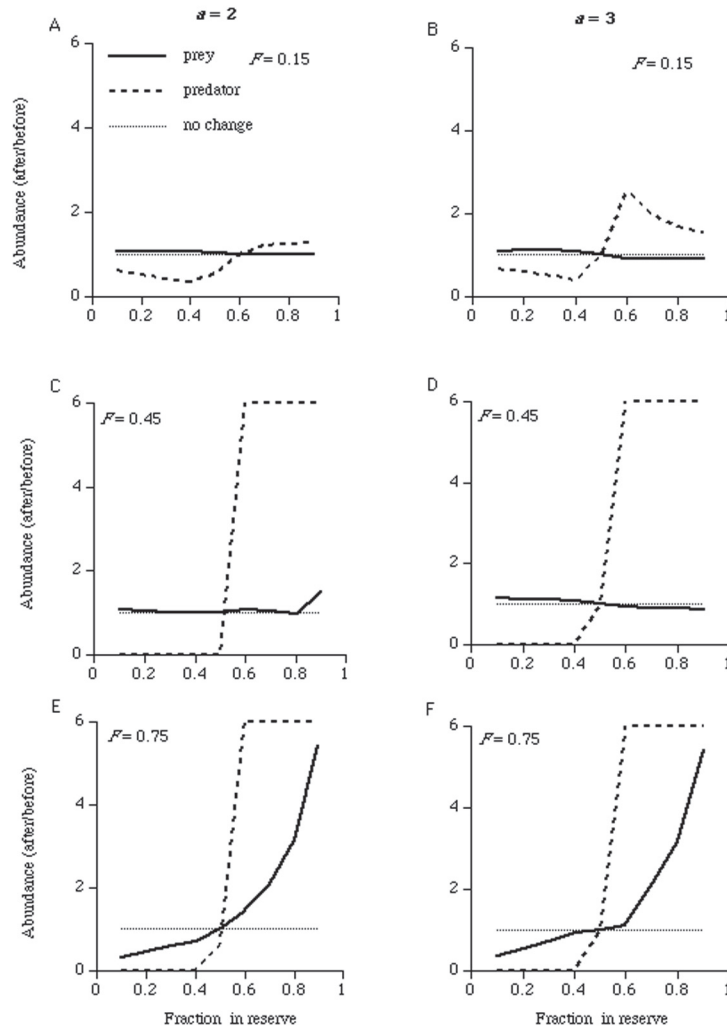
Figure 3. Effects of reserve size and fishing rates on prey and predator populations for different values of the predator attack rate and conversion efficiency ($a = 2$, panels A,C,E,; $a = 3$, panels B,D,F). Effects of protection were quantified as the ratio between total population abundances (sums of populations in the reserve and the fished area) after and before the reserve establishment. Abundance ratios are plotted as a function of the fraction of the total area within the reserve (r) for fishing rates (F) set at 0.15 (A,B), 0.45 (C,D), and 0.75 (E,F). Other parameters are $\lambda = 1.5$ and $\mu = 0.5$.

At the highest fishing rate ($F_N = F_P = 0.75$), predators persist only when large fractions of the habitat are protected within the no-take reserve (Figs. 2–4F). Increased predation rates on the prey associated with the positive effect of protection on predator population size are compensated for by the direct positive effect of protection on the prey. Thus, under all parameter combinations, allocating a large fraction of the habitat to the no-take reserve has a positive effect on both species (Figs. 2–4F).

Results about effects of protection measured as the ratios between densities inside and outside the reserve mirror those from ratios of total population sizes after and before
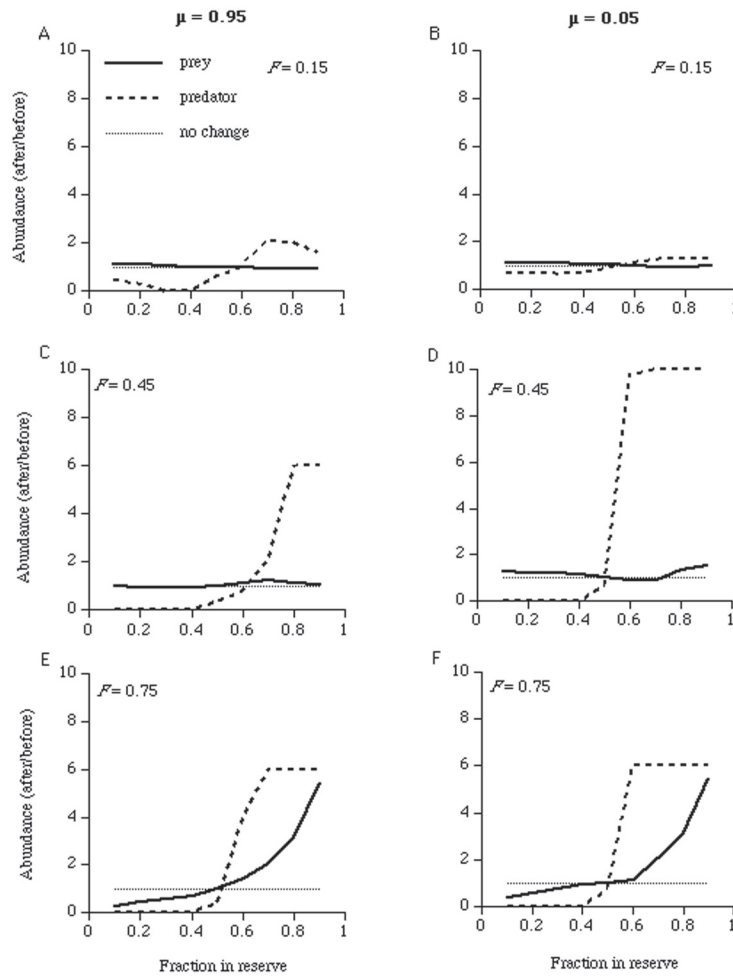
Figure 4. Effects of reserve size and fishing rates on prey and predator populations for different values of the predator larval dispersal rate ($\mu = 0.95$, panels A,C,E; $\mu = 0.05$, panels B,D,F). Effects of protection were quantified as the ratio between total population abundances (sums of populations in the reserve and the fished area) after and before the reserve establishment. Abundance ratios are plotted as a function of the fraction of the total area within the reserve (r) for fishing rates (F) set at 0.15 (A,B), 0.45 (C,D), and 0.75 (E,F). Other parameters are $\lambda = 1.5$ and $a = 2.5$.

reserve establishment, and only one example is reported (Fig. 5). As with patterns for total population sizes (Figs. 2–4A,B), at low fishing rates allocating increasing fractions of the habitat to the reserve has opposite effects on the responses of the predator and the prey for most reserve configurations ($F_N = F_P = 0.15$; Fig. 5A,B). When the reserve encompasses less than half of the habitat, only prey densities are increased in the reserve relative to the fished area. At larger reserve sizes, predator densities increase within the reserve, with detrimental effects for the prey (Fig. 5A,B). Densities of both the predator and prey are increased within the reserve relative to the fished area only when approximately half of the habitat is included within the reserve, and benefits for the predator are
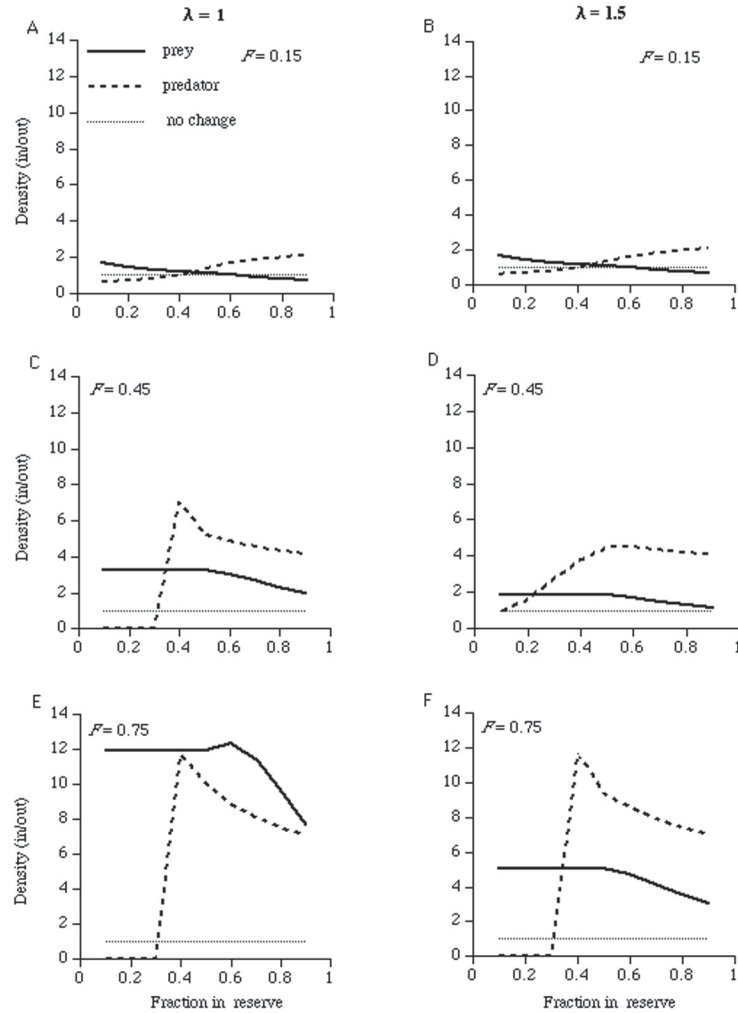
Figure 5. Effects of reserve size and fishing rates on prey and predator populations for different values of the prey population growth rate ($\lambda = 1$, panels A,C,E; $\lambda = 1.5$, panels B,D,F). Note that effects of protection are quantified here as the ratio between the ratios of prey and predator densities inside and outside the reserve. Density ratios are plotted as a function of the fraction of the total area within the reserve (r) for fishing rates (F) set at 0.15 (A,B), 0.45 (C,D), and 0.75 (E,F). Other parameters are $a = 2.5$ and $\mu = 0.5$.

not sufficient to support intense predation on the prey (Fig. 5A,B). At high fishing rates ($F_N = F_P = 0.45$ and $F_N = F_P = 0.75$), prey densities are always higher inside the reserve than in the fished portion of the population (Fig. 5C,D,E,F). Predators cannot persist if small fractions of the habitat are protected. When reserves are sufficiently large, predator densities are always greater within the reserve than in fished areas (Fig. 2C,D,E,F).

DISCUSSION

Simulated predator and prey population dynamics exhibited complex and in some cases counterintuitive responses to varying combinations of life-history characteristics of the two species, reserve size, and fishing intensity, even in this simple two-patch predator-prey model. In particular, (1) the dynamics of each species and responses to management measures depended both on its life-history characteristics and those of other species in the system; (2) management measures that were beneficial to one species could be detrimental to the other species; (3) vulnerability to overfishing and the consequences of species interaction for long-term species persistence depended on the trophic level that the species occupied; and (4) reserve area and fishing intensity interacted in complex ways in their effects on the predator-prey system, so their effects should always be considered jointly rather than separately from each other.

Despite their complexity, these results provide several interesting insights. In theory, counterintuitive prey declines following protection may be expected at low fishing rates and relatively large reserve sizes, regardless of the particular combination of life-history parameters describing the species population growth and their interaction. In contrast, at high fishing intensities trade-offs in the benefits of protection to the two species are predicted only for parameter values leading to large predator population sizes. These include traits of both the prey (the prey growth rates, i.e., the productivity of the predator's resource) and the predator (a combined measure of its attack rate and conversion efficiency and its larval dispersal rate). Thus, combinations of life-history and management parameters limiting the predator population size alleviated the negative impacts of predation on the prey and led, in some cases, to increased densities within the reserves and increased total population sizes for both species. These general results suggest that multispecies management of fishery species is likely to pose trade-offs and may require strategies combining no-take reserves with regulation of fishing intensity. For example, Supriatna and Possingham (1998) used a spatially structured predator-prey model to study optimal harvesting of separate subpopulations connected through dispersal. Their results indicate that prey living in the same patch with a relatively efficient predator should be harvested more conservatively than the other subpopulation and that prey subpopulations that act as sources for the other subpopulation should also be harvested more conservatively. Similarly, trade-offs in the conservation and management of species linked through trophic interactions may require the simultaneous establishment of marine reserves and variation in fishing intensity on these different species.

Reserve effects quantified as the ratio of species abundances inside and outside the reserve appear to be more sensitive to variation in critical parameters than reserve effects quantified as the ratio of species abundances after and before reserve establishment. For example, the ratio of prey abundance after and before reserve establishment appears to be relatively insensitive to variation in prey growth rate and predator attack and dispersal rates until fishing effort exceeds 50% (Figs. 2,3,4). In contrast, the ratio of prey abundances inside and outside the reserve is sensitive to variation in prey growth rate at all levels of fishing effort (Fig. 5).

Our results suggest that the consequences of a management decision are likely to depend on the trophic level that a species occupies. As in models investigating species extinction and recolonization of areas of varying size (Holt, 1996) and effects of habitat destruction on species occupying different trophic levels (May, 1994; Bascompte and Solé, 1998; Melián and Bascompte, 2002), predators in our model are at greater risk of

extinction than prey species and require larger reserve sizes to benefit from protection. Fishing at different trophic levels influences predators in two ways: (1) by directly removing individuals from the predator population and (2) by reducing resource availability for the predator by increasing prey mortality. Although these results apply only to specialist predators, similar conclusions may be reached for predators that rely largely, though not exclusively, on one prey species. The combined effects of these two mechanisms by which fishing on both the predator and the prey influence the predator's abundance produce a clear threshold reserve size below which predator abundance after reserve establishment is much lower than that before (Figs. 2–4). This result arises because, when reserve size is small, the predator is negatively affected both by direct fishing pressure on adults and indirectly through depletion of its resource as a result of fishing pressure on the prey. Once reserve size exceeds this threshold (about 40% of habitat within reserve), sufficient numbers of predators are protected inside the reserve that abundances start to increase, causing a small decline in prey abundance.

This model is clearly an oversimplified representation of a real predator-prey system, let alone of marine food webs. We used several simplifications, including assuming (1) a pairwise species interaction instead of a multispecies food web; (2) a specialist rather than generalist consumer (most marine consumers are generalists), thus ignoring predator switching at low prey densities; (3) a linear functional response for the predator; (4) dependence of larval production only on local population dynamics and absence of any outside source of propagules; (5) nonoverlapping generations, not an accurate assumption for most invertebrate and fish species of interest, which are typically long-lived and iteroparous; and (6) only a two-patch system, probably not adequate to describe the complex metapopulation structure of each species. Although all of these are important biological features of marine systems, their simultaneous incorporation would make for an extremely complicated model with few useful insights. Our aim was to examine possible effects of varying fishing intensities combined with spatial protection in a marine reserve on an interaction between two species by means of the simplest possible model. Including some of the complexities listed above in our model would probably produce different results. We therefore examined a subset of the effects that species interactions could generate in marine reserves. Additional effects are likely to arise from inclusion of multiple species, generalistic predatory behaviors, nonlinear functional responses, and multiple patches.

Spencer and Collie (1995) incorporated alternative prey and a nonlinear predatory functional response into a predator-prey model depicting interactions between spiny dogfish (*Squalus acanthias*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank. Results indicate that although the prey dynamics are similar to those from a model without alternative prey (Collie and Spencer, 1994), this model better explained the observed increases in spiny dogfish at low haddock abundances. Predation on pelagic species may maintain predators at high abundances despite declines in groundfish prey in this system (Spencer and Collie, 1995). In the scenario we represented in our model, the presence of an alternative prey, also lightly fished outside the reserve, may increase predator abundances and further increase the predator's top-down effect on the focal prey. In contrast, alternative prey and higher predator population growth rates may compensate for fishing mortality at high fishing rates and lead to lower prey abundances even at high fishing rates. A promising next step will be to determine whether our results are robust to the inclusion of different characteristics of predator-prey systems and modeling assumptions.

Even under the simplified conditions of our model, inclusion of species interactions radically changes predictions about reserve efficacy from those of single-species models. Interestingly, including a species interaction often influenced not only the magnitude but also the direction of a species' response to changes in reserve size or fishing intensity. A management intervention that appears, from life history and dispersal characteristics, to benefit a species may be detrimental because of interactions with other species in the system. Relaxation of some of the assumptions of this model and inclusion of more realistic patterns of species interactions may further increase the variability and unpredictability of the responses of suites of interacting species to management measures (Yodzis, 1988). As a result, additional modeling investigations of marine food webs are needed that will further our understanding of the complex effects of species interactions on reserve efficacy (see, e.g., Walters 2000).

It is of great concern that, although we may be able to make sensible recommendations about the size, shape, and placement of reserves for one species (Botsford et al., 2003), the efficacy of that reserve for meeting multispecies objectives is uncertain. The complexity of species responses to management observed in this simple predator-prey system indicates that biotic interactions add uncertainty to predictions about the long-term persistence of exploited species. In the absence of such mechanistic understanding of the effects of species interactions on species dynamics and responses to management, uncertainty calls for precautionary management of marine assemblages (Lauck et al., 1998). An alternative approach to modeling species interactions in marine food webs to meet multispecies goals is to use siting algorithms to conserve representative proportions of different habitats (see, e.g., Possingham et al., 2000).

Although recognition and incorporation into precautionary management approaches of the additional uncertainty about the efficacy of management interventions associated with species interactions is crucial, it is important to attempt to reduce such uncertainty through continued research. In particular, existing and proposed networks of marine reserves provide an invaluable opportunity to increase our mechanistic understanding of the effects of reserves on assemblages of interacting species. As more studies of marine reserves focusing on multiple species become available, more compelling generalizations about the conditions more likely to lead to species declines resulting from species interactions can be drawn.

A review of empirical examples of indirect effects of protection through trophic interactions revealed two general trends: (1) most examples are from shallow coastal systems underlain by hard substrate (kelp forests, rocky reefs, coral reefs, and rocky shores), and (2) a large number of case studies concerned large, relatively sedentary herbivorous invertebrates (sea urchins and limpets; Pinnegar et al., 2000). These patterns may arise, however, because shallow hard bottoms and large, sedentary species are more amenable to the observations and manipulations needed for documenting these effects, rather than because specific biological characteristics increase the likelihood of indirect effects (Pinnegar et al., 2000). Therefore, generalizations about what environments, species, and management regimes are more likely to result in species declines from cascading trophic interactions are difficult to draw on the basis of the available studies.

Our results indicate that empirical studies of reserve effects on groups of interacting species should include quantification of fishing rates outside reserves and of the species demographic rates, in addition to static measures such as abundances or biomass. As with results of the single-species model by Gerber et al. (2002), fishing intensities and population growth rates (of both species, for the two-species case) are the parameters

that are most important in determining species responses to a particular reserve configuration. More realistic models and empirical studies should therefore include at least these parameters.

In contrast to the rich theory of predator-prey and host-parasitoid interactions in patchy environments developed for the terrestrial realm (Murdoch and Oaten, 1975; Reeve, 1988; Hassell et al., 1991, 1994; Murdoch et al., 1992; Taylor, 1998, Bascompte and Solé, 1998), few spatially structured models of species interactions are available for marine systems (Hilborn and Walters, 1987; Murphy, 1995; Spencer and Collie, 1995, Supriatna and Possingham, 1998), and only one modeling approach has explicitly addressed the issue of marine reserves (Walters et al., 1997, 1999; Walters, 2000). More models and data on the dynamics of interacting species are needed for understanding and management of marine multispecies assemblages in the face of increasing fishing intensity and habitat destruction. The model we have presented greatly simplifies the complexities of marine food webs. Even under these simplifying assumptions, however, our results indicate that species interactions significantly influence both individual species responses to management schemes and the long-term persistence of species assemblages and that the magnitude and direction of these influences depend on the effects of both reserve characteristics and fishing intensity.

ACKNOWLEDGMENTS

LITERATURE CITED

Agardy, T. 1997. Marine protected areas and ocean conservation. R. G. Landes Press, Austin; Academic Press, San Diego, California. 244 p.

Attwood, C. G. and B. A. Bennett. 1995. Modeling the effect of marine reserves on the recreational shore-fishery of the south-western cape, South Africa. S. Afr. J. Mar. Sci. 16: 227–240.

Babcock, R. and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. Can. J. Fish. Aquat. Sci. 56: 1668–1678.

Bascompte, J. and R. V. Solé. 1998. Effects of habitat destruction in a predator-prey metapopulation model. J. Theor. Biol. 195: 383–393.

Boersma, D. P. and J. K. Parrish. 1999. Limiting abuse: marine protected areas, a limiting solution. Ecol. Econ. 31: 287–304.

Bohnsack, J. A. 1996. Maintenance and recovery of reef fishery productivity. Pages 283–313 *in* N. V. C Polunin and C. M. Roberts, eds. Management of reef fisheries. Chapman and Hall, London.

Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecol. Appl. 13: S25–S31.

Castilla, J. C. 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends Ecol. Evol. 14: 280–283.

Collie, J. S. and P. D. Spencer. 1994. Modeling predator-prey dynamics in a fluctuating environ-
    ment. Can. J. Fish. Aquat. Sci. 51: 2665–2672.
Cowen, R. K. 1985. Large scale pattern of recruitment in the labrid, *Semicossyphus pulcher*: causes
    and implications. J. Mar. Res. 43: 719–742.
DeMartini, E. E. 1993. Modeling the potential for fishery reserves for managing Pacific coral reef
    fishes. Fish. Bull., U.S. 91: 414–427.
Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea
    otters linking oceanic and nearshore ecosystems. Science 282: 473–476.
Fanshawe, S., G. R. VanBlaricom, and A. A. Shelly. 2003. Restored top carnivores as detriments
    to the performance of marine protected areas intended for fishery sustainability: a case study
    with red abalones and sea otters. Conserv. Biol. 17: 273–283.
Fisher, J. A. D. and K. T. Frank. 2002. Changes in finfish community structure associated with an
    offshore fishery closed area on the Scotian Shelf. Mar. Ecol. Prog. Ser. 240: 249–265.
Gerber, L. R, L. W. Botsford, A. Hastings, H. P. Possingham, S. D. Gaines, S. R. Palumbi, and S. J.
    Andelman. 2003. Population models for marine reserve design: a retrospective and prospective
    synthesis. Ecol. Appl. 13: S47–S64.
_____, P. M. Kareiva, and J. Bascompte. 2002. The interplay of life history attributes and
    fishing pressure in evaluating efficacy of marine reserves. Biol. Conserv. 106: 11–18.
Halpern, B. S. 2003. The impact of marine reserves: does size matter? Ecol. Appl. 13: S117–
    S137.
Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press,
    Princeton. 237 p.
_____, H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect popula-
    tion dynamics. Nature 353: 255–258.
_____, _____, and _____. 1994. Species coexistence and self-organizing spa-
    tial dynamics. Nature 370: 290–292.
Hilborn, R. and C. J. Walters. 1987. A general model for simulation of stock and fleet dynamics in
    spatially heterogeneous fisheries. Can. J. Fish. Aquat. Sci. 44: 1366–1369.
Holt, R. D. 1996. Food webs in space: an island biogeographic perspective. Pages 313–323 *in* G.
    A. Polis and K. O. Winemiller, eds. Food webs: integration of patterns and dynamics. Chap-
    man and Hall, New York.
Lauck, T., C. W. Clarke, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary
    principles in fisheries management through marine reserves. Ecol. Appl. 8: S72–S78.
Levin, S. A. and C. P. Goodyear. 1980. Analysis of an age-structured fishery model. J. Math. Biol.
    9: 245–274.
Ludwig, D. 1998. Management of stocks that may collapse. Oikos 83: 397–402.
_____ and C. J. Walters. 1981. Measurement errors and uncertainty in parameter estimates for
    stock and recruitment. Can. J. Fish. Aquat. Sci. 38: 711–720.
Mangel, M. 1998. No-take reserves for sustainability of harvested species and a conservation
    invariant for marine reserves. Ecol. Lett. 1: 87–90.
May, R. M. 1974. Stability and complexity in model ecosystems. Princeton University Press,
    Princeton.
_____. 1994. The effect of spatial scale on ecological questions and answers. Pages 1–17 *in*
    P. J. Edwards, R. M. May, and N. R. Webb, eds. Large-scale ecology and conservation biology.
    Blackwell Scientific, Oxford.
Melián, C. J. and J. Bascompte. 2002. Food web structure and habitat loss. Ecol. Lett. 5: 37–46.
Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. In press. Trajectories and correlates
    of community change in no-take marine reserves. Ecol. Appl.
Mosqueira, I., I. M. Côté, S. Jennings, and J. D. Reynolds. 2000. Conservation benefits of marine
    reserves for fish populations. Anim. Conserv. 4: 321–332.
Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9: 1–
    131.

_____, C. J. Briggs, R. M. Nisbet, W. S. C. Gurney, and A. Stewart-Oaten. 1992. Aggregation and stability in metapopulation models. Amer. Nat. 140: 41–58.

Murphy, E. J. 1995. Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs. J. Anim. Ecol. 64: 333–347.

National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. Natl. Academy Press, Washington, D.C. 272 p.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol. Evol. 14: 483–488.

Palumbi, S. R. 2001. The ecology of marine protected areas. Pages 509–530 *in* M. Bertness, S. Gaines and M. Hay, eds. Marine community ecology. Sinauer, Sunderland, Massachusetts.

Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M. L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D'Anna, and C. Pipitone. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ. Conserv. 27: 179–200.

Possingham, H., I. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–306 *in* S. Ferson and M. Burgman, eds. Quantitative methods in conservation biology. Springer, New York.

Pringle, J. D. 1986. California spiny lobster (*Panulirus interruptus*) larval retention and recruitment: a review and synthesis. Can. J. Fish. Aquat. Sci. 43: 2142–2152.

Reeve, J. D. 1988. Environmental variability, migration, and persistence in host-parasitoid systems. Amer. Nat. 132: 810–836.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11: 559–623.

_____. 1977. The historical development. Pages 1–26 *in* J. A. Gulland, ed. Fish population dynamics. Wiley, New York.

Roberts, C. M. and N. V. C. Polunin. 1993. Marine reserves: simple solutions to managing complex fisheries? Ambio 22: 363–368.

Shears, N. T. and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132: 131–142.

Sladek-Nowlis, J. and C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. Fish. Bull., U.S. 97: 604–616.

Spencer, P. D. and J. S. Collie. 1995. A simple predator-prey model of exploited marine fish populations incorporating alternative prey. ICES J. Mar. Sci. 53: 615–628.

Supriatna, A. K. and H. P. Possingham. 1998. Optimal harvesting for a predator-prey metapopulation. Bull. Math. Biol. 60: 49–65.

Taylor, A. D. 1998. Environmental variability and the persistence of parasitoid-host metapopulation models. Theor. Pop. Biol. 53: 98–107.

Tegner, M. J. 1993. Southern California abalones: can stocks be rebuilt using marine harvest refugia? Can. J. Fish. Aquat. Sci. 50: 2010–2018.

_____ and R. A. Butler. 1985. The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. Calif. Fish Game 71: 150–163.

Walters, C. 2000. Impact of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Bull. Mar. Sci. 66: 745–757.

_____, V. Christensen, and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7: 139–172.

_____, D. Pauly, and V. Christensen. 1999. Ecospace: prediction of mesoscale spatial patterns of trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2: 539–554.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69: 508–515.

ADDRESSES: (F.M.) *Hopkins Marine Station, Stanford University, Oceanview Blvd., Pacific Grove, California 93950. E-mail <micheli@stanford.edu>.* (P.A.) *Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637.* (J.B.) *Integrative Ecology Group, Estación Biológica de Doñana, E-41080, Sevilla, Spain.* (L.R.G.) *Department of Biology, Arizona State University, Tempe, Arizona 85287.*