

# Predation, competition, and the recovery of overexploited fish stocks in marine reserves

Marissa L. Baskett, Mary Yoklavich, and Milton S. Love

**Abstract:** Community interactions alter the management actions necessary to recover overfished species using marine reserves. For example, in communities where a larger species preys on their juveniles' competitors, overfishing of the larger species may cause prey population expansion; subsequent increased competition for the juveniles of the overfished species may impede its recovery within reserves. We explore the implications of such community interactions for reserve design with a model of a subtidal rockfish (genus *Sebastes*) system from the Northeast Pacific Ocean within a no-take reserve. Ignoring community interactions, the model predicts that a reserve large enough for internal recruitment to counterbalance mortality will allow recovery of the overfished species. However, after incorporating community interactions, the model predicts that two alternative stable states exist: one where the overfished species dominates and one where the prey dominates. In the community model, the ability of an overfished system to recover to the equilibrium where the overfished species dominates after reserve establishment depends on the initial densities of both species, and a larger reserve is required for recovery to be possible.

**Résumé :** Les interactions au sein de la communauté modifient les actions requises pour rétablir les espèces surexploitées à l'aide de réserves marines. Par exemple, dans les communautés où une espèce plus grande fait de la prédation sur les compétiteurs de ses petits, une surpêche de l'espèce plus grande peut causer une expansion de la population de proies; la compétition subséquente qui en résulte pour les jeunes de l'espèce surexploitée peut alors nuire à son rétablissement au sein des réserves. Nous examinons les implications de telles interactions communautaires pour la planification de réserves à l'aide d'un modèle d'un système sublittoral de sébastes (genre *Sebastes*) dans une réserve sans capture. Si l'on ne tient pas compte des interactions de la communauté, le modèle prédit qu'une réserve assez grande pour que le recrutement interne contrebalance la mortalité permet le rétablissement de l'espèce surexploitée. Cependant, une fois les interactions communautaires incorporées, le modèle indique qu'il existe deux états stables de recharge, l'un où c'est l'espèce surexploitée qui prédomine et l'autre où c'est la proie. Dans le modèle communautaire, lorsque l'espèce surexploitée domine après l'établissement de la réserve, la capacité du système surexploité à atteindre de nouveau l'équilibre dépend des densités initiales des deux espèces; une réserve de plus grande taille est alors requise pour permettre le rétablissement de l'espèce.

[Traduit par la Rédaction]

## Introduction

In intensively fished ecosystems, abundance of species at the top of the food web often declines, and as a result, fisheries shift to target species at lower trophic levels (Pauly et al. 1998). In addition, fisheries have a greater long-term negative impact on species with lower population growth rates, later maturation, larger organism size, and greater longevity than on species with faster production (Jennings et al. 1998; Heino and Godø 2002). The bias in fisheries' effects on trophic level and reproductive strategies may significantly alter ecosystem structure and function, in which case community dynamics may influence the recovery of depleted stocks.

For example, with intense fishing, marine communities may shift to new stable states in which trophic interactions, lower production rates, or a combination of the two prevent overfished species from recovering (Heino and Godø 2002). In general, alternative stable states involve multiple possible dominating species or groups of species in an ecosystem, and in this paper, we focus on the case in which multiple stable states exist for a particular set of conditions rather than a new stable state arising as conditions (e.g., temperature regime, fishing effort) change. Empirical evidence suggests that the existence of alternative stable states is possible, although unproven, in many marine ecosystems (Petraitis and Dudgeon 2004). Anthropogenic disturbances to ecosystems, such as the dominating influence of fisheries in marine

Received 8 June 2005. Accepted 23 November 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 25 April 2006.  
J18733

**M.L. Baskett,<sup>1</sup>** Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA.

**M. Yoklavich.** Southwest Fisheries Science Center (NOAA Fisheries), National Marine Fisheries Service, Fisheries Ecology Division, 110 Shaffer Road, Santa Cruz, CA 95060, USA.

**M.S. Love.** Marine Science Institute, University of California at Santa Barbara, Santa Barbara, CA 93106, USA.

<sup>1</sup>Corresponding author (e-mail: [mbaskett@princeton.edu](mailto:mbaskett@princeton.edu)).

ecosystems, alter the local stability of the alternative states and, therefore, the resilience to a shift between states (Scheffer et al. 2001; McClanahan et al. 2002; Collie et al. 2004).

Alternative stable states are theoretically feasible in a variety of simple models of ecological systems (May 1977), including models of intraguild predation (Holt and Polis 1997; Mylius et al. 2001) in which predator and prey species compete for a common resource. Intraguild predation occurs frequently in marine and terrestrial ecosystems (Polis et al. 1989). The existence of alternative states in communities with intraguild predation, including the specific case in which competition and predation occur during different life history stages, means that the final state of the communities depends on which species dominates initially (Polis and Holt 1992). Therefore, dominance of an intraguild prey may cause recovery efforts of the large predator species to fail in fisheries (Polis and Holt 1992). For example, one possible explanation for the lack of recovery of Newfoundland Atlantic cod (*Gadus morhua*) is the “cultivation effect” suggested by Walters and Kitchell (2001): with fewer adult cod to prey on smaller species that compete with or prey on juvenile cod, increased abundance of the smaller species has reduced the recruitment rate of juvenile cod (Swain and Sinclair 2000). Analogously, Barkai and McQuaid (1988) demonstrated that predation reversal between rock lobsters (*Jasus lalandii*) and whelks (*Burnupena* spp.) prevented the reintroduction of rock lobsters to a whelk-dominated community.

Cultivation effects may also influence rockfish (*Sebastes* spp.) communities in the rocky subtidal zone of the North-east Pacific Ocean. In rockfish communities, as in many marine communities, fishing efforts disproportionately affect larger, slow-growing, late-maturing species such as the yelloweye rockfish (*Sebastes ruberrimus*) compared with smaller, fast-growing, early-maturing, nonfished species such as pygmy rockfish (*Sebastes wilsoni*). These co-occurring species can interact when the juveniles of the larger species compete with the smaller species, as well as when the adults of the larger species prey on the smaller species. The smaller rockfish species represents one component of the larger species’ varied diet; for example, yelloweye rockfish prey on Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), flatfishes, shrimps, and crabs, as well as smaller rockfishes (Love et al. 2002).

Before anthropogenic disturbance dominated the system, predation and competition pressure from the larger species likely kept the smaller species at low population densities, except in suboptimal habitats not occupied by larger species. Now overfishing has substantially reduced population densities of the larger species, thereby releasing predation and competition pressures and likely causing a subsequent explosion in the smaller species’ populations in the higher quality habitat previously dominated by the larger species. From surveys of rock habitats in deep water off California and Oregon, larger individuals of several overfished species of rockfishes, such as canary (*Sebastes pinniger*) and bocaccio (*Sebastes paucispinis*), as well as yelloweye rockfish, are in low numbers or almost absent, whereas dwarf species such as halfbanded (*Sebastes semicinctus*) and squarespot (*Sebastes hopkinsi*) rockfishes, as well as pygmy rockfishes, dominate the fish assemblages in these areas (Stein et al.

1992; Yoklavich et al. 2000, 2002). Though fisheries closures are implemented in response to overfishing, competition between expanded populations of the smaller species and juveniles of the larger species may slow or prevent the overfished larger species from recovering (MacCall 2002; Mangel and Levin 2005). Stock assessments and rebuilding plans for overfished populations currently use single-species models (Punt 2003), which ignore the interactions described above. Regardless of whether species interactions cause shifts to alternative stable states or simply slow recovery following anthropogenic disturbance, the outcome is a reason for concern (Knowlton 2004), and management decisions may need to account for community interactions.

Permanent spatial closures, or no-take marine reserves, provide an alternative form of fisheries management that may reduce the likelihood of overfishing (e.g., Lauck et al. 1998; Mangel 2000; Apostolaki et al. 2002) and the chance of shifts in coastal marine community structure following anthropogenic disturbance. Generally, marine reserves serve to protect biodiversity and ecosystem function within protected areas by reducing anthropogenic impact (Allison et al. 1998), and reserves may benefit fisheries outside reserves for intensively harvested fisheries (Man et al. 1995; Holland and Brazee 1996; Sladek Nowlis and Roberts 1999), depending on movement and reproductive rates (Hilborn et al. 2004). In systems with alternative stable states, marine reserves may increase the yield of depleted stocks (Steele and Beet 2003).

Although the general response of marine communities to reserve establishment can be an increase in numbers and biomass (Halpern and Warner 2002), the combination of historical overfishing and community interactions may impede recovery of specific species with reserve establishment. In addition, accounting for community interactions may influence the reserve size necessary for recovery to be possible (Walters 2000). Because the collapse of previously dominant species such as Atlantic cod has contributed to systemic changes in community composition and interactions (Choi et al. 2004), recovery of such species is necessary to achieve the goals of marine reserves to protect ecosystem structure and function (Murray et al. 1999).

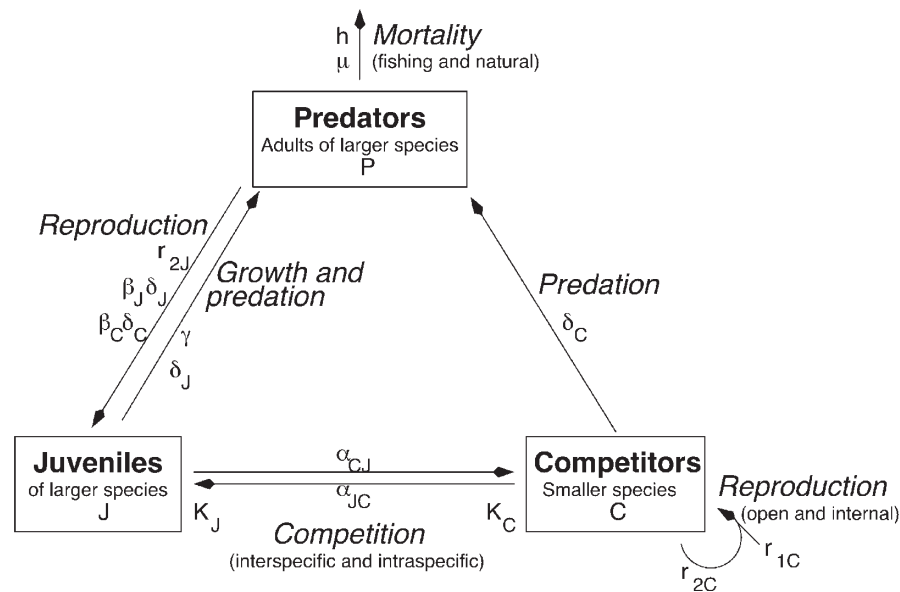
By exploring the feasibility of alternative stable states, simple mathematical models help inform empirical studies and large simulations (Scheffer and Carpenter 2003). Furthermore, theoretical knowledge of thresholds between alternative stable states can educate conservation decisions and planning (Huggett 2005). Here we propose a model to determine how reserve area affects the recovery of overfished species while accounting for “cultivation effect” community interactions. We use the above-described competition–predation interactions between rockfish species as our model system. As a simplified treatment of a complex system, the community model presented here allows a qualitative assessment of the importance of various processes and parameters that could influence expectations to recover ecosystem structure and function via marine reserves (Essington 2004).

## Materials and methods

### Model summary

The model represents a community of interacting rockfish species with three groups (Fig. 1): smaller rockfish species

**Fig. 1.** Schematic of the model. See Appendix A for explanation of parameter symbols.



(competitors), juveniles of larger rockfish species (juveniles), and adults of larger rockfish species (predators). Juveniles and competitors experience both interspecific and intra-specific competition for space. We assume that competitors have partially open population dynamics: their reproduction depends on both an internal recruitment rate and a constant external recruitment rate from populations in the suboptimal habitat. Predators prey primarily on competitors, but also on juveniles of their own species. For the predation dynamics, we use the simplest functional response possible whereby predation increases directly with prey density (see below for test of the importance of this assumption). Juveniles grow (mature) into predators. Predators produce more juveniles based on conversion of energy, gained from predation, into reproductive potential; prey include competitors, juveniles, and other species assumed to be constantly available. The closed predator–juvenile dynamics reflect the “scorched earth” assumption that populations of larger rockfish species are depleted outside the reserve (see below for test of the importance of this assumption). Predators experience natural mortality, as well as fishing mortality resulting from edge effects on the border of the reserve.

The model follows population densities (fish per unit area) over time within a no-take reserve. To determine the effect of reserve area on the rockfish community dynamics, we define the parameters as functions of reserve area. Given competition for space, carrying capacities are proportional to area. Predation rates, which depend on prey encounter rates and therefore prey per unit area, are inversely proportional to area. External recruitment for competitors is proportional to area and reflects increased probability of larvae settling in the reserve with increased area. Internal recruitment rates for competitors and predators vary with reserve width and length according to the percent retention of larvae given a dispersal kernel for each species (Appendix A, Fig. A1). Finally, fishing mortality for predators depends on the probability of predators crossing the reserve boundaries and therefore varies with the perimeter-to-area ratio of the reserve (Appendix

A, Fig. A2), as well as on the amount of fishing effort outside the reserve.

For a detailed mathematical formulation of the model, see Appendix A. To analyze the model, we determine the possible equilibria states (i.e., population densities where there is no change over time) and local stability of each equilibrium (i.e., whether a system starting near the equilibrium will go toward it (locally stable) or away from it (locally unstable)) for a range of reserve lengths. Where parameter values are uncertain, we test a range of values. In addition, we test the effect of relaxing some assumptions made in developing the model. First, we compare the Laplace dispersal kernel, used for mathematical simplicity, with a normal dispersal kernel, which may be more a realistic representation of larval dispersal. Second, we try a more realistic predation function that includes handling time and thus predation saturation at high prey densities (type II predation, as opposed to the linear type I predation in the main model). Third, we relax the scorched earth assumption by modeling the exchange between protected and fished areas in a reserve network (Appendix A, Fig. A3).

### Parameters

In the model analysis, we base the parameter values for the larger species on yelloweye rockfish (*S. ruberrimus*) and the parameter values for the smaller species on pygmy rockfish (*S. wilsoni*; Table 1). In general, rockfish have a diversity of life histories from which to choose representative species for parameter values (Love et al. 2002). Yelloweye rockfish are large (maximum total length of 91 cm), slow-growing, late-maturing (age at 50% maturity around 20 years), long-lived (maximum age of at least 118 years), and heavily fished. This species extends from northern Baja California to the Aleutian Islands, commonly inhabiting depths of 91–180 m (Love et al. 2002). On the US west coast, spawner abundance fell below the target level in 1991 and was estimated at 24.1% of the unfished level in 2002 (Methot et al. 2002). Pygmy rockfish are small (maximum

**Table 1.** Parameter values used to develop the model for community interactions inside marine reserves, including ranges tested and alternate values for relaxing assumptions.

Parameter		Default value	Alternate value(s)	Units	Reference(s)
Open recruitment	$r_{A1C}$	0.001	0.00067–0.0015	$C \cdot m^{-2} \cdot year^{-1}$	
Internal recruitment	$r_{A2C}$	0.0271	0.0194–0.0379	$year^{-1}$	Love et al. 2002; Ralston et al. 2003
	$r_{A2J}$	0.3486	0.249–0.488	$year^{-1}$	Love et al. 2002; Anderson 1984
Prey conversion	$\beta_{AC}$	0.003		$J \cdot C^{-1}$	Charnov et al. 2001
	$\beta_{AJ}$	0.003		$J \cdot J^{-1}$	Charnov et al. 2001
Mean dispersal distance	$\bar{D}_C$	30 000	20 000 – 60 000	m	Shanks et al. 2003; Kinlan and Gaines 2003
	$\bar{D}_J$	30 000	20 000 – 60 000	m	Shanks et al. 2003; Kinlan and Gaines 2003
Carrying capacities	$K_{AC}$	0.213	0.213–0.89	$C \cdot m^{-2}$	Yoklavich et al. 2000; Stein et al. 1992
	$K_{AJ}$	0.028	0.019–0.028	$J \cdot m^{-2}$	Yoklavich et al. 2000
Competition coefficients	$\alpha_{JC}$	1		$C \cdot J^{-1}$	
	$\alpha_{CJ}$	1		$J \cdot C^{-1}$	
Predation attack rates	$\delta_{AC}$	912.5	547.5–2555	$(P \cdot m^{-2})^{-1} \cdot year^{-1}$	Johnson 2004
	$\delta_{AJ}$	547.5	54.75–912.5	$(P \cdot m^{-2})^{-1} \cdot year^{-1}$	
Predation handling times	$\tau_C$	0	$2.74 \times 10^{-8}$	year	Mylius et al. 2001
	$\tau_J$	0	$2.74 \times 10^{-8}$	year	Mylius et al. 2001
Growth	$\gamma$	0.05		$year^{-1}$	Love et al. 2002
Natural mortality	$\mu$	0.05		$year^{-1}$	Methot et al. 2002
Fishing mortality	$h_A$	0.2	0.1–0.7	$year^{-1}$	
Habitat width	$\omega$	4828.03	4828.03–6759.24	m	
Reserve width	$W$	4828.03		m	
Reserve length	$L$ (or $L_R$ )	50 000	1000 – 100 000	m	
Region length	$L_T$	$L$	200 000	m	
Number of reserves	$N_R$	1	1–5	Reserves	

**Note:** For units: m, metres; C, competitors; J, juveniles; P = predators (number of fish).

total length of 23 cm), relatively short-lived (maximum age of 26 years), and unfished and extend from southern California to the Gulf of Alaska at depths of 44–200 m (Love et al. 2002). Yelloweye and pygmy rockfishes are two species with overlapping ranges but divergent life histories with which to represent the general groups of large, longer-lived and small, shorter-lived species, respectively, in our community model.

Although pygmy rockfish have the most representative life history of the dwarf rockfish species that have increased after overfishing of larger species, not all parameter values are available for this unfished species; therefore, we use a slightly larger (maximum total length of 35 cm), longer-lived (maximum age of 32 years) species, shortbelly rockfish (*S. jordani*), to determine internal recruitment values for the smaller species (Love et al. 2002). To calculate internal recruitment, we solve the continuous-time Euler equation for intrinsic growth rate (i.e.,  $r$  in  $1 = \int l(x)m(x)\exp(-rx)dx$ , where  $l(x)$  is survivorship and  $m(x)$  is fecundity at age  $x$ ). We base survivorship on the mortality rate in Methot et al. (2002) for yelloweye rockfish (which also provides the model parameter value for adult yelloweye rockfish natural mortality) and in Ralston et al. (2003) for shortbelly rockfish. To calculate fecundity, Love et al. (2002) provide age at maturity (the inverse of which also provides the parameter value for growth from juveniles into adult yelloweye rockfish), maximum age, age–length relationships, and length–weight relationships for both rockfish species. We convert weight to egg production based on maximum size and egg

production for yelloweye rockfish (Love et al. 2002) and using the weight–fecundity relationship for shortbelly rockfish (Ralston et al. 2003). Finally, we convert egg production to fecundity in terms of larval recruitment using larval survivorship estimates: Ralston et al. (2003) provide larval survivorship estimates for shortbelly rockfish, and we use the general *Sebastes* spp. larval survivorship in Anderson (1984) for yelloweye rockfish.

For external recruitment in the smaller species, we test the range of values for which coexistence between the two species is possible. In the reserve network model, we reduce the smaller species' external recruitment by a factor of 10, because larval dispersal from regions outside the reserve are now accounted for, but larval dispersal from shallow, sub-optimal habitat is still possible. For predation–reproduction conversion in the larger species, we assume 10% of the prey eaten contributes to maintenance, growth, and reproduction. The proportion of the 10% energetic gain that contributes to reproduction is the gonadosomatic index, estimated from the allometric relationships described by Charnov et al. (2001; the analogous approach specific to viviparous fish by Gunderson (1997) yields similar parameter values). We test larval dispersal distances for which coexistence between the two species was possible within a range of feasible values (20–500 km; Kinlan and Gaines 2003; Shanks et al. 2003). To convert average dispersal distance to dispersal kernel parameters, we use the formulas from Lockwood et al. (2002).

To determine carrying capacities, we use estimates from the coasts of central California (Yoklavich et al. 2000) and



Oregon (Stein et al. 1992) for pygmy rockfish and from the central California coast for yelloweye rockfish (Yoklavich et al. 2000). In determining competition coefficients, given the absence of quantitative measures of competitive interactions between our model species, we make the baseline assumption that juveniles of the larger species and the smaller species are equally aggressive. Competitive superiority of the smaller species arises from the greater carrying capacity and, therefore, ability to use the same resource (space, which provides a refuge from predation; note that this ignores competition for food) more efficiently. For predation attack rates, we generally assume that cannibalism is less frequent than predation on the smaller species (although we test a range of values that includes equal attack rates for juveniles and competitors), within the range of feasible values reported by Johnson (2004). We base predation handling time on Mylius et al. (2001).

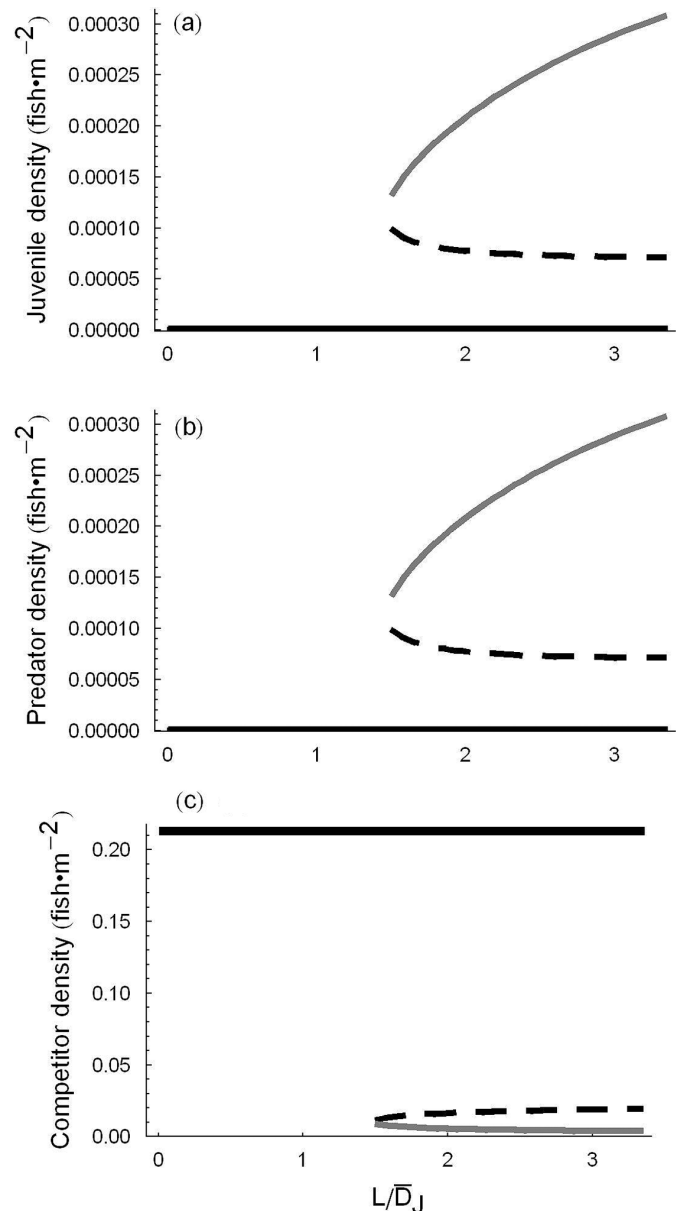
We assume that reserve width (perpendicular to the coastline) is equal to California's jurisdictional boundary (3 nautical miles offshore (1 nautical mile = 1852 m)). In addition, we assume that the habitat width ends the same distance from the coast as the reserve width, again testing a range of values. We tested a range of values (1–100 km) for reserve length based on expected adult movement (Love et al. 2002) and larval dispersal distances (Kinlan and Gaines 2003; Shanks et al. 2003).

## Results

There are up to three biologically relevant (i.e., real and nonnegative) equilibria for the system described above. The first equilibrium, where the juvenile and predator densities are zero and competitor density is at its carrying capacity, is always locally stable when competitors outcompete juveniles (see Appendix A for analytic proof). It is possible for equilibrium densities of the larger species to be exactly zero because, with the conservative assumption of scorched earth, the dynamics are closed for the larger species: there is no input from outside the reserve for the larger species. Given the open nature of marine systems, a stable equilibrium with exactly zero density is unlikely (low densities would be more realistic). Therefore, this result emphasizes the fact that our model is not appropriate for quantitative predictions, but rather is useful for qualitative assessment of relevant processes.

Numerically, within all of the parameter values tested, the second equilibrium, with intermediate juvenile, predator, and competitor densities, is always locally unstable; the third equilibrium, with high juvenile and predator densities and low competitor densities, is always locally stable. The interior equilibria, where the larger species density is nonzero, do not exist unless the reserve is large enough for internal recruitment (recruitment after the loss from spillover beyond reserve boundaries) to outweigh competition and mortality for the larger species (Fig. 2; note that for all figures in which we present equilibrium densities for varying reserve length, solid lines represent locally stable equilibria and broken lines represent locally unstable equilibria). This result parallels the classic result of critical patch size from spatially explicit diffusion models in which a patch (in this case, the reserve) must be large enough for within-patch

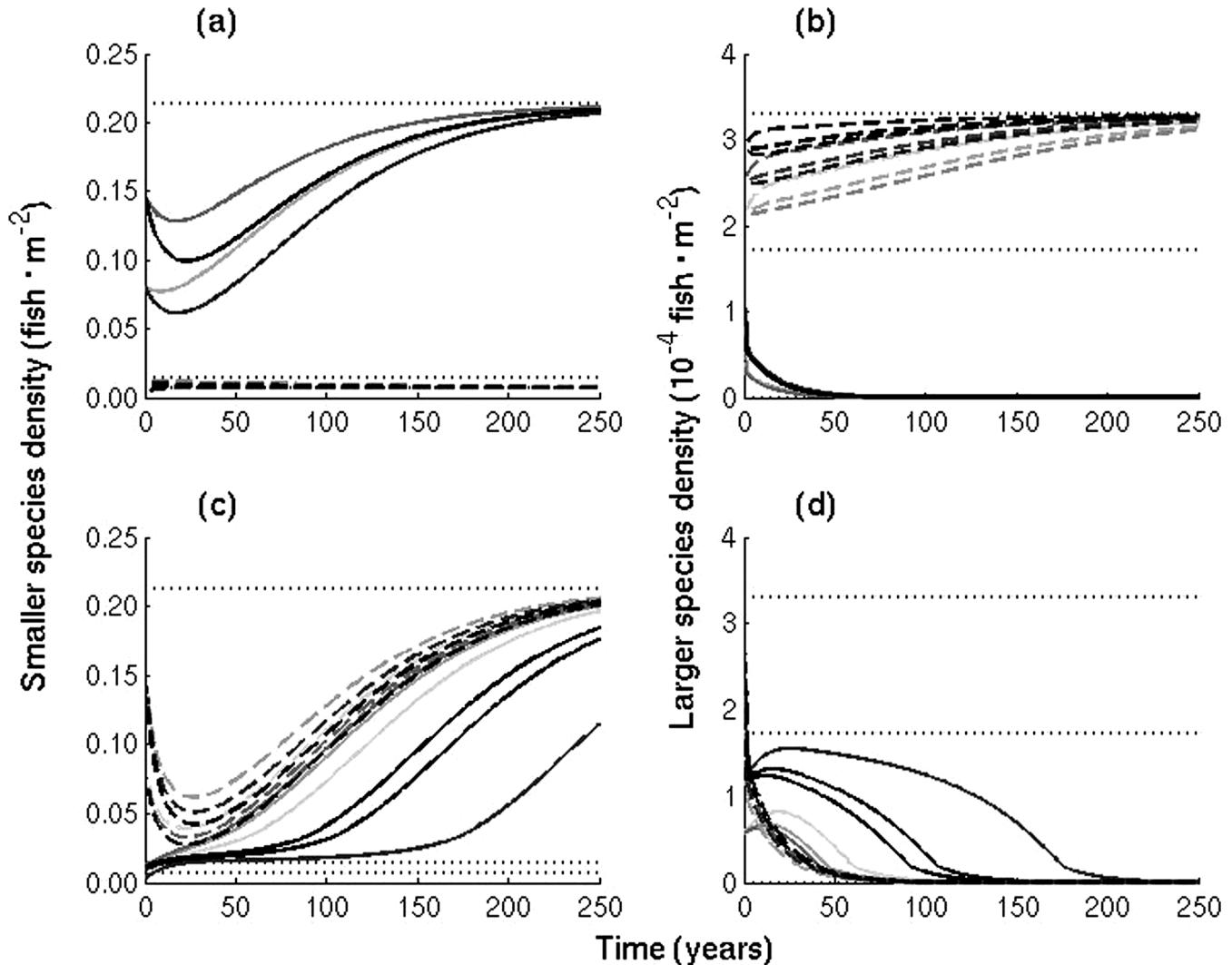
**Fig. 2.** (a) Juvenile, (b) predator, and (c) competitor equilibria densities dependent on reserve length scaled by mean juvenile dispersal distance ( $L/\bar{D}_j$ ). The solid black lines represent the equilibrium with no larger species and the smaller species at its carrying capacity (smaller species dominated equilibrium), which is locally stable. The broken black lines represent the equilibrium with intermediate larger and smaller species densities (threshold equilibrium), which is locally unstable. The shaded lines represent the equilibrium with high larger species density and low smaller species density (larger species dominated equilibrium), which is locally stable.



reproduction to outweigh loss over patch edges in order for a population to persist (Skellam 1951; Kierstead and Slobodkin 1953).

Therefore, in reserves larger than a critical reserve size, two alternative stable states exist. The additional unstable equilibrium sets a threshold as an upper limit for the smaller species and lower limit for the larger species. If the smaller species density is below and the larger species density is

**Fig. 3.** Time trajectories for the smaller (competitors) and larger (juveniles + predators) species densities (fish·m<sup>-2</sup>) with varying initial conditions. (a–b) Simulations in which one species starts above and the other below the threshold equilibrium (solid lines for smaller species above and larger species below, broken lines for smaller species below and larger species above; dotted lines represent equilibrium values; different grayscale for each simulation). (c–d) Simulations in which the smaller and larger species start both below or both above the threshold (solid lines for both below and broken lines for both above; dotted lines represent equilibrium values; different grayscale for each simulation).



above this “threshold equilibrium” (broken lines in Fig. 2), then the smaller species will decline and the larger species will increase to the “larger species dominated equilibrium” densities (high larger species density and low smaller species density; solid shaded lines in Fig. 2), which is presumably representative of the state before overfishing. Alternately, if the smaller species density is above and the larger species density is below the threshold equilibrium, then the smaller species will increase and the larger species will decline to the “smaller species dominated equilibrium” (no larger species and high smaller species density; solid black lines in Fig. 2). The larger species dominated equilibrium density for the larger species increases with reserve length (Figs. 2a, 2b).

#### Impact of initial conditions

To determine the relative importance of smaller and larger species’ initial densities, we numerically integrated the model to explore predicted time trajectories with varying ini-

tial conditions. As expected, simulations that begin near locally stable equilibria tend toward those equilibria: if the smaller species starts above the threshold equilibrium and the larger species starts below the threshold equilibrium, the system goes to the smaller species dominated equilibrium (solid lines in Figs. 3a and 3b); if the smaller species starts below the threshold equilibrium and the larger species starts above the threshold equilibrium, the system goes to the larger species dominated equilibrium (broken lines in Figs. 3a and 3b). In addition, within the initial values and parameters tested, if both the larger species and the smaller species start below the threshold equilibrium or both start above the threshold equilibrium, then the system goes to the smaller species dominated equilibrium (solid lines for both below and broken lines for both above in Figs. 3c and 3d). In other words, in simulations that did not begin near a locally stable equilibrium and in which one species would need to cross the threshold equilibrium in order for the system to reach a

locally stable equilibrium, the system went to the smaller species dominated equilibrium in all of the simulations explored here. Thus, recovery to the desired state of the larger species dominated equilibrium within a reserve depends not only on the larger species starting with a high enough density, but also on the smaller species starting with a low enough density.

### Impact of predation and competition

When predation and competition are not included in the model, there are two biologically relevant equilibria: with zero or with nonzero predator and juvenile densities. The nonzero equilibrium exists and is locally stable only when the zero equilibrium is locally unstable (see Appendix A for analytic proof); therefore, alternative stable states do not exist, as in the case with community interactions (where the smaller species dominated and the larger species dominated equilibria are both locally stable). Without interspecific interactions, the model predicts that larger species will recover as long as the reserve is large enough for reproduction within the reserve to counteract mortality, regardless of initial conditions (Fig. 4), whereas the model with interspecific interactions predicts that initial conditions determine the potential for the larger species to recover (Figs. 2–3). Furthermore, the model with interspecific interactions requires a larger reserve for equilibria with nonzero larger species density to exist and therefore for recovery to be possible (Fig. 2 versus Fig. 4).

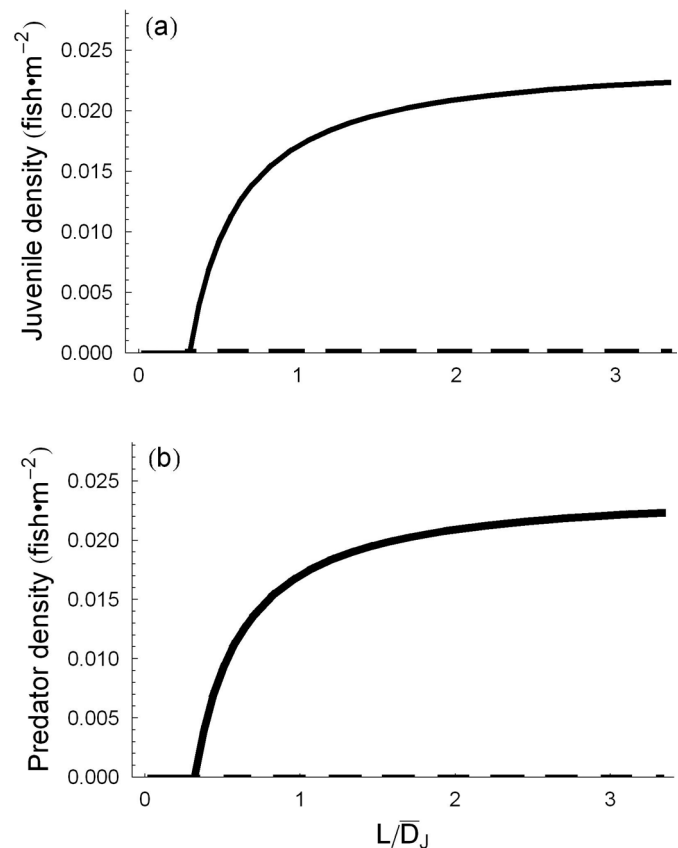
### Equilibria dependence on uncertain parameter values and assumptions

In this section we summarize the key results for varying uncertain parameter values and relaxing assumptions made in developing the basic model (for detailed results, see Appendix B).

Parameters important for estimating threshold equilibrium density for the smaller species are predation on the smaller species, predation on juveniles of the larger species, and juvenile carrying capacity. Parameters important for estimating threshold equilibrium density for the larger species are predation on the smaller species, juvenile carrying capacity, and the smaller species external recruitment. Finally, parameters important for estimating both the reserve size necessary for recovery to be possible and the larger species density at the recovered state are predation on the smaller species, predation on juveniles of the larger species, juvenile carrying capacity, habitat width compared with reserve width, the smaller species external recruitment, the larger species internal recruitment, and the larger species dispersal distance (Appendix B, Figs. B1–B6).

Although uncertain parameter values can substantially change quantitative predictions of our model, the model predictions do not depend greatly on the predatory dynamics assumed or the shape of the dispersal kernel (as has been found in other marine reserve models; Lockwood et al. 2002). However, the scorched earth assumption that larger species outside the reserve do not contribute to the reserve population does substantially impact the quantitative outcome, particularly the threshold equilibrium densities within the reserve (Fig. 5). Furthermore, fragmenting a single reserve

**Fig. 4.** Equilibrium (a) juvenile and (b) predator densities dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_j$ ) when ignoring predation and competition. Solid and broken lines indicate stable and unstable equilibria, respectively.

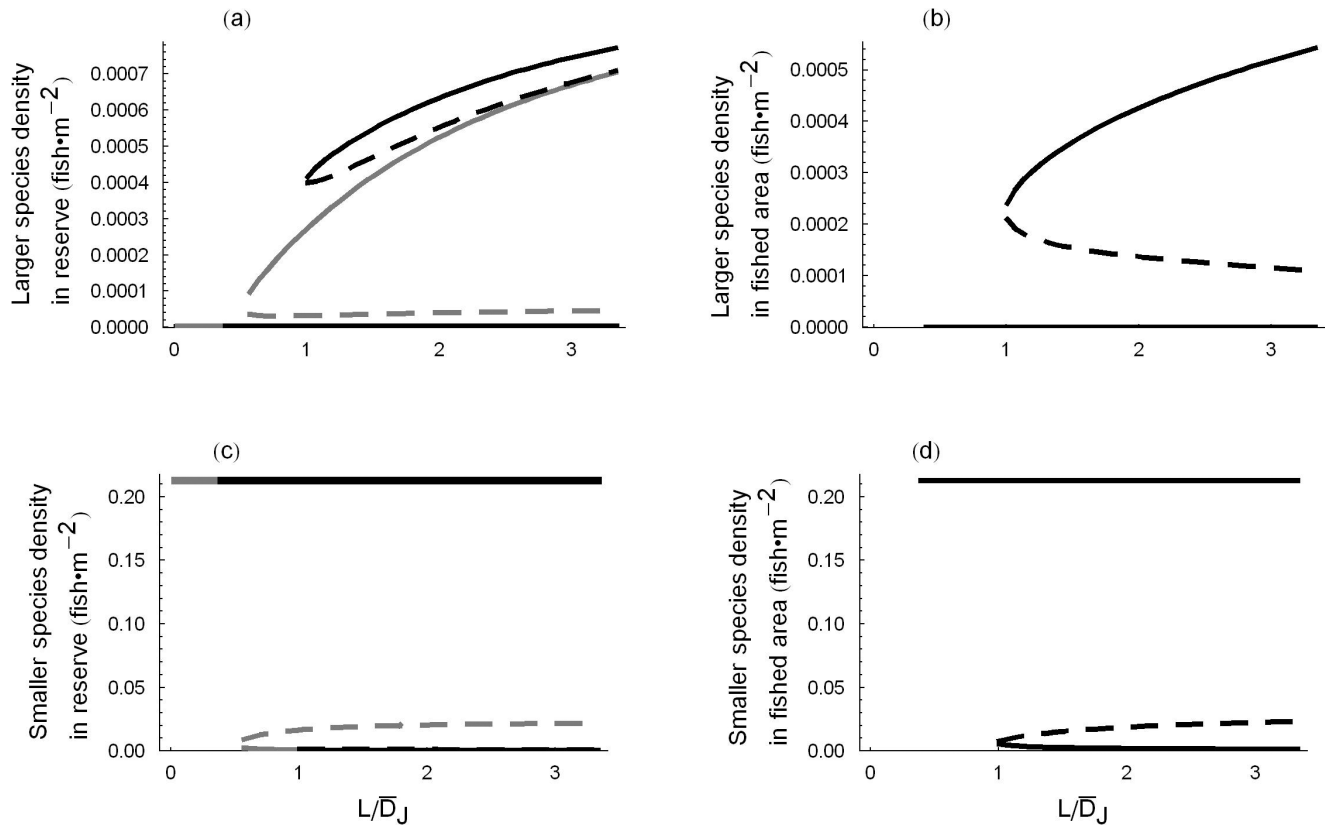


into a network of reserves alters the within-reserve equilibrium density for the larger species (Appendix B, Fig. B7).

### Discussion

Negative community interactions such as predation and competition may impede the recovery of overfished species in marine reserves. To explore one scenario where this is a concern, we presented a model of a rockfish community in which species are identified as overfished “larger species” and unfished “smaller species”. The larger species competes with the smaller species as juveniles and preys on the smaller species as adults. As with other models in which the predator and prey compete for common resource (e.g., Polis and Holt 1992; Mylius et al. 2001), numerical analysis of our model indicates that two alternative stable states exist, one in which the larger species dominates and one in which the smaller species dominates, with an unstable threshold equilibrium between the two. In contrast, the equivalent model without predation and competitive community interactions has only one stable state. Therefore, the model without community interactions predicts that any overfished rockfish will recover within a marine reserve as long as the reserve is large enough for recruitment to outweigh mortality, whereas the model with community interactions predicts that recovery depends on both reserve size and the initial densities of the interacting species in the rockfish community.

**Fig. 5.** Equilibria densities (fish·m<sup>-2</sup>) for (a–b) larger and (c–d) smaller species, dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_J$ ), inside and outside reserves (black lines); shaded lines indicate basic model with “scorched earth” assumption (i.e., areas outside reserve not modeled). Solid and broken lines indicate stable and unstable equilibria, respectively.



Specifically, both the initial density of the larger species must be large enough and that of the smaller species must be small enough for recovery to take place within a marine reserve. Similarly, Walters and Kitchell (2001) hypothesize that community interactions such as the ones modeled here can explain unexpected recruitment depensation in Ecosim simulations, in which case recovery does not necessarily follow reduced take. Because initial community composition may be vital for the successful restoration of ecosystem structure and function, choosing areas with high abundance of overfished species, and possibly low abundance of interacting species such as competitors, may be more important than choosing areas with generally high biomass and diversity when making reserve placement decisions. Further actions to enhance densities of larger species and (or) reduce densities of smaller species within a reserve may be necessary as well. However, such measures may be difficult to implement in the rockfish system modeled here. In addition, given that we intend this model for qualitative assessment, further research is needed to make more specific recommendations on management actions required to promote recovery of overfished stocks given community interactions. In particular, our model ignores countless aspects of reality, such as environmentally driven fluctuations in recruitment, that could alter theoretical predictions.

Along with altering the initial conditions necessary for recovery, consideration of community interactions increases the reserve size necessary for the larger species to persist within the reserve and for recovery to be possible regardless

of initial conditions. Analogously, in models and simulations without marine reserves but with varying fishing mortality, scenarios that incorporate community interactions require a lower fishing rate to maintain sustainable yield compared with scenarios without community interactions (Walters and Kitchell 2001; MacCall 2002). Both the larger reserve and lower fishing mortality requirements arise from the need for recruitment by the overfished species to outweigh negative interactions with unfished species. The increase in reserve size necessary for protection of ecosystem structure in this and other models of community interactions (Walters 2000) indicates the importance of such interactions in designing reserves to achieve biodiversity goals.

For both the reserve size necessary for recovery and the various equilibria densities, the quantitative predictions of our model vary substantially with values for poorly known parameters such as predation and recruitment, as well as with the scorched earth assumption of no input from unprotected areas. Therefore, future models or simulations that are designed for quantitative rather than qualitative predictions will require a better understanding of parameter values and will likely need to incorporate contributions from both protected and unprotected areas to ensure accuracy. Another outcome of the version of our model that incorporates unprotected areas is that the recovered state in which the larger species has high density within the reserve corresponds to higher density for the larger species outside the reserve as well, even at a fishing rate outside the reserve that would lead to population collapse if the reserve were not there. In



other words, if the larger species can recover from overfishing within the reserve, it will lead to an increase in larger species density outside the reserve and prevent stock collapse from overfishing. This result parallels Steele and Beet's (2003) outcome from a single-species model that the establishment of reserves can increase the yield of depleted stocks with alternative stable states, as well as reinforces the role, suggested from single-species models (e.g., Guénette and Pitcher 1999; Apostolaki et al. 2002), that reserves may play in enhancing resilience to overfishing.

In addition to the predation and competitive interactions modeled here, incorporating community interactions in marine reserve models generally alters reserve design recommendations and expectations after reserve establishment. For example, in Mangel and Levin's (2005) model of a target species with offshore adults and inshore juveniles, when ignoring community interactions, establishing an inshore reserve is more effective in terms of recovery rate and recovered-state biomass than establishing an offshore reserve or stopping all take. However, when they incorporated an inshore predator, establishing an inshore reserve is the least effective policy in their model. Furthermore, Micheli et al. (2004) show that the counterintuitive outcome of population declines after marine reserve establishment is feasible in a predator-prey model with exchange between protected and unprotected areas, dependent on fishing mortality outside the reserve. Finally, Ecospace simulations indicate that incorporating community interactions can reduce the potential for small reserves to protect target species (Walters 2000). In general, predictions from community models such as the ones described above and the one presented here are preferable to the traditional single-species approach to fisheries modeling when they include key interactions (Hollowed et al. 2000).

In summary, even with its simplified representation of rockfish communities, our model indicates that community interactions substantially alter the conditions necessary for recovery of overfished species within marine reserves. Given the additional initial density requirements and increased reserve size necessary for recovery when incorporating community interactions, the model results suggest that recovery from overfishing within reserves may require management action beyond the elimination of fishing mortality. Regardless of whether the community interactions result in prevented recovery, as is possible in models with alternative stable states, or slowed recovery, these theoretical predictions indicate the importance of considering community interactions in conservation planning (Knowlton 2004). In the variety of systems in which relevant community interactions occur, from the rockfish system explored here to Atlantic cod to rock lobsters (Barkai and McQuaid 1988; Swain and Sinclair 2000; MacCall 2002), a better understanding of such interactions is vital to policy decisions such as reserve design and expectations after reserve establishment.

## Acknowledgments

Discussions with Simon Levin, Steve Pacala, Alec MacCall, Steve Ralston, Mark Carr, and Dave Fluharty were extremely helpful in developing the ideas and model. This paper benefited from comments on an earlier version by John Field, Heather Leslie, Simon Levin, and two anonymous

reviewers. M.L.B. received support for this research from the National Science Foundation Graduate Research Fellowship Program and the Burroughs Wellcome Fund Training Program in Biological Dynamics (No. 1001781). This work was conducted as part of the Development of Tools for the Practical Design of Marine Reserves Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant No. DEB-00-72909), the University of California at Santa Barbara, and the State of California.

## References

- Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* **8**: S79–S92.
- Anderson, J.T. 1984. Early life-history of redfish (*Sebastes* spp.) on Flemish Cap. *Can. J. Fish. Aquat. Sci.* **41**(7): 1106–1116.
- Apostolaki, P., Milner-Gulland, E.J., McAllister, M.K., and Kirkwood, G.P. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. *Can. J. Fish. Aquat. Sci.* **59**: 405–415.
- Barkai, A., and McQuaid, C. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* (Washington, D.C.), **242**(4875): 62–64.
- Charnov, E.L., Turner, T.F., and Winemiller, K.O. 2001. Reproductive constraints and the evolution of life histories with indeterminate growth. *Proc. Natl. Acad. Sci. U.S.A.* **98**(16): 9460–9464.
- Choi, J.S., Frank, K.T., Leggett, W.C., and Drinkwater, K. 2004. Transition to an alternate state in a continental shelf ecosystem. *Can. J. Fish. Aquat. Sci.* **61**: 505–510.
- Collie, J.S., Richardson, K., and Steele, J.H. 2004. Regime shifts: can ecological theory illuminate the mechanisms? *Prog. Oceanogr.* **60**(2–4): 281–302.
- Essington, T.E. 2004. Getting the right answer from the wrong model: evaluating the sensitivity of multispecies fisheries advice to uncertain species interactions. *Bull. Mar. Sci.* **74**(3): 563–581.
- Guénette, S., and Pitcher, T.J. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fish. Res.* **39**: 295–303.
- Gunderson, D.R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can. J. Fish. Aquat. Sci.* **54**: 990–998.
- Halpern, B.S., and Warner, R.R. 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* **5**: 361–366.
- Heino, M., and Godø, O.R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bull. Mar. Sci.* **70**: 639–656.
- Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K.L., Garcia, S., Hall, S.J., Kirkwood, G.P., Sainsbury, K., Stefansson, G., and Walters, C. 2004. When can marine reserves improve fisheries management? *Ocean Coast. Manag.* **47**(3–4): 197–205.
- Holland, D.S., and Brazee, R.J. 1996. Marine reserves for fisheries management. *Mar. Resour. Econ.* **11**: 157–71.
- Hollowed, A.B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., and Rice, J.C. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J. Mar. Sci.* **57**(3): 707–719.
- Holt, R.D., and Polis, G.A. 1997. A theoretical framework for intraguild predation. *Am. Nat.* **149**(4): 745–764.

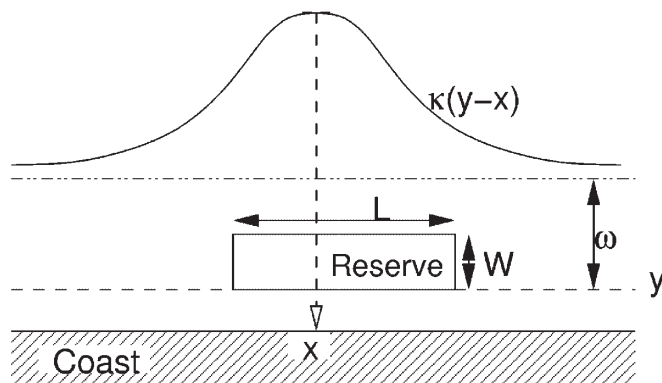
- Huggett, A.J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biol. Conserv.* **124**: 301–310.
- Jennings, S., Reynolds, J.D., and Mills, S.C. 1998. Life history correlates of responses to fisheries exploitation. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **265**: 333–339.
- Johnson, D. 2004. Early, post-settlement mortality and the population dynamics of nearshore rockfish. Ph.D. dissertation, University of California at Santa Cruz, Santa Cruz, California.
- Kierstead, H., and Slobodkin, L.B. 1953. The size of water masses containing plankton blooms. *J. Mar. Res.* **12**: 141–147.
- Kinlan, B.P., and Gaines, S.D. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, **84**(8): 2007–2020.
- Knowlton, N. 2004. Multiple "stable" states and the conservation of marine ecosystems. *Prog. Oceanogr.* **60**(2–4): 387–396.
- Lauck, T., Clark, C.W., Mangel, M., and Munro, G.R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol. Appl.* **8**: S72–S78.
- Lockwood, D.R., Hastings, A., and Botsford, L.W. 2002. The effects of dispersal patterns on marine reserves: does the tail wag the dog? *Theor. Popul. Biol.* **61**: 297–309.
- Love, M.S., Yoklavich, M., and Thorsteinson, L. 2002. The rockfishes of the Northeast Pacific. The University of California Press, Berkeley, California.
- MacCall, A.D. 2002. Fishery-management and stock-rebuilding prospects under conditions of low-frequency environmental variability and species interactions. *Bull. Mar. Sci.* **70**: 613–628.
- Man, A., Law, R., and Polunin, N.V.C. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. *Biol. Conserv.* **71**: 197–204.
- Mangel, M. 2000. Irreducible uncertainties, sustainable fisheries and marine reserves. *Evol. Ecol. Res.* **2**: 547–557.
- Mangel, M., and Levin, P.S. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **360**: 95–105.
- May, R.M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature (London)*, **269**(5628): 471–477.
- McClanahan, T., Polunin, N., and Done, T. 2002. Ecological states and the resilience of coral reefs. *Conserv. Ecol.* **6**(2): 18.
- Methot, R., Wallace, R., and Piner, K. 2002. Status of yelloweye rockfish off the U.S. west coast in 2002. National Marine Fisheries Service, Portland, Oregon.
- Micheli, F., Amarasekare, P., Bascompte, J., and Gerber, L.R. 2004. Including species interactions in the design and evaluation of marine reserves: some insights from a predator–prey model. *Bull. Mar. Sci.* **74**(3): 653–669.
- Murray, S.N., Ambrose, R.F., Bohnsack, J.A., Botsford, L.W., Carr, M.H., Davis, G.E., Dayton, P.K., Gotshall, D., Gunderson, D.R., Hixon, M.A., Lubchenco, J., Mangel, M., MacCall, A., McArdle, D.A., Ogden, J.C., Roughgarden, J., Starr, R.M., Tegner, M.J., and Yoklavich, M.M. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries*, **24**: 11–25.
- Mylius, S.D., Klumpers, K., de Roos, A.M., and Persson, L. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.* **158**: 259–276.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F., Jr. 1998. Fishing down marine food webs. *Science (Washington, D.C.)*, **279**: 860–863.
- Petratis, P.S., and Dudgeon, S.R. 2004. Detection of alternative stable states in marine communities. *J. Exp. Mar. Biol. Ecol.* **300**(1–2): 343–371.
- Polis, G.A., and Holt, R.D. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* **7**(5): 151–154.
- Polis, G.A., Myers, C.A., and Holt, R.D. 1989. The ecology and evolution of intraguild predation — potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* **20**: 297–330.
- Punt, A.E. 2003. Evaluating the efficacy of managing West Coast groundfish resources through simulations. *Fish. Bull.* **101**: 860–873.
- Ralston, S., Bence, J.R., Eldridge, M.B., and Lenarz, W.H. 2003. An approach to estimating rockfish biomass based on larval production, with application to *Sebastes jordani*. *Fish. Bull.* **101**(1): 129–146.
- Scheffer, M., and Carpenter, S.R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**(12): 648–656.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature (London)*, **413**(6856): 591–596.
- Shanks, A.L., Grantham, B.A., and Carr, M.H. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* **13**: S159–S169.
- Skellam, J.G. 1951. Random dispersal in theoretical populations. *Biometrika*, **38**(1–2): 196–218.
- Sladek Nowlis, J., and Roberts, C.M. 1999. Fisheries benefits and optimal design of marine reserves. *Fish. Bull.* **97**: 604–616.
- Steele, J.H., and Beet, A.R. 2003. Marine protected areas in 'non-linear' ecosystems. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **270**: S230–S233.
- Stein, D.L., Tissot, B.N., Hixon, M.A., and Barss, W. 1992. Fish–habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fish. Bull.* **90**: 540–551.
- Swain, D.P., and Sinclair, A.F. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **57**: 1321–1325.
- Walters, C. 2000. Impacts 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.
- Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* **58**: 39–50.
- Whipple, S.J., Link, J.S., Garrison, L.P., and Fogarty, M.J. 2000. Models of predation and fishing mortality in aquatic ecosystems. *Fish. Fish.* **1**: 22–40.
- Yoklavich, M., Greene, H.G., Cailliet, G., Sullivan, D., Lea, R., and Love, M. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fish. Bull.* **98**: 625–641.
- Yoklavich, M.M., Cailliet, G.M., Lea, R.N., Greene, H.G., Starr, R., deMarignac, J., and Field, J. 2002. Deepwater habitat and fish resources associated with the Big Creek Ecological Reserve. CalCOFI (California Cooperative Oceanic Fisheries Investigations), Rep. **43**: 120–140. Available at [http://www.calcofi.org/newhome/publications/CalCOFI\\_Reports/V43/V43\\_toc.htm](http://www.calcofi.org/newhome/publications/CalCOFI_Reports/V43/V43_toc.htm).

## Appendix A. Model details

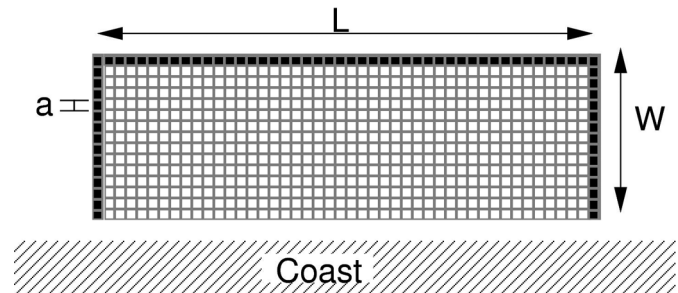
The smaller rockfish species, represented by  $C$  (competitors), have open recruitment at rate  $r_{1C}$  from the suboptimal habitat, as well as internal recruitment at rate  $r_{2C}$ . Assuming depletion of the larger, fished rockfish species outside the reserve (scorched earth), juveniles of the larger species, represented by  $J$ , only have internal recruitment at a rate of  $r_{2J}$ .

**Table A1.** Variables, parameters, and relation to reserve area.

Number	Density	
<b>Variables</b>		
$C$	$\rho_C A$	Competitors (smaller species)
$J$	$\rho_J A$	Juveniles (of larger species)
$P$	$\rho_P A$	Predators (adults of larger species)
<b>Parameters</b>		
$r_{1X}$	$r_{A1X} A$	Open recruitment rate for $X$ ( $C$ or $J$ )
$r_{2X}$	$r_{A2X} \frac{W}{\omega} \int_0^L \int_0^L \frac{\kappa_X(y-x)}{L} dy dx$	Internal recruitment rate for $X$ (see Fig. A1)
$V_X$	$\bar{D}_X$ or $\frac{\pi}{2} \bar{D}_X^2$	Variance in dispersal distance for kernel $\kappa_X(y-x)$ (Laplace or normal, respectively) <sup>a</sup>
$K_X$	$K_{AX} A$	Carrying capacity of $X$
$\alpha_{XY}$		Competitive effect of $X$ on $Y$
$\delta_X$	$\delta_{AX}/A$	Predation rate of predators on $X$
$\tau_X$		Handling time for $X$ in type II predation
$\beta_X$	$\beta_{AX} \frac{W}{\omega} \int_0^L \int_0^L \frac{\kappa_X(y-x)}{L} dy dx$	Conversion factor of predation on $X$ into reproductive capacity
$\gamma$		Growth rate from juveniles to predators
$\mu$		Natural mortality for predators
$h$	$h_A \left( \frac{2W+L}{LW} \right)$	Fishing mortality in predators (see Fig. A2)
$A$	$LW$	Reserve area = length $\times$ width
$N_R$		Number of reserves in a reserve network

<sup>a</sup>Lockwood et al. 2002.**Fig. A1.** Length  $L$  parallel to the coast and width  $W$  perpendicular to the coast characterize a theoretical reserve. The dispersal kernel  $\kappa(y-x)$  (either normal or Laplace) represents the settlement distribution along the coast (each point  $y$ ) of offspring originating at point  $x$ . At each settlement point  $y$ , individuals are equally likely to settle at any distance perpendicular to coast within the suitable habitat width,  $\omega$ .

The reserve has carrying capacities  $K_C$  for the competitors and  $K_J$  for the juveniles, and the juveniles and competitors compete according to constants  $\alpha_{JC}$  and  $\alpha_{CJ}$ . The adults of the larger species, represented by  $P$  (predators), prey on the competitors and juveniles at rates  $\delta_C$  and  $\delta_J$ , respectively. This predation is converted into reproductive capacity according to  $\beta_C$  and  $\beta_J$ ;  $r_{2J}$  represents additional reproductive capacity due to constant predation on other prey not included in the dynamics below. The growth rate of juveniles into adult predators is  $\gamma$ , the natural adult mortality rate is  $\mu$ ,

**Fig. A2.** The checked area represents a reserve of length  $L$  and width  $W$ , each check of size  $a \times a$  represents an adult territory, and the solid checks on the perimeter of the reserve are vulnerable to fishing edge effects.

and the fishing mortality rate as a result of edge effects on the border of the reserve is  $h$ . Then competitor, juvenile, and predator populations vary over time ( $t$ ) according to :

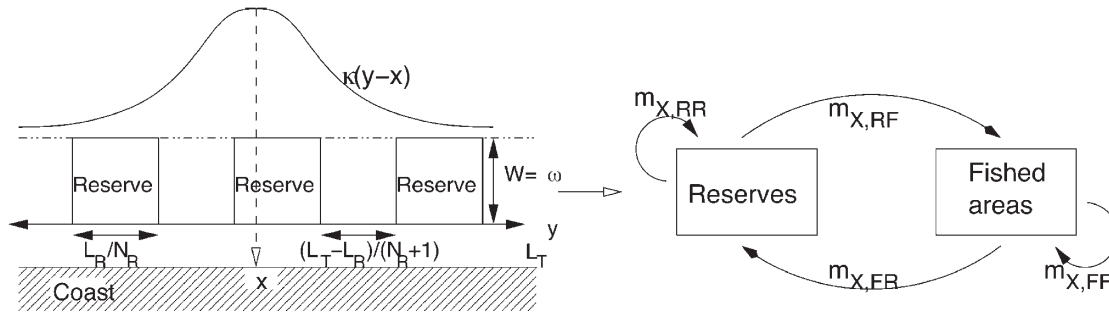
$$(A1) \quad \frac{dC}{dt} = \frac{r_{1C} + r_{2C}C}{K_C} (K_C - C - \alpha_{JC}J) - \delta_C PC$$

$$(A2) \quad \frac{dJ}{dt} = \frac{P(r_{2J} + \beta_J \delta_J J + \beta_C \delta_C C)}{K_J} (K_J - J - \alpha_{CJ}C) - (\delta_J P + \gamma)J$$

$$(A3) \quad \frac{dP}{dt} = \gamma J - (\mu + h)P$$

(Fig. 1). Here we use Lotka–Volterra dynamics based on their frequent and historical use in ecological dynamics, in-

**Fig. A3.** Integrating and summing the dispersal kernel ( $\kappa(y-x)$ ) over reserves and (or) fished areas in a reserve network (with width  $W$  equal to habitat width  $\omega$  and total reserve network length  $L_R$  out of region length  $L_T$  divided into  $N_R$  reserves) yields the movement rates ( $m_{x,yz}$ ) within and between reserves and fished areas for each species.



cluding multispecies fisheries dynamics, as well as for mathematical simplicity and the use of relatively few (albeit difficult to estimate) parameters (Whipple et al. 2000).

### Density dynamics

To redefine the model in terms of population density (fish per unit area) rather than number of individuals, let  $\rho_C = C/A$ ,  $\rho_J = J/A$ , and  $\rho_P = P/A$ . Given the area relationships in Table A1, eqs. A1–A3 become

$$(A4) \quad \frac{d\rho_C}{dt} = \frac{r_{AC} + r_{2C}[L, W]\rho_C}{K_{AC}} (K_{AC} - \rho_C - \alpha_{JC}\rho_J) - \delta_{AC}\rho_P\rho_C$$

$$(A5) \quad \frac{d\rho_J}{dt} = \frac{\rho_P(r_{2J}[L, W] + \beta_J[L, W]\delta_{AJ}\rho_J + \beta_C[L, W]\delta_{AC}\rho_C)}{K_{AJ}} \times (K_{AJ} - \rho_J - \alpha_{CJ}\rho_C) - (\delta_{AJ}\rho_P + \gamma)\rho_J$$

$$(A6) \quad \frac{d\rho_P}{dt} = \gamma\rho_J - (\mu + h[L, W])\rho_P$$

### Analysis

We primarily use local stability analysis of our community model. The leading eigenvalue  $\lambda$  of the Jacobian matrix of eqs. A4–A6 evaluated at an equilibrium ( $\hat{\rho}_C, \hat{\rho}_J, \hat{\rho}_P$  such that  $\frac{d\rho_C}{dt} = \frac{d\rho_J}{dt} = \frac{d\rho_P}{dt} = 0$ ) indicates the local stability of that equilibrium: if  $\lambda < 0$ , then the above equilibrium is locally stable; if  $\lambda > 0$ , then the above equilibrium is locally unstable.

One biologically relevant equilibrium for system A4–A6 is  $\hat{\rho}_C = K_{AC}$ ,  $\hat{\rho}_J = \hat{\rho}_P = 0$ , or with competitors at their carrying capacity and juveniles and predators not present. The three eigenvalues of system A4–A6 evaluated at this equilibrium are

$$(A7) \quad \lambda_1 = -\frac{r_{AC} + r_{2C}K_{AC}}{K_{AC}}$$

$$(A8) \quad \lambda_2 = -\frac{1}{2}(\gamma + \mu + h) - \frac{1}{2}\sqrt{(\gamma - (\mu + h))^2 + 4\gamma(r_{2J} + \beta_C\delta_{AC}K_{AC})\left(1 - \alpha_{CJ}\frac{K_{AC}}{K_{AJ}}\right)}$$

$$(A9) \quad \lambda_3 = -\frac{1}{2}(\gamma + \mu + h) + \frac{1}{2}\sqrt{(\gamma - (\mu + h))^2 + 4\gamma(r_{2J} + \beta_C\delta_{AC}K_{AC})\left(1 - \alpha_{CJ}\frac{K_{AC}}{K_{AJ}}\right)}$$

Given that all parameter values are positive,  $\lambda_1$  and  $\lambda_2$  have a negative real part.  $\lambda_3$  has a negative real part if

$$(A10) \quad \mu + h > (r_{2J} + \beta_C\delta_{AC}K_{AC})\left(1 - \alpha_{CJ}\frac{K_{AC}}{K_{AJ}}\right)$$

or the larger species mortality outweighs its recruitment reduced by a factor based on competition with the smaller species. Note that inequality A10 is always true if  $\alpha_{CJ} < K_{AJ}/K_{AC}$ , or the smaller species is a superior competitor to the juveniles of the larger species, which is true for all parameter values used here. Therefore, when the smaller species is the superior competitor (and, more generally, when inequality A10 holds), all eigenvalues are negative and the equilibrium is locally stable.

For analysis of additional equilibria, we numerically solve for the equilibria and calculate the leading eigenvalue of the Jacobian matrix evaluated at those equilibria using the parameter values in Table 1. An analytical exploration of the generality of the numerical results shown here is worth future theoretical investigation.

### Equivalent system without predation and competition

Without the competition and predation ( $\alpha_{CJ} = \alpha_{JC} = \delta_{AC} = 0$ ; i.e., removing the smaller species from the system), there are two biologically relevant equilibria. Based on local stability analysis as described above, the trivial equilibrium,  $\hat{\rho}_J = \hat{\rho}_P = 0$ , is locally stable if  $\mu + h[L, W] > r_{2J}[L, W]$  (mortality outweighs reproduction). For the nontrivial equilibrium,  $\hat{\rho}_J = \gamma\frac{K_{AJ}}{r_{2J}}\left(\frac{r_{2J}}{\mu + h} - 1\right)$ ,  $\hat{\rho}_P = K_{AJ}\left(1 - \frac{\mu + h}{r_{2J}}\right)$ , the

condition for its biological existence (nonnegative densities) and local stability are identical:  $r_{2J}[L, W] > \mu + h[L, W]$  (reproduction outweighs mortality), exactly the reverse of the stability condition for the trivial equilibrium. Therefore, if reproduction outweighs mortality, the system will go to positive equilibrium densities; otherwise, the juveniles and predators will decline to zero.



## Relaxing assumptions

### Type I predation

For mathematical simplicity, the above model uses a linear (type I) functional response of predators to prey density; however, a saturating (type II) functional response is more biologically realistic. To determine whether incorporating type II functional response significantly impacts the results, system A4–A6 with type II predation is

$$(A11) \quad \frac{d\rho_C}{dt} = \frac{r_{A1C} + r_{2C}[L, W]\rho_C}{K_{AC}} (K_{AC} - \rho_C - \alpha_{JC}\rho_J) - \frac{\delta_{AC}\rho_P\rho_C}{1 + \tau_C\delta_{AC}\rho_C + \tau_J\delta_{AJ}\rho_J}$$

$$(A12) \quad \frac{d\rho_J}{dt} = \frac{\rho_P}{K_{AJ}} \left( r_{2J}[L, W] + \frac{\beta_J[L, W]\delta_{AJ}\rho_J + \beta_C[L, W]\delta_{AC}\rho_C}{1 + \tau_C\delta_{AC}\rho_C + \tau_J\delta_{AJ}\rho_J} \right) (K_{AJ} - \rho_J - \alpha_{CJ}\rho_C) - \rho_J \left( \frac{\delta_{AJ}\rho_P}{1 + \tau_C\delta_{AC}\rho_C + \tau_J\delta_{AJ}\rho_J} + \gamma \right)$$

$$(A13) \quad \frac{d\rho_P}{dt} = \gamma\rho_J - (\mu + h[L, W])\rho_P$$

We numerically compare equilibria densities and local stabilities for the system with type I and type II predation over a range of reserve lengths with the default parameters listed in Table 1.

### Scorched earth

To relax the scorched earth assumption that overfishing negates any contribution of predator populations outside the reserve to juvenile populations inside the reserve, we model the dynamics within and exchange between reserves (with competitor, juvenile, and predator populations  $C_R$ ,  $J_R$ , and  $P_R$ , respectively) and fished areas (with competitor, juvenile, and predator populations  $C_H$ ,  $J_H$ , and  $P_H$ , respectively) according to

$$(A14) \quad \frac{dC_R}{dt} = \frac{r_{A1C}A_R + r_{A2C}(m_{C,RR}C_R + m_{C,FR}C_H)}{K_{AC}A_R} (K_{AC}A_R - C_R - \alpha_{JC}J_R) - \delta_{AC}A_RP_R C_R$$

$$(A15) \quad \frac{dC_H}{dt} = \frac{r_{A1C}A_H + r_{A2C}(m_{C,FF}C_H + m_{C,RF}C_R)}{K_{AC}A_H} (K_{AC}A_H - C_H - \alpha_{JC}J_H) - \delta_{AC}A_HP_H C_H$$

$$(A16) \quad \frac{dJ_R}{dt} = \frac{1}{K_{AJ}A_R} (m_{J,RR}P_R(r_{A2J} + \delta_{AJ}A_R\beta_{AJ}J_R + \delta_{AC}A_R\beta_{AC}C_R) + m_{J,FR}P_H(r_{A2J} + \delta_{AJ}A_H\beta_{AJ}J_H + \delta_{AC}A_H\beta_{AC}C_H)) \\ \times (K_{AJ}A_R - J_R - \alpha_{CJ}C_R) - (\delta_{AJ}A_RP_R + \gamma)J_R$$

$$(A17) \quad \frac{dJ_H}{dt} = \frac{1}{K_{AJ}A_H} (m_{J,FF}P_H(r_{A2J} + \delta_{AJ}A_H\beta_{AJ}J_H + \delta_{AC}A_H\beta_{AC}C_H) + m_{J,RF}P_R(r_{A2J} + \delta_{AJ}A_R\beta_{AJ}J_R + \delta_{AC}A_R\beta_{AC}C_R)) \\ \times (K_{AJ}A_H - J_H - \alpha_{CJ}C_H) - (\delta_{AJ}A_HP_H + \gamma)J_H$$

$$(A18) \quad \frac{dP_R}{dt} = \gamma J_R - \left( \mu + h_A \frac{L_R + N_R W}{L_R W} \right) P_R \quad (A19) \quad \frac{dP_H}{dt} = \gamma J_H - (\mu + h_A) P_H$$

In the above system, there is no adult movement, and all movement occurs as a result of larval dispersal. Movement parameters  $m_{X,RR}$  and  $m_{X,FF}$  represent the portion of larvae retained within reserves and fished areas, respectively, whereas  $m_{X,FR}$  is the proportion of larvae that move from fished to reserve areas and  $m_{X,RF}$  is the proportion of larvae that move from reserve to fished areas. Integrating and summing the dispersal kernel over reserves or fished areas yields the retention and exchange rates for each species  $X$  ( $C$  or  $J$ ; Fig. A3). Because we do not explicitly account for adult movement, predators in reserves still experience edge-effects fishing. Again, we numerically analyze the equilibria values and local stabilities of system A14–A19 with the parameter values in Table 1.

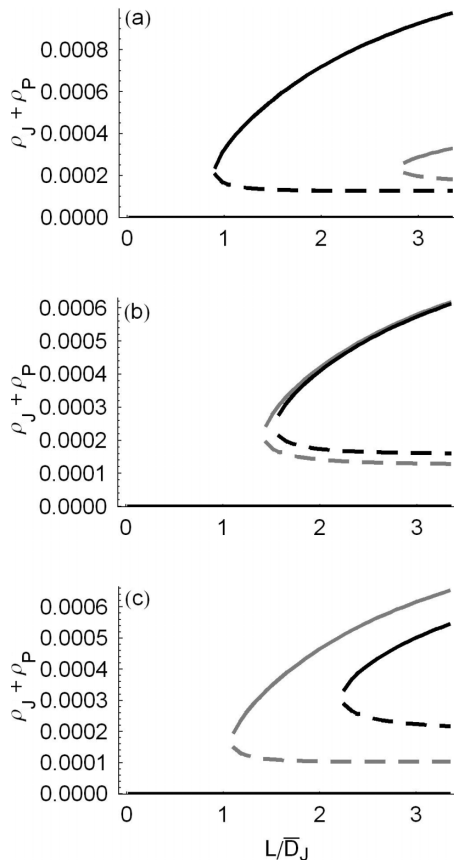
## Reference

Lockwood, D.R., Hastings, A., and Botsford, L.W. 2002. The effects of dispersal patterns on marine reserves: does the tail wag the dog? *Theor. Popul. Biol.* **61**: 297–309.

## Appendix B. Exploration of uncertain parameter values and assumptions

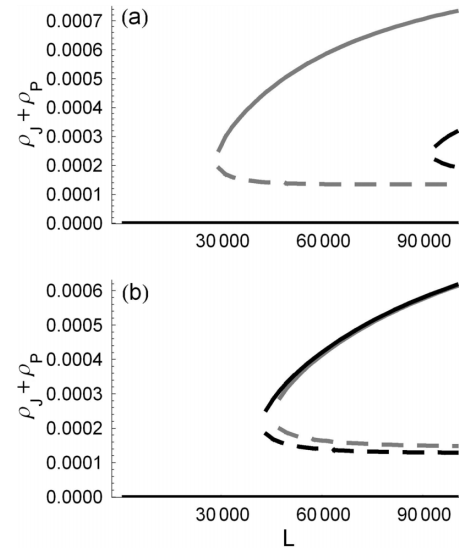
Here we determine the impact of changing uncertain parameter values on our results. Rather than a formal sensitivity analysis, we explore biologically feasible ranges to determine which parameters may require more precise values in order to make quantitative predictions. In the following graphs, shaded lines represent lower limits and black lines represent upper limits of uncertain parameter ranges.

**Fig. B1.** Equilibria densities (fish·m<sup>-2</sup>) for larger species dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_J$ ) for ranges of recruitment rate values with (a) juvenile internal recruitment ranges, (b) competitor internal recruitment ranges, and (c) competitor external recruitment ranges. Solid and broken lines indicate stable and unstable equilibria, respectively; shaded and black lines indicate lower and upper bounds for value ranges, respectively.



Decreasing recruitment rates, increasing dispersal distances, and increasing habitat width all have the similar affect of decreasing within-reserve recruitment, by decreasing reproduction, decreasing retention, and decreasing the proportion of the habitat covered by the reserve, respectively. Therefore, changes in these parameters have similar effects on equilibrium values. Specifically, because of decreased within-reserve recruitment, decreasing the juvenile internal recruitment rate, increasing the juvenile dispersal distance, and increasing habitat width all substantially increase the reserve size necessary for the threshold and larger species dominated equilibria to exist and decrease the larger species dominated equilibrium density for the larger species (Figs. B1a, B2a, and B3, respectively). Analogous changes in parameter values for the smaller species have less of an impact on equilibrium values. Qualitatively, decreasing the competitor internal recruitment rate, decreasing the competitor external recruitment rate, and increasing the competitor dispersal distance all decrease the reserve size necessary for the threshold and larger species dominated equilibria to exist and decrease the threshold equilibrium density for the larger species (decreasing the smaller species' external recruitment increases the larger species density at the larger species dominated equilibrium as well), pre-

**Fig. B2.** Equilibria densities (fish·m<sup>-2</sup>) for larger species dependent on reserve length ( $L$ , m) for ranges of values for dispersal distance for (a) juveniles and (b) competitors. Solid and broken lines indicate stable and unstable equilibria, respectively; shaded and black lines indicate lower and upper bounds for value ranges, respectively.



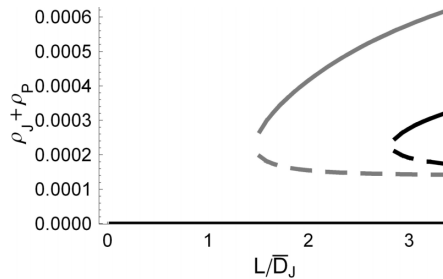
sumably because of decreased competition for the larger species' juveniles with the decreased recruitment for the smaller species (Figs. B1b, B1c, and B2b, respectively). Beyond affecting the reserve lengths for which the equilibria exist, changes in these parameters have little affect on the smaller species equilibria densities (results not shown). In addition, choosing a Laplace or normal dispersal kernel does not impact the qualitative results of the model (Fig. B4).

Altering carrying capacities tests the effect of altering competition between the juveniles and the competitors. Decreasing the juvenile carrying capacity increases the reserve size necessary for the threshold and larger species dominated equilibria to exist, increases the threshold equilibrium density for the larger species, decreases the threshold equilibrium density for the smaller species, and decreases the larger species dominated equilibrium density for the larger species, all presumably because of the greater competitive disadvantage (Figs. B5a, B5b). The primary effect of increasing the smaller species carrying capacity is to increase its density at the smaller species dominated equilibrium to the new carrying capacity (Figs. B5c, B5d).

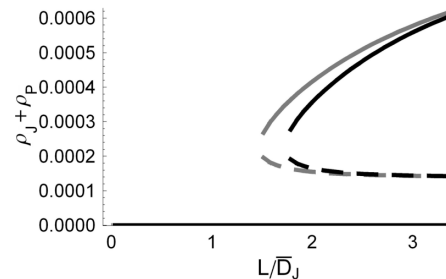
Within the parameter ranges tested, changing the fishing mortality outside the reserve has virtually no impact on the smaller or larger species equilibria densities (results not shown).

Altering predation parameter values has a substantial impact on equilibrium predictions. Both increasing predation on juveniles and decreasing predation on competitors increase the reserve size necessary for the threshold and larger species dominated equilibria to exist, decrease the threshold equilibrium density for the smaller species, and decrease the larger species dominated equilibrium density for the larger species (Fig. B6). Furthermore, decreasing predation on competitors increases the threshold equilibrium density for the larger species (Fig. B6c). A likely ex-

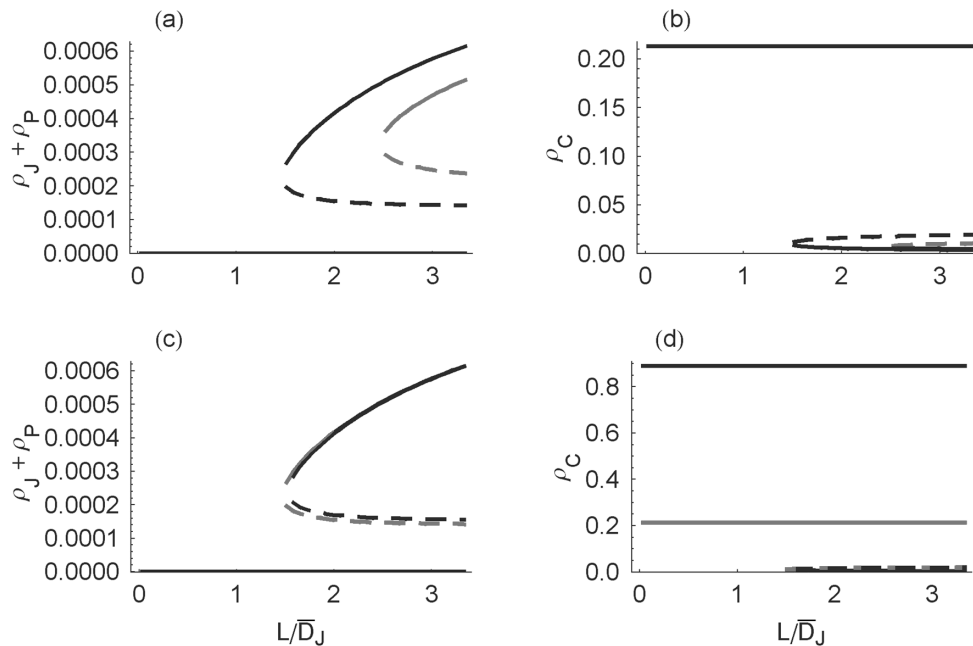
**Fig. B3.** Equilibria densities (fish·m<sup>-2</sup>) for larger species dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_j$ ), for a range of habitat widths (impacting percent of habitat that the reserve covers). Solid and broken lines indicate stable and unstable equilibria, respectively; shaded and black lines indicate lower and upper bounds for value ranges, respectively.



**Fig. B4.** Equilibria densities (fish·m<sup>-2</sup>) for larger species dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_j$ ) using the Laplace dispersal kernel (shaded lines) and the normal dispersal kernel (black lines). Solid and broken lines indicate stable and unstable equilibria, respectively.



**Fig. B5.** Equilibria densities (fish·m<sup>-2</sup>) for larger and smaller species dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_j$ ) for ranges of values for carrying capacity for (a–b) juveniles and (c–d) competitors. Solid and broken lines indicate stable and unstable equilibria, respectively; shaded and black lines indicate lower and upper bounds for value ranges, respectively.

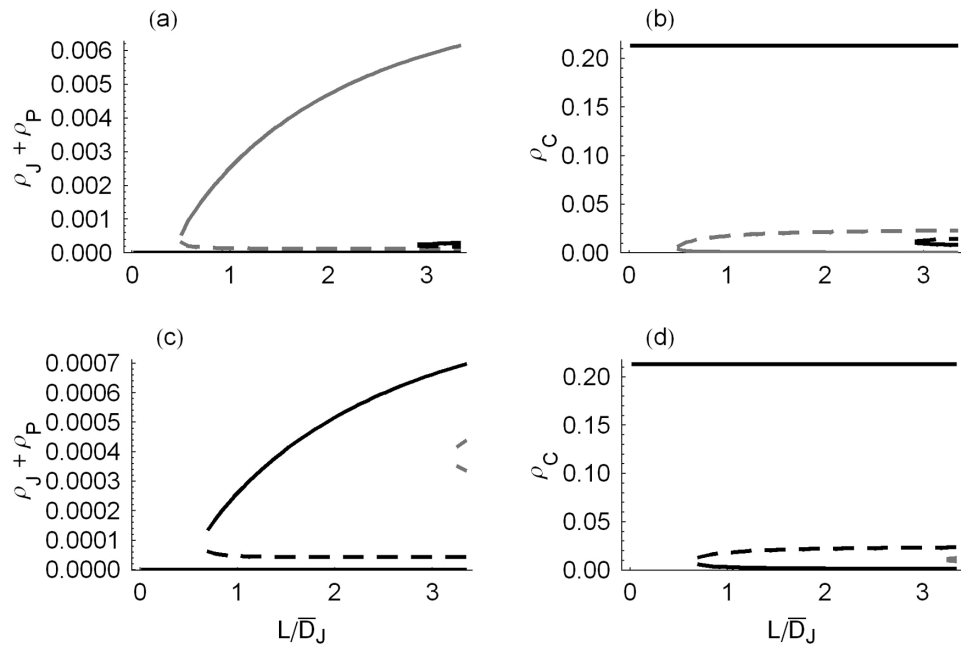


planation for these trends is increased juvenile mortality and decreased predation pressure offsetting competition with increased juvenile predation and decreased competitor predation, respectively. Incorporating handling time and prey saturation in the predation dynamics has little impact on equilibrium predictions (results not shown).

We explore the effect of relaxing the scorched earth assumption and explicitly modeling exchange between protected and fished areas with numerical analysis. With the parameter values tested, the protected-fished exchange model has the same qualitative equilibrium outcome as the scorched earth

model: two alternative stable states (smaller species dominated and larger species dominated equilibria) and an unstable threshold in between, both in the reserve and in the fished areas (Fig. 5). However, incorporating exchange between protected and unprotected areas substantially increases the threshold equilibrium density for the larger species inside the reserve and decreases the threshold equilibrium density for the small species inside the reserve (Figs. 5a, 5c). Increasing the number of reserves in a reserve network primarily decreases the threshold and larger species dominated equilibria densities for the larger species (Fig. B7).

**Fig. B6.** Equilibria densities (fish·m<sup>-2</sup>) for larger and smaller species dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_j$ ) for ranges of values for predation rate on (a–b) juveniles and (c–d) competitors. Solid and broken lines indicate stable and unstable equilibria, respectively; shaded and black lines indicate lower and upper bounds for value ranges, respectively.



**Fig. B7.** Equilibria densities (fish·m<sup>-2</sup>) for larger species in (a) reserves and (b) fished areas dependent on reserve length scaled to mean juvenile dispersal distance ( $L/\bar{D}_j$ ) for a range of number of reserves in a reserve network. Solid and broken lines indicate stable and unstable equilibria, respectively; shaded and black lines indicate lower and upper bounds for value ranges, respectively.

