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Review

Designing marine reserves for interacting species: Insights from theory

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ABSTRACT

The primary goals of marine reserves include protecting biodiversity and ecosystem structure. Therefore, a multispecies approach to designing and monitoring reserve networks is necessary. To gain insight into how the interactions between species in marine communities may affect reserve design, we synthesize marine reserve community models and community models with habitat destruction and fragmentation, and we develop new extensions of existing models. This synthesis highlights the potential for species interactions to alter reserve design criteria; in particular, accounting for species interactions often leads to an increase in reserve size necessary to protect populations. Accounting for species interactions also indicates the need to base reserve design and monitoring on a variety of species, especially long-distance dispersers, inferior colonizers, and specialists. Finally, the new model extensions highlight how, given dispersal, source populations outside reserves as well as increases in fished populations after reserve establishment may negatively affect reserve populations of competitors or prey. Therefore, multispecies harvest dynamics outside reserves and before reserve establishment are critical to determining the appropriate reserve size, spacing, and expectations after establishment. These models highlight the importance of species interactions to reserve design and provide guidelines for how this complexity can begin to be incorporated into conservation planning.

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1. Introduction

While heavily impacting marine ecosystems (Botsford et al., 1997; Myers and Worm, 2003), anthropogenic activities such as fisheries alter the structure of marine communities (Jackson et al., 2001; Frank et al., 2005). Fisheries alter community structure through direct biomass removal as well as biases in the species impacted. In particular, fisheries more negatively affect larger, slower-growing, longer-living species (Jennings et al., 1998; Heino and Godø, 2002), and fisheries tend to target species at higher trophic levels (Pauly et al., 1998).

Marine reserves, or no-take zones, reduce anthropogenic impacts such as overfishing, bycatch, and habitat damage from fishing gear (Allison et al., 1998). The primary goals of marine reserves include protecting biodiversity and ecosystem structure and function (Allison et al., 1998; Leslie, 2005). However, like fisheries, marine reserves have a biased effect on different species in a community. For example, reserves better protect species with shorter dispersal distances because such species are more likely to stay within reserve boundaries (Botsford et al., 2001, 2003).

Because higher trophic level species tend to have greater dispersal distances in marine systems (Kinlan and Gaines, 2003), the hardest species to protect within reserves (long-distance dispersers) also may be the species most heavily impacted outside reserves (top predators). Furthermore, a greater variation in and potential for dispersal exists in marine systems compared to terrestrial systems (Carr et al., 2003). Therefore, the biases in reserves' and fisheries' impacts relative to dispersal distance, trophic level, and life history suggest that a multispecies approach may be particularly important for effective marine reserve network design.

In addition to classic reserve network design questions such as reserve size and spacing, dispersal and species interactions may affect expectations after reserve establishment, an understanding of which is important for reserve monitoring and determining reserve effectiveness. While most species increase in biomass and abundance after reserve establishment (Halpern, 2003), one may expect the prey or competitors of previously fished species to decline after re-

serve establishment (Micheli et al., 2004a,b). Providing empirical evidence for species declines with protection due to increased predation or competition, a meta-analysis of 30 temperate and tropical reefs found lower abundances in no-take reserves compared to reference (fished) conditions for 19% of fish species on average and for sedentary species not targeted by fisheries in particular (Micheli et al., 2004b). However, the potential for species declines may depend on the intensity of fishing outside reserves and reserves' ability to protect long-distance dispersers, especially if prey disperse less and therefore are better protected in reserves than predators (Micheli et al., 2004a).

To determine the potential implications of a multispecies approach for marine reserves, we present a synthesis of published and new models that account for species interactions, organized by interaction type (competition, predation, and mutualism). Models of marine reserves have been extensively explored (reviewed by Guénette et al. (1998); Gerber et al. (2003)); however, in their review Gerber et al. (2003) identified the inclusion of species interactions as a critical gap in marine reserve theory. In addition to primarily being single-species models, the existing theoretical investigations often focus on the implications of reserve establishment for fisheries outside protected areas (Gerber et al., 2003). On the other hand, given the biodiversity and ecosystem structure goals of marine reserves, most reserve siting programs used for designing reserve networks focus on achieving biodiversity criteria based on static species and habitat distributions (e.g. Sala et al., 2002; Fernandes et al., 2005). Therefore, as a first step toward connecting dynamic single-species models and static multispecies approaches to reserve design, we explore how community dynamics affect predictions for marine reserves.

In this synthesis, we review the few recent marine reserve models that incorporate species interactions (predominantly published after Gerber et al.'s (2003) review). Given the rarity of such models, we also review general community models with habitat destruction and fragmentation or spatially heterogeneous mortality. We include these models because reserve networks can be thought of as the remnants after habitat

destruction and fragmentation and because harvest mortality is spatially heterogeneous in regions with marine reserve networks. In particular, the critical amount of habitat destruction before species extinctions occur within a community indicates the critical reserve size needed to protect biodiversity (analogous to critical patch size models for single species; e.g. Skellam, 1951; Kierstead and Slobodkin, 1953). Finally, because community models with habitat destruction and fragmentation often ignore dynamics outside reserves, we extend existing models to explore the impact of fishing regime outside reserves and before reserve establishment on model predictions.

The multispecies approach explored here is one of several components of a more holistic, ecosystem-based approach to marine management (Botsford et al., 1997; Pikitch et al., 2004). Rather than compare species interactions to the many factors important to marine reserve design (see reviews by Allison et al., 1998; Bohnsack, 1998; Fogarty, 1999; Guerry, 2005; Sale et al., 2005), we use simple models to inform the development and application of a community-level approach to reserve design. In addition, we focus primarily on questions of protecting community structure within reserves rather than the potential for fisheries benefits outside reserves (for a discussion of this issue, see Halpern and Warner, 2003; Hilborn et al., 2004; Roberts et al., 2005). Overall, this synthesis serves to identify what types of indirect effects due to species interactions may be expected in reserve networks as well as identify critical dynamics and assumptions for reserve design given species interactions.

2. Competition

2.1. Synthesis of competition models

Two recent models have explored the impact of competitive interactions on marine reserves. First, a metacommunity model where local competition for space drives large-scale patterns suggests that present species distributions may not be good criteria for reserve placement and reserve network design itself could affect large-scale distributions (Guichard et al., 2004). Second, in a model where the adults of a fished species prey on smaller, unfished species including their juveniles' competitors, competition increases the reserve size necessary to recover overfished species and that recovery depends on the initial densities of all interacting species; therefore, multiple species' densities may be an important factor in reserve placement decisions (Baskett et al., 2006). Both models indicate the importance of competition for reserve design decisions such as size and placement.

For models of competition and habitat destruction, one well-studied case is the competition-colonization trade-off, where two species coexist when the inferior competitor is a superior colonizer. A simple two-species, competition-colonization, spatially implicit metacommunity model demonstrates that habitat destruction, modeled by the loss of available patches, leads to the loss of the superior competitor before the superior colonizer (Nee and May, 1992). The authors assume that the superior competitor colonizes patches occupied by the superior colonizer at the same rate as empty patches; therefore, the critical amount of habitat

loss that causes the loss of the superior competitor has the same value in the community model as the analogous single-species model of the superior competitor only.

The predicted loss of the superior competitor first holds for extensions of the basic model that incorporate an arbitrary number of species in the competition-colonization trade-off (Tilman et al., 1994, 1997), an additional trophic level (Kareiva and Wennergren, 1995), local dispersal in spatially explicit simulations (e.g. Dytham, 1994; Tilman et al., 1997), different patterns of fragmentation in simulations with local dispersal (Dytham, 1995b,a; Tilman et al., 1997), delayed reproduction (Tilman et al., 1997), distance-dependent colonization and population size-dependent extinction and reproduction (Moilanen and Hanski, 1995), and population size-dependent coexistence and extinction in simulations with local dispersal (Huxel and Hastings, 1998). However, the prediction breaks down and the superior colonizer may be more vulnerable to habitat destruction in spatially explicit models where the superior colonizer disperses farther than the superior competitor (Klausmeier, 1998), especially with high levels of habitat fragmentation (Neuhauser, 1998).

The above models generally predict that the superior competitor can be the most abundant species before any habitat loss occurs, depending on the original amount of habitat. As habitat destruction occurs, the superior competitor declines and the superior colonizer increases until the superior competitor goes extinct, at which point the superior colonizer declines with habitat destruction (Nee and May, 1992). These dynamics lead to the counterintuitive suggestion that conservation efforts may need to focus on more abundant species. Contrary to this theory, empirical evidence from various terrestrial systems suggests that superior competitors increase with, and that rare species are more vulnerable to, habitat fragmentation (McCarthy et al., 1997). However, in an empirical study of a competitive coral community, habitat destruction led to the loss of superior competitors first; in this community, superior competitors tended to be the less common species (Stone et al., 1996). Modifying the above models for this coral community, with colonization dependent on population size and greater mortality for superior colonizers, causes habitat destruction to drive superior competitors extinct first (Stone, 1995), with theoretical predictions matching the empirical outcome (Stone et al., 1996).

Beyond the competition-colonization trade-off, habitat fragmentation alters theoretical communities with other competitive interactions. Departing from the strong competition in the competition-colonization models, a two-species metacommunity model of weak competition predicts that the inferior colonizer is the most vulnerable to habitat destruction, regardless of its place in the competitive hierarchy (Klausmeier, 2001). In a metacommunity model of two competitively superior habitat specialists and one competitively inferior habitat generalist, habitat destruction and fragmentation drive the specialists extinct first (Marvier et al., 2004). In a Lotka–Volterra (logistic, with coexistence dependent on each species being affected by the other less than by itself) metacommunity model, habitat destruction, modeled as reduced carrying capacity, more negatively affects slower-growing species (Doncaster et al., 2003). In spatially explicit Lotka–Volterra competition models, habitat degradation and

destruction can cause a reversal in competitive dominance (Cantrell et al., 1998; Neuhauser, 1998), and the superior competitor can be more vulnerable to habitat destruction, especially when the superior competitor is a long-distance disperser (Neuhauser, 1998). Including biased movement towards the center of a patch in a Lotka–Volterra competition model demonstrates that critical patch size increases with increasing movement and decreasing growth and movement bias (Gopalsamy, 1977).

In addition to reserve size, models such as those described above can provide insight into the debate on whether to establish a single large or several small reserves (SLOSS). For example, in a competition-colonization model with local dispersal, more clumped patterns of habitat fragmentation are less detrimental than scattered patterns of fragmentation (Dytham, 1995b), which suggests that fewer large reserves would be more effective than several small reserves at protecting such communities. In a neutral competition model, fragmentation into several small reserves increases the number of species protected in a reserve network by reducing competition, but the presence of long-distance dispersal decreases the impact of fragmentation (Chave et al., 2002). Therefore, the effect of fragmentation depends on both the competitive and dispersal dynamics.

Generally, the above models predict which type of species is most vulnerable to habitat destruction and fragmentation, and therefore which species should be the focus for determining the reserve size necessary to protect competitive communities. Such focal species tend to be inferior colonizers (which are often assumed to be superior competitors) and specialists, depending on the type of competitive interactions and the relative dispersal distances of the interacting species. Furthermore, the time delay after habitat destruction before the predicted extinctions occur (“extinction debt”; Tilman et al., 1994) calls into question whether short-term monitoring programs can reliably measure the effectiveness of protected areas (Kareiva and Wennergren, 1995). Short-term (~5 years) monitoring programs may be the most cost-effective at determining the optimal reserve design to achieve reserve goals for

supplying adjacent fisheries (Gerber et al., 2005). However, time lags from the interaction between habitat loss and community dynamics may make much longer-term monitoring programs necessary for determining the optimal reserve design to achieve persistence and biodiversity goals.

2.2. Competition-colonization model extension

2.2.1. Model

One important assumption in using habitat destruction and fragmentation models to inform reserve network design is that areas outside the reserves are uninhabitable. Rather than uninhabitable, areas outside marine reserves are usually regions of elevated mortality for fished species. To determine the importance of this assumption, we extend an existing model to include the dynamics in areas outside the reserve(s). Because of the importance of dispersal highlighted in the Introduction, we use a model that accounts for variation in dispersal: Klausmeier’s (1998) spatially explicit competition-colonization model.

Klausmeier’s (1998) model follows the abundance of each species at each point in time and location on a linear habitat of limited length. Species may differ in their colonization rates, natural mortality rates, and mean dispersal distances, where dispersal occurs according to the exponential dispersal kernel. As colonization rate increases, competitive ability decreases, where colonizing species always displace inferior competitors and cannot settle in locations with superior competitors. To this framework we add species-dependent harvest mortality rates as functions of space, where no harvest occurs for locations in reserves and constant-effort harvest occurs outside reserves (Fig. 1a; Eq. (A.1) in Appendix A). Note that we use a constant-effort harvest strategy in all of the model extensions presented here for mathematical tractability and because it is a commonly-used management strategy in marine fisheries (Hilborn and Walters, 1992).

We simulate this model using two or three species and the colonization, natural mortality, and dispersal parameters

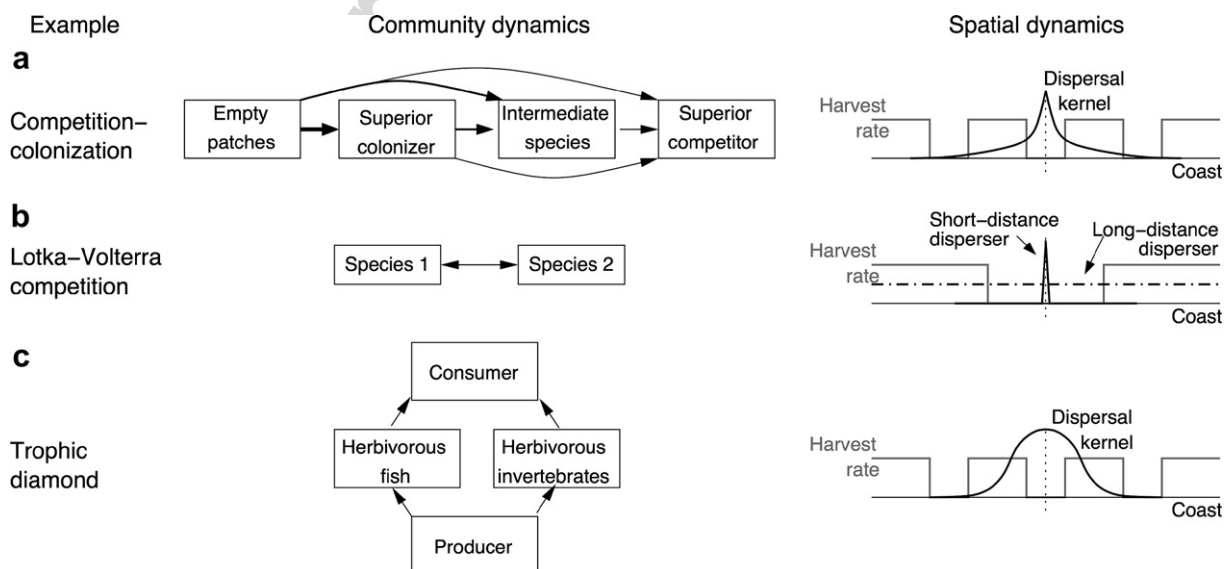


Fig. 1 – Box models of the community dynamics and illustrations of the spatial dynamics for the three model extensions.

from Klausmeier (1998). While Klausmeier (1998) increases suitable habitat length, we set the total habitat length to twice the maximum length in Klausmeier (1998) and implement reserve networks protecting up to half of that habitat. As in Klausmeier (1998), we test two dispersal scenarios: all species with equal dispersal distance and dispersal distance decreasing with increasing competitive ability (i.e., superior colonizers disperse farther). For each dispersal scenario, we test three harvest scenarios: all species fished, superior competitor fished, or superior colonizer fished. For each fished species, we explore two possible harvest rates to test a range of values relative to the species' dynamics: the less intensive harvest rate of half the natural mortality rate, and the more intensive harvest rate of half the colonization rate.

2.2.2. Results

Regardless of whether all species have equal dispersal (Fig. 2) or dispersal increases with colonization ability (Fig. 3), the results given the original assumption that unprotected areas are uninhabitable differ substantially from results based on simulations that follow the dynamics in harvested areas. In particular, compared to models that assume unprotected areas are uninhabitable (panels e–f in Figs. 2 and 3), models

that account for harvested-area dynamics (panels a–d in Figs. 2 and 3) predict that the superior colonizer (dotted lines in Figs. 2 and 3) is more vulnerable to lack of protection and therefore that larger reserve networks are required to protect the entire community. While only established for the parameter values explored here, this trend also occurs in simulations with all species fished, two-species simulations, simulations with less intensive harvesting, and simulations where natural mortality increases with competitive ability (results not shown).

The increased vulnerability of the superior colonizer in simulations that account for harvested-area dynamics likely occurs because competitor populations in harvested areas disperse into reserves, a negative interaction unaccounted for in the original model. Somewhat counterintuitively, the superior colonizer is the most vulnerable species even when it is not fished outside reserves (panels a–b in Figs. 2 and 3) because fishing the superior competitor outside reserves benefits the intermediate species that can out-compete the superior colonizer. The effect on the vulnerability of the superior colonizer highlights the importance of accounting for dynamics outside protected areas to multispecies approaches to reserve design.

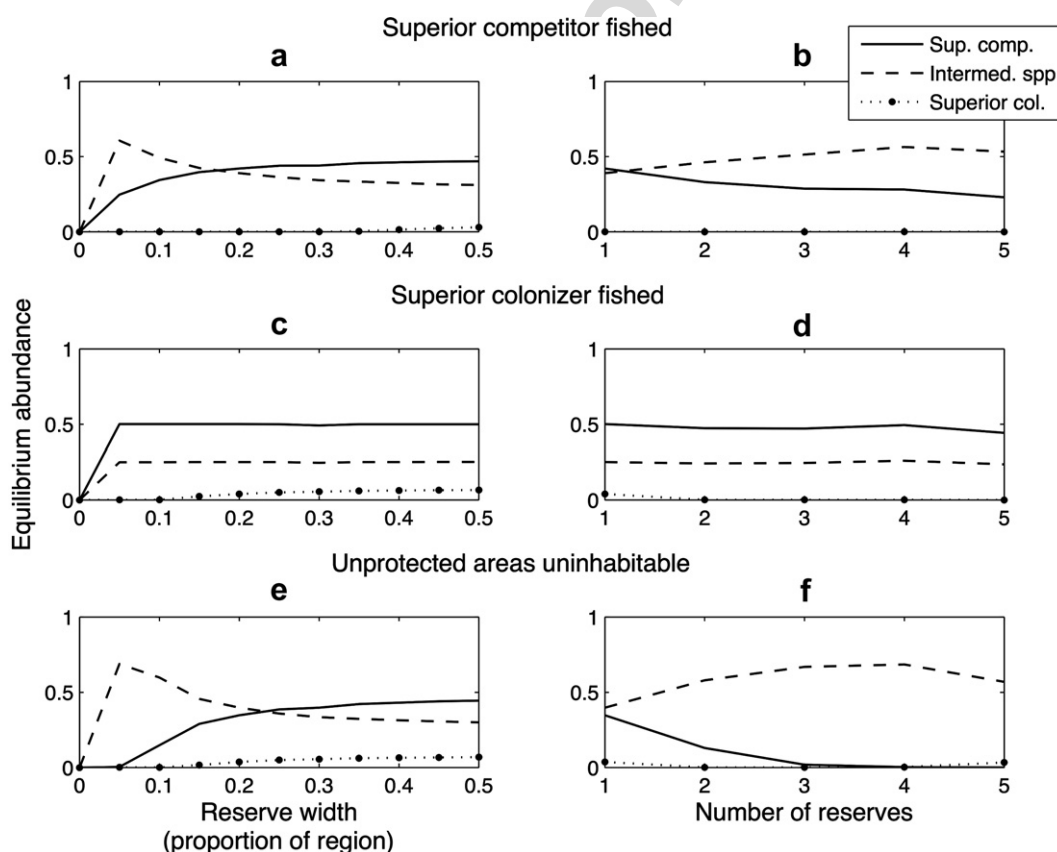


Fig. 2 – Results from three-species competition-colonization simulations (Eq. (A.1)), assuming all three species have equal dispersal rates. The above graphs show the average equilibrium abundance (proportion occupied patches) within protected areas, depending on total proportion of the habitat protected in one reserve (panels a, c, and e) or the number of reserves in the reserve network with 20% of the coast protected in total (panels b, d, and f). Equilibrium superior competitor densities are in the solid lines, intermediate species in the dashed line, and superior colonizer in the dotted lines. Different assumptions for the unprotected area dynamics (superior competitor fished in panels a–b, superior colonizer fished in panels c–d, unprotected areas are uninhabitable in panels e–f) are across the rows.

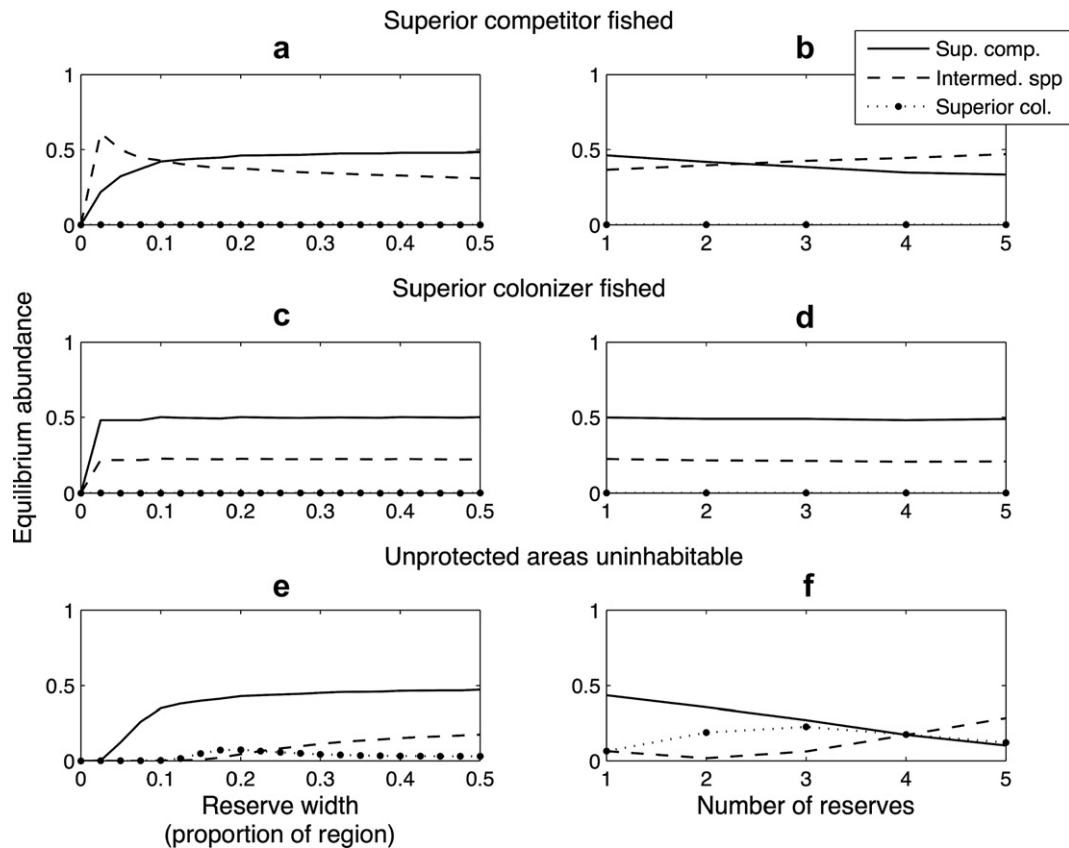


Fig. 3 – Results from three-species competition-colonization simulations (Eq. (A.1)), assuming dispersal rate increases with colonization rate. The above graphs show the average equilibrium abundance (proportion occupied patches) within protected areas, depending on total proportion of the habitat protected in one reserve (panels a, c, and e) or the number of reserves in the reserve network with 20% of the coast protected in total (panels b, d, and f). Equilibrium superior competitor densities are in the solid lines, intermediate species in the dashed line, and superior colonizer in the dotted lines. Different assumptions for the unprotected area dynamics (superior competitor fished in panels a–b, superior colonizer fished in panels c–d, unprotected areas are uninhabitable in panels e–f) are across the rows.

2.3. Lotka–Volterra competition model extension

2.3.1. Model

To explore the effect of harvest outside reserves on competitive dynamics beyond the competition-colonization trade-off, we also adjust a Lotka–Volterra competition model (Cantrell and Cosner, 1998). As with the competition-colonization example above, we choose the model by Cantrell and Cosner (1998) because it incorporates spatial dynamics, in this case through diffusion. In addition, the analytical evaluation in Cantrell and Cosner (1998) allows for more generalized conclusions than the numerical results in the above extension.

Cantrell and Cosner's (1998) model follows the population sizes in space and time of two competing species on a linear habitat. The species differ in their diffusion (dispersal) constants, population growth (birth minus death) rates, carrying capacities, and competitive effects on the other species. Cantrell and Cosner (1998) allow the latter three parameters to vary in space; we apply their analysis to marine reserves by allowing only the population growth rate to vary in space, with reduced population growth due to constant-effort harvest mortality outside reserves (Fig. 1b; Eqs. (B.1) and (B.2) in Appendix B).

Cantrell and Cosner's (1998) analysis of this model, which assumes reflecting boundaries and extreme values for the dispersal parameters, allows determination of the critical reserve size necessary to protect both species. Beyond the point where both species have extremely short-distance dispersal relative to the reserve length and the population dynamics' time scale, only local dynamics affect coexistence, and the persistence of both species becomes independent of reserve size and harvest mortality outside reserves. However, if one or both species are extremely long-distance dispersers, coexistence depends on both reserve size and the harvest mortalities outside reserves. Here we explore the critical reserve size necessary to protect both species as a function of the harvest mortality rates outside reserves (based on inequalities (B.3)–(B.5) in Appendix B).

2.3.2. Results

When both species are long-distance dispersers, the critical reserve length depends on the harvest rate for both species (Fig. 4a). However, when one species is a long-distance disperser and the other a short-distance disperser, the critical reserve length depends primarily on the harvest rate for the long-distance disperser (Fig. 4b). Therefore, harvest rates for

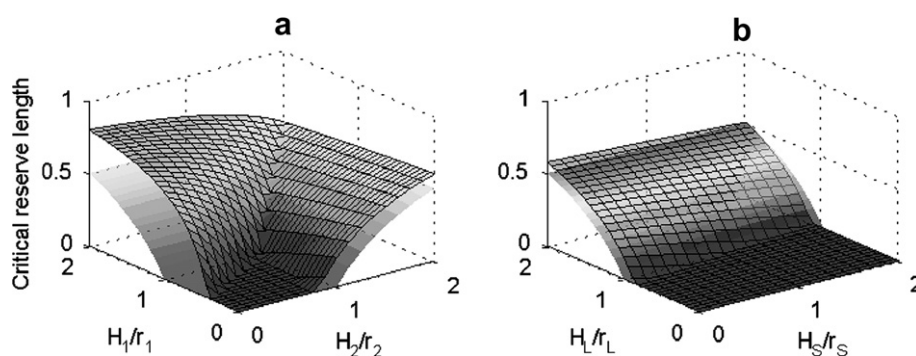


Fig. 4 – Plot of critical reserve length (proportion of coastline) necessary to protect two competing species depending on harvest rate (represented here as a multiple of production rate) for each species, where both are long-distance dispersers (1 and 2 in panel a; plot of In Eq. (B.3)) or one is a long-distance disperser and one is a short-distance disperser (L and S, respectively, in panel b; plot of In Eqs. (B.4) and (B.5)). Surfaces with or without grid lines indicate critical reserve length when accounting for or ignoring competition, respectively. Parameter values are $K_1 = 10^6$, $K_2 = 2 \times 10^6$, $r_1 = 0.8$, $r_2 = 0.4$, $a_{12} = 0.3$, $a_{21} = 0.4$ (see Eqs. (B.1) and (B.2)), where species 1 and 2 are the long and short distance dispersers, respectively, in panel (b).

longer-distance dispersers tend to dictate reserve size, which echoes the tendency for the superior colonizer to determine the critical reserve size in the competition-colonization model extension above. Furthermore, particularly in the case where both species are long-distance dispersers, accounting for competition increases the reserve length necessary to protect both species compared to calculations that ignore competition (i.e., competition coefficients are zero; surfaces without grid lines in Fig. 4). Along with paralleling previous model results by highlighting the importance of competitive and dispersal dynamics to reserve design (e.g. the vulnerability of long-distance dispersers in Gopalsamy, 1977; Klausmeier, 1998; Neuhauser, 1998), these results indicate the potential for harvest mortality to impact critical reserve size.

2.4. Empirical support

Empirical evidence supports the theoretical potential for competition to lead to species declines inside reserves. For example, red abalones and red sea urchins are two harvested species that compete for food and space in temperate rocky ecosystems. Increasing red sea urchin harvest may have led to increases in red abalones outside reserves; within no-take reserves, as red sea urchin populations have increased due to protection from harvesting, red abalone populations have declined (Karpov et al., 2001). In contrast, because abalone have a shorter larval duration, and thus less dispersal potential, than sea urchins (Grantham et al., 2003), a single-species perspective (e.g. Botsford et al., 2001) might predict that reserves would better protect abalone. Therefore, both empirical and theoretical evidence indicate that the interaction between competition and harvest regime outside reserves is critical to predicting reserve efficacy.

3. Predation

3.1. Synthesis of predation models

Marine reserve models that account for trophic dynamics fall into two categories: simple predator–prey models and com-

plex food web simulations. First, in a simple two-patch predator–prey model the response to reserve establishment depends both on the species' life histories and the management regime (harvest intensity for each species and reserve size), and predators require larger reserves than prey (Micheli et al., 2004a). Incorporating stochasticity into a two-patch predator–prey model indicates that reserve establishment may increase fisheries rent and decrease catch variability, which depends on the predation and movement dynamics (Greenville and MacAulay, 2006). In addition, in a model of a species with offshore adults and inshore juveniles that experience predation, incorporating species interactions changes whether inshore and/or offshore reserves are the most effective management strategy (Mangel and Levin, 2005). Indicating the importance of ontogenetic shifts in predation vulnerability as well as in habitat, in a resource-based predator–prey model motivated by the empirical findings of Mumby et al. (2006), prey size refugia (i.e., larger prey escaping predation) greatly reduces the chance of trophic cascades occurring after reserve establishment (Baskett, 2006).

In a complex food web simulation, a detailed community model of the Florida coral reef ecosystem indicates that reserve network effectiveness at enhancing the sustainability of multispecies fisheries depends on movement dynamics and reserve placement in areas such as high-productivity habitats (Ault et al., 2005). The food webs simulated in spatially explicit ECOSPACE models indicate that cascading predator–prey responses to reserve establishment are feasible (Walters et al., 1999; Walters, 2000), and accounting for species interactions leads to larger sizes necessary for effective reserves (Walters, 2000). Furthermore, in ECOSPACE simulations, accounting for predator movement in response to prey density leads to an increased need to minimize reserve perimeter to area ratio (Walters et al., 1999) and to create multi-use buffer zones around reserves (Salomon et al., 2002). While incorporating movement responses to both food availability and predation risk into ECOSPACE simulations has little effect on reserve efficacy, incorporating variability in ocean circulation reduces predictions for reserve efficacy (Martell et al., 2005). Overall, these models highlight the importance

of predation to reserve design decisions such as size, fragmentation into a network, placement, and expectations for monitoring.

For predator–prey models with habitat destruction (recently reviewed by Ryall and Fahrig (2006)), the most basic model focuses on two species: a prey and its specialist predator. Because the predator depends entirely on the prey for persistence and not vice versa, the predator is always equally or more vulnerable to habitat destruction. In a spatially implicit metacommunity approach to this system, the critical amount of habitat destruction that causes predator extinction depends on local extinction and colonization parameters for both species (May, 1994).

The basic result of increased vulnerability with trophic level, dependent on all species' parameters, holds for model extensions that incorporate an additional trophic level in the food chain (Holt, 1997; Kondoh, 2003), enhanced prey within-patch extinction due to predation (Bascompte and Solé, 1998), prey colonization from predator–prey patches as well as prey-only patches (Prakash and de Roos, 2002), and local dispersal in spatially explicit simulations (Bascompte and Solé, 1998). In three-to-four species metacommunity models with variable food web structure, the vulnerability of the top predator to habitat destruction depends on food web structure: it is greater in top-down controlled food webs compared to donor-controlled food webs, and it is greatest in food webs with intraguild predation, intermediate in simple food chains or food webs with apparent competition, and least in food webs with omnivory (Melián and Bascompte, 2002). In addition to food web structure, spatial dynamics are important to theoretical predictions of the critical patch size needed for top predator and community persistence. For example, in two-to-three species Lotka–Volterra predator–prey models where habitat degradation only directly affects prey dynamics, compared to the analogous spatially implicit models spatially explicit simulations predict increased vulnerability of the top predator to habitat degradation (Nakagiri et al., 2001; Nakagiri and Tanaka, 2004). Similarly, in a three-species food chain, unlike the analogous spatially implicit metacommunity model spatially explicit simulations with local dispersal can predict the simultaneous collapse of the entire community at low levels of habitat destruction due to overgrazing (given a high colonization rate for the intermediate species relative to the top predator; Kondoh, 2003).

Relaxing the assumption of a specialist predator can alter the relative vulnerability of the predator and prey. The addition of a second prey to the basic predator–prey metacommunity model, where the prey are specialists to different habitats and the generalist predator can consume both, leads to complicated persistence criteria that involve parameters for all three species (Holt, 1997). Furthermore, adding an alternative prey that is constantly available to the basic predator–prey metacommunity model and spatially explicit simulations (with local dispersal) results in the potential for habitat destruction to cause prey extinction before predator extinction (depending on the predator's reliance on the alternative prey; Swihart et al., 2001). In two-species predator–prey models where the predator movement is greater than the within-patch (reaction–diffusion) prey movement, the critical patch size for prey persistence compared to the prey-only model in-

creases if the predator is a generalist that can persist outside the patch (Cantrell et al., 2002). A similar increase in critical patch size for prey persistence occurs if the predator movement is independent of prey density; however, the critical patch size does not change if predators track prey density because predators leave patches with low prey density (Cantrell and Cosner, 1996). Therefore, the interaction between the degree of prey specialization and movement behavior is critical to predicting prey vulnerability.

Overall, models with specialist predators indicate that the species most vulnerable to habitat destruction, and therefore the species on which to base reserve size, is the top predator (May, 1994; Holt, 1997; Bascompte and Solé, 1998; Prakash and de Roos, 2002). Alternatively, models with generalist predators indicate the possible need for conservation focus on prey of generalist predators and specialist over generalist predators (Swihart et al., 2001). Regardless of whether the predator is a generalist or specialist, the critical reserve size necessary to protect the most vulnerable species usually depends on parameters for all interacting species (May, 1994; Holt, 1997; Bascompte and Solé, 1998; Swihart et al., 2001; Prakash and de Roos, 2002) and food web structure (Melián and Bascompte, 2002), which indicates the importance of predation for effective marine reserve design. Finally, one two-species metacommunity model indicates that alternative stable states, with and without the predator, are possible at some levels of habitat destruction (Prakash and de Roos, 2002). In this scenario, even if a reserve is large enough for predator persistence to be feasible (i.e., for the state with the predator to exist), the initial densities (i.e., densities at reserve establishment) of both species may determine whether the community tends toward the state with or without the predator in the reserve.

3.2. Trophic model extension

3.2.1. Model

As stated above, an important assumption in models with habitat destruction is that unprotected areas are uninhabitable. To explore the impact of dynamics outside reserves to predator–prey systems, we simulate two, three, and four-species trophic systems.

The trophic model follows the population sizes of producers, herbivorous invertebrates, herbivorous fish, and piscivorous consumers in space and time. All species groups move according to diffusion on a linear coastline, with different diffusion constants for each species. The producers have logistic-growth population dynamics and experience mortality from herbivorous fish and invertebrate predation at constant rates. Herbivorous fish and invertebrates convert energy gained from predation on producers into reproduction and experience constant natural mortality, location-dependent harvest mortality, and saturating predation mortality from the generalist consumers. Consumers convert energy gained from predation on herbivores into reproduction and experience constant natural mortality and location-dependent harvest mortality. The harvest mortality for herbivores and consumers varies in space such that zero harvest occurs in reserves and constant-effort harvest occurs outside reserves. This four-species trophic diamond (apparent competition)

system (Fig. 1c; Eqs. (C.1)–(C.4) in Appendix C) can also be used to explore a three-species food chain by removing one herbivore, or a two-species predator–prey system by removing the consumer and one herbivore.

We base the simulation parameters on the analogous parameter values reported in McClanahan and Sala's (1997) temperate rocky reef simulation (which explores the effect of fisheries but not marine reserves on ecosystem structure), using algae for the producers, sea urchins for the herbivorous invertebrates, herbivorous fish, and piscivores for the consumers. In addition, we estimate dispersal rates from the trend of increasing dispersal with trophic level in Kinlan and Gaines (2003). We assume that the length of the region being managed is 1000 km (e.g. Sala et al., 2002) and that the boundaries of the region are fatal. For harvest mortalities outside reserves, we use a rate of 0.8 year⁻¹ for consumers and 0.4 year⁻¹ for herbivores to model the general trend that higher trophic level species are more heavily fished (Pauly et al., 1998). We choose intensive harvest mortalities for a conservative approach to exploring the reserve network design necessary to protect community structure.

For the numerical simulations, we initiate population sizes at the expected (locally stable) equilibrium values with harvesting and without spatial dynamics. Next we numerically integrate the model (Eqs. (C.1)–(C.4)) with the entire region harvested for 100 time steps to let the system reach the harvested equilibrium with spatial dynamics. Then we change

the harvesting functions to have reserves, or regions with zero harvesting. After 50 time steps (sufficient time to reach the new equilibrium), we calculate proportion change in population size from the harvested state for all species both inside and outside reserves. For the reserve populations, we compare this proportion change to the proportion difference between the harvested state and the expected natural state based on analogous simulations where harvesting is zero throughout time and space.

3.2.2. Results

In the simulations, within the parameter values used here, the expected cascading effects generally occur after reserve establishment: in two-species simulations the predator increases and prey decreases, and in three and four-species simulations the consumer increases, herbivore(s) decrease, and producer increases very slightly (sample results in Fig. 5). Note that these simple simulations do not account for prey size refugia, cannibalism, omnivory, or other biological complexities which may reduce the likelihood of trophic cascades (Polis et al., 2000; Mumby et al., 2006). The changes are greater in reserves than in harvested areas. Within-reserve changes are greatest for larger reserve networks with less fragmentation (fewer reserves); outside-reserve changes are greatest for larger reserve networks with more fragmentation, presumably due to increased spillover with fragmentation. Populations within reserves approach the expected natural (unharvested) state for

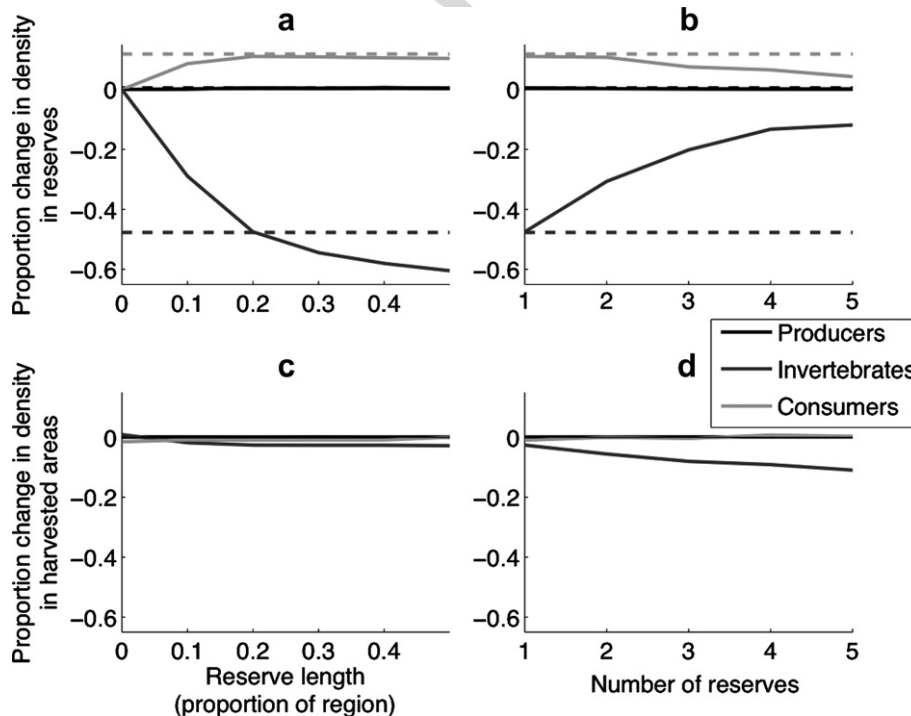


Fig. 5 – Sample results of the trophic model numerical simulations (Eqs. (C.1)–(C.4)) with a three-species trophic chain where both consumers and invertebrates are fished outside reserves: proportion change inside (panels a–b) and outside (panels c–d) reserves from harvested state after reserve network establishment, depending on total proportion of the habitat protected in a single reserve (panels a, c) or the number of reserves in the reserve network with 20% of the coast protected in total (panels b, d). Black lines represent produces, medium gray invertebrates, and light gray consumers. Solid lines indicate changes in reserve networks, and dashed lines indicate proportion difference between the expected natural state (no fishing) and harvested state.

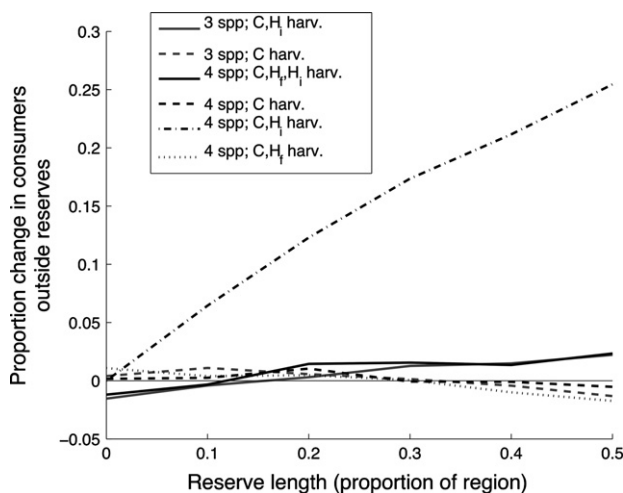


Fig. 6 – Proportion change from harvested state after reserve network establishment for consumers outside reserves in the trophic simulations (Eqs. (C.1)–(C.4)), depending on total proportion of the habitat protected in a network of five reserves. Different lines represent different trophic structure (three species trophic chain in gray or four species trophic diamond in black) and different harvest scenarios: dashed lines for consumers (C) only harvested, solid lines for all non-producers harvested, dash-dotted line for consumers and invertebrates (H_i) harvested, and dotted line for consumers and herbivorous fish (H_i) harvested.

large ($\geq 20\%$ of the coastline protected) reserve networks fragmented into few (≤ 2) reserves.

These trends vary with the harvest scenario in two cases. First, harvested consumers in areas outside reserves are more likely to increase after reserve establishment when invertebrates are fished outside reserves as well (sample results in Fig. 6). This occurs because, when multiple trophic levels experience fishing, top predators benefit both from reduced mortality and increased prey in reserves, and the resulting greater increases in top predators are more likely to spill over into unprotected areas.

Second, unlike consumers and invertebrates, herbivorous fish densities in reserves do not approach the expected natu-

ral state in large, un-fragmented reserve networks if they are fished before reserve establishment (dotted lines in Fig. 7). However, they can persist in large reserves while harvested in unprotected areas if they are not harvested before reserve establishment (dashed lines in Fig. 7). In addition, in two-species herbivorous fish-producer simulations they always recover to the expected natural state in large, un-fragmented reserve networks (results not shown). Therefore, the potential lack of herbivorous fish recovery in the four-species simulations is likely due to the lower productivity of herbivorous fish compared to invertebrates and increased predation by consumers after reserve establishment both causing the system to remain in an alternative state with herbivorous fish depleted. Thus the recovery of harvested herbivorous fish may depend on initial population sizes as well as protection in reserves. As mentioned above, a similar dependency on initial conditions for the recovery of top predators occurs in the marine reserve model where adults of a fished species prey on their juveniles' competitors (Baskett et al., 2006) and in a two-species predator-prey model with habitat destruction (Prakash and de Roos, 2002).

Finally, one expectation is that simulations with longer-distance dispersers require larger reserves for community recovery to the expected natural state. While smaller reserve sizes are necessary in two-species simulations with invertebrates (the shortest-distance dispersing harvested species) and producers, the reserve size necessary for community recovery is similar for three- and four-species simulations with consumers (the longest-distance dispersers) compared to two-species simulations with herbivorous fish and producers (results not shown). Therefore, within the parameters tested here, harvest rates relative to species' productivities may be more important than dispersal distance in predicting community-level responses to the establishment of large reserve networks.

3.2.3. Empirical support

In empirical support of the theoretical importance of harvest dynamics relative to dispersal distance, response to reserves increases with home range size and species with low adult mobility are more likely to decline in reserves; these trends contrary to the expectation that reserves better protect short-distance dispersers occur because low-mobility species

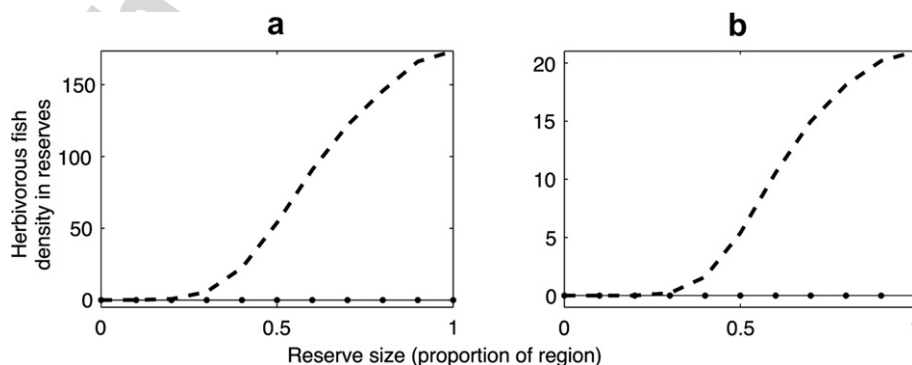


Fig. 7 – Equilibrium herbivorous fish density in four-species trophic diamond simulations (Eqs. (C.1)–(C.4)), given various harvest scenarios outside a single no-take reserve after reserve establishment. Dotted and dashed lines indicate herbivorous fish are and are not harvested before reserve establishment, respectively. (a) All species harvested and (b) consumer, herbivorous fish harvested.

tend to experience less harvest mortality (Micheli et al., 2004b; Palumbi, 2004). Empirical studies of marine reserves also demonstrate the potential for species interactions to slow the recovery of overfished species in reserves. For example, competition with sea urchins may impede the recovery of herbivorous fish in a Kenyan marine reserve (McClanahan and Kaunda-Arara, 1996). In addition, in a Canadian marine reserve previously dominant larger-bodied species (such as skate and halibut) have not recovered while the newly dominant smaller-bodied species (such as herring and mackerel) increased through time (Fisher and Frank, 2002). This impeded recovery with the theoretical possibility of alternative stable states highlights the importance of species interactions and harvest before reserve establishment to expectations after reserve establishment and reserve placement (i.e., what community composition may be appropriate when deciding which locations to protect).

4. Mutualism

Compared to competition and predation, far fewer models have been developed to explore the impact of habitat fragmentation and destruction on mutualism. In a two-species metacommunity model where one mutualist requires the second for reproduction and the second requires the first for both reproduction and survival (much like plant–pollinator interactions), habitat destruction causes the simultaneous loss of both species (Nee et al., 1997). In a two-species metacommunity model with mutualism through enhanced colonization, habitat destruction leads to either the simultaneous loss of both species or the loss of the poorer colonizer first (Klausmeier, 2001). Extending this model to include reduced extinction as well as enhanced colonization as the mutualistic mechanism leads to a similar conclusion that habitat destruction leads to either the simultaneous loss of both species (given strong mutualism) or to the loss of the “weaker” (greater extinction:colonization ratio) species first (given weak mutualism; Prakash and de Roos, 2004). An analogous spatially explicit model with local dispersal predicts that dispersal can enhance persistence given strong mutualism or large habitat loss, particularly with more species in the mutualistic community (Prakash and de Roos, 2004). In large-scale simulations of mutualistic metacommunities, including a realistic representation of the interaction network’s nestedness and variation in degree of specialization decreases the critical amount of habitat loss before any extinctions occur (Fortuna and Bascompte, 2006). However, their inclusion increases the amount of habitat loss that causes the entire community to collapse, with specialists more vulnerable to habitat destruction (Fortuna and Bascompte, 2006).

As in the competition and trophic models, these mutualistic models indicate that specialists (Fortuna and Bascompte, 2006) and poorer colonizers (Klausmeier, 2001; Prakash and de Roos, 2004) tend to be more vulnerable to habitat destruction and thus should be the focus of conservation decisions such as reserve size. In addition, analogous to the basic predator–prey models, the critical amount of habitat destruction that causes extinction depends on the colonization and extinction rates for both species (Nee et al., 1997) and the

strength of the mutualistic interaction (Prakash and de Roos, 2004). Unlike competitive and trophic interactions, incorporating mutualistic interactions can cause community persistence at levels of habitat destruction that would otherwise cause extinctions (Prakash and de Roos, 2004); therefore, incorporating mutualistic interactions may decrease the reserve size necessary to protect communities. Also analogous to the models reviewed above, two mutualistic models predict alternative stable states, with and without one or both of the species, at some levels of habitat destruction (Klausmeier, 2001; Prakash and de Roos, 2004), in which case the end community state may depend on initial conditions. Again, this potential dependency of recovering all species in a community on the densities at reserve establishment as well as reserve size can impact expectations after reserve establishment and reserve placement criteria.

Positive interactions, from coral–algal symbioses to species–habitat relationships, are vital to many marine ecosystems. For example, coincident with the decline of live coral in Papua New Guinea reserves, several coral-associated fish species declined, likely due to loss of juvenile recruitment habitat (Jones et al., 2004); thus species–habitat links may be critical to species recoveries in marine reserves. Furthermore, preliminary exploration of a three-species trophic chain model with recruitment facilitation indicates that positive interactions may affect the time scale of species response to reserve establishment and spillover from reserves to harvested areas, and therefore expectations for reserve monitoring (Baskett, in review). Because of the importance of mutualistic interactions in marine ecosystems, the theoretical impact of mutualism and other positive interactions on reserve design warrants further study (as is the case with positive interactions in ecological theory in general; Bruno et al., 2003). Given that a generalized theoretical framework for positive interactions is still in development, an example model to explore the design of marine reserve networks for mutualistic communities requires in-depth investigation beyond the scope of this synthesis.

5. Conclusions

Competitive, trophic, and mutualistic interactions impact the theoretical targets for designing reserve networks and expectations after reserve establishment (Table 1). In the reviewed marine reserve models and models with habitat destruction, species interactions are important to predicting effective reserve size, spacing, placement, and monitoring targets. Because specific predictions vary with interaction type and model assumptions, empirically identifying and exploring key interactions in marine ecosystems will be necessary for a multispecies approach to marine reserve design. Assumptions critical to the outcomes of competition models include relative dispersal distances (Klausmeier, 1998; Neuhauser, 1998); critical assumptions for trophic models include the degree of specialization (Holt, 1997; Swihart et al., 2001), and predator movement in response to prey density (Cantrell and Cosner, 1996; Walters et al., 1999). This significance of movement and dispersal echoes the importance of dispersal in single-species marine reserve models (e.g. Attwood and

Table 1 – Summary of implications from existing models and new model extensions

	Review of community models with habitat destruction	Review of marine reserve community models	New extensions of existing models
Implications for reserve design	<ul style="list-style-type: none"> – Reserve size likely to depend on interactions between multiple species; relationship varies with interaction type 	<ul style="list-style-type: none"> – Larger and less fragmented reserve networks necessary when account for species interactions – Species interactions indicate potential need to base reserve placement on habitat productivity, community composition, or ontogenetic shifts in habitat use 	<ul style="list-style-type: none"> – Larger reserves necessary when account for species interactions (Fig. 4) – Effective reserve size and placement depend on harvest outside reserves and before reserve establishment (Figs. 2,3 and 7)
Expectations after reserve establishment	<ul style="list-style-type: none"> – Time delay before extinctions in a community occur – Recovery may depend on population densities at reserve establishment 	<ul style="list-style-type: none"> – Trophic cascades likely in general, but unlikely in communities with prey size refugia – Recovery may depend on population densities at reserve establishment 	<ul style="list-style-type: none"> – Trophic cascades likely (Fig. 5) – Recovery may depend on population densities at reserve establishment (Fig. 7)
Vulnerable species	<ul style="list-style-type: none"> – Long-distance dispersers – Poorer colonizers – Specialists – Top predators – Prey of generalist predators 	<ul style="list-style-type: none"> – Top predators 	<ul style="list-style-type: none"> – Long-distance dispersers (Figs. 3 and 4) – Competitors of species that are not harvested outside reserves (Figs. 2 and 3)
Key dynamics	<ul style="list-style-type: none"> – Dispersal/movement – Degree of specialization (e.g., on habitat or prey) 	<ul style="list-style-type: none"> – Dispersal/movement – Variable ocean circulation – Harvest regime outside reserves – Ontogenetic shifts (e.g., in habitat or trophic level) 	<ul style="list-style-type: none"> – Dispersal (Figs. 3 and 4) – Harvest regime before reserve establishment and outside reserves (Figs. 2–4, 6 and 7)

Bennett, 1995; Botsford et al., 2001, 2003; Lockwood et al., 2002; Gaylord et al., 2005; Sanchirico et al., 2006). Therefore, future theoretical efforts that construct more detailed, realistic models (e.g., ECOSPACE simulations; Christensen and Walters, 2004) should be particularly careful when forming the above assumptions.

In marine reserve models ranging from simple community models (Baskett et al., 2006, Lotka–Volterra competition example here) to complex simulations (Walters, 2000), accounting for competition and predation leads to an increase in reserve size necessary to protect all species in a community. Thus, in locations with little data on interaction dynamics, incorporating species interactions into reserve design decisions may require increasing the optimal reserve size predicted for single species by an “insurance factor,” analogous to incorporating disturbances (Allison et al., 2003). In addition, given limited data, one possible approach to designing reserves for multiple species is to focus on species for which their maintenance would likely ensure adequate protection for other species in the community. Informing this approach, one generalization from the reviewed models with habitat destruction and the new extensions presented here is that specialists, top predators, inferior colonizers, and long-distance dispersers tend to be the more vulnerable species.

5.1. The importance of dynamics outside reserves

The model extensions presented here highlight the importance of the harvest regime outside reserves for effective reserve network design and monitoring given species interactions. In particular, the harvest regime outside reserves may be a key factor influencing the reserve size necessary to protect communities with competition-colonization trade-offs and Lotka–Volterra competition (Figs. 2–4). In addition, the harvest regime before reserve establishment may be critical to predicting the potential spillover of reserve benefits to harvested areas for top predators and the recovery of intermediate consumers (e.g., herbivores) after reserve establishment (Figs. 6 and 7).

Ignoring dynamics outside reserves and assuming that unprotected areas are uninhabitable is the conservative approach in single-species reserve design models because it indicates the reserve size necessary for persistence regardless of impacts outside reserve. For example, accounting for the contribution of areas outside reserves can substantially decrease the reserve size necessary to protect the critical fraction of natural larval settlement required for population sustainability (Botsford et al., 2001). However, accounting for multispecies interactions introduces the potential for unfished predators or competitors outside reserves to negatively impact protected populations. Therefore, considering unprotected areas uninhabitable may no longer serve as the conservative assumption for multispecies approaches to designing reserve networks to protect biodiversity and ecosystem structure.

Similar to the importance of harvest dynamics to the biodiversity goals explored here, harvest regime is critical to predicting fisheries benefits of reserves in single-species models. Specifically, reserves are more likely to benefit fisheries for more heavily fished species (e.g. Man et al., 1995; Holland

and Braze, 1996; Sladek Nowlis and Roberts, 1999; Gerber et al., 2003; Botsford et al., 2004; Kaplan and Botsford, 2005; Hart, 2006). Providing empirical support for this theoretical importance of harvest dynamics, meta-analyses of marine reserve empirical studies indicate that harvest intensity may be the primary predictor of a species’ response to reserve establishment (Côté et al., 2001; Micheli et al., 2004b). In addition, in an analysis and model of a complex Caribbean coral reef food web, harvest regime and variable interaction strength are important to predicting the potential for trophic cascades (Bascompte et al., 2005). Thus both empirical and theoretical evidence suggest that key species interactions and harvest dynamics outside reserves are critical to predicting community responses to reserve establishment.

5.2. Future directions

In response to the degradation of marine ecosystems, many scientists and managers support an ecosystem-based approach to management (Botsford et al., 1997; Pikitch et al., 2004). Two key components of ecosystem-based management are moving from a single-species approach to a multispecies approach and implementing spatial zoning, including marine reserves (Botsford et al., 1997; Pikitch et al., 2004). Our conclusions indicate that an understanding of interaction types, harvest regime, and movement are critical to effectively implementing these components of ecosystem-based management.

Along with indicating the general effects of species interactions on reserve design, the most vulnerable species to habitat destruction, and the importance of movement dynamics and harvest dynamics outside reserves, this synthesis highlights major gaps and important issues that require further investigation. First, the implications of positive interactions for reserve design and the persistence of multispecies assemblages in the face of habitat destruction are poorly understood. Second, most theoretical studies of reserve design with population or community dynamics focus on optimal reserve size and spacing. However, when considering competitive and trophic dynamics in marine reserve models, placement decisions based on factors such as habitat productivity, species densities, or ontogenetic shifts in habitat use may be vital to reserve effectiveness (Guichard et al., 2004; Ault et al., 2005; Mangel and Levin, 2005; Baskett et al., 2006). Therefore, the effect of factors such as habitat heterogeneity on dynamic models of reserve design merits further study. Finally, predictions from theoretical models are still largely untested and more work needs to relate theoretical hypotheses to empirical case studies.

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Appendix A. Details of the competition-colonization model extension

Adjusting Eq. (6) from Klausmeier (1998), we assume that each species i has abundance $p_i(x, t)$ at location x and time t , colonization rate c_i , natural mortality m_i , and harvest mortality $h_i(x)$, which is zero in protected area(s) and H_i in unprotected areas (constant effort harvest). Species disperse along a linear coastline of total length L according to the exponential dispersal kernel $k_i(x) = \frac{\alpha_i}{2} \exp(-\alpha_i|x|)$ with mean dispersal distance $1/\alpha_i$. A colonizing species instantaneously displaces competitive inferiors and never settles in locations with competitive superiors. Competitive dominance increases and colonization decreases with decreasing i . Thus each species' dynamics are (Fig. 1a):

$$\begin{aligned} \frac{\partial p_i(x, t)}{\partial t} = & \int_{-L/2}^{L/2} c_i k_i(x-y) p_i(y, t) dy \left[1 - \sum_{j=1}^i p_j(x, t) \right] \\ & - (m_i + h_i(x)) p_i(x, t) - p_i(x, t) \sum_{j=1}^{i-1} \int_{-L/2}^{L/2} c_j k_j(x-y) p_j(y, t) dy. \end{aligned} \quad (\text{A.1})$$

Appendix B. Details of the Lotka-Volterra competition model extension

Rewriting Eq. (3.2) from Cantrell and Cosner (1998), we assume that each species i has population size n_i and randomly disperses along a linear coastline of length L_T with D_i . Also, each species i has population growth rate r_i , has carrying capacity K_i , and experiences competitive effect from species j α_{ij} . The harvest mortality $h_i(x)$ varies with location x such that it is zero in a reserve with length L_R and is H_i outside the reserve (constant effort harvest). Thus the species dynamics are (Fig. 1b):

$$\frac{\partial n_1}{\partial t} = D_1 \frac{\partial^2 n_1}{\partial x^2} + n_1 \left(\frac{r_1}{K_1} (K_1 - n_1 - \alpha_{12} n_2) - h_1(x) \right) \quad (\text{B.1})$$

$$\frac{\partial n_2}{\partial t} = D_2 \frac{\partial^2 n_2}{\partial x^2} + n_2 \left(\frac{r_2}{K_2} (K_2 - n_2 - \alpha_{21} n_1) - h_2(x) \right). \quad (\text{B.2})$$

Eqs. (B.1) and (B.2) are analytically tractable when we consider extreme values for the dispersal parameters and reflecting (i.e., no flux or zero Neumann) boundary conditions (Cantrell and Cosner, 1998). If both species are extremely short-distance dispersers ($D_1, D_2 \rightarrow 0$ relative to the reserve length as well as the time scale for the population growth, competition, and harvest mortality dynamics; see the Appendix in Cantrell and Cosner (1998) for the detailed mathematical conditions), only local dynamics affect coexistence. Therefore, beyond the constraints of a large enough reserve (and of the relevant harvest rate time scale) relative to the dispersal

dynamics, coexistence is independent of reserve length or harvest rate outside reserves (Eq. (3.9) in Cantrell and Cosner, 1998). If both species are extremely long-distance dispersers ($D_1, D_2 \rightarrow \infty$), the condition for coexistence within a no-take reserve is:

$$r_i \left(1 - \frac{K_j}{K_i} \alpha_{ij} \right) > \left(1 - \frac{L_R}{L_T} \right) \left(H_i - \frac{r_i K_j}{r_j K_i} \alpha_{ij} H_j \right) \quad (\text{B.3})$$

(equivalent to Eq. (3.18) in Cantrell and Cosner, 1998). If one species is a short-distance disperser ($D_S \rightarrow 0$) and the other is a long-distance disperser ($D_L \rightarrow \infty$), the conditions for coexistence within a no-take reserve are:

$$r_S - \alpha_{SL} r_L > \left(1 - \frac{L_R}{L_T} \right) (H_S - \alpha_{SL} H_L) \quad (\text{B.4})$$

$$r_L \left(1 - \frac{K_S}{K_L} \alpha_{LS} \right) > - \left(1 - \frac{L_R}{L_T} \right) \frac{r_L K_S}{r_S K_L} \alpha_{LS} H_S \quad (\text{B.5})$$

(equivalent to Eqs. (3.14)–(3.15) in Cantrell and Cosner, 1998).

Appendix C. Details of the trophic model extension

In the trophic model, the producers (P), herbivorous invertebrates (H_i) and fish (H_f), and piscivorous consumers (C) move according to diffusion rates D_P, D_{H_i}, D_{H_f} , and D_C , respectively, along a linear coastline with absorbing boundaries (i.e., the boundary is fatal, or zero Dirichlet boundary conditions). The producers reproduce at rate r and have carrying capacity K . The herbivores consume the producers at rates δ_{H_i} and δ_{H_f} (linear, or Type I, functional response), which is converted into reproduction with efficiencies β_{H_i} and β_{H_f} . The consumers prey on the herbivores at rates δ_{C_i} and δ_{C_f} , which saturates due to the handling times τ_i and τ_f (Type II functional response), and the consumers' predation-reproduction conversion efficiencies are β_{C_i} and β_{C_f} . The herbivores and consumer experience natural mortality, at rates u_{H_i}, u_{H_f} , and u_C , and constant effort harvest mortality outside reserves, at rates F_{H_i}, F_{H_f} , and F_C . Therefore, the harvest function for species Y , $f_Y(x)$, equals F_Y for location x outside reserves and 0 for x inside reserves. Thus the dynamics of the four species groups are (Fig. 1c):

$$\frac{\partial P}{\partial t} = D_P \frac{\partial^2 P}{\partial x^2} + P \left(r \left(1 - \frac{P}{K} \right) - \delta_{H_i} H_i - \delta_{H_f} H_f \right) \quad (\text{C.1})$$

$$\frac{\partial H_i}{\partial t} = D_{H_i} \frac{\partial^2 H_i}{\partial x^2} + H_i \left(\beta_{H_i} \delta_{H_i} P - \frac{\delta_{C_i} C}{1 + \tau_i \delta_{C_i} H_i + \tau_f \delta_{C_f} H_f} - u_{H_i} - f_{H_i}(x) \right) \quad (\text{C.2})$$

$$\frac{\partial H_f}{\partial t} = D_{H_f} \frac{\partial^2 H_f}{\partial x^2} + H_f \left(\beta_{H_f} \delta_{H_f} P - \frac{\delta_{C_f} C}{1 + \tau_i \delta_{C_i} H_i + \tau_f \delta_{C_f} H_f} - u_{H_f} - f_{H_f}(x) \right) \quad (\text{C.3})$$

$$\frac{\partial C}{\partial t} = D_C \frac{\partial^2 C}{\partial x^2} + C \left(\frac{\beta_{C_i} \delta_{C_i} H_i + \beta_{C_f} \delta_{C_f} H_f}{1 + \tau_i \delta_{C_i} H_i + \tau_f \delta_{C_f} H_f} - u_C - f_C(x) \right). \quad (\text{C.4})$$

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