Reciprocal feedbacks between spatial subsidies and reserve networks in coral reef meta-ecosystems

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Abstract. Top-down processes such as predation and herbivory have been shown to control the dynamics of communities across a range of ecosystems by generating trophic cascades. However, theory is only beginning to describe how these local trophic processes interact with spatial subsidies in the form of material (nutrient, detritus) transport and organismal dispersal to (1) shape the structure of interconnected (meta-) ecosystems and (2) determine their optimal management via reserve networks. Here, we develop a meta-ecosystem model to understand how the reciprocal feedbacks between spatial subsidies and reserve networks modulate the importance of top-down control in a simple herbivorous fish–macroalgal–coral system. We show that in large and isolated reserve networks where connectivity between protected and unprotected areas is limited, spatial subsidies remain largely confined to reserves. This retention of spatial subsidies promotes the top-down control of corals and macroalgae by herbivores inside reserves but reduces it outside reserves. Conversely, in small and aggregated reserves where connectivity between protected and unprotected areas is high, the spillover of spatial subsidies causes a reduction in top-down control of corals and macroalgae by herbivores inside reserves and an increase in the strength of top-down control outside reserves. In addition, we demonstrate that there is a trade-off between local and regional conservation objectives when designing reserve networks: small and aggregated reserves based on the extent of dispersal maximize the abundance of corals and herbivores regionally, whereas large and isolated reserves always maximize the abundance of corals within reserves, regardless of the extent of dispersal. The existence of such “conservation traps,” which arise from the fulfillment of population-level objectives within local reserves at the cost of community-level objectives at regional scales, suggests the importance of adopting a more holistic strategy to manage complex and interconnected ecosystems.

Key words: corals; dispersal; material transport; meta-ecosystem; reserve networks; spatial management; spatial subsidies; top-down control; trophic cascades

INTRODUCTION

Recent meta-analyses have shown that no-take marine reserves (areas protected from all destructive and extractive activities) can be powerful management tools because they tend to (1) increase the biomass and abundance of organisms within their boundaries (Halpern 2003, Lester et al. 2009) and (2) improve the yields of overfished species via spillover of adults and larvae into neighboring exploited areas (Roberts et al. 2001, Gell and Roberts 2003, Gaines et al. 2010). Although initial work suggested that marine reserves might not be effective for managing mobile species found in temperate regions, a recent global meta-analysis has shown that reserves established in temperate regions tend to have equivalent or stronger positive biological effects than those found in tropical regions (Lester et al. 2009). However, this mean tendency belies strong differences between individual reserves, with some exhibiting weak positive or even negative effects on critical biological metrics such as biomass and density (Lester et al. 2009). Despite this strong variation in individual performance, the overall potential of no-take reserves to fulfill both conservation and fisheries objectives across a range of tropical and temperate regions has prompted calls for the adoption of reserve networks to manage ecosystems interconnected by the movement of material (e.g., nutrients,
detritus) and organisms (i.e., meta-ecosystems; Loreau et al. 2003, Pikitch et al. 2004, McLeod and Leslie 2009). Such a strategic shift from the population biology of target species to the spatial ecology of entire communities is critical (Mangel and Levin 2005, Gouhier et al. 2013) because regional processes that mediate connectivity can have a large impact on the overall performance of reserve networks (Botsford et al. 2001, 2003, Gaines et al. 2010).

Theory suggests that for reserve networks to be effective, (1) reserve size has to be large relative to the scale of organismal dispersal to allow individual reserves to become self-sustaining via self-recruitment, or (2) the spacing of individual reserves needs to be small enough to maintain connectivity via organismal dispersal to promote network persistence (Botsford et al. 2001, 2003, 2009, White et al. 2010). Furthermore, the optimal size of individual marine reserves depends on the main objective of reserve networks (Hastings and Botsford 2003). Networks designed primarily to manage fisheries should be composed of small reserves in order to maximize spillover into exploited areas, whereas 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). Although the impact of organismal dispersal is well appreciated in metapopulations (Botsford et al. 2001, 2003) and metacommunities (Basket et al. 2007, White and Samhouri 2011, Gouhier et al. 2013), the joint effects of material transport and organismal dispersal on the optimal size and spacing of reserve networks for managing meta-ecosystems remains largely unknown.

Extending reserve network theory to meta-ecosystems is particularly important for marine environments because strong oceanographic currents promote the exchange of spatial subsidies such as material (e.g., nutrients, detritus) and organisms (e.g., propagules and adults) between geographical locations (Carr et al. 2003). Yet despite the importance of regional material transport and organismal dispersal, we are only beginning to appreciate how these processes interact with local species interactions to control the structure and optimal spatial management of meta-ecosystems (Gouhier et al. 2010, 2013, Gravel et al. 2010a, Massol et al. 2011). Filling this gap in our understanding is critical because increased spatial subsidies due to regional oceanographic or anthropogenic factors have been shown to affect the health and structure of interconnected ecosystems. For example, elevated levels of dissolved organic matter and detritus from terrestrial run-off can promote productivity at multiple trophic levels and alter the strength of trophic interactions in neighboring streams and estuaries (Polis et al. 1997, Cederholm et al. 1999, Smith et al. 1999). Similarly, by bringing cold and nutrient-rich waters from the deep ocean to the surface, coastal upwelling currents subsidize the base of marine food webs and alter the strength of local trophic and non-trophic species interactions (Menge 2000, Menge et al. 2003, Menge and Menge 2013). Such spatial subsidies can also influence the relative importance of local top-down vs. regional forcing on meta-ecosystem dynamics by promoting the strength of trophic cascades (Leroux and Loreau 2008), especially if the scales of material transport and organismal dispersal differ (Gravel et al. 2010b), as is the case in marine systems.

Despite traveling through the same medium, waterborne material and organisms can be transported over markedly different scales by oceanographic currents. Material such as inorganic nutrients or detritus may travel regionally for hundreds of kilometers via wind-driven currents and the ocean conveyor belt (Menge 2000), or they may be confined to relatively small scales by strong coastal fronts such as those found along the California Bight (Woodson et al. 2012). The spatial extent of organismal dispersal can be even more variable because it depends upon the complex interaction between organismal behavior, pelagic larval duration, water temperature, and oceanographic currents (Grantham et al. 2003, Kinlan et al. 2005, O’Connor et al. 2007, Jones et al. 2009). For instance, larvae may remain passive, akin to inorganic nutrients, at the onset of their development and travel far from their natal site via oceanographic currents before deploying active swimming behavior (Cowen et al. 2006). Alternatively, larvae may limit the spatial extent of their dispersal by returning to their natal sites via (1) vertical migration within the water column guided by olfactory cues (Gerlach et al. 2007) or (2) entrainment within local eddies (Lobel and Robinson 1986). Overall, these different scales of material transport and organismal dispersal are expected to have a strong impact on the structure of communities across scales, the relative importance of local vs. regional processes, and the spatial management of interconnected ecosystems via reserve networks (Gaines et al. 2010, White and Samhouri 2011).

Here, we use a mathematical model to understand how local top-down and regional processes interact to shape the structure and dynamics of a coral reef meta-ecosystem managed via reserve networks. Specifically, we model the interactions between corals, macroalgae, and herbivorous fish in a tropical marine meta-ecosystem. We focus on this system because previous work has identified (1) local top-down control via herbivory as a critical process for understanding the shift from coral to macroalgal dominance (Hughes 1994, Mumby et al. 2007) and (2) reserves as a key management tool for preventing macroalgal dominance and promoting the long-term persistence of corals (Mumby et al. 2006). Indeed, the reduction of herbivorous fish density due to overfishing combined with occasional but strong disturbances can allow macroalgae to outcompete corals for space (Mumby et al. 2007). By preventing overfishing, reserves can reduce
the abundance of macroalgae by increasing the density and grazing effects of herbivorous fish, which in turn, promote the recovery of corals (Mumby et al. 2006, 2007). However, little is known about how regional subsidies such as material transport and organismal dispersal between coral reefs can affect community structure and the effectiveness of reserves by modifying the strength of local top-down herbivory (Loreau et al. 2003, Gravel et al. 2010a,b). Hence, we use our model to determine how differential rates of material transport and organismal dispersal affect (1) the relative importance of local top-down and regional processes on the structure of ecosystems across scales, and (2) the optimal size and spacing of reserve networks.

**Methods**

**The meta-ecosystem model**

We developed a generic herbivore–macroalgae–coral meta-ecosystem model consisting of a set of $L = 200$ local ecosystems coupled in space via material transport and organismal dispersal (Fig. 1). Each local ecosystem $x$ consists of five compartments: herbivores ($H$), corals ($C$), macroalgae ($M$), detritus ($D$), and nutrients ($N$). The herbivores $H(x)$ in ecosystem $x$ die at rate $m_H$, are harvested at rate $h_H$, and consume macroalgae $M$ according to a saturating Type II functional response with attack rate $a$ and handling time $v$. The herbivores disperse to adjacent ecosystems at rate $d_H$ based on a Gaussian dispersal kernel $\kappa_H$. Corals $C(x)$ in local ecosystem $x$ die at rate $m_C$ and colonize empty space via larval recruitment, with larvae being produced at rate $r_C$ and dispersing from neighboring ecosystems $y$ according to a Gaussian kernel $\kappa_C$. Because corals obtain much of their resources from their association with symbiotic dinoflagellates (e.g., Stat et al. 2008), we assumed their larval production was not dependent upon the availability of nutrients. However, relaxing this assumption by modeling coral larval production as a saturating function of nutrient uptake yields the same qualitative results.

Macroalgae $M(x)$ in local ecosystem $x$ die at rate $m_M$, are consumed by herbivores at rate $a$, and colonize empty space via propagules, which (1) are produced according to a saturating (Monod) function of nutrient concentration with maximum growth rate $r_M$ and half-saturation constant $k$ and (2) disperse from neighboring ecosystems $y$ according to a Gaussian kernel $\kappa_M$. Macroalgae and corals thus compete for free space according to a simple lottery model (i.e., no competitive hierarchy; Mumby et al. 2007). Dead herbivores, corals, and macroalgae contribute to the detritus compartment, whose material is lost at rate $\gamma$ and recycled at rate $\varepsilon$ of material that is lost from the detritus compartment at rate $\gamma$. The nutrient compartment decreases due to loss at rate $\varepsilon$ and...
nutrient uptake by macroalgae at rate $r_M$. Nutrients are transported to neighboring ecosystems at rate $d_N$ based on a Gaussian kernel $\kappa_N$. These processes are modeled via the following set of integro-differential equations for each ecosystem $x$:

$$\frac{dH(x)}{dt} = \frac{aM(x)H(x)}{1 + aM(x)} - m_H H(x) - h_H H(x) - d_H H(x) + \int_{-\infty}^{\infty} d_H(y)\kappa_H(x-y)dy$$
$$\frac{dC(x)}{dt} = \left[ \int_{-\infty}^{\infty} r_C C(y)\kappa_C(x-y)dy \right] (1 - M(x) - C(x)) - m_C C(x)$$
$$\frac{dM(x)}{dt} = \left[ \int_{-\infty}^{\infty} r_M N(y)M(y)\kappa_M(x-y)dy \right] (1 - M(x) - C(x)) - m_M M(x) - \frac{aM(x)H(x)}{1 + aM(x)}$$
$$\frac{dD(x)}{dt} = m_M M(x) + m_H H(x) + m_C C(x) - \gamma D(x) - d_D D(x) + \int_{-\infty}^{\infty} d_D(y)\kappa_D(x-y)dy$$
$$\frac{dN(x)}{dt} = q - \varepsilon N(x) + f_D d_D(x) - \frac{r_H N(x)}{k + N(x)} M(x) - d_N N(x) + \int_{-\infty}^{\infty} d_N(y)\kappa_N(x-y)dy.$$

(1)

Each model compartment’s normalized Gaussian kernel is defined as

$$\kappa_i(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(x-x_0)^2}{2\sigma^2}}$$

where $\mu$ is the advection rate (mean) and $\sigma^2$ is the diffusion rate (variance). The herbivore, coral, and macroalgal compartments all disperse via the same Gaussian kernel with mean $\mu_i$ and variance $\sigma_i^2$. This type of kernel was used because it accurately depicts the dispersal patterns of marine organisms inhabiting the coastal ocean (Siegel et al. 2003). Material in the detritus and nutrient compartments is transported according to a Gaussian kernel with mean $\mu_i$ and variance $\sigma_i^2$. From herein, the transport of the nutrient and detritus compartments will be referred to collectively as “material transport.” The model equations (Eq. 1) were solved numerically using the Runge-Kutta algorithm in MATLAB (function ode45; MATLAB, MathWorks, Natick, Massachusetts, USA).

**Model parameterization, behavior, and sensitivity**

Because we wanted to model a generic herbivore–macroalgal–coral meta-ecosystem, our parameter values were not based on a specific set of species at a given location. Rather, we selected biologically plausible parameter values (e.g., growth > mortality for all biotic compartments) that allowed the model to reach a locally stable (interior) point equilibrium (i.e., where all compartments persist) for harvesting rates ranging from 0 to 0.8. Our choice of parameter values was constrained in order to avoid limit cycles due to the Type II functional response of herbivores and the logistic growth of macroalgae. We also constrained the parameter space to values that generated very low herbivore abundances in unprotected areas in order to simulate strong harvesting pressure. We then randomly selected parameter values within this restricted parameter space.

To complement this selection approach, we determined the robustness of our results to the parameter values by conducting a sensitivity analysis (Table 1). Specifically, we computed the sensitivity of the equilibrium of each state variable $V$ in the model (i.e., where $V$ represents $H$, $C$, $M$, $N$, and $D$) to each parameter $P$ by numerically computing all the partial

<table>
<thead>
<tr>
<th>Parameter, by model compartment</th>
<th>Description</th>
<th>Value</th>
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<tbody>
<tr>
<td>Herbivores ($H$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>Attack rate</td>
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</tr>
<tr>
<td>$\nu$</td>
<td>Handling time</td>
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<tr>
<td>$m_H$</td>
<td>Mortality rate</td>
<td>0.1</td>
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<tr>
<td>$h_H$</td>
<td>Harvesting rate</td>
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</tr>
<tr>
<td>$d_H$</td>
<td>Dispersal rate</td>
<td>0.1</td>
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<tr>
<td>Corals ($C$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r_C$</td>
<td>Colonization rate</td>
<td>5</td>
</tr>
<tr>
<td>$m_C$</td>
<td>Mortality rate</td>
<td>0.1</td>
</tr>
<tr>
<td>$d_C$</td>
<td>Dispersal rate</td>
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<tr>
<td>Macroalgae ($M$)</td>
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<td></td>
</tr>
<tr>
<td>$r_M$</td>
<td>Maximum growth rate</td>
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</tr>
<tr>
<td>$k$</td>
<td>Half-saturation constant</td>
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</tr>
<tr>
<td>$m_M$</td>
<td>Mortality rate</td>
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</tr>
<tr>
<td>$d_M$</td>
<td>Dispersal rate</td>
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<tr>
<td>Detritus ($D$)</td>
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<td></td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Loss rate</td>
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</tr>
<tr>
<td>$d_D$</td>
<td>Transport rate</td>
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</tr>
<tr>
<td>Nutrients ($N$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$q$</td>
<td>External input</td>
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</tr>
<tr>
<td>$f$</td>
<td>Recycling rate</td>
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<tr>
<td>$\varepsilon$</td>
<td>Loss rate</td>
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</tr>
<tr>
<td>$d_N$</td>
<td>Transport rate</td>
<td>0.1</td>
</tr>
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derivatives $\partial \bar{V}/\partial P$ (Chitnis et al. 2008). We then normalized each sensitivity value to obtain the proportional sensitivity or elasticity by multiplying by the parameter value $P$ and dividing by the equilibrium value of the state variable $\bar{V}$ (i.e., $(\partial \bar{V}/\partial P) \bar{V}$). A large positive (negative) sensitivity or elasticity indicates that increasing the parameter will cause a large increase (decrease) in the equilibrium value of the state variable (Chitnis et al. 2008).

**Implementing marine reserve networks**

We used the reserve network allocation scheme developed by Gouhier et al. (2013). Specifically, we implemented no-take marine reserve networks (i.e., no harvesting within reserves) across the meta-ecosystem using a periodic square wave function. The reserve network consisted of $L = 200$ sites with harvesting rate $h_H(x)$ for site $x$ along the coastline (Fig. 1B)

$$h_H(x) = \frac{\text{sign} \left[ \sin \left( 2\pi \phi \frac{x}{L} \right) \right]}{L} + \bar{h}_H$$

We varied the spatial harvesting rate $h_H(x)$ for herbivores while keeping the regional mean harvesting rate $\bar{h}_H = 0.4$ constant across the meta-ecosystem. The amplitude $\lambda = 0.4$ determines the difference in harvesting rate between uniformly spaced reserves (i.e., protected areas) and unprotected areas. The frequency $\phi$ determines the size and spacing (i.e., distance between the center) of the reserves. By keeping the regional mean harvesting rate constant, we modeled a conservative scenario whereby marine reserves do not reduce the overall harvesting rate $\bar{h}_H$. Instead, any reduction in harvesting within reserves is met with a commensurate increase in harvesting outside reserves (Gouhier et al. 2013). We set the percentage of protected coastline to 50% for all simulations presented here. This value falls within the 20–70% range advocated by both theoretical and empirical studies (e.g., Airame et al. 2003, Gaines et al. 2010). Our results also hold for percentages of protected coastline ranging 20–40% (see Appendix A).

We tested the effectiveness of 30 different no-take marine reserve designs ranging from networks of many small and aggregated reserves to a single large and isolated reserve. For each reserve design, we simulated the dynamics of a meta-ecosystem consisting of $L = 200$ sites for a total of 8000 time steps. From time step 0 to 5000, the simulations ran without reserves. Then, from time step 5001 to 8000, the simulations incorporated reserves. Only the last 2000 time steps of the simulations were analyzed in order to avoid transient dynamics (Gouhier et al. 2013). For each compartment, mean equilibrium abundance was assessed regionally (across the entire meta-ecosystem) and locally (within reserves vs. outside reserves) in order to determine the effectiveness of reserve networks in achieving conservation goals.

The mean equilibrium abundances were converted to percentage of change relative to baseline scenarios without reserves (i.e., spatially uniform harvesting rate $h_H(x) = \bar{h}_H = 0.4$) in order to measure the net effect of the spatial variation in harvesting (Gouhier et al. 2013).

**Quantifying the strength of top-down control**

To determine the effects of reserve networks on the strength of trophic cascades and top-down control in meta-ecosystems, we computed (log) response ratios regionally and locally (inside vs. outside reserves). Specifically, to quantify top-down control, we used the natural logarithm of the ratio of equilibrium macroalgal abundance ($LR$) in the absence ($\hat{M}_{H_0}$) vs. presence ($\hat{M}_{H}$) of herbivores $LR = \ln (\hat{M}_{H_0}/\hat{M}_{H})$. This metric has been used extensively in both empirical and theoretical studies to document the strength of trophic cascades (e.g., Shurin et al. 2002, Leroux and Loreau 2008), and is easy to interpret biologically since it represents the proportional change in macroalgal abundance due to herbivores. Hence, more positive (negative) values of $LR$ denote stronger (weaker) top-down control.

**Determining the effects of differential material transport and organismal dispersal**

To determine the effects of differences in the scale of material transport and organismal dispersal on the effectiveness of reserve networks, we (1) varied the ratio $\sigma^2_t/\sigma^2_d$ between the variance of the Gaussian kernel $\sigma^2_t$ describing dispersal and the variance of the Gaussian kernel describing transport, and (2) set the mean of both kernels to zero (i.e., $\mu_d = \mu_t = 0$). To model a suite of scenarios ranging from the small-scale dispersal of species exhibiting homing behavior (Jones et al. 2009) to the large-scale dispersal typically observed in species with long pelagic larval durations (Grantham et al. 2003, Siegel et al. 2003, O’Connor et al. 2007), we fixed the extent of material transport (i.e., the spatial neighborhood around a source ecosystem over which ~95% of the material is transported) to ~13% of the spatial domain by setting the variance of the Gaussian kernel $\sigma^2_t = 6.94^2$ and varied the dispersal to material transport ratio $\sigma^2_d/\sigma^2_t$ using the following values: {0.06, 0.25, 0.53, 0.81, 1.0, 1.28, 1.47, 1.75, 2.03}. These ratios correspond to the following organismal dispersal extent expressed in terms of the percentage of the spatial domain: {2%, 6%, 9%, 12%, 13%, 15%, 16%, 17%, 19%}.

We also simulated the effects of varying the scale of material transport on the effectiveness of reserve networks. To do so, we fixed the extent of organismal dispersal (i.e., the spatial neighborhood around a source ecosystem over which ~95% of the organisms disperse) by setting the variance of the Gaussian dispersal kernel.
to $\sigma_x^2 = 6.94^2$ and setting the material transport to dispersal scale ratio $\sigma_y^2/\sigma_x^2$ to the following values: \{0.06, 0.25, 0.53, 0.81, 1.0, 1.28, 1.47, 1.75, 2.03\}. These ratios correspond to the following material transport extent expressed in terms of the percentage of the spatial domain: \{2\%, 6\%, 9\%, 12\%, 13\%, 15\%, 16\%, 17\%, 19\%\}. Although we focused on the effects of the variance in organismal dispersal and material transport kernels (i.e., diffusion), our results also hold when we vary the means of the kernels to simulate marine meta-ecosystems experiencing strong advective currents (see Appendix B).

**RESULTS**

**The effects of top-down control and reserve networks in closed (meta-) ecosystems**

We begin by analyzing the behavior of a closed ecosystem to generate a baseline expectation in the absence of organismal dispersal and material transport. Doing so will allow us to more readily interpret the effects of regional processes and reserve networks in meta-ecosystems. In closed ecosystems, the equilibrium abundance of herbivores, corals, macroalgae, and the stock of nutrients/detritus are largely determined by top-down processes. Indeed, the equilibrium abundance of corals and macroalgae is most sensitive to herbivore parameters such as the harvesting, mortality, and attack rates (Fig. 2). Reducing the harvesting and mortality rates or increasing the attack rate of the herbivore decreases the abundance of macroalgae and increases that of corals due to reduced competition for space (Fig. 2B,C), which in turn, increases the nutrient stock due to reduced nutrient uptake by macroalgae (Fig. 2E). This classical trophic cascade thus demonstrates that in the absence of organismal dispersal and material transport, the structure of local ecosystems is largely determined by top-down herbivory.

In spatially managed and closed meta-ecosystems, Jensen’s inequality can be used to explain patterns of abundance at the regional scale because reserve networks alter the spatial distribution (i.e., the spatial variance) of the harvesting rate without affecting its mean value (Ruel and Ayres 1999). Specifically, 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, herbivore and coral abundance are both decreasing and decelerating functions of the harvesting rate (Fig. 3A,C). Hence, Jensen’s inequality predicts (and our simulations confirm) that increasing the spatial variance of the harvesting rate by implementing reserve networks reduces the regional mean abundance across the entire meta-ecosystem because abundance increases less within reserves than it decreases outside reserves (Fig. 3B,D). Conversely, macroalgae abundance and nutrient stock are both accelerating functions of the harvesting rate (Fig. 3E,G). Thus, both regional macroalgal abundance and nutrient stock increase in the presence of reserve networks (Fig. 3F,H). This is an important result because it demonstrates that increasing the spatial variation of harvesting in closed meta-ecosystems can attenuate trophic cascades at the regional scale by simultaneously promoting nutrients and the macroalgae that consume them. Hence, in closed meta-ecosystems, nonlinear spatial averaging due to Jensen’s inequality trumps the effect of trophic cascades at the regional scale despite strong top-down effects occurring both inside and outside reserves.

Overall, these results suggest that when trophic cascades are attenuated at regional scales, spatial processes such as organismal dispersal and material transport that reduce the differences in abundance or nutrient stock between protected and unprotected areas (i.e., spatial variance) will (1) promote the regional abundance of herbivores and corals but (2) reduce the regional abundance of macroalgae and the regional stock of nutrients due to the effects of nonlinear spatial averaging.

**The effects of organismal dispersal on the optimal size and spacing of reserve networks**

For large and isolated reserve networks (i.e., size and spacing greater than extent of dispersal), we largely recover the results predicted by Jensen’s inequality and observed in closed meta-ecosystems (blue-colored lines in Fig. 4). Specifically, the regional abundance of corals and herbivores generally decreases relative to the baseline scenario of no reserves because the abundance of corals and herbivores generally decreases more within reserves than it falls outside reserves (Fig. 4A–F). Conversely, because macroalgae abundance generally increases more outside reserves than it decreases inside reserves, regional macroalgae abundance generally increases relative to the baseline scenario of no reserves (Fig. 4G–I). However, contrary to closed meta-ecosystems, regional nutrient stock is always 10–40\% higher than that observed in baseline scenarios of no reserves because reduced macroalgal abundance within reserves allows nutrient stock to rise faster within reserves than it falls outside reserves (Fig. 4J–L). The attenuation of trophic cascades at regional scales observed in closed meta-ecosystems is thus lost in open meta-ecosystems due to the exchange of spatial subsidies between protected and unprotected areas. This shows that spatial management via reserve networks can alter the strength of top-down control and the resulting distribution of important ecosystem properties such as nutrient availability across scales.

Smaller and more aggregated reserve networks (i.e., size and spacing smaller than or equal to the extent
Fig. 2. Proportional sensitivity (elasticity) of state variables representing the abundance or stock of (A) herbivores, (B) corals, (C) macroalgae, (D) nutrients, and (E) detritus for each parameter in a closed ecosystem (no organismal dispersal or material transport). Parameter definitions are provided in Table 1.
of dispersal) typically prove more beneficial for the regional abundance of herbivores and corals (Fig. 4A, D). Indeed, reserve networks based on the extent of dispersal maximize the spillover of coral larvae and herbivores from protected to unprotected areas. These spatial subsidies counteract the disproportional reduction in coral and herbivore abundance predicted to occur outside reserves based on Jensen’s inequality and the decelerating nonlinear response of coral and herbivore abundance to harvesting (Fig. 4C, F). Although the abundance of corals and herbivores within reserves is always higher than that observed in baseline no reserve scenarios (Fig. 4B, E), herbivore abundance reaches a maximum when reserve networks are based on the extent of dispersal because of increased reciprocal exchanges of spatial subsidies between protected and unprotected areas (Fig. 4B). Hence, by minimizing the differences in abundance between protected and unprotected areas that emerge as a result of spatial variation in harvesting, reserve networks based on the extent of dispersal maximize the regional abundance of both corals and herbivores.
The size and spacing of reserve networks has a significant impact on the strength of top-down control in meta-ecosystems (Fig. 4M–O). In small and aggregated reserve networks where greater connectivity...
promotes the spillover of spatial subsidies from protected to unprotected areas, the strength of top-down control decreases inside reserves and increases outside reserves with decreasing network size/spacing (Fig. 4N vs. O). When reserve networks are large and isolated, connectivity between protected and unprotected areas becomes limited, which leads to the accumulation of spatial subsidies within reserves and an increase (decrease) in the strength of top-down control inside (outside) reserves with increasing network size/spacing (Fig. 4N vs. O).

Despite experiencing a reduction in their abundance within protected areas in large and isolated reserve networks, herbivores exert more dominant top-down control by reducing the abundance of macroalgae and thus indirectly promoting the abundance of corals (Fig. 4E,H). Hence, despite reducing the abundance of herbivores, large and isolated reserve networks are more beneficial to corals in protected areas than small and aggregated reserve networks, regardless of the extent of dispersal (Fig. 4E). Overall, the mismatch between the response of corals and macroalgae (monotonic) vs. herbivores (unimodal) to the size and spacing of reserve networks is the product of the complex interplay between local top-down control and spatial subsidies.

*The effects of material transport on the optimal size and spacing of reserve networks*

In general, increasing the scale of material transport and fixing the extent of dispersal leads to the same qualitative results (Fig. 5). Reserve networks based on the extent of dispersal maximize herbivore and coral abundance (Fig. 5A,D) and minimize macroalgae abundance and nutrient stock regionally (Fig. 5G,J). Large and isolated reserve networks maximize the abundance of corals and minimize the abundance of both macroalgae and herbivores within protected areas (Fig. 5B,E,H). Herbivores are able to compensate for this reduction in abundance by exerting greater top-down control of macroalgae (Fig. 5N). Although increasing the scale of material transport does not affect the optimal size and spacing of reserve networks, it does alter the quantitative patterns of abundance regionally, inside and outside reserves. Specifically, by promoting the exchange of spatial subsidies from protected to unprotected areas, increasing the scale of material transport reduces the nutrient stock regionally and within reserves (Fig. 5J,K), but increases macroalgae and the herbivores that consume them regionally and outside reserves (Fig. 5A,C,G,I). The increased abundance of macroalgae regionally and outside reserves leads to a concomitant reduction in coral abundance due to greater competition for space (Fig. 5D,F).

The magnitude and spatial distribution of the quantitative changes in response to increased material transport are largely predictable based on the strength of top-down control. Indeed, because top-down control is always greater inside than outside reserves (Fig. 5N vs. O), increasing the scale of material transport has a muted effect on the abundance of corals and macroalgae within protected areas (Fig. 5E,H). This is because any increase in nutrient availability is taken up by macroalgae (Fig. 5K) and then rapidly converted to herbivore biomass (Fig. 5B). However, outside reserves where the strength of top-down control is limited, increasing the scale of material transport leads to stronger quantitative responses. Specifically, the greater exchange of nutrients from protected to unprotected areas due to increased material transport causes macroalgae to increase and corals to decrease because of greater competition for space (Fig. 5F,I), particularly in large and isolated reserve networks where top-down control is at its weakest (Fig. 5O). Overall, these results suggest that although the scale of material transport modulates the relative effectiveness of reserve networks, it does not alter their optimal size and spacing.

**DISCUSSION**

We have shown that spatial subsidies in the form of organismal dispersal and material transport can generate dramatic feedbacks that determine the strength of trophic cascades and the optimal size and spacing of reserve networks for managing meta-ecosystems. These reciprocal feedbacks can lead to unexpected changes in meta-ecosystem functioning and mismatches in the response of trophically coupled species that, when unaccounted for, can lead to hidden “conservation traps” whereby local population-level conservation objectives are fulfilled at the cost of more desirable regional community-level objectives. Hence, adopting a more holistic framework that integrates processes across scales would improve our ability to both understand and manage complex meta-ecosystems.

**Spatial subsidies mediate the strength of trophic cascades in meta-ecosystems**

Despite the recognition that natural ecosystems are inherently shaped by processes operating at multiple spatial scales, local patterns of abundance and diversity have historically been linked to local abiotic and biotic factors. Only relatively recently has spatial ecology emphasized the importance of feedbacks between local and regional processes for understanding ecological patterns and ecosystem function across scales (Loreau et al. 2003, Leibold et al. 2004, Holyoak et al. 2005, Massol et al. 2011). One of the most prominent empirical examples of such feedbacks is the critical role that the supply of marine material plays in determining the structure and dynamics of terrestrial communities.
Fig. 5. The effect of varying the extent of material transport on the mean abundance of herbivores, corals, macroalgae, and nutrient stock regionally (mean across entire meta-ecosystem; first column; A, D, G, J), inside reserves (second column; B, E, H, K), outside reserves (third column; C, F, I, L), and the strength of top-down control (M–O) for networks with different sizes and spacing. The x-axes depict the size/spacing of reserve networks as the percentage of the total coastline. The extent of dispersal was fixed at 13% of the spatial domain. The values on the y-axes are expressed as the percentage of change relative to the baseline scenario of no reserves represented by the black dashed line.

on isolated islands (reviewed by Polis et al. 1997). Building on these cross-ecosystem exchanges, Leroux and Loreau (2008) showed that increased allochthonous inputs from a donor system tended to strengthen top-down control and trophic cascades in a single recipient ecosystem regardless of its structure or the trophic level at which the allochthonous inputs arrived (Leroux and Loreau 2008). This led the authors to
suggest that ecosystems that receive greater levels of allochthonous inputs tend to exhibit stronger trophic cascades.

Our work extends these results by explicitly considering how reciprocal regional feedbacks mediate the strength of trophic cascades in spatially managed meta-ecosystems. In the absence of connectivity (either material transport or organismal dispersal), we showed that trophic cascades become attenuated at the regional scale, as adjacent trophic levels increase in response to greater spatial variance in harvesting generated by the establishment of reserve networks. This attenuation at regional scales is particularly surprising because trophic cascades occur both within and outside reserves, with adjacent trophic levels responding in opposite ways to spatial variance in harvesting. Hence, without connectivity, the relationships between adjacent trophic levels and the strengths of trophic cascades observed locally (i.e., within or outside reserves) are not maintained at regional scales due to the effects of nonlinear spatial averaging. However, restoring connectivity between ecosystems generates strong and matching trophic cascades at local and regional scales.

Overall, the increased exchange of material or organisms between ecosystems strengthens local and regional trophic cascades. The high connectivity of marine ecosystems may thus explain their tendency to exhibit stronger trophic cascades than terrestrial ecosystems, which are typically characterized by relatively low levels of connectivity (Shurin et al. 2002). Our results also demonstrate that more complex spatial models that explicitly account for connectivity between ecosystems are critical for correctly predicting the strength of trophic cascades across scales.

Using spatial management to control the distribution of trophic cascades

Although the establishment of reserves has a tendency to promote the abundance of species within their boundaries, some species experience clear and pronounced declines (Halpern 2003, Lester et al. 2009). These reductions in abundance can often be attributed to the strengthening of antagonistic trophic and competitive interactions following the reduction of fishing-induced mortality in species that typically occupy top trophic levels (reviewed by Baskett et al. 2007). Such reductions in abundance can have a negative impact on the performance of reserves, especially if the species experiencing declines are critical for achieving commercial or conservation objectives.

Our results demonstrate that the reduction in abundance of target species due to trophic cascades can be controlled by altering the size and spacing of reserve networks. Indeed, by maximizing connectivity among protected sites within individual reserves, networks of large and isolated reserves maximize the strength of trophic cascades within their boundaries. Conversely, by maximizing connectivity between protected and unprotected sites, networks of small and aggregated reserves maximize the strength of trophic cascades beyond their boundaries. Hence, the size and spacing of reserve networks can be used to both predict and control the spatial distribution of trophic cascades across meta-ecosystems. These predictions have important implications because they suggest that one must consider both the direct and indirect effects of connectivity when designing reserve networks.

Although the direct effects of connectivity on the effectiveness of reserve networks are well known for metapopulations (Botsford et al. 2001, 2003, Hastings and Botsford 2003), the indirect effects of connectivity on the strength and the distribution of trophic cascades only emerge in metacommunity and meta-ecosystem frameworks that explicitly model species interactions across scales. The inclusion of such species interactions can have profound impacts on reserve design principles. For instance, metapopulation-based approaches suggest that connectivity largely determines the ability of reserve networks to maximize conservation or commercial objectives (Botsford et al. 2003, Hastings and Botsford 2003, Sale et al. 2005, Gaines et al. 2010). Specifically, networks that seek to maximize commercial objectives should be composed of small reserves in order to increase connectivity between protected and unprotected areas and thus promote the spillover of adults or larvae beyond their boundaries. However, networks that seek to maximize conservation objectives should be composed of large reserves in order to increase connectivity between protected areas and thus increase the retention of adults or larvae within their boundaries.

In metacommunities where both the predator and the prey are harvested, the effect of connectivity on trophic cascades can significantly alter these guidelines (Goughier et al. 2013). Indeed, networks of small and aggregated reserves based on the extent of dispersal maximize the regional abundance of the predator but minimize the regional abundance of the prey because of strong trophic cascades within reserves. Conversely, networks of large and isolated reserves maximize the regional abundance of the prey but minimize the regional abundance of the predator by reducing the strength of trophic cascades. Hence, connectivity’s indirect effects on community-level processes such as trophic cascades can trump its direct population-level effects when determining the optimal size and spacing of reserve networks for spatially coupled sets of interacting species. These results largely hold for more complex (meta) communities that range from competitive guilds to keystone modules (Baskett et al. 2007).
Although we did not include predators in our model, the indirect effects of connectivity on community-level processes observed in predator–prey metacommunities (Gouhier et al. 2013) largely carry over to coral reef meta-ecosystems. Indeed, we showed that at the regional scale, corals and herbivores benefit the most from small and aggregated reserves based on the extent of organismal dispersal that maximizes both spillover and the strength of trophic cascades, whereas macroalgae benefit the most from large and isolated reserves that minimize the strength of trophic cascades. In this case, the same optimal reserve network can be used to simultaneously (1) promote the abundance of target species such as herbivores and corals and (2) reduce the prevalence of macroalgae.

Critically, the optimal size and spacing of reserve networks for achieving both goals does not depend on the extent of material transport. The minimal impact of material transport is likely due to the strong top-down control in this system, which rapidly converts nutrient supply into herbivore biomass. Variation in the extent of material transport would likely be much more important in systems characterized by limited nutrient availability or weak top-down control (e.g., donor-controlled systems). Overall, our results suggest that the extent of connectivity and the trophic position of target species jointly determine the optimal size and spacing of reserve networks. Hence, managing species that occupy higher trophic levels in terrestrial ecosystems characterized by low levels of dispersal and high levels of self-recruitment (Carr et al. 2003) would require networks of small and aggregated reserves that match the limited extent of connectivity.

We assumed that all species disperse according to identical and spatiotemporally homogeneous kernels. However, there is mounting evidence that dispersal varies across species (Kinlan and Gaines 2003) and spatiotemporally in marine environments due to complex oceanographic currents (Siegel et al. 2008). Such interspecific and spatiotemporal heterogeneity in dispersal could affect the optimal size and spacing of reserve networks by altering the spatial coupling between sites and the strength of trophic cascades within sites. Indeed, by dispersing over broader scales, species occupying higher trophic levels (Kinlan and Gaines 2003) could generate greater spillover effects and stronger trophic cascades. Conversely, spatiotemporal heterogeneity in dispersal could lead to a decoupling between species that could reduce spillover effects and weaken both trophic cascades and competitive displacement (Berkley et al. 2010). Understanding how these two sources of dispersal heterogeneity interact will be critical in order to design effective static reserve networks in an inherently dynamic world.

Avoiding conservation traps by adopting a meta-ecosystem-based management strategy

The dependence of reserve network performance on connectivity can be problematic in marine ecosystems because organisms typically disperse via strong and dynamic oceanographic currents that produce complex patterns of recruitment that can be difficult to predict at annual to decadal scales (Siegel et al. 2008). Uncertain connectivity patterns can thus limit the ability of reserve networks to address conservation or commercial objectives.

We have shown that irrespective of the extent of organismal dispersal (and thus connectivity), large and isolated reserve networks can achieve population-level conservation objectives by maximizing the abundance of corals within protected areas. Specifically, by increasing retention within protected areas, large and isolated reserves promote the strength of top-down control exerted by herbivores on macroalgae, thus allowing corals to reach high abundances within reserves. This suggests that even in situations where connectivity is poorly known, networks consisting of large and isolated reserves can still be used to meet certain conservation needs within protected areas. However, these local population-level objectives pale in comparison to the regional community-level objectives that become attainable once the extent of organismal dispersal is known. This is because large and isolated reserve networks maximize the abundance of corals within protected areas but minimize coral and herbivore abundance regionally, whereas small and aggregated reserves based on the extent of organismal dispersal maximize the abundance of both corals and herbivores regionally. Such conservation traps, which inadvertently lead to the fulfillment of population-level objectives within local reserves at the cost of community-level objectives at regional scales, demonstrate the importance of understanding connectivity and modeling reciprocal spatial feedbacks between protected and unprotected areas in order to design effective reserve networks for meta-ecosystems.

The existence of such reciprocal spatial feedbacks highlights the limitations of early reserve models. Indeed, reserve theory was initially based on worst case scenario models that treated unprotected areas as uninhabitable regions where species mortality was essentially infinitely high (reviewed by Baskett et al. 2007). Although informative, these models could not describe the regional dynamics that arose from the feedbacks between protected and unprotected areas. They thus focused on identifying optimal strategies for maximizing local (within-reserve) conservation objectives. However, we have shown that when we relax that assumption by modeling unprotected areas as extremely inhospitable (but not uninhabitable) locations for harvested species, the feedbacks between protected and unprotected areas can have dramatic effects on the optimal size and spacing of reserve networks needed to achieve local population- vs. regional community-level conservation objectives. Overall, these results suggest that a shift from population biology to spatial community ecology is critical.
to avoid such conservation traps and design effective reserve networks for interconnected ecosystems.

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Literature Cited


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