SIMPLE FISHERIES AND MARINE RESERVE MODELS OF INTERACTING SPECIES: AN OVERVIEW AND EXAMPLE WITH RECRUITMENT FACILITATION

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ABSTRACT

Accounting for species interactions is a key component of ecosystem-based management. Simple models of species interactions provide a framework for making qualitative comparisons and identifying critical dynamics. A review of multispecies-fisheries and marine-reserve models indicates that incorporating species interactions leads to decreased theoretical predictions for sustainable yield and harvest rates and to increased theoretical predictions for the reserve size necessary to protect populations; ontogenetic shifts in interactions also have a significant effect on multispecies model predictions. While previous models have explored negative species interactions (i.e., predation and competition), this paper presents an example marine reserve model with a positive interaction: a spiny lobster-sea urchin-red algae trophic chain where red algae facilitate lobster recruitment. Model results indicate that recruitment facilitation primarily affects the time scale of the species dynamics and the lobster spillover from reserves to harvested areas; the direction of these changes depends on the no-facilitation baseline. Overall, these models indicate the importance of incorporating species interactions into fisheries and reserve management decisions.

INTRODUCTION

Global declines in harvested species have led to a call for a more holistic, ecosystem-based approach to fisheries management (Botsford et al. 1997; Pikitch et al. 2004). One of the central components of ecosystem-based management (EBM) is a multispecies approach (Larkin 1996; Pikitch et al. 2004; Marasco et al. 2005). In general, interspecific biodiversity is vital to marine ecosystem functional properties, such as productivity and stability (Worm et al. 2006). In addition, interactions between species may affect management metrics such as maximum sustainable yield (Hollowed et al. 2000) and, when overfishing occurs, could impede the recovery of depleted stocks (Walters and Kitchell 2001; Heino and Godø 2002; MacCall 2002).

Simple models provide insight into how species interactions may affect management decisions. For the purposes of this paper, simple models have few (two to four)

species or aggregated groups of species (e.g., trophic guilds), follow deterministic dynamics on the level of populations (as opposed to individuals), and have a limited number of parameters (e.g., May et al. 1979), in contrast to large-scale simulations which have complex food web structure and/or variable climatic and oceanographic conditions (e.g., Field et al. 2006). While these approaches represent extremes on a continuum of possible model complexity, most models fall into one of these two categories.

Models, from simple community models to large-scale simulations, are always a simplified representation of the biological reality. While simple community models are less realistic, they can make important contributions to management decisions. For example, simple models can provide qualitative predictions, in some cases with the same degree of accuracy as more complicated simulations (Essington 2004; May 2004). This relative accuracy is possible because including the dynamics that have the greatest impact on model outcomes is more important to theoretical predictions than including a high level of biological detail in complicated simulations that neglect such key dynamics (for examples from disease management, see May 2004).

Furthermore, while the parameters in simple community models may be more abstract and therefore more difficult to measure (Whipple et al. 2000), the existence of fewer dynamics and parameters allows for more sensitivity analysis than possible in complicated simulations. In some cases, an analytic solution can be derived, which enables all potential outcomes to be determined. Overall, simple models provide greater insight into which dynamics and parameters have a large impact on model predictions. Therefore, such models help determine which processes may be necessary to incorporate into complicated simulations in order to ensure predictive power, and they help identify some key ecological processes or variables to estimate empirically (Whipple et al. 2000; Essington 2004).

The goal of this paper is to explore the effect of incorporating species interactions in simple models relevant to marine management. The incorporation of species interactions into traditional (non-spatial) fisheries man-

agement models has been reviewed by Bax (1998), Hollowed et al. (2000), Whipple et al. (2000), and Latour et al. (2003); the more recent development of incorporating species interactions into marine reserve models has been reviewed by Baskett et al. (2007). Because these approaches have previously been reviewed only separately, this paper provides a brief synopsis of the conclusions from these models and reviews and synthesizes the conclusions from both fisheries and marine reserve models. In addition, this paper presents a new example model.

As with theoretical ecology in general (Bruno et al. 2003), multispecies marine management models have focused on the negative interactions of predation and competition, while positive interactions are relatively under-explored despite their prevalence in marine ecosystems (with exceptions, e.g., see Thompson et al. 2006 for a mutualistic model relevant to marine populations, and see Rogers-Bennett and Pearse 2001 for an empirical study of the influence of facilitation on species responses to marine reserve establishment). Therefore, the example model I present incorporates recruitment facilitation into the dynamics of interacting species in marine reserves and harvested areas. Specifically, the model follows the trophic dynamics of spiny lobsters (*Panulirus interruptus*), sea urchins (*Strongylocentrotus* spp.), and red algae (*Gelidium* spp.), as well as the potential for spiny lobsters to preferentially recruit to red algae. Generalities arising from the overview and example model indicate how species interactions may affect marine management and help to identify topics for future research.

Overview of existing models

Interacting species in fisheries models

The interspecific dynamic most frequently incorporated into fisheries management models is predation (e.g., Larkin 1966; May et al. 1979; Brauer and Soudack 1981; Shirakihara and Tanaka 1981; Beddington and Cooke 1982; Yodzis 1994; Ströbele and Wacker 1995; Spencer and Collie 1996; Basson and Fogarty 1997; Dai and Tang 1998; Flaaten 1998; Essington 2004). In addition, some models account for competition directly (e.g., Larkin 1963; Shirakihara and Tanaka 1978; Kirkwood 1982; Ströbele and Wacker 1991; Semmler and Sieveking 1994) or indirectly in trophic models with multiple predators and/or prey (e.g., Collie and DeLong 1999), and a few models account for mutualism (e.g., Ströbele and Wacker 1991; Wacker 1999). Because of the additional predation mortality incorporated, the primary effect of including trophic interactions in the modeled species' demography is an increase in mortality rates; incorporating trophic interactions has little effect on the average recruitment of the modeled species (Hollowed et al. 2000). Incorporating species interactions such as preda-

tion can provide a mechanistic explanation for some of the variability in recruitment, mortality, age structure, and size structure (Hollowed et al. 2000).

The additional mortality factored in when incorporating predation into models causes decreases in the predicted yield per recruit and in spawner biomass per recruit and increases in the predicted recovery time compared to single species approaches (Hollowed et al. 2000). Furthermore, the total yield and maximum sustainable yield (MSY) in simple multispecies models with trophic and/or competitive interactions are less than the equivalent yield predictions from the analogous single-species models summed over all species (Pope 1975; May et al. 1979; Kirkwood 1982; Collie and DeLong 1999). How much predation affects yield predictions depends on the type of predation assumed (Yodzis 1994; Flaaten 1998). Landings and MSY predictions can also be lower than single-species predictions in more complicated community simulations such as Ecosim models, but the opposite trend is possible as well with the added food web complexity (Walters et al. 2005).

In addition, the harvest rates that maximize yield in single-species models are often unsustainable in the corresponding multispecies models that account for competitive and trophic interactions, both (1) because the single-species models overestimate sustainable harvest rates (May et al. 1979; Ströbele and Wacker 1991; Essington 2004) and (2) because the multispecies models have the capacity to have unstable equilibria, multiple stable states, and limit cycles when assuming strong and/or nonlinear species interactions (Shirakihara and Tanaka 1978; Brauer and Soudack 1981; Shirakihara and Tanaka 1981; Beddington and Cooke 1982; Kirkwood 1982; Semmler and Sieveking 1994; Spencer and Collie 1996; Basson and Fogarty 1997; Dai and Tang 1998). Overestimates of sustainable harvest rates generally result from species negatively affecting each others' productivities and, in trophic models, from the potential for harvest on a prey species to decrease the food availability and, therefore, productivity of a predator species; these dynamics are ignored in single-species models but accounted for in multispecies models (note that increased sustainable harvest rates can occur in mutualistic models due to the positive impact of the species on each others' productivities; Ströbele and Wacker 1991). Second, when unstable equilibria, multiple stable states, and limit cycles are possible, the dynamics of interacting species can create the potential for fishing to cause sudden shifts to an undesirable ecological state, such as a state with lower or collapsed populations of target species ("ecologically unsustainable yield" sensu Zabel et al. 2003). Similarly, Ecosim simulations indicate that fishing every species at its single-species MSY harvest rate would lead to a collapse in top predators in more complex food

webs (Walters et al. 2005). Overall, species interactions can have a profound impact on the basic metrics of sustainable fisheries management.

Interacting species in marine reserve models

Fisheries substantially alter the structure of marine ecosystems through direct take and indirect impacts that cascade through species interactions (Pauly et al. 1998; Jackson et al. 2001). One of the primary goals of no-take marine reserves is to protect biodiversity and ecosystem structure and function (Allison et al. 1998; Leslie 2005). Therefore, multispecies marine reserve models often address the question of how to design reserves to protect marine communities given the ecosystem impacts of fisheries outside reserves and before the reserves are established (the focus of the review by Baskett et al. 2007). This focus on conservation goals of reserves differs from single-species marine reserve models (reviewed by Guénette et al. 1998; Gerber et al. 2003), which primarily address the potential for reserves to reduce uncertainty in or enhance sustainable fisheries yield. While including the insights into designing reserves to achieve conservation goals from multispecies models, the overview below highlights model results that relate to sustainable fisheries management.

As in the fisheries models reviewed above, multispecies marine reserve models focus on negative species interactions (i.e., predation and competition) which reduce the modeled species' productivities. Because species are assumed to have negative effects on each other, incorporating species interactions increases the predicted reserve size necessary to protect self-sustaining populations, both in simple models (Baskett et al. 2006; 2007) as well as in more complex simulations such as Ecospace models (Walters 2000). Species interactions also alter reserve placement criteria. For example, incorporating predation on inshore juveniles for a species with an ontogenetic shift from inshore to offshore habitats changes the relative effectiveness of inshore and offshore reserves (Mangel and Levin 2005). In addition, a predator-prey model in which trophic level shifts with age indicates that reserve placement may need to be based on the current densities of the interacting species, including unfished prey species, to ensure the recovery of overfished predators (Baskett et al. 2006).

Along with reserve design, simple multispecies models provide insight into expectations after reserve establishment and, therefore, into appropriate goals for monitoring and determining reserve success. For example, two models predict the potential existence of alternative stable states, with or without a targeted species (Baskett et al. 2006; 2007). In this case, species interactions, such as competition, may impede the recovery of depleted species, depending on the species' densities

at reserve establishment (Baskett et al. 2006; 2007). However, when that recovery does occur, reserves may promote resilience of the targeted species population to any overfishing in the harvested areas outside reserves (Baskett et al. 2006).

In another example, a simple trophic model demonstrates that spillover from reserves to harvested areas is more likely for top predators when assuming both a predator and its prey were fished before the reserve was established because, subsequently, the productivity of the predator population within the reserve benefits from both reduced mortality and increased prey availability (Baskett et al. 2007). Furthermore, while reserves are generally expected to reduce variation in catch (e.g., see single-species models by Sladek Nowlis and Roberts 1999; Mangel 2000), incorporating predation into a stochastic marine reserve predator-prey model may increase variation in dispersal and, therefore, spillover to harvested areas (Greenville and MacAulay 2006). Therefore, species interactions affect expectations for both the recovery of community structure within reserves and the potential for reserves to promote sustainable fisheries in harvested areas.

Finally, both simple trophic models and complicated ecosystem simulations predict that trophic cascades, and therefore declines of some species, are feasible after reserves are established (Walters 2000; Micheli et al. 2004; Baskett et al. 2007). This potential for cascades may be overestimated because simple trophic models often ignore additional biological dynamics that typically reduce the potential for cascades, such as omnivory and refugia from predation (Polis et al. 2000). For example, incorporating prey size refugia, or the potential for larger prey to escape predation, greatly decreases the theoretical likelihood of trophic cascades after reserve establishment (Baskett 2006). Because fewer prey are available to predators when incorporating prey size refugia, predators recover more slowly in reserves and, in the absence of reserves, the threshold harvest mortality for fishing predators to depletion is lower (Baskett 2006). In this model, as well as in the models by Mangel and Levin (2005) and Baskett et al. (2006), the size/age-dependency of the interaction is critical to predicting how species interactions affect both reserve design issues, such as monitoring, and fisheries management issues, such as sustainable harvest.

Example model:
Incorporating positive interactions

Multispecies fisheries and marine reserve models have focused on predation and competition, and positive interactions are under-explored. Unlike negative interactions, incorporating positive interactions into models can lead to increases in the interacting species' productivi-

ties. Therefore, it might be expected that incorporating positive interactions may have the opposite effect compared to negative interactions on management decisions, such as an increase in sustainable harvest rates (e.g., Ströbele and Wacker 1991) and/or a decrease in the reserve size necessary to protect populations. Metacommunity models of mutualism and habitat destruction confirm this expectation by showing that critical patch size, and therefore critical reserve size, decreases with increasing mutualism strength (e.g., Prakash and de Roos 2004). However, such metacommunity models assume that areas outside reserves are uninhabitable, which differs from marine systems with habitable, but harvested, regions outside reserves. Accounting for dynamics outside reserves is particularly important in the context of a multispecies approach in managing marine systems because of the potential for unharvested species to have non-reserve populations that, given movement such as larval dispersal, affect reserve populations of harvested species (Baskett et al. 2007).

One type of positive interaction common to marine systems is recruitment facilitation (Bruno and Bertness 2001). Specifically, dispersing larvae of a wide range of fish and invertebrates often preferentially recruit to the habitat formed by invertebrates and algae (Bruno and Bertness 2001; Carr and Syms 2006). In many temperate rocky subtidal systems, these positively interacting species are also components of trophic cascades, where herbivores graze algae and consumers prey on herbivores, and the reduction of consumer populations through fisheries often leads to herbivore increases and algal declines (Pinnegar et al. 2000). Given recruitment facilitation, declines in algae from fisheries-induced trophic cascades (plus the myriad of other direct anthropogenic impacts on algae such as habitat disturbance from fishing gear and sedimentation) can lead to reduced recruitment of targeted species (Planes et al. 2000). Therefore, protection of recruitment habitat in marine reserves can also help protect community structure and harvested species (Planes et al. 2000).

As an initial step toward exploring the potential effect of positive interactions on marine management decisions, this paper presents an example multispecies marine reserve model with and without facilitation. In particular, the model focuses on a trophic (producer-herbivore-consumer) chain where both the herbivore and consumer are harvested and the producer facilitates the recruitment of the consumer. The model parameters are based on a Northeast Pacific rocky subtidal system with two harvested invertebrates, spiny lobsters (*Panulirus interruptus*) and sea urchins (*Strongylocentrotus* spp.), and red algae (*Gelidium* spp.), where red algae facilitate spiny lobster recruitment (fig. 1A). Harvesting of urchin predators such as spiny lobsters can shift this ecosystem from
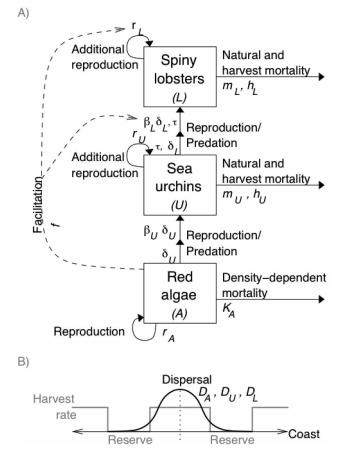

Figure 1. Outline of the spiny lobster–sea urchin–red algae facilitation model (equations 1–3). (A) ecological dynamics; (B) spatial dynamics.

diverse kelp forests (with high densities of many algae such as *Gelidium* spp.) to urchin-dominated barrens (with low densities of many algae); a goal of marine reserve networks is to protect the kelp forest community from such shifts (Behrens and Lafferty 2004a, b).

In the model, sea urchins and spiny lobsters prey on red algae and sea urchins, respectively, and convert that predation into reproductive capacity which increases the rate of recruitment above a baseline amount (as predation on red algae and sea urchins are each one of many sources of urchin and lobster reproduction; Sousa et al. 1981, Tegner and Levin 1983). For the spiny lobster, this total recruitment (which is the predation-to-reproduction conversion plus the constant baseline) indicates the maximum possible recruitment. In the model with facilitation, how much of this recruitment occurs depends on the red algae population size. Specifically, given the preferential recruitment of *P. interruptus* to *Gelidium* spp. (Castañeda-Fernández de Lara et al. 2005), the facilitation model assumes that an increased density of red algae indicates increased algal cover, and therefore increases the rate at which lobster larvae encounter their preferred settlement habitat; thus, increasing the density of algae

TABLE 1
Parameter values for the spiny lobster–sea urchin–red algae facilitation model (fig. 1; equations 1–3).

Description	Parameter	Value	Source[*]
Red algae recruitment	r_A	10/yr	
Urchin constant recruitment	r_U	0.4/yr	Pfister and Bradbury (1996)
Lobster constant recruitment	r_L	0.3/yr	Tegner and Levin (1983)
Lobster–red algae facilitation constant	f	0.05/A	Castañeda-Fernández de Lara et al. (2005)
Red algae carrying capacity	K	3 A	Castañeda-Fernández de Lara et al. (2005)
Urchin natural mortality	m_U	0.5/yr	Kenner (1992)
Lobster natural mortality	m_L	0.35/yr	
Urchin harvest mortality	H_U	0.1/yr	Morgan et al. (2000)
Lobster harvest mortality	H_L	0.1/yr	
Urchin predation on red algae	δ_U	0.2/U/yr	Sousa et al. (1981)
Lobster predation on urchins	δ_L	0.1/L/yr	Tegner and Levin (1983)
Lobster predation handling time	τ	10^{-8} yr	
Urchin predation-recruitment conversion	β_U	0.4 U/A	Kenner (1992)
Lobster predation-recruitment conversion	β_L	0.1 L/U	
Red algae average dispersal distance	V_A[**]	1 km	Kinlan and Gaines (2003), Sosa et al. (1998)
Urchin average dispersal distance	V_U[**]	10 km	Edmands et al. (1996)
Lobster average dispersal distance	V_L[**]	10 km	

[*]Parameter values are based on both the values reported in these sources and the values that produce biologically reasonable dynamics in the model.
[**]Diffusion constant for each species D_X ($X = A$, U, or L for algae, urchins, or lobsters) calculated from average dispersal distance V_X by $D_X = (\pi/4)(V_X/Y)^2$ (Lockwood et al. 2002), where $Y = 1{,}000$ km is the length of the coastline.

increases the realized proportion of the potential spiny lobster recruitment beyond a baseline recruitment proportion. In addition, spiny lobsters and sea urchins experience natural and harvest mortality, and red algae experience density-dependent mortality. Finally, in the model, spiny lobster, sea urchin, and red algae movement occurs as diffusion along an idealized linear coastline to represent random (larval and adult) dispersal, and harvest varies in space in order to model harvested areas interspersed with no-take reserves (fig. 1B).

Model details

Let L, U, and A represent the spiny lobster, sea urchin, and red algal densities, respectively. In addition, let δ_U and δ_L be the urchin and lobster predation rates, respectively, on algae and urchins, with linear (type-I functional response) predation by urchins and lobster predation saturating with handling time τ (type-II functional response), as handling time is more likely to affect lobster consumption of urchins than urchin grazing of algae. Predation is converted into reproduction with efficiencies β_U and β_L, while r_U and r_L are the constant recruitment rates for urchins and lobsters, respectively. The recruitment rate for the red algae is r_A, and its carrying capacity is K. m_U and m_L are the natural mortality rates for the urchins and lobsters, respectively; the urchin and lobster harvest mortalities, $h_U(x)$ and $h_L(x)$, vary with location x such that they are equal to the constant-effort harvest rates, H_U and H_L, for x outside reserves and equal to zero for x inside reserves. Algae, urchin, and lobster dispersal in space occurs according to diffusion constants D_A, D_U, and D_L on a linear coastline. Note that these diffusion constants are independent of life-history stage and therefore represent both adult movement and larval dispersal. Finally, the proportion of the total possible lobster recruitment beyond a baseline amount increases linearly with algal density according to the constant f. Given the above definitions, the model dynamics are shown below (fig. 1). One mathematical constraint in the above model is that the baseline reproductive rates (r_U, r_L) must be less than the mortality rates (m_U, m_L) to avoid exponential growth in the sea urchins and spiny lobsters. Therefore, while red algae and sea urchins are not the only resources available for sea urchins and spiny lobsters, respectively, their presence is necessary for the predators' persistence.

$$\frac{\partial L}{\partial t} = D_L \frac{\partial^2 L}{\partial x^2} + \left(\left(\frac{1 + fA}{1 + fK} \right) \left(r_L + \frac{\beta_L \delta_L U}{\beta_L \delta_L U} \right) - (m_L + h_L(x)) \right) L \qquad (1)$$

$$\frac{\partial U}{\partial t} = D_U \frac{\partial^2 U}{\partial x^2} + \left(r_U + \beta_U \delta_U A - \left(\frac{\delta_L U}{1 + \tau \delta_L U} + (m_U + h_U(x)) \right) \right) U \qquad (2)$$

$$\frac{\partial A}{\partial t} = D_A \frac{\partial^2 A}{\partial x^2} + \left(r_A \left(1 - \frac{A}{K} \right) - \delta_U U \right) A \qquad (3)$$
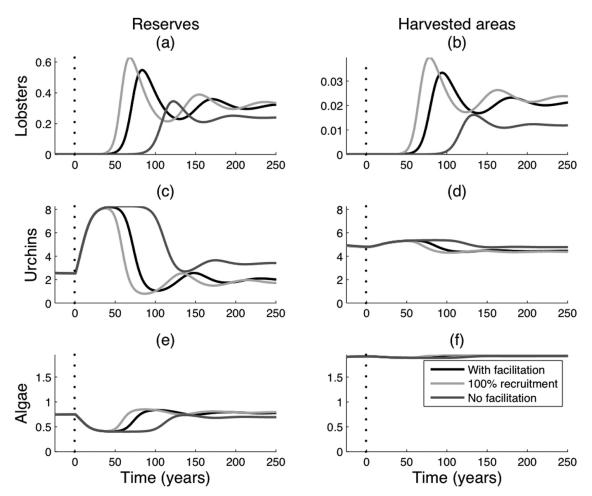
Figure 2.   Sample time trajectories of the facilitation model (in black) and the two baseline simulations without facilitation: none of the otherwise red algae-facilitated recruitment happens (in dark grey) or all of the otherwise red algae-facilitated recruitment happens (in light grey). (A-B) spiny lobster densities (note different y-axes); (C-D) sea urchin densities; (E-F) red algae densities; (A, C, and E) densities within reserves; (B, D, and F) densities within harvested areas. Dotted lines indicate time of reserve implementation.

I numerically analyzed the lobster, urchin, and algal dynamics given parameter values within biologically feasible ranges for *P. interruptus*, *Strongylocentrotus* spp., and *Gelidium* spp., respectively (tab. 1; Sousa et al. 1981; Tegner and Levin 1983; Kenner 1992; Edmands et al. 1996; Pfister and Bradbury 1996; Sosa et al. 1998; Morgan et al. 2000; Kinlan and Gaines 2003; Castañeda-Fernández de Lara et al. 2005). I assumed absorbing boundary conditions (moving beyond the edge of the habitat is fatal) on the linear habitat (coastline). First, I initialized all population densities at the expected (locally stable) equilibrium densities with fishing in the spatially implicit version of the model (i.e., $D_A = D_U = D_L = 0$). Second, I numerically integrated the system with harvesting along the entire coastline beyond the time where the system reaches an equilibrium with spatial dynamics (100 years). Third, I implemented spatially variable harvest rates in order to model reserves and continue numerical integration beyond the time where the system has reached the new equilibrium (250 years). In

addition to sample time trajectories, I present equilibrium results for varying reserve size and number of reserves in a reserve network.

Model results
In order to compare model results with facilitation to those without facilitation, I established two baseline models without facilitation, i.e., where spiny lobster recruitment is independent of red algae. In the first baseline, none of the additional recruitment that happens in the presence of red algae in the facilitation model occurred (i.e., $A = 0$ in equation 1; the "no-facilitation-recruitment" model). In the second baseline, spiny lobster recruitment always occurred at the maximum possible amount regardless of the red algae density (i.e., as if the red algae density were at its carrying capacity in the facilitation model, or $f = 0$ in equation 1; the "100% recruitment" model).

Given the parameter values used here, regardless of the inclusion of facilitation, the reserve populations fol-
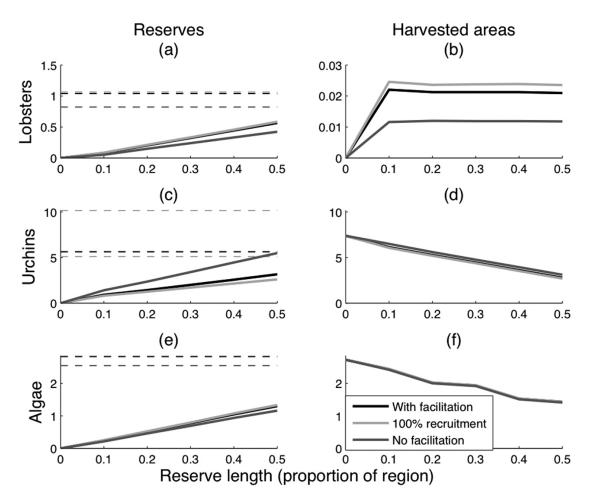
Figure 3. Equilibrium densities as a function of reserve size (proportion of the coastline protected in a single no-take reserve) for the facilitation model (in black) and the two baseline simulations without facilitation: none of the otherwise red algae-facilitated recruitment happens (in dark grey) or all of the otherwise red algae-facilitated recruitment happens (in light grey). (A-B) spiny lobster densities (note different y-axes); (C-D) sea urchin densities; (E-F) red algae densities; (A, C, and E) densities within reserves; (B, D, and F) densities within harvested areas. Broken lines indicate equilibrium density with no harvesting at any location (i.e., the expected natural state).

low time trajectories after reserve establishment where initially sea urchins increase and red algae decreases; then once the spiny lobsters start to increase, a cascade of decreasing sea urchins and increasing red algal occurs, with such oscillations eventually damping out to an equilibrium (fig. 2A, C, E). Harvested populations follow similar dynamics with lower magnitude oscillations (fig. 2B, D, F), probably due to the lower spiny lobster population sizes. While the inclusion of facilitation does not affect which populations increase or decrease, it does affect their time scale, with an intermediate response in the facilitation model; the fastest response was in the 100% recruitment model (where the lobsters have the greatest productivity), and the slowest response in the no-facilitation-recruitment model (where the lobsters have the lowest productivity).

In addition, facilitation has little effect on the reserve size necessary for the recovery of spiny lobsters and community structure (fig. 3A, C, E). However,

facilitation does affect the predicted spiny lobster population densities in harvested areas, which are connected to the amount of larval and adult spillover from reserves; harvested-area spiny lobster density increases with potential lobster productivity (i.e., no-facilitation-recruitment less than facilitation less than 100% recruitment; fig. 3B). If the total area protected is constant and the reserve network is fragmented into smaller, more numerous reserves, lobster populations in the reserve decrease and harvested populations increase due to greater export from reserves to harvested populations and less self-replenishment within reserves (fig. 4A, B). Eventually reserves may become too fragmented to protect populations within reserves and therefore provide a source population for harvested areas; this potential loss of lobster reserve spillover is less likely in the simulations with facilitation or 100% recruitment than in the simulations with no-facilitation-recruitment (fig. 4B).
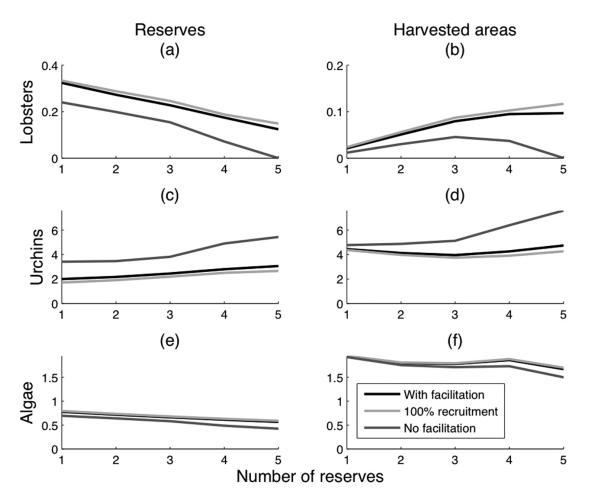
Figure 4. Equilibrium densities as a function of number of reserves in a reserve network with 30% of the coastline protected in total for the facilitation model (in black) and the two baseline simulations without facilitation: none of the otherwise red algae-facilitated recruitment happens (in dark grey) or all of the otherwise red algae-facilitated recruitment happens (in light grey). (A-B) spiny lobster densities (note different y-axes); (C-D) sea urchin densities; (E-F) red algae densities; (A, C, and E) densities within reserves; (B, D, and F) densities within harvested areas.

DISCUSSION

Conclusions from the facilitation model

In the example marine reserve multispecies model presented here, a spiny lobster–sea urchin–red algae trophic chain, recruitment facilitation of the spiny lobster to red algae primarily affects the time scale of the community recovery within reserves (fig. 2) and the potential for spiny lobster spillover (due to adult movement and larval dispersal) from reserves to harvested areas (fig. 3B). The potential for interspecific facilitation to affect the rate of recovery parallels both multispecies fisheries models (Hollowed et al. 2000) and multispecies marine reserve models (e.g., Baskett 2006), which indicates that negative species interactions may reduce the rate of species recoveries from intensive fishing. Furthermore, single-species marine reserve models predict similar results to those presented here where increasing network frag-

mentation into more, smaller reserves may initially increase spillover and reserve benefits to harvested populations (e.g., Hastings and Botsford 2003; Neubert 2003; Gaylord et al. 2005), while the concurrent reduced protection within reserves may eventually cause reduced spillover potential in highly fragmented reserve networks (e.g., DeMartini 1993). The results here indicate that such negative effects of fragmentation are less likely when the target species has a higher productivity, such as through recruitment-enhancing facilitation (fig. 4).

The direction of these changes when facilitation is included depends on the assumed baseline. Specifically, incorporating recruitment facilitation leads to a faster (fig. 2) and greater (fig. 3) response compared to ignoring all recruitment that may occur with facilitation, as one would expect for a positive interaction. The greater equilibrium density of spiny lobsters both outside and inside reserves associated with this greater response with

facilitation indicates a potential for enhanced yield from lobsters in harvested areas and an enhanced ability for reserves to buffer against environmental variability, and therefore reduce uncertainty in fisheries yield, which is a potential benefit of reserves suggested by single-species models (e.g., Sladek Nowlis and Roberts 1999; Mangel 2000). However, incorporating recruitment facilitation leads to a slower (fig. 2) and slightly smaller (fig. 3) response compared to assuming that the maximum facilitation-associated recruitment always occurs. In either case, these effects on the time scale and the extent of response indicate that variation in the strength of facilitation and trophic interactions may partly explain variation in how species such as spiny lobsters respond to reserve establishment. Overall, empirical research on recruitment facilitation that explores the outcome without the attracting species as well as on the faciliatory interaction would help determine how facilitation may affect expectations for reserve establishment.

The simple model used here ignores many biological realities, from additional dynamic species in the system to variable oceanic conditions. In addition, our results only apply to the parameter values used in the numerical analysis. How the magnitude of harvest before reserve establishment and outside reserves varies with species can be particularly important to predicting the effect of reserve establishment in multispecies models (Baskett et al. 2007). If, for example, urchin harvest exceeds lobster harvest, establishing a reserve may lead to an increase in urchin populations and a decrease in red algae, which may negatively affect lobster recruitment in the facilitation model. Given the prevalence of facilitation in marine ecosystems both specific to recruitment dynamics and in general (Bruno and Bertness 2001; Carr and Syms 2006), the effect of facilitation on fisheries and marine reserve management decisions warrants future theoretical and empirical investigations. As highlighted above, the results presented here indicate that a careful consideration of the no-facilitation baseline is necessary to accurately predict the effect of facilitation on any future model predictions.

Overall conclusions

Simple models can help identify key dynamics that have a substantial effect on theoretical predictions. The simple multispecies models discussed here indicate that species interactions are themselves such key dynamics: predation, competition, and facilitation have the potential to affect basic fisheries management decisions such as sustainable harvest rates (e.g., May et al. 1979), reserve design decisions such as size (e.g., Baskett et al. 2006), and interpretation of the response of species and communities to reserve establishment. Within reserve models, the exchange between protected and unpro-

tected areas is critical to predicting both reserve benefits to harvested areas (as occurs with single-species models; e.g., Attwood and Bennett 1995; Gaylord et al. 2005) and the reserve design necessary to achieve conservation goals such as protecting community structure (Baskett et al. 2007).

Finally, ontogenetic shifts in habitat use (Mangel and Levin 2005), trophic level (Baskett et al. 2006), and predation susceptibility (Baskett 2006) are critical to effective reserve placement, size, and expectations after establishment. Similarly, ontogenetic shifts can be important to model predictions in single-species reserve models (e.g., St. Mary et al. 2000) and non-spatial multispecies fisheries models (Bax 1998). Therefore, such size/age-dependent dynamics may be particularly important to explore further with simple models, incorporate into more complicated multispecies simulations (e.g., Bax and Eliassen 1990; Christensen and Walters 2004; Pope et al. 2006), and investigate in empirical research (Field et al. 2006).

While quantitative predictions from multispecies models are rarely possible without in-depth empirical investigation of species interactions, qualitative trends across multiple models provide potential management recommendations. For example, in both fisheries and marine reserve models, negative species interactions tend to increase recovery time from any overfishing that may occur. Therefore, the species dynamic with the slowest time scale should determine the monitoring time scale (May et al. 1979), and empirical investigations of the time scale as well as the strength of species interactions would help inform multispecies management decisions.

In addition, incorporating negative species interactions decreases the maximum sustainable yield and sustainable harvest rates in fisheries models and increases the reserve size necessary to protect self-sustaining populations in marine reserve models. Positive species interactions may have the opposite effect, but the results from the recruitment facilitation example model suggest that the magnitude of this effect is uncertain and its direction depends on the baseline considered. Therefore, when data on key species interactions are not available, one management action may be to put a precautionary buffer into management decisions, such as harvest rate and reserve size, based on traditional single-species approaches (Baskett et al. 2007).

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