

## Designing effective reserve networks for nonequilibrium metacommunities

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**Abstract.** The proliferation of efficient fishing practices has promoted the depletion of commercial stocks around the world and caused significant collateral damage to marine habitats. Recent empirical studies have shown that marine reserves can play an important role in reversing these effects. Equilibrium metapopulation models predict that networks of marine reserves can provide similar benefits so long as individual reserves are sufficiently large to achieve self-sustainability, or spaced based on the extent of dispersal of the target species in order to maintain connectivity between neighboring reserves. However, these guidelines have not been tested in nonequilibrium metacommunity models that exhibit the kinds of complex spatiotemporal dynamics typically seen in natural marine communities.

Here, we used a spatially explicit predator–prey model whose predictions have been validated in a marine system to show that current guidelines are not optimal for metacommunities. In equilibrium metacommunities, there is a community-level trade-off for designing effective reserves: Networks whose size and spacing are smaller than the extent of dispersal maximize global predator abundance but minimize global prey abundance because of trophic cascades, whereas the converse is true for reserve networks whose size and spacing are larger than the extent of dispersal. In nonequilibrium metacommunities, reserves whose size and spacing match the extent of spatial autocorrelation in adult abundance (i.e., the extent of patchiness) escape this community-level trade-off by maximizing global abundance and persistence of both the prey and the predator. Overall, these results suggest that using the extent of adult patchiness instead of the extent of larval dispersal as the size and spacing of reserve networks is critical for designing community-based management strategies. By emphasizing patchiness over dispersal distance, our results show how the apparent complexity of nonequilibrium communities can actually simplify management guidelines and reduce uncertainty associated with the assessment of dispersal in marine environments.

*Key words:* dynamic resources; metacommunities; nonequilibrium; patchiness; reserve networks; spatial management; trophic cascades.

### INTRODUCTION

Fisheries can have strong ecological and evolutionary impacts on marine communities by preferentially extracting large individuals from long-lived and slow-growing species that often occupy higher trophic levels (Botsford et al. 1997, Pauly et al. 1998, 2002, Baskett et al. 2007, Jorgensen et al. 2007, Palkovacs 2011). The intensive nature of large-scale commercial fishing practices can also inflict significant collateral damage on noncommercial species and marine habitats (Botsford et al. 1997, Pauly et al. 2002, Carr et al. 2003).

Marine reserves—areas protected from all destructive and extractive activities—can play an important role in reversing some of the harm caused by such unsustainable fishing practices (Allison et al. 1998, Halpern 2003,

Lubchenco et al. 2003, Lester et al. 2009, Gaines et al. 2010). Recent meta-analyses have shown that marine reserves protect marine habitats and increase the biomass, abundance, species richness, and size of organisms within their boundaries (Halpern 2003, Lester et al. 2009). Additionally, the spillover of adults and larvae from reserves into neighboring exploited areas can significantly improve the yields of overfished species (Roberts et al. 2001, Gell and Roberts 2003, Gaines et al. 2010). Indeed, theory has shown that managing fisheries via marine reserves can produce yields that are equivalent to those obtained under traditional quota-based techniques (Hastings and Botsford 1999, Botsford et al. 2003). Hence, marine reserves can both protect endangered communities within and promote the growth of exploited stocks beyond their boundaries.

To serve both conservation and fishery goals, marine reserves must be large enough to protect species within and promote spillover effects beyond their boundaries, but not so large as to prohibitively diminish access to

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exploited species and thus reduce fishery yields (Gerber et al. 2003, Gaines et al. 2010). This inherent trade-off has spurred much interest into the optimal placement and size of reserves (Hastings and Botsford 1999, Botsford et al. 2001, 2003, Gaines et al. 2010). Theory has shown that networks of marine reserves are better than single reserves of equivalent size because networks can (1) reduce the local societal costs (i.e., the limited access to resources) associated with single large reserves by distributing them more evenly over space, (2) protect species across a larger portion of their range, and (3) provide spatial redundancy that can buffer against local or spatially autocorrelated catastrophes and variability in both environmental and oceanographic conditions (Allison et al. 1998, 2003, Gaines et al. 2003, 2010, Lubchenco et al. 2003, Wagner et al. 2007). However, this buffer against extrinsic variability comes at a cost: The effectiveness of reserve networks is critically dependent upon the size and spacing of individual reserves (Botsford et al. 2001, 2003, Gaines et al. 2003).

Conventional wisdom suggests that individual marine reserves should be at least as large as the mean dispersal distance of the target species in order to retain enough larvae to achieve self-sustainability, or spaced according to the extent of dispersal in order to maintain connectivity in the form of larval subsidies between reserves (Carr et al. 2003, Shanks et al. 2003, Sale et al. 2005, Halpern et al. 2006). Indeed, single-species models have shown that reserve networks can be effective if (1) the mean dispersal distance is small relative to reserve size so that individual reserves are self-sustaining or (2) the mean dispersal distance is large enough to connect reserves and promote network persistence (Botsford et al. 2001, 2003, 2009, Gaines et al. 2010, White et al. 2010b). The optimal size of individual marine reserves depends on the main objective of reserve networks (Hastings and Botsford 2003). Reserve networks designed primarily to manage fisheries should be composed of small reserves in order to maximize spillover into exploited areas, whereas reserve networks designed to meet conservation targets should be composed of large reserves that minimize spillover (Allison et al. 1998, Hastings and Botsford 2003, Sale et al. 2005, Gaines et al. 2010).

Theory has mainly focused on single-species models to develop these reserve design principles, yet by curtailing all harvesting activities within designated areas, marine reserves inherently affect entire communities (Botsford et al. 1997, Guichard et al. 2004, Baskett et al. 2007, Gaines et al. 2010). Recent work has shown that protecting entire communities typically requires networks of larger reserves in order to counteract the indirect negative effects caused by competitive and trophic interactions between species within and beyond reserve boundaries (reviewed by Baskett et al. 2007). Indeed, by promoting the abundance of previously exploited species such as predators, consumers, and superior competitors, marine reserves can set off trophic

cascades and competitive effects that reduce the abundance of prey and inferior competitors (Baskett et al. 2007, Gaines et al. 2010). Increasing the size and decreasing the spacing of reserve networks reduces the strength of these trophic and competitive effects by limiting connectivity and spillover (Baskett et al. 2007). Hence, in addition to the trade-off between conservation and fishery goals affecting the optimal size and spacing of reserves, there are also inherent community-level trade-offs (i.e., “winning” and “losing” species) that must be weighed carefully in order to design effective reserve networks for (meta)communities of interacting species.

Although reserve models are increasingly incorporating realistic features of natural marine systems such as species interactions (Baskett et al. 2007, White and Samhouri 2011), dispersal (Botsford et al. 2001, Guichard et al. 2004, Kaplan 2006), and environmental stochasticity (Blowes and Connolly 2012), the implications of nonequilibrium fluctuations in abundance remain underexplored (Guichard et al. 2004, Hsieh et al. 2005, 2006, Anderson et al. 2008, Siegel et al. 2008). Understanding the consequences of such nonequilibrium dynamics is particularly important for marine reserve design because (1) natural systems typically exhibit strong temporal variation in abundance (Kendall et al. 1998, Hsieh et al. 2006, Rouyer et al. 2008, Shelton and Mangel 2011a) and (2) harvesting tends to increase the amplitude of population fluctuations and promote the risk of catastrophic collapse in response to environmental stochasticity (Hsieh et al. 2006, Anderson et al. 2008, Shelton and Mangel 2011a). Nonequilibrium theory suggests that current reserve guidelines based on equilibrium models could actually promote global extinction risk because increasing connectivity between interconnected and fluctuating marine populations can both amplify and (spatially) synchronize their dynamics (Earn et al. 2000, Liebhold et al. 2004, Gouhier et al. 2010a). Moreover, when strong population fluctuations are coupled in space via dispersal, they often generate complex spatiotemporal patterns of abundance characterized by autocorrelated variability (i.e., patchiness) at spatial scales that exceed the extent of dispersal (Fig. 1d, e; Jansen and De Roos 2000, Guichard et al. 2004, Guichard 2005, Gouhier et al. 2010b). Hence, current guidelines emphasizing the importance of promoting connectivity by basing reserve networks on the extent of dispersal may not necessarily translate from equilibrium theory to the nonequilibrium world.

Here, we used a predator–prey metacommunity model whose predictions have been validated in a natural marine system (Gouhier et al. 2010b) to determine how changes in the underlying dynamical regime affect the design of reserve networks. We show that for equilibrium metacommunities, current reserve guidelines based on the extent of dispersal lead to a community-level trade-off by simultaneously maximizing global predator abundance and minimizing prey abundance due to

trophic cascades. In nonequilibrium metacommunities, current reserve guidelines minimize the persistence of both species and minimize the abundance of the prey, whereas reserve networks based on the (larger) extent of patchiness maximize the abundance and persistence of both the prey and the predator. Hence, our results demonstrate that the underlying dynamical regime has strong implications for designing effective marine reserve networks to manage trophically structured metacommunities.

THE METACOMMUNITY MODEL

We used a spatially explicit version of the classical Rosenzweig and MacArthur (1963) predator-prey model to simulate the dynamics of an array of  $L$  coastal communities connected by a Gaussian dispersal kernel (Fig. 1a, b). The prey ( $N_1$ ) undergoes logistic growth with intrinsic rate of increase  $r = 0.5$  and carrying capacity  $K$ , and the specialist predator ( $N_2$ ) has a type II (saturating) functional response with attack rate  $a = 0.2$ , prey handling time  $v = 1$ , and natural mortality rate  $m = 0.2$ . Using a type III functional response to simulate the dynamics of a generalist predator and its prey yield qualitatively identical results (see Appendix A). The prey and the predator are harvested at rates  $h_1$  and  $h_2$ , respectively. Although the model allows for each species to be harvested at a different rate, we chose to use the same rate for both the prey and predator (i.e.,  $h_1 = h_2$ ). The predator-prey dynamics are modeled using the following set of differential equations for each site  $x$ :

$$\begin{aligned} \frac{dN_1(x)}{dt} &= rN_1(x) \left( 1 - \frac{N_1(x)}{K} \right) \\ &\quad - \frac{aN_1(x)N_2(x)}{1 + avN_1(x)} - h_1(x)N_1(x) - dN_1(x) \\ &\quad + \int_{-L/2}^{L/2} dN_1(y)k(x-y)dy \\ \frac{dN_2(x)}{dt} &= \frac{aN_1(x)N_2(x)}{1 + avN_1(x)} - mN_2(x) - h_2(x)N_2(x) \\ &\quad - dN_2(x) + \int_{-L/2}^{L/2} dN_2(y)k(x-y)dy \end{aligned} \tag{1}$$

where  $d = 1$  represents the proportion of the prey and the predator that disperse (herein referred to as the dispersal rate). Dispersal,

$$\int_{-L/2}^{L/2} dN_i(y)k(x-y)dy$$

is modeled as the convolution of the product of the dispersal rate  $d$  and the abundance vector  $N_i$  of species  $i$  with

$$k(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp[-(x - \mu)^2/2\sigma^2]$$

a normalized Gaussian dispersal kernel with mean  $\mu$  representing alongshore advection and variance  $\sigma^2$  representing diffusion (Siegel et al. 2003). The dispersal kernel was kept constant across all simulations with mean  $\mu = 0$  and variance  $\sigma^2 = 1$  (Fig. 1b). Symmetrical Laplace or Weibull dispersal kernels yield results that are qualitatively identical to those presented here. The model equations (Eq. 1) were solved numerically using an explicit Runge-Kutta (4, 5) formula in MATLAB (function ode45; MATLAB 2012).

*Simulating equilibrium and nonequilibrium dynamics in metacommunities*

We used the Rosenzweig-MacArthur predator-prey model to simulate local dynamics because its asymptotic behavior can shift from a point equilibrium to limit cycles in response to increased productivity of the prey (Rosenzweig 1971). Hence, by increasing productivity (i.e., carrying capacity  $K$ ), we were able to use the same modeling framework to determine the effects of marine reserve networks on equilibrium and nonequilibrium metacommunities. It is important to note that our results do not depend on the specific values of each parameter, but rather on their combined influence on the dynamical regime of the predator-prey model (i.e., point equilibrium for  $K = 7$  vs. limit cycles for  $K = 40$ ; see Appendix B).

We assessed the effects of marine reserve networks on both equilibrium and nonequilibrium metacommunities to determine whether current guidelines developed using equilibrium models were optimal for managing natural marine populations, which typically show strong variability in space and time (Hsieh et al. 2005, Anderson et al. 2008, Rouyer et al. 2008, Worm et al. 2009, Gouhier et al. 2010b). Once communities characterized by such variability (e.g., self-sustained oscillations) are coupled via localized dispersal, they can generate complex spatiotemporal patterns of abundance whose statistical properties match those observed in intertidal systems along the west coast of the United States (Gouhier et al. 2010b). These complex spatiotemporal patterns arise because localized dispersal intermittently decouples regional and local dynamics (Fig. 1a; Briggs and Hoopes 2004, Gouhier et al. 2010a). Specifically, localized dispersal generates an ephemeral negative correlation between immigration and local abundance that dampens and spatially desynchronizes fluctuations in neighboring populations by (1) promoting growth when local abundance is low and (2) limiting growth when local abundance is high (Fig. 1a; Briggs and Hoopes 2004, Gouhier et al. 2010a). Over time, repeated bouts of localized dispersal (re)couple local and regional dynamics by generating a positive correlation between immigration and local abundance that both amplifies and synchronizes local population fluctuations (Fig. 1a;

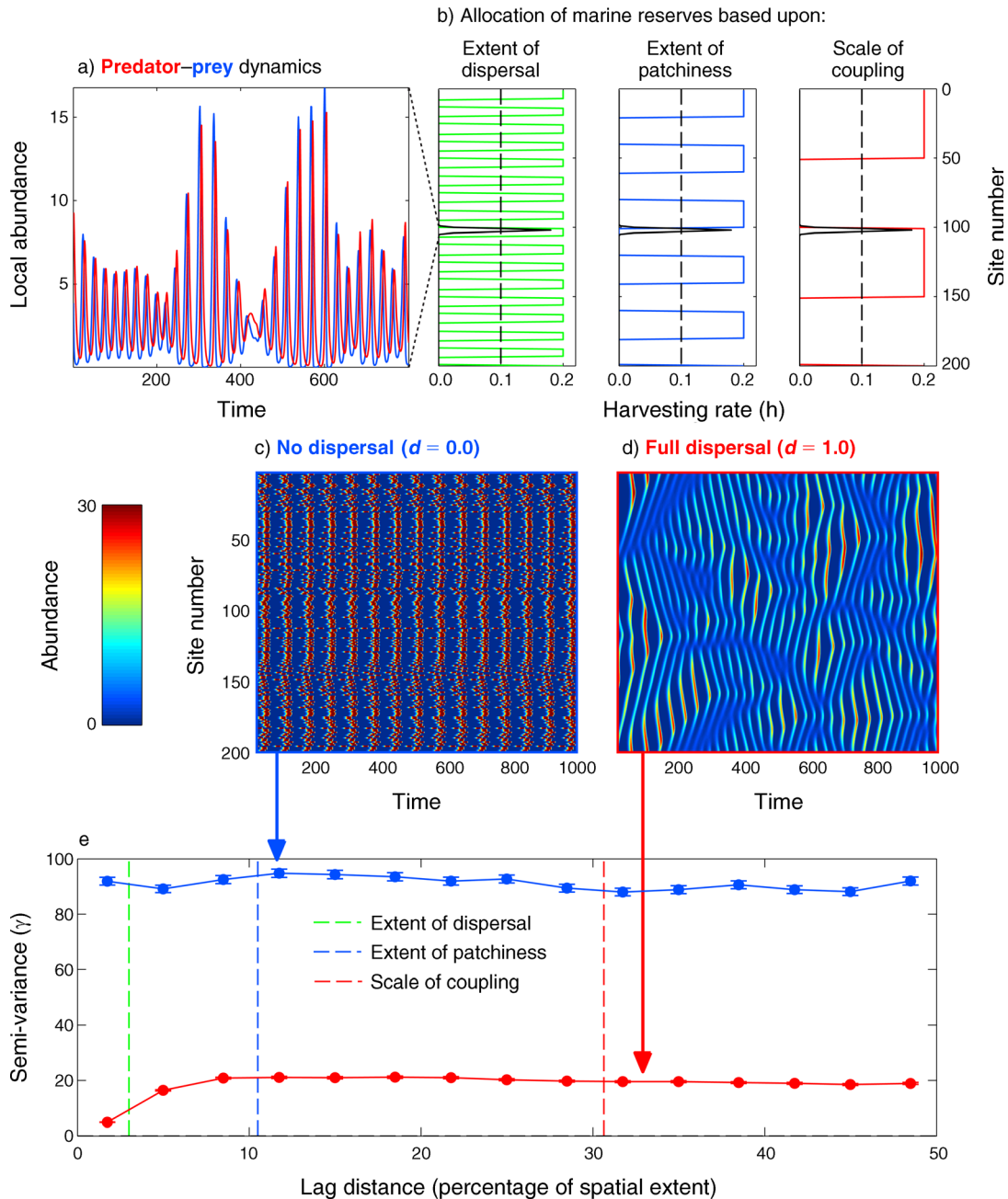


FIG. 1. Dynamics of the predator-prey metacommunity model at local and regional scales, and description of marine reserve networks. (a) Localized dispersal between predator (red line) and prey (blue line) communities undergoing limit cycles (carrying capacity  $K = 40$ ) generates complex patterns of abundance within sites by decoupling immigration from local abundance. (b) A fraction  $d$  of individuals disperses to neighboring populations via a Gaussian dispersal kernel (black curve). Marine reserves are allocated by using a square waveform with a given amplitude and frequency to vary the harvesting rate spatially. The frequency of the waveform is used to control the distance between the edges of the reserves and create marine reserve networks based upon the extent of dispersal (green), the extent of patchiness (blue), or the scale of coupling (red). The vertical dashed line indicates the mean harvesting rate across the metacommunity, which is kept constant at 0.1 for all simulations in this paper. (c, d) The prey abundance time series in nonequilibrium metacommunities with no reserves and either no dispersal ( $d = 0$ ; blue) or full dispersal ( $d = 1$ ; red). (c) In the absence of dispersal, populations fluctuate independently, so the semi-variance remains high across all lag distances [blue line in panel (e)]. (d) When the rate of dispersal is full, dispersal interacts with local population fluctuations to generate autocorrelation in abundance (i.e., patchiness) at spatial scales that are much larger than the extent of dispersal [red line in panel (e)]. Semi-variance increases monotonically with lag distance until it reaches a plateau at the extent of patchiness. (e) Shown are means  $\pm$  SE. The vertical dashed lines represent (1) the extent of dispersal (green), defined as the distance at which  $>99\%$  of individuals disperse; (2) the extent of patchiness (blue), defined as the size of clusters of populations undergoing autocorrelated fluctuations; and (3) the scale of coupling (red), defined as the distance between clusters of populations undergoing autocorrelated fluctuations in abundance.



Gouhier et al. 2010b). Overall, these processes generate nonstationary spatiotemporal patterns of abundance (Fig. 1e) with (1) a characteristic extent of patchiness (i.e., the size of clusters of populations undergoing autocorrelated fluctuations; Fig. 1e) and (2) a scale of coupling (i.e., the distance between clusters of populations undergoing similar fluctuations in abundance; Fig. 1e; Gouhier et al. 2010b).

*Quantifying patterns of population abundance  
in nonequilibrium metacommunities*

We used isotropic (semi-)variograms to quantify spatial patterns of autocorrelated fluctuations in population abundance in nonequilibrium metacommunities prior to the establishment of marine reserves. Specifically, for each post-transient time step, we used the semi-variance function  $\gamma(l)$  to quantify the spatial semi-variance of population abundance  $N_i$  between pairs of sites  $x_i$  as a function of the lag distance  $l$  that separates them (Fortin and Dale 2005):

$$\gamma(l) = \frac{1}{2n(l)} \sum_{i=1}^n [N_i(x_i) - N_i(x_i + l)]^2 \quad (2)$$

with  $n(l)$  representing the number of pairs of sites located within distance  $l$  of one another. We then fit a spherical model  $\hat{\gamma}(l)$  to the experimental variogram  $\gamma(l)$  obtained at each post-transient time step (Fortin and Dale 2005):

$$\hat{\gamma}(l) = c_0 + c_1 \left[ \frac{3l}{2a} - \frac{1}{2} \left( \frac{l}{a} \right)^3 \right] \quad \text{for } 0 < l < a \quad (3)$$

$$\hat{\gamma}(l) = c_0 + c_1 \quad \text{for } l \geq a$$

with  $c_0$  representing the nugget (the semi-variance at lag distance zero),  $a$  representing the spatial range/the extent of patchiness (the size of clusters of populations with autocorrelated abundance), and  $c_1$  representing the sill (the semi-variance at the spatial range; Fortin and Dale 2005). We then averaged the spatial range  $c_1$  across all post-transient time steps to quantify the extent of patchiness in abundance for both the prey and the predator (Fig. 1b–e). We also used the variograms to quantify the scale of coupling by determining the nonzero lag distance at which the semi-variance reaches the lowest local minimum at each time step, and then taking the average of that lag distance across all time steps (Fig. 1b–e). The scale of coupling thus corresponds to the mean distance between clusters of populations undergoing autocorrelated fluctuations in abundance. These analyses were only performed for nonequilibrium metacommunities because under equilibrium conditions, populations do not fluctuate and are thus perfectly spatially autocorrelated across all lag distances. Hence, the extent of patchiness is essentially infinite and the scale of coupling does not exist.

*Implementing marine reserve networks*

We modeled marine reserve networks by varying the harvesting rate  $h_i$  spatially using a periodic square wave function (Fig. 1b). The amplitude  $\lambda$  of the square wave function controls the difference in harvesting rate between reserves (i.e., protected areas) and unprotected areas, whereas the frequency  $\phi$  of the square wave function controls both the size of and the distance between the center of marine reserves (Fig. 1b). Implementing marine reserves in a metacommunity consisting of  $L$  sites thus yields harvesting rate  $h_i(x)$  for site  $x$  along the coastline:

$$h_i(x) = \lambda \text{sign} \left[ \sin \left( 2\pi\phi \frac{x}{L} \right) \right] + \bar{h}_i \quad (4)$$

where  $\lambda$  and  $\phi$  are the amplitude and the frequency of the square wave function, respectively, and  $\bar{h}_i = 0.1$  is the global mean harvesting rate for the predator and the prey. We used the same square wave function to model harvesting for the prey and the predator (i.e.,  $h_1(x) = h_2(x)$ ). Although this periodic function (Eq. 4) generates uniformly spaced reserves, our results also hold for irregularly spaced networks (see Appendix C). We kept the total protected area in our simulations constant at 50% of the coastline, a value that falls within the 20–70% range advocated by both theoretical and empirical studies (e.g., Airame et al. 2003, Gell and Roberts 2003, Gaines et al. 2010). Supplementary simulations using a slightly different siting algorithm indicate that our results hold when the total protected area represents less than 50% of the coastline. Our implementation of marine reserves is conservative because we assume that global mean harvesting rates remain constant across the entire metacommunity even after the implementation of marine reserves ( $\bar{h}_i = 0.1$ ). Our study thus describes the worst case scenario whereby marine reserves do not reduce exploitation overall, but merely displace it beyond their boundaries (Ewers and Rodrigues 2008, Gaines et al. 2010). This compensatory increase in harvesting effort outside of reserves represents the simplest adaptive behavior possible by parties interested in exploiting these resources (e.g., fishing fleets).

We tested the effectiveness of 30 different marine reserve designs that ranged from a single large reserve to networks of many smaller reserves. We focused primarily on three types of reserve networks (Fig. 1): (1) reserve networks that maximize spillover from protected to unprotected areas by using the extent of dispersal (defined as the distance at which >99% of individuals from a source population have dispersed) as the size and spacing of reserves (Fig. 1b); (2) reserve networks whose size and spacing are equal to the extent of patchiness (defined as the size of clusters of populations undergoing autocorrelated fluctuations; Fig. 1b–e); and (3) reserve networks whose size and spacing are equal to the scale of coupling (defined as the distance between clusters of populations undergoing autocorrelated fluctuations in abundance; Fig. 1b–e). Since marine reserves can refer to

areas that benefit from either partial or full protection from all extractive activities (Lester et al. 2009), we evaluated the performance of reserve networks for a range of protection levels by varying the amplitude  $\lambda$  of the square wave function describing the spatial variation in harvesting rate  $h_i$  such that  $0 < \lambda \leq \bar{h}_i$ . This allowed us to assess the performance of fully protected/no-take reserves ( $\lambda = \bar{h}_i$ , difference in harvesting rate of 100% between protected and unprotected areas) and partially protected reserves ( $0 < \lambda < \bar{h}_i$ , difference in harvesting rate of <100% between protected and unprotected areas).

All simulations were run for metacommunities consisting of 200 sites with periodic boundary conditions for a total of 8000 time steps: From time step 0 to 5000 without reserves and from time step 5001 to 8000 with reserves. The analyses were conducted over the last 2000 time steps in order to avoid transient dynamics. However, conducting our analyses immediately after the establishment of reserves (i.e., from time step 5001) yielded results that were qualitatively similar to those presented here. We used mean prey and predator abundance assessed (1) globally, (2) within, and (3) outside reserves to determine the effectiveness of reserve networks in achieving conservation goals (Gerber et al. 2003). We also measured total yield of each species (i.e., total amount of predator or prey harvested) to evaluate the effectiveness of reserve networks as fishery management tools. Additionally, we determined the effect of marine reserve networks on persistence in nonequilibrium metacommunities by measuring the probability of extinction of all populations (i.e., global extinction risk) and local populations (i.e., local extinction risk) in response to a global perturbation, which we defined as normally distributed white noise with a mean of zero and a variance of  $10^3$  (Earn et al. 2000). The global perturbation was applied to the abundance of each population at each time step and the global probability of extinction was calculated by determining the proportion of time steps for which all populations saw their abundance reach zero. The local probability of extinction was calculated by determining the proportion of populations that saw their abundance reach zero at each time step. Local and global extinction risk were measured for the predator, the prey, and both species (i.e., extinction of the entire community). These measures of extinction risk allowed us to quantify the amount of spatial redundancy and resilience that each type of marine reserve network provided against large-scale, catastrophic events. Extinction risk was not assessed for equilibrium metacommunities because such populations do not fluctuate, so any catastrophic event that is strong enough to cause the extinction of the predator, the prey, or the entire community within a given site will do so across the entire metacommunity.

All metrics (abundance, yield, extinction risk) were converted to percentage change relative to baseline

scenarios without reserves (i.e., spatially uniform harvesting rate) in order to facilitate comparisons across dynamical regimes (i.e., comparing equilibrium and nonequilibrium metacommunities). For example, metric  $\omega(\lambda, \varphi)$  obtained for a reserve network with a level of protection of  $\lambda$  and an inter-reserve distance of  $\varphi$  was converted to percentage change relative to the same metric  $\omega(0, \varphi)$  obtained in the absence of reserves:

$$\frac{\omega(\lambda, \varphi) - \omega(0, \varphi)}{\omega(0, \varphi)} \times 100.$$

The results documented using the percentage changes are qualitatively identical to those observed in the raw data.

## RESULTS

### *The effects of harvesting in closed communities*

We begin by generating baseline results on the impact of reserve-mediated changes in harvesting on closed communities (i.e., in the absence of dispersal) undergoing equilibrium and limit cycle dynamics. Contrasting these results with those obtained using equilibrium and nonequilibrium metacommunity models will allow us to fully appreciate the effects of dispersal on the effectiveness of reserve networks for managing interconnected marine systems. We now show that nonlinear averaging in space and time leads to opposite effects of harvesting on mean abundance in equilibrium and nonequilibrium metacommunities.

*Nonlinear spatial averaging.*—Since all marine reserve networks considered here alter the spatial distribution (i.e., the spatial variance) of the harvesting rate without affecting its mean value (Fig. 1b), we can use Jensen's inequality to understand the effect of marine reserves on global mean abundance. Jensen's inequality states that for accelerating (decelerating) nonlinear functions, the variance of the independent variable tends to amplify (depress) the response variable (Ruel and Ayres 1999). In our model, abundance is the response variable and is an accelerating (decelerating) function of harvesting for the prey (predator). Jensen's inequality predicts that in the absence of dispersal, increased spatial variance in harvesting due to the implementation of marine reserves will tend to increase (decrease) the global mean abundance of the prey (predator) (see Appendix B: Fig. B2). An increase (decrease) in global mean abundance occurs because populations experiencing high harvesting rates (i.e., unprotected sites) contribute more (less) to global mean abundance than those experiencing low harvesting rates (i.e., protected sites) (Appendix B: Fig. B2). Hence, our null expectation based on closed equilibrium communities is that increasing the spatial variance of the harvesting rate by increasing the level of protection within marine reserves will increase the global mean abundance of the prey and reduce the global mean abundance of the predator in equilibrium metacommunities.

*Nonlinear spatiotemporal averaging.*—In enriched communities undergoing limit cycles, spatial variance in harvesting also alters mean abundance by reducing the amplitude and increasing the frequency of population fluctuations (see Appendix B: Fig. B3). Because population fluctuations are bounded by zero and have asymmetrical shapes, increasing their frequency will tend to increase mean abundance whereas reducing their amplitude will tend to decrease mean abundance (Appendix B: Fig. B3b, d). These opposing effects of harvesting on the frequency and amplitude of population fluctuations cause mean prey (predator) abundance to be a decelerating (accelerating) function of harvesting (Appendix B: Fig. B4a, c). Because of Jensen's inequality, increasing the spatial variance of the harvesting rate by implementing reserves will thus decrease (increase) mean prey (predator) abundance (Appendix B: Fig. B4b, d). Hence, our null prediction based on closed communities undergoing limit cycles is that increasing the spatial variance of the harvesting rate by increasing the level of protection within marine reserves will reduce the global mean abundance of the prey and increase the global mean abundance of the predator in nonequilibrium metacommunities. Overall, these results obtained with closed communities show that the underlying dynamical regime (i.e., equilibrium vs. limit cycles) has a profound influence on the effect of spatial variance in harvesting on the mean abundance of both the prey and the predator.

#### *The effects of reserve networks in equilibrium metacommunities*

The net impact of increasing the level of protection on global abundance depends on the size and spacing of individual reserves (Fig. 2). When the size and spacing of reserves is much larger than the extent of dispersal (i.e.,  $\gg 3\%$  of spatial extent), we recover the results obtained in closed equilibrium communities because protected areas are largely isolated from unprotected areas (Appendix B: Fig. B2 vs. Fig. 2): Increasing the level of protection causes global prey (predator) abundance to increase (decrease). Specifically, increasing the level of protection increases (reduces) predator abundance within (outside) reserves and reduces prey abundance within reserves because of trophic cascades (Fig. 2c–f).

Networks whose size and spacing are smaller than the extent of dispersal maximize predator spillover from protected to unprotected areas, and thus maximize predator abundance outside reserves while reducing predator abundance within reserves (Fig. 2d, f). Because the increase in predator abundance within reserves more than compensates for its reduction outside reserves, predator global abundance is maximized when networks are characterized by small inter-reserve spacing (Table 1, Fig. 2b). Although reserve networks with small sizes and spacing increase predator global abundance, they never increase total predator yield beyond the levels reached without reserves (Fig. 2h) because the increase in

predator global abundance is driven by the increase in predator abundance within reserves, where harvesting rates, and thus yields, are low or zero (Fig. 2d). Reserve networks characterized by larger sizes and spacing minimize total yield and predator abundance both globally and outside reserves by reducing predator spillover from protected to unprotected areas (Fig. 2b, f, h). Results for prey abundance essentially mirror those of the predator because of trophic cascades: Prey abundance is maximized (minimized) within (outside) reserves for networks whose size and spacing are small, and minimized (maximized) for networks whose size and spacing are large (Fig. 2a, c, e). By increasing prey abundance outside reserves, networks whose size and spacing are large increase total prey yield by 5–50%. Conversely, networks whose size and spacing are small reduce prey abundance outside reserves and total prey yield by 5–10% (Table 1, Fig. 2e, g). Note that, because populations in equilibrium metacommunities do not fluctuate, reserve networks based on the extent of patchiness do not promote the abundance of either the prey or the predator (Table 1, Fig. 2a, b).

Overall, reserve networks whose size and spacing is smaller than the extent of dispersal are optimal for the predator because they maximize global predator abundance by striking the right balance between retaining subsidies within protected areas and allowing them to spillover into unprotected areas (Table 1). However, reserve networks characterized by much larger sizes and spacing are optimal for the prey because such networks reduce predator spillover from protected to unprotected areas and thus limit the effects of trophic cascades outside reserves (Table 1). Designing effective reserves for equilibrium metacommunities thus involves a community-level trade-off: Networks characterized by small reserve size and spacing maximize predator abundance and minimize prey abundance/yield, whereas the converse is true for networks characterized by large spacing.

#### *The effects of reserve networks in nonequilibrium metacommunities*

In nonequilibrium metacommunities, increasing the level of protection (1) increases (reduces) predator abundance within (outside) reserves (Fig. 3d, f), and (2) increases the disparity in the performance of different reserve designs (Fig. 3). Networks whose size and spacing match the extent of dispersal (i.e.,  $\sim 3\%$  of spatial extent) are suboptimal because by promoting spillover between protected and unprotected areas, they generate strong trophic cascades that minimize global prey abundance (Fig. 3a) and the persistence of both the predator and the prey (Fig. 4), and only provide a mild increase in global predator abundance (Fig. 3b). Networks whose size and spacing match the extent of spatially autocorrelated fluctuations in population abundance (i.e., the extent of patchiness which represents  $\sim 11\%$  of the spatial extent; Fig. 1e and Appendix

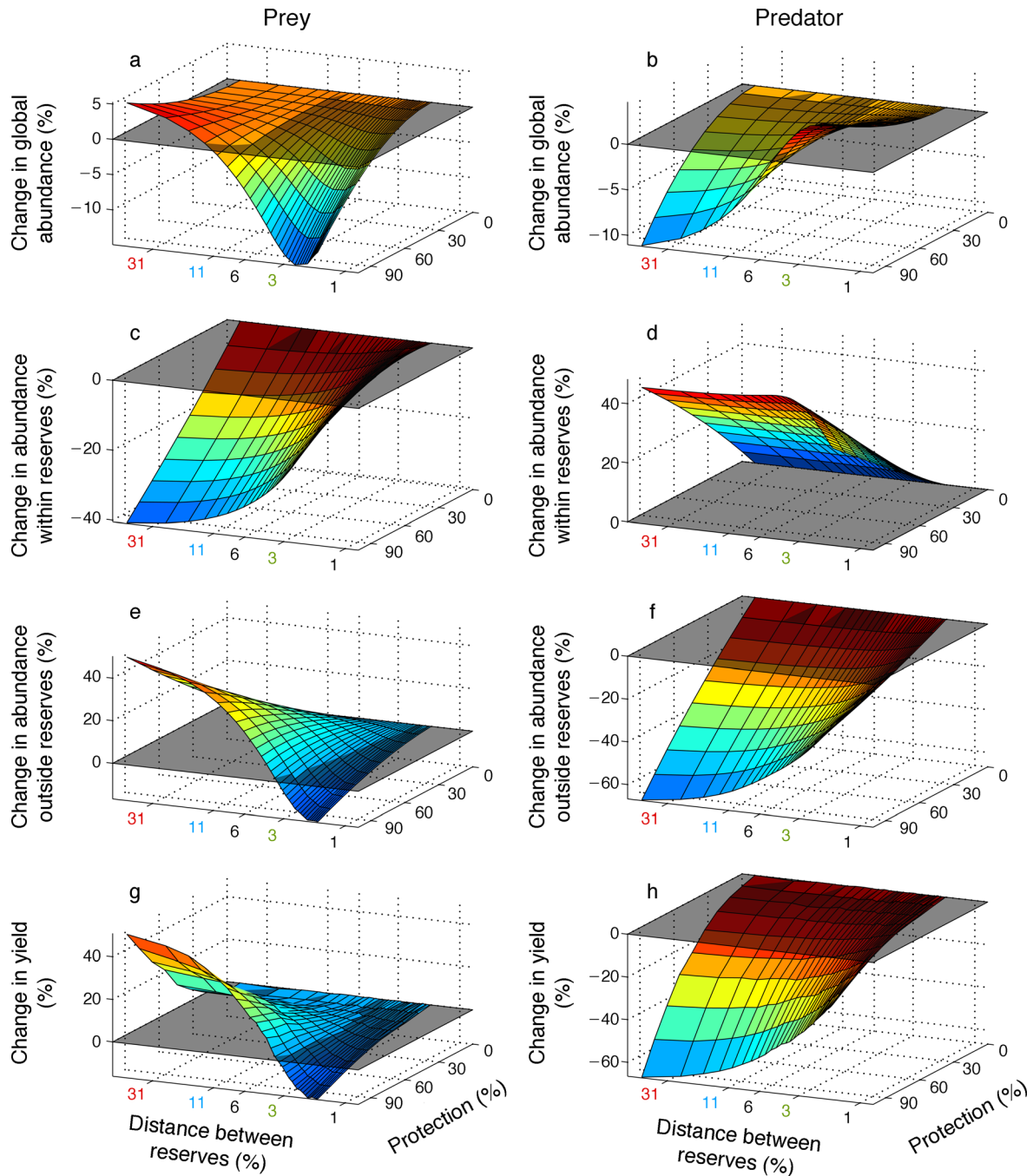


FIG. 2. The effect of varying the level of protection and the distance between reserves (expressed as the percentage of spatial extent) on prey and predator (a, b) global mean abundance, (c, d) mean abundance within reserves, (e, f) mean abundance outside reserves, and (g, h) total yield for equilibrium metacommunities ( $K = 7$ ) with full dispersal. Each metric is measured as the percentage change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate) represented by the gray horizontal surface. The mean predator and prey harvesting rates are set to 0.1. The green, blue, and red axis tick labels indicate the extent of dispersal, the extent of patchiness, and the scale of coupling, respectively. Results are means from 10 replicate simulations.

D: Fig. D1) maximize predator abundance within reserves (Fig. 3d). Although these networks reduce predator abundance outside reserves by limiting spillover from protected to unprotected areas (Fig. 3f), the increase in predator abundance within reserves more

than compensates for its reduction in unprotected areas (Fig. 3d). Hence, reserve networks based on the extent of patchiness maximize global predator abundance (i.e., increase global predator abundance by 10–15% relative to no reserves; see Table 1, Fig. 3b) and persistence (Fig.



TABLE 1. The performance of different no-take marine reserve designs based on their effect on global mean abundance and total yield for equilibrium (carrying capacity  $K = 7$ ) and nonequilibrium metacommunities ( $K = 40$ ).

Performance metric and marine reserve design	Change in equilibrium metacommunities (%)		Change in nonequilibrium metacommunities (%)	
	Prey	Predator	Prey	Predator
Global mean abundance				
Extent of dispersal	-14	4	-21	5
Extent of patchiness	-1	-6	5	11
Scale of coupling	4	-10	1	3
Total yield				
Extent of dispersal	-6	-38	-22	-30
Extent of patchiness	35	-58	32	-28
Scale of coupling	48	-64	38	-28

*Note:* The values represent the percentage change of each metric for marine reserve designs described in rows, relative to baseline simulations of metacommunities with no reserves.

4). Because the increase in global predator abundance is entirely attributable to the increase in predator abundance within reserves where harvesting is low or zero, increasing the level of protection always reduces total predator yield (Fig. 3h).

Prey abundance within reserves generally decreases with the level of protection because of trophic cascades (Fig. 3c). When the spacing between reserves is greater than the extent of dispersal, prey abundance outside reserves increases because the reduction in predator spillover from protected to unprotected areas limits trophic cascade effects (Fig. 3e). This increase in prey abundance outside reserves leads to a 5–30% increase in total prey yield (Table 1, Fig. 3g). However, when the spacing between reserves is equal to or smaller than the extent of dispersal, prey abundance outside reserves, total prey yield, and prey persistence all reach minimal levels (Figs. 3e, g, and 4). Networks whose size and spacing approach the extent of patchiness maximize prey abundance outside reserves and thus increase the spillover of prey subsidies into protected areas (Fig. 3c, e). In doing so, these networks minimize the effects of trophic cascades on prey abundance within reserves and thus maximize both global prey abundance and persistence (Figs. 3a, c, and 4).

Overall, the optimal reserve networks for the predator are those whose spacing is approximately equal to the extent of patchiness because these networks maximize predator persistence and abundance globally by maximizing both abundance within reserves and spillover into unprotected areas (Table 1). Importantly, these same networks are also optimal for the prey because they maximize (1) prey persistence, (2) prey abundance globally and outside reserves, and (3) total prey yield, and minimize trophic cascade effects within reserves because of prey spillover from unprotected to protected areas (Table 1). Hence, in contrast to equilibrium metacommunities, there is no community-level trade-off for designing effective reserve networks for nonequilibrium metacommunities: Reserve networks whose size

and spacing match the extent of patchiness maximize the persistence and global abundance of both the predator and the prey.

## DISCUSSION

Despite the strong spatiotemporal variability of natural marine systems and the amplifying effect of fishing (Kendall et al. 1998, Hsieh et al. 2006, Anderson et al. 2008, Shelton and Mangel 2011a), current reserve principles designed for either managing fisheries or conserving communities are largely based on single-species equilibrium models that assume a steady state in space and time. This discrepancy between equilibrium theory and the nonequilibrium world has strong implications for the way we manage dynamic resources via networks of reserves. Using a validated predator–prey metacommunity model (Gouhier et al. 2010b), we have shown that the current emphasis on promoting connectivity by basing reserve networks on the extent of dispersal is not optimal for managing interconnected communities. In equilibrium models, reserves based on these guidelines generate a quasi zero sum game at the community level, whereby the gains achieved in the abundance of the prey (predator) are offset by concomitant reductions in the abundance of the predator (prey) because of strong spatial and trophic coupling. In nonequilibrium models, reserves based on current guidelines reduce the persistence and yield of both species, minimize the abundance of the prey, and provide only a marginal boost to the abundance of the predator. However, reserve networks based on the (larger) spatial scale of variability that emerges from the interaction between local population fluctuations and dispersal simultaneously maximize the persistence and abundance of both species by reducing spatial coupling and trophic cascades while maintaining connectivity. Paradoxically, by generating variability at large spatial scales, nonequilibrium metacommunities characterized by unpredictable spatiotemporal patterns of abundance appear to be easier to manage via reserve

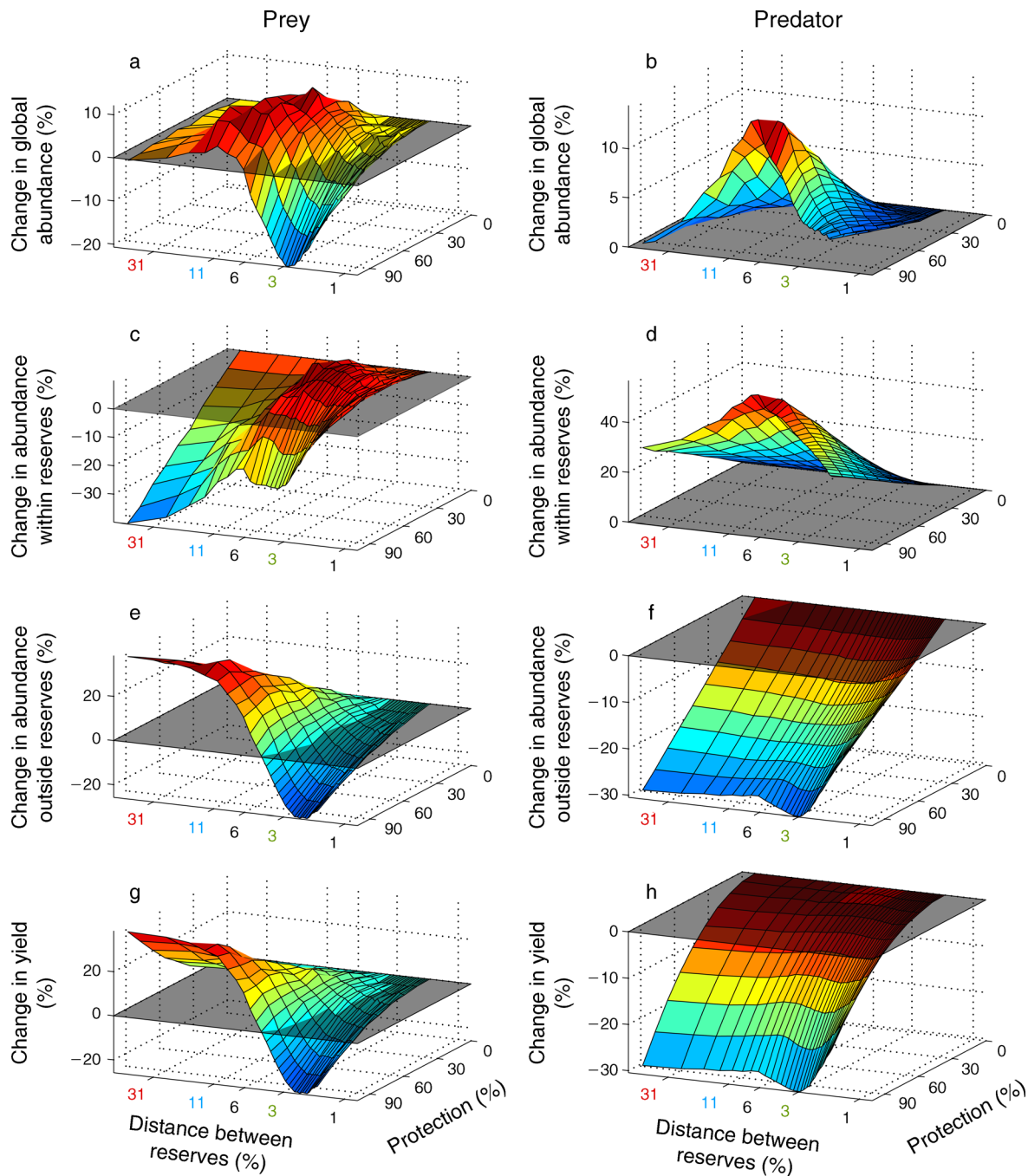


FIG. 3. The effect of varying the level of protection and the distance between reserves (expressed as the percentage of spatial extent) on prey and predator (a, b) global mean abundance, (c, d) mean abundance within reserves, (e, f) mean abundance outside reserves, and (g, h) total yield for nonequilibrium metacommunities ( $K = 40$ ) with full dispersal. Each metric is measured as the percentage change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate) represented by the gray horizontal surface. The mean predator and prey harvesting rates are set to 0.1. The green, blue, and red axis tick labels indicate the extent of dispersal, the extent of patchiness, and the scale of coupling, respectively. Results are means from 10 replicate simulations.

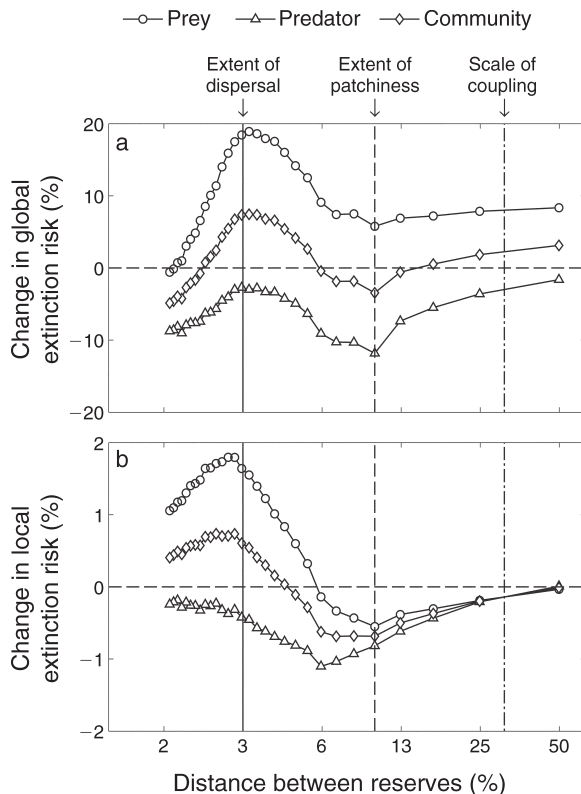


FIG. 4. The effect of varying the distance between no-take marine reserves (expressed as the percentage of spatial extent) on (a) global and (b) local extinction risk for the prey (circles), the predator (triangles), and entire communities (diamonds) in nonequilibrium metacommunities ( $K = 40$ ). The vertical lines indicate the extent of dispersal (solid), the extent of patchiness (dashed), and the scale of coupling (dot-dashed). The extinction risk is measured as the percentage change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate) represented by the horizontal dashed line. The mean predator and prey harvesting rates are set to 0.1. Results are means from 10 replicate simulations.

networks than equilibrium metacommunities exhibiting much simpler dynamics. Overall, these results suggest that existing reserve principles must be amended to account for realistic patterns of population fluctuations in order to promote the persistence and productivity of trophically structured metacommunities.

#### *Cross-scale ecological feedbacks: spatial implications of temporal dynamics*

*From hot spots to hot moments.*—Because of the inherent complexity of marine environments, the dearth of quantitative information about key biological processes, and the need for urgent action, “tactical” reserve siting algorithms have often used environmental variables as proxies for ecological patterns in order to select the optimal location, size, and spacing of reserves (Airame et al. 2003, Leslie et al. 2003, Roberts et al. 2003, Cook and Auster 2005, Ball et al. 2009). For

example, placing reserves in areas that contain a variety of habitat types (e.g., habitat hot spots) is expected to produce desirable ecological outcomes such as increased species abundance and diversity. When ecological data on the abundance and distribution of species obviates the need for environmental proxies, biological hot spots can be targeted directly for protection via reserves. These tactical reserve siting approaches thus assume that the relationship between environmental proxies and ecological properties remains largely frozen in time or that the distribution of species stays relatively fixed in space. However, marine communities are anything but stationary in time or space (Hsieh et al. 2006, Anderson et al. 2008, Rouyer et al. 2008, Gouhier et al. 2010b, Shelton and Mangel 2011a). Hence, siting algorithms cannot always rely on static patterns or hot spots; they must also account for dynamic ecological processes in order to make accurate recommendations regarding the optimal location, size, and spacing of reserves.

Complementary “strategic” approaches have long espoused this perspective and explicitly modeled the impact of reserves on ecological dynamics in order to distill general design principles (Botsford et al. 2001, 2003, Gerber et al. 2003, Hastings and Botsford 2003). The consensus view that has emerged from these (mostly) single-species, equilibrium models is that increasing connectivity by basing reserve networks on the extent of dispersal is crucial for promoting the persistence and productivity of spatially structured populations (Botsford et al. 2001, 2003, Hastings and Botsford 2003, Gaines et al. 2010). But in the nonequilibrium world, connectivity can actually destabilize spatial ecological systems and increase global extinction risk by both amplifying and spatially synchronizing population fluctuations (Earn et al. 2000, Liebhold et al. 2004, Gouhier et al. 2010a). This complex effect of connectivity on persistence cautions against focusing too narrowly on the extent of dispersal and connectivity when designing reserve networks.

The widespread use of equilibrium models in reserve theory has also promoted the tacit assumption that ecological processes and patterns share a common scale. According to this perspective, to preserve ecological patterns such as the regional distribution of species, reserve networks ought to be based on the scale of their causal process, namely dispersal. In a nonequilibrium world, this assumption does not necessarily hold because local and regional processes can interact synergistically to generate nonstationary patterns of abundance (i.e., patchiness) at much larger spatial scales (Levin 1992, Guichard et al. 2003, Guichard 2005, Gouhier et al. 2010b). Our simulations show that these cross-scale ecological feedbacks between local and regional processes have strong implications for the spatial management of natural resources. Indeed, reserve networks based on the extent of dispersal promote global extinction risk, whereas reserve networks based on the extent of patchiness reduce global extinction risk and

increase the abundance of all species. Given the ubiquity of cross-scale feedbacks across a range of spatial ecological systems (Levin 1992, Jansen and de Roos 2000, Guichard et al. 2004, Gouhier and Guichard 2007, Gouhier et al. 2010b), our results suggest that a shift from the extent of dispersal to the extent of patchiness may lead to more effective reserve networks for protecting interconnected and dynamic ecological communities.

The causes of population fluctuations in marine systems are a matter of intense debate, especially for harvested species (Anderson et al. 2008, Shelton and Mangel 2011a, b, Sugihara et al. 2011). Here, we have focused on a specific type of nonequilibrium dynamics that arises when endogenously generated local fluctuations are spatially coupled via localized dispersal (Briggs and Hoopes 2004, Gouhier et al. 2010b). In such systems, localized dispersal decouples regional and local dynamics by creating an intermittent negative correlation between immigration and local abundance that spatially desynchronizes and dampens population fluctuations (“cold moments,” see Fig. 1a; Briggs and Hoopes 2004, Gouhier et al. 2010a). However, repeated bouts of dispersal eventually (re)couple local and regional dynamics, and thus spatially synchronize and amplify population fluctuations (“hot moments,” see Fig. 1a). This intermittent decoupling between local and regional dynamics is responsible for generating the large-scale patterns of autocorrelated fluctuations that allow reserve networks based on the extent of patchiness to maximize the abundance of all species in nonequilibrium metacommunities. Our results regarding the optimal reserve networks for nonequilibrium metacommunities thus apply to any system that can generate this negative correlation between immigration and local abundance (Briggs and Hoopes 2004), whether it be via disturbance–recovery dynamics in single-species models (Guichard et al. 2003, Gouhier and Guichard 2007, Gouhier et al. 2010b), disturbance and recruitment facilitation between competitors in two-species models (Guichard 2005), nonlinear trophic interactions between a generalist or a specialist predator and its prey (see Fig. 3 and Appendix A; Jansen and de Roos 2000, Gouhier et al. 2010b), or asymmetrical and nonlinear trophic interactions in tri-trophic keystone community modules (Gouhier et al. 2010a). However, these reserve design recommendations do not hold when nonequilibrium dynamics arise because of exogenous forcing via spatially uncorrelated or autocorrelated environmental fluctuations (see Appendix E). Indeed, in such stochastically forced equilibrium metacommunities, the exogenous fluctuations are either spatially uncorrelated or positively correlated, so the decoupling between immigration and local abundance that drives large-scale patchiness does not occur. Hence, the reserve recommendations for stochastically forced equilibrium metacommunities are identical to those for equilibrium metacommunities (Appendix E): Networks of small

(large) and aggregated (isolated) reserves maximize the abundance of the predator (prey). Overall, these results highlight the importance of identifying the relative importance of endogenous (Hsieh et al. 2005, Gouhier et al. 2010b) and exogenous (Shelton and Mangel 2011a) drivers of population fluctuations in marine systems for designing effective reserve networks. Importantly, because our simulations show that the emergence of large-scale patchiness can serve as a signature of spatially coupled endogenous fluctuations, we suggest that computing the spatial extent of patchiness in adult abundance may be critical for determining whether reserve networks based on the extent of dispersal or the extent of patchiness are optimal for managing natural systems.

Classical strategic models have focused almost exclusively on ecological processes, but there is growing recognition that we need to heed the lessons of tactical approaches by incorporating environmental heterogeneity into a new generation of dynamic models in order to determine the joint influence of biotic and abiotic factors on the effectiveness of reserve networks (Blowes and Connolly 2012). For instance, spatially autocorrelated environmental stochasticity can synchronize the dynamics of geographically isolated subpopulations and thus potentially promote regional extinction risk (Moran 1953). Since this “Moran effect” and connectivity both typically decay with distance, the net impact of altering the spacing of reserve networks on metapopulation persistence will depend on the relative influence of connectivity and the Moran effect on stability (Blowes and Connolly 2012). Ultimately, determining the optimal size and spacing of reserve networks will thus require information about the rate at which both environmental and ecological processes wax and wane with geographical distance.

*From metapopulations to metacommunities.*—Despite the historical emphasis on single species, recent work has called for the development of reserve networks that protect entire (meta)communities or (meta)ecosystems (Mangel and Levin 2005, Baskett et al. 2007, McLeod and Leslie 2009, White and Samhuri 2011). Although desirable, this shift toward ecosystem-based management presents a new challenge: How can we construct reserve networks that will maximize the persistence of trophically and spatially coupled species? To circumvent the difficulties associated with quantifying species interactions and connectivity in nature, initial strategies elected to target environmental surrogates of biodiversity such as niche space (e.g., habitat and biogeographical diversity) in order to design reserves that would benefit whole communities (Airame et al. 2003, Leslie et al. 2003, Roberts et al. 2003). Surrogate strategies provide an excellent starting point for allocating reserves, but because species inherently interact with one another in space, these methods must be supplemented by dynamic models in order to predict how the



effects of reserves will propagate across (meta)communities via networks of species interactions and dispersal.

There are two main issues with extending reserve principles designed for single-species equilibrium models to multi-species assemblages: species-specific dispersal distances and species interactions. Although single-species models can focus on a unique scale of dispersal to promote connectivity and persistence, multi-species models must account for interspecific differences in dispersal distances and rates in order to design reserve networks that will serve entire communities (Kinlan and Gaines 2003). One potential solution is to adopt networks of irregularly spaced reserves in order to cater to the dispersal ability of each species (Airame et al. 2003). Although irregularly spaced reserve networks have little effect in single-species (Kaplan and Botsford 2005) or multi-species models where all species have the same dispersal properties (see Appendix C), they may benefit assemblages of species with different dispersal abilities by creating sub-networks, each promoting the connectivity of a different subset of species. However, our results suggest that the effectiveness of heterogeneous reserve networks will depend on the local and regional impact of competitive or trophic species interactions.

Indeed, species interactions can actually trump the importance of connectivity when designing reserve networks. In competitive and trophic communities composed of species with different dispersal abilities, networks of larger and more isolated reserves are better than networks of smaller and more aggregated reserves because the interspecific benefits of weaker trophic cascades outweigh the intraspecific costs of reduced connectivity (Baskett et al. 2007). Similarly, in trophically structured communities composed of species with comparable dispersal patterns due to strong oceanographic coupling, trophic cascades can turn what would be a net “source” population in a single-species metapopulation framework into a net “sink” population once species interactions are accounted for in a metacommunity context (White and Samhuri 2011). Designing reserve networks for equilibrium metacommunities thus requires a community-level trade-off: One can promote the abundance and persistence of one trophic level, but only at the cost of another. Altering the spatial coupling by varying the spacing of reserve networks can dampen this community-level trade-off or tilt the balance towards either trophic level, but it cannot abolish it completely and simultaneously benefit both trophically coupled species.

In nonequilibrium metacommunities, this community-level trade-off is avoidable because cross-scale ecological feedbacks between local population fluctuations and dispersal create patterns of abundance (or patchiness) at large spatial scales (Fig. 1). By generating this separation of scales between ecological processes (dispersal) and patterns (distribution of abundance), these cross-scale ecological feedbacks spatially decouple the intraspecific

benefits of connectivity from the interspecific costs of trophic cascades. Networks that exploit this separation of scales by using the extent of patterns (i.e., the extent of patchiness) as the size and spacing of reserves are thus able to maximize the abundance and persistence of both trophically coupled species (Figs. 3 and 4). Overall, this suggests that cross-scale ecological feedbacks between local dynamics and dispersal have critical implications for the spatial management of trophically and spatially coupled communities via reserve networks.

Adopting a metacommunity rather than a metapopulation perspective also has strong consequences for designing reserve networks that can address both conservation and fishery goals. Although reserve networks based on the extent of patchiness are able to maximize total prey yield, they are never predicted to increase the total yield of the predator because strong trophic cascades within reserves reduce prey spillover (and thus predator abundance) in unprotected areas where harvesting mainly occurs (Fig. 3). However, when trophic coupling is relatively weak between the predator and its prey (e.g., generalist predator; see Appendix A), reserve networks based on the extent of patchiness can simultaneously maximize the (1) global mean abundance, (2) persistence, and (3) total yield of both the predator and its prey, and thus optimally satisfy both conservation and fishery goals (Appendix A: Table A2 and Figs. A6–A7). Hence, the trade-off in the design of reserve networks needed to optimally achieve conservation or fishery objectives in metapopulation contexts (Hastings and Botsford 2003) disappears for (weakly) trophically structured metacommunities (Appendix E). A shift from (meta)population to (meta)community and (meta)ecosystem approaches (Mangel and Levin 2005, Baskett et al. 2007, McLeod and Leslie 2009) is thus critical for designing reserve networks that can simultaneously address both conservation (maximize abundance) and fishery (maximize yield) objectives.

#### *Managing uncertainty in a variable world*

*The paradox of predictability.*—Predicting and managing the abundance of marine species can be extremely difficult due to the strong temporal variability of natural populations and the amplifying effect of fishing (Hsieh et al. 2006, Anderson et al. 2008, Shelton and Mangel 2011a). Reserve networks can reduce the uncertainty related to the assessment of species abundance, but because the effectiveness of reserves can be strongly dependent on accurate estimates of dispersal and connectivity, their use introduces a new source of uncertainty due to the limited information about the dispersal distance of most marine organisms (Botsford et al. 2001, 2009). Our understanding of dispersal in marine environments is relatively poor because organisms typically produce millions of tiny larvae that are difficult to track in space and time because they spend anywhere from days to weeks under the influence of

strong oceanographic currents before becoming competent and settling (Shanks et al. 2003). Quantifying dispersal can be especially onerous in coastal waters because chaotic coastal oceanographic currents can entrain larvae and lead to complex spatiotemporal patterns of connectivity between nearshore populations (Siegel et al. 2008). Although average connectivity can be approximated via simple dispersal kernels over multiple generations, annual connectivity patterns are highly variable in space and time (Siegel et al. 2008). Overall, this suggests that dispersal and connectivity in marine systems are inherently dynamic and unpredictable due to the chaotic nature of oceanographic currents. The unpredictability of connectivity may thus fundamentally limit the applicability of reserve networks whose effectiveness depends on accurate estimates of dispersal.

Our results show that the performance of reserve networks in equilibrium metacommunities (Fig. 2) and stochastically forced equilibrium metacommunities (Appendix E) is strongly dependent on reasonable estimates of dispersal distance. Even when the dispersal distance is perfectly known, reserve networks can only be configured to maximize the abundance of either the prey or the predator (but not both) because of strong trophic cascades in equilibrium metacommunities. However, in nonequilibrium metacommunities, the performance of reserve networks is dependent on knowledge about the extent of adult variability (i.e., patchiness; Fig. 3), a metric that is relatively easy to measure by applying geospatial statistics to existing data sets (Fig. 1), and not larval dispersal, which typically requires genetic analyses coupled with physical oceanographic models (e.g., White et al. 2010a). Furthermore, reserve networks based on the extent of patchiness are able to simultaneously maximize the abundance and persistence of both the prey and the predator. Hence, there exists a “paradox of predictability” whereby nonequilibrium metacommunities characterized by complex and unpredictable spatiotemporal patterns of abundance are easier to manage via reserve networks than equilibrium metacommunities exhibiting much simpler and predictable dynamics. These results suggest that being able to predict the spatiotemporal patterns of larval dispersal and adult abundance is neither necessary nor sufficient for designing effective reserve networks for nonequilibrium metacommunities. Thus, despite displaying unpredictable patterns of connectivity (Siegel et al. 2008) and abundance (Berkley et al. 2010) due to chaotic coastal currents, interconnected and dynamic marine communities may be manageable using simple, static reserve networks.

*Monitoring dynamic and interconnected communities.*—The natural variability of interconnected marine systems has strong implications for the implementation of successful management and monitoring programs. Current approaches are largely based on static metrics such as the maximum sustainable yield or the total

abundance of target species. However, in nonequilibrium systems, static snapshots of these metrics are less important than measuring their variability over time because changes in the latter can serve as early warning signs for impending catastrophic collapses due to environmental stochasticity (Scheffer et al. 2009). For example, fishing has been shown to induce a “double jeopardy” for exploited populations by both reducing the mean and elevating the temporal variability of species abundance (Hsieh et al. 2006). Hence, managers must keep track of both the mean and the temporal variability (e.g., coefficient of variation) of species abundance in order to assess the extinction risk of natural populations. Furthermore, because nonequilibrium systems typically undergo strong cyclical fluctuations, evaluations based on static metrics collected over a limited period may lead to erroneous conclusions about the true state of monitored populations and the effectiveness of recovery programs. Managing nonequilibrium systems will thus require a shift from static to dynamic metrics in order to provide a more complete and accurate assessment of the health of natural systems.

Calculating these dynamic metrics will require the kind of spatially and temporally replicated surveys that are regularly conducted prior to and following the establishment of reserves (Lester et al. 2009, Gaines et al. 2010). These types of spatiotemporal datasets could prove crucial for testing nonequilibrium theory and determining the drivers of population fluctuations in natural systems. The fundamental insights gained from these datasets regarding the causes of fluctuations could then be used to design better reserve networks that reduce the temporal and spatial variability of populations. Such mutually beneficial feedbacks between fundamental and applied research would foster a better understanding of the natural world and improve our stewardship of its invaluable resources.

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## SUPPLEMENTAL MATERIAL

### Appendix A

The effects of a type III predator functional response on the effectiveness of reserve networks (*Ecological Archives* A023-077-A1).

### Appendix B

The effects of harvesting on closed predator-prey communities with a type II functional response (*Ecological Archives* A023-077-A2).

### Appendix C

The effects of irregularly spaced reserve networks on metacommunities with a type II functional response (*Ecological Archives* A023-077-A3).

### Appendix D

The effects of reserve networks on the dynamics of nonequilibrium metacommunities with a type II functional response (*Ecological Archives* A023-077-A4).

### Appendix E

The effects of reserve networks on stochastically forced equilibrium metacommunities (*Ecological Archives* A023-077-A5).