A reserve paradox: introduced heterogeneity may increase regional invasibility

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Abstract

No-take marine protected areas (MPAs) typically lead to population abundances that are much more spatially heterogeneous compared to conventional fisheries management. Higher abundances inside marine reserves may sustain regional populations through spillover of larvae, but this induced spatial heterogeneity can also have undesirable consequences. Displacing fishing effort into a smaller area may offset larval export from MPAs and locally reduce populations within fished areas by intensifying effort per area. Using a novel community perspective, we show that this displacement can increase the local and regional community's susceptibility to invasion by nonindigenous species. This study illustrates the types of multispecies trade-offs that are inherent to spatially explicit forms of management and highlights the pressing need to transition from single-species analyses to examining community responses to management schemes across broader biological and spatial scales. Our results demonstrate the potentially negative regional consequences of anthropogenically-driven spatial heterogeneities in aquatic and terrestrial systems.

Introduction

Aquatic species invasions are occurring worldwide at a staggering rate (Cohen & Carlton 1998; Ruiz *et al.* 2000), and pose one of the greatest threats to marine biodiversity (Grosholz 2002; Bax *et al.* 2003; Albins & Hixon 2008) with ecological, economic, and human health repercussions. It is clear that marine protected areas (MPAs, also referred to simply as "reserves") are not immune to bioinvasions (Simberloff 2000; Byers 2005; Klinger *et al.* 2006), despite the conjecture that more diverse marine communities may be less susceptible to invasion (Stachowicz *et al.* 2002). However, it is uncertain whether MPAs may play a role in hindering or facilitating the spread of introduced species on a broader regional scale. It is critical to address whether MPAs can enhance stocks of desirable native species and simultaneously inhibit the establishment of potentially invasive exotics, or instead are likely to benefit *both* native and invasive species.

In the recent scientific literature and resource management community, MPAs have been touted as a management tool with potentially less downside for the fishing industry compared to more traditional catch and effort restrictive schemes. This judgment comes from simple single-species models (see reviews in Gerber *et al.* 2003; Pelletier & Mahevas 2005; Pelletier *et al.* 2008) and empirical assessments based on the distribution of species across MPA boundaries (e.g., Halpern 2003; Kaunda-Arara & Rose 2004; Claudet *et al.* 2008). Here, instead, we use a model to focus on the interplay between management and heterogeneity in a multispecies context. The insights will not only be informative for studies of marine reserves, but will also tie into more general ecological questions pertaining to the impact of space on the dynamics of interacting species.

Numerous studies of marine reserves have highlighted important differences between spatial redistribution of effort (as with MPAs) and spatially homogeneous reductions in fishing pressure through conventional forms of fisheries regulations such as catch quotas, size limits, and gear regulations (Roberts *et al.* 2005). For all but the most mobile species, the establishment of no fishing zones is

likely to cause more spatially heterogeneous distributions of harvested species than conventional management. This can be a desirable outcome, creating local "source" stocks inside MPAs to maintain population persistence and replenish fished "sinks" outside reserve boundaries. However, the overall impact of MPAs will depend on population exchange across their boundaries (Hastings & Botsford 1999), and how fishing effort is redistributed after reserve establishment (Mangel 1998; Halpern *et al.* 2004; Byers & Noonburg 2007; Kellner *et al.* 2007).

Recent theoretical and empirical studies indicate that predictions from single-species models may be misleading in a community context because they ignore multispecies interactions (Micheli *et al.* 2004b). For example, Micheli *et al.* (2004a) and Baskett *et al.* (2006, 2007a) show that inclusion of predator–prey interactions may substantially change predictions about reserve efficacy compared with estimates from single-species models. Their work showed that accounting for species interactions across reserve boundaries, under certain circumstances, predicts reduced reserve effectiveness from both a conservation and fisheries standpoint because one or both trophic levels may incur negative consequences from spatial protection measures. Recent observations have also documented changes in fish assemblages both inside and outside MPAs (e.g., Guidetti 2007; Watson *et al.* 2007). These studies reveal that including trophic structure and dynamics may change predictions of reserve efficacy and that a more complete picture of the community can shed light on potential advantages and shortcomings of MPAs as long-term ecosystem-based tools.

The spread of marine invasive species is accelerating globally, but few empirical studies have explicitly addressed this threat in the context of marine reserves. One example is the 45-year documentation of an introduced Australasian barnacle spreading into Ireland's Lough Hyne Marine Nature Reserve and becoming a dominant and widespread species throughout Europe's coastal waters (Lawson *et al.* 2004). Byers (2005) investigated potential mechanisms driving the increased density of a heavily harvested nonindigenous clam (*Venerupis*

philippinarum) inside reserves, when the native confamilial *Protothaca staminea* did not respond to reserve protection. Whitfield *et al.* (2007) addressed the need to assess potential reserve locations based upon the burgeoning invasive lionfish population (*Pterois volitans*) in the Atlantic Ocean and suggested that their rapid establishment "may be due in part to resource availability that results from over-fishing of potential competitors such as groupers." This Indo-Pacific carnivore can also have substantial negative impacts on the recruitment of native fishes (Albins & Hixon 2008) and poses an extensive threat to coral reef conservation efforts throughout the eastern United States and Caribbean, but data on which to base management decisions are almost nonexistent. Furthermore, the theoretical basis needed to understand the issue of interaction between invasive species and MPAs has not been developed, and there is little predictive knowledge of how reserve efficacy might affect and be affected by this pervasive marine threat.

Whether MPA implementation will block or foster the invasion of nonindigenous species is fundamentally a question of species coexistence. Even if a native species would resist the invasion of a competitor under unfished conditions, the relative competitive ability of that native (and thus its resistance to invasion) will be reduced in fished areas. This heterogeneity in population density caused by protection will be amplified by an effect uniquely created by marine reserve establishment. As a reserve or MPA network is implemented or increases in size, fishing pressure outside its boundaries also increases given that some or all of the displaced effort moves into the remaining fished areas, which may make the regional community more susceptible to invasion by nonindigenous species (Figure 1).

Although reserves were not present, the role of over-fishing *per se* in permitting an invasive to enter a system is discussed by Daskalov *et al.* (2007). Reducing native populations in fished areas reduces the competitive effect on the invasive species, thus allowing the invasive species to gain a foothold from which it can spread.
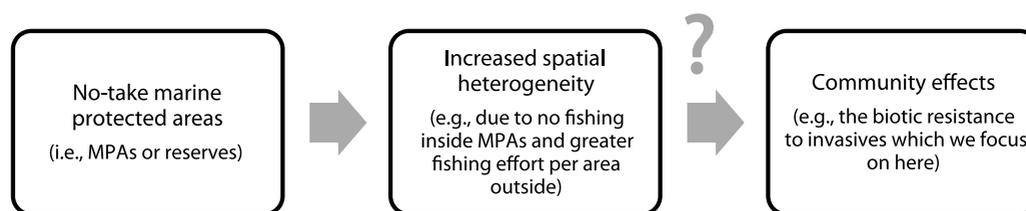

Figure 1 A schematic of the reserve paradox model hypothesis: Does displacing fishing effort make the community more or less susceptible to invasion by nonindigenous species? The models explored in this paper illustrate the extent to which management-induced heterogeneity in fishing effort and population levels can open up new opportunities for invasive species to become established.

There are general issues of how invasive species react to resource availability in a spatially heterogeneous environment (Melbourne *et al.* 2007). Widespread and abundant propagule dispersal may facilitate the regional spread of introduced species that initially take hold in fished areas (Hollebone & Hay 2007), especially if the nonindigenous species has a demographic advantage such as higher fecundity or lower mortality. Using a spatially implicit model, we demonstrate the importance of including species interactions when assessing marine reserve effectiveness and impacts. We determine the minimum reserve size needed to maintain persistence of a native fished species which is threatened by a competing exotic and discuss whether marine reserves can be effective tools in suppressing invasion by nonindigenous species.

Although our focus is on marine communities, the lessons and insights from MPAs should certainly apply to terrestrial systems as well (Parrish *et al.* 2003). In terrestrial communities, spatial heterogeneity can arise from preserving critical habitat or from anthropogenic activities (Gascon *et al.* 2000). These kinds of spatial heterogeneities can increase the threat of invasive species and our general approach can provide insight for other systems with spatial complexity.

Theoretical approach

We base our analysis on a Lotka–Volterra model of exploitation competition with no underlying spatial heterogeneity modified to include fishing mortality. Since we focus on equilibrium behavior, our results are not highly sensitive to the choice of functional form of density dependence. If fishing is spatially unrestricted (i.e., no MPA), population dynamics at each location within the region are described as

$$\frac{dn_i}{dt} = b_i n_i \left(1 - \frac{n_i}{k_i} - a_{i,j} \frac{n_j}{k_i}\right) - d_i n_i - q_i e_i n_i$$
$$e_i = E_i / L \qquad (1)$$

where n_i is the density of species i. The first term on the right-hand side of the equation includes three processes: density-independent production at a per capita fecundity rate b_i, recruitment, and density-dependent settlement. The interspecific competitive interaction strength is defined as $a_{i,j}$ and k_i is the carrying capacity reflecting a limiting resource (e.g., space). The second and third terms describe density-independent natural and fishing-induced mortality, respectively, where q_i is the species-specific catchability coefficient and e_i is the local fishing effort on that species. Note that fishing effort per unit area, e_i is dependent upon the total fishing effort, E_i, and

is homogeneously distributed across a region of habitat of length L. Competing species are assumed to overlap spatially within this region. As noted, for simplicity, all demographic and competitive parameters are homogenous across the region, but can be species specific.

Species coexistence can be altered by changes in mortality and other demographic rates as a result of fishing. For example, as fishing effort per area (E_i/L) increases or per capita fecundity (b_i) decreases, it becomes more difficult for a harvested species to persist in the face of competition.

With MPAs, we continue the homogeneity assumptions of habitat, species distributions, and fishing effort *within* each area. Larval dispersal is represented as a global pool and there is no postsettlement movement (as in Hastings & Botsford 2003), as would be appropriate for a wide range of marine species, including invertebrates, reef fish, and other territorial species, etc. Population dynamics inside and outside MPAs can be described by two coupled equations with subscripts R and U representing reserve and unprotected areas, respectively:

$$\frac{dn_{iR}}{dt} = b_i \left[\frac{n_{iU}(L - L_R) + n_{iR}(L_R)}{L}\right]$$
$$\times \left(1 - \frac{n_{iR}}{k_i} - a_{i,j} \frac{n_{jR}}{k_i}\right) - d_i n_{iR}$$
$$\frac{dn_{iU}}{dt} = b_i \left[\frac{n_{iU}(L - L_R) + n_{iR}(L_R)}{L}\right] \qquad (2)$$
$$\times \left(1 - \frac{n_{iU}}{k_i} - a_{i,j} \frac{n_{jU}}{k_i}\right) - d_i n_{iU} - q_i e_i n_{iU}$$
$$e_i = E_i / (L - L_R)$$

The first term on the right side of both equations includes the arrival of propagules from the larval pool that are produced in the reserve and unprotected areas, and is multiplied by the density-dependent settlement term. The final term in the equation for the dynamics in the unprotected area shows that as the total area protected from fishing, L_R, becomes larger, fishing effort is compressed into a smaller space and effort per unit area, $e_i = E_i/(L - L_R)$, becomes greater.

Results and discussion

As a first theoretical approach to evaluating the spatial heterogeneity induced by MPAs, we focus on the regional impact of MPAs on community invasibility. Our approach is biased toward persistence of the indigenous species (N), assuming that it is the superior competitor in its native range. Thus, the introduced species (I) cannot invade in the absence of fishing (i.e., $a_{I,N} \geq a_{N,I}$). Relaxation of this assumption favors invasion and successful establishment
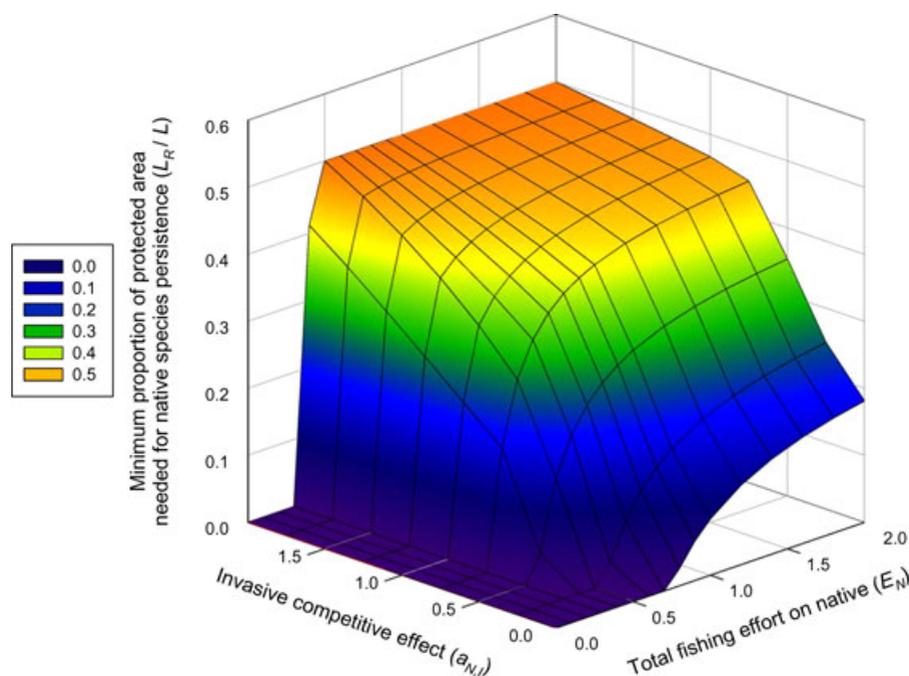
Figure 2 The minimum proportion of total area to be protected from fishing (L_R/L) that maintains persistence of a targeted native species (N) as a function of interspecific competition ($a_{N,I}$) and total fishing effort (E_N). The range of the interspecific competitive effect of the invasive species (I) on the native species ($a_{N,I}$) includes the intraspecific competition rate of 1. Values of $a_{N,I}$ greater than 1 mean that the competitive effect of the invasive species on the native is greater than the effect of the native on itself. Other parameter values used in Equation (2) are as follows: $L = 1, a_{I,N} = 2, b_N = b_I = 1, K_N = K_I = 100, d_N = d_I = 0.25, q_N = q_I = 1, E_I = 0$. Initial densities were set at $n_N = K_N, n_I = K_I/10$ and the model is evaluated at the stable equilibrium. The criteria for persistence requires that species density is at or greater than 1. This pattern qualitatively holds for a larger set of parameter values if $a_{I,N} \geq a_{N,I}$ and the native is demographically similar or superior (e.g., $b_N - d_N \geq b_I - d_I$).

of the introduced species and increases the likelihood of its local and regional dominance.

Like single-species models, this analysis illustrates that MPAs can be beneficial in sustaining native fished populations within their boundaries. The results reported here are based on a parameter set such that a reserve or reserve network encompassing 20% of the total region would sustain the native population in the absence of competition, an estimate that is within the range of existing single-species models which generally predict that 15%–33% of the coastline would need to be protected for population persistence under very intense harvesting pressure. The model predictions hold more generally for a larger parameter set and may underestimate the impact that management-induced spatial heterogeneity could have on community susceptibility if the invasive species is considerably demographically superior.

Given that an introduced species is not likely to be initially targeted at the beginning of its establishment phase due to low abundances and/or lack of experience with this resource, we first assume that the introduced

species is not fished (i.e., $e_I = 0$). We consider alternative scenarios with fishing on the introduced species below. As total fishing effort increases and/or the competitive impact of the introduced species on the native becomes stronger, maintaining population persistence of the native requires from 0% to 50% of the total region to be protected from fishing (Figure 2). Accounting for competition necessitates a larger reserve for persistence of native species than if there were no interspecific interactions (also see Baskett *et al.* 2007a).

Even with larval spillover from the reserve, compressing effort into a smaller area can locally reduce native populations within fished areas by intensifying effort per area. Thus, MPAs may in reality facilitate bioinvasions and invasive coexistence by increasing resource availability in unprotected areas, thereby providing opportunities for invasion by nonindigenous species into fished areas. This initial establishment and local dominance outside reserve boundaries can then allow the invader to seed the larger region with its propagules. Whether the targeted population represents a single species or an assemblage of indigenous fished species in a single functional
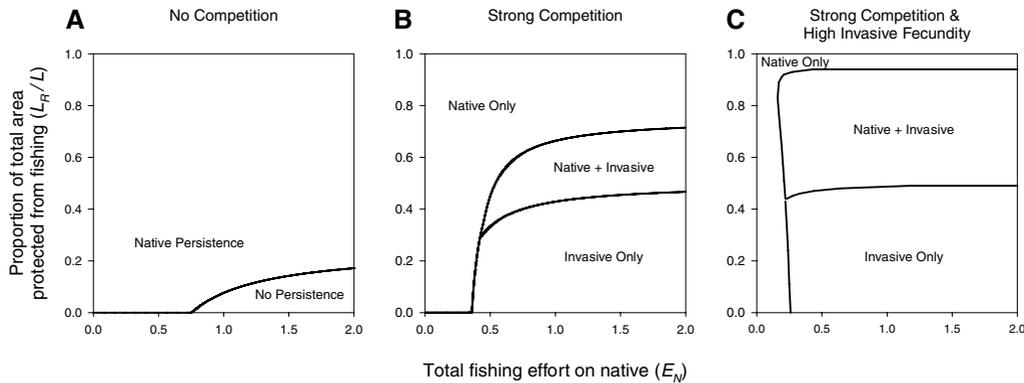
Figure 3 Persistence of native and invasive species as a function of total fishing effort on the native (E_N) and the proportion of total area protected from fishing (L_R/L). Parameter values for each panel are the same as those used in Figure 2 unless otherwise indicated. (A) No interspecific competition ($a_{I,N} = a_{N,I} = 0$), so persistence of the native species is independent of the invasive species' existence. (B) Strong interspecific competition favoring the native species ($a_{I,N} = 2, a_{N,I} = 1$). (C) Strong interspecific competition as in B plus high invasive fecundity rate ($b_I = 5, b_N = 1$). These patterns are qualitatively similar for a broader set of parameter values when the species trade-offs are competitive dominance of the native (B) and a demographic advantage of the invasive (C).

group, a key point of this model is that by reducing native population densities, fishing lessens the intensity of competition for limiting resources. As a result, coexistence of native and introduced species is more likely under MPA management schemes (Figure 3). Furthermore, this increased susceptibility to invasion is a robust result, not depending upon 100% of the effort being displaced. A high (much higher than any existing or proposed reserve and presumably unrealistic) proportion of the total area would need to be protected from fishing in order to inhibit bioinvasions both within MPA boundaries and regionally (Figure 3B). In a worst-case scenario when invasive species are demographically superior (e.g., higher fecundity rates or lower mortality), implementation of an MPA can change a native dominated system into one with only the invasive (Figure 3C), an effect we call the "reserve paradox." This reserve paradox is a consequence of the negative impact of the spatial heterogeneity induced by shifting fishing effort to outside the MPA. These patterns are qualitatively similar for a broader set of parameter values when the species trade-offs are competitive dominance of the native (Figure 3B) and a demographic advantage of the invasive (Figure 3C).

It is important to distinguish between the nature of species invasions under two types of management regime. With spatially unrestricted fishing (conventional management), the native, a strong competitor, is able to exclude the exotic until fishing effort becomes too high at which point the region becomes solely occupied by the introduced species. Thus invasion is tantamount to elimination of the native species. This is not the case with MPA management, under which the native species may persist inside reserves while the invasive gains a foothold in

fished areas of low native density. The greater the demographic superiority of the invasive, the more pronounced the effects predicted here will be as the reserve size increases. Therefore, it is reasonable to predict that MPAs can provide conservation benefits to native species even when subjected to competitive pressures (Figure 3B), but it is unlikely that protected areas will simultaneously inhibit invasions.

As shown in more general models of competition in heterogeneous environments (Melbourne *et al.* 2007), coexistence criteria depend on the demographic and competitive differences between competitors across space, and relative mortality from fishing. Fishing either the native or invasive will clearly decrease that species' likelihood of persistence, but the predicted trend of increased coexistence with MPA implementation holds unless the invasive species is heavily fished (Figure 4), especially when it is demographically superior. Fishing the invasive species would increase the region of native persistence (shifting curves down and to the right in Figure 3B toward the curve in Figure 3A) and decrease the region of coexistence, but targeting the invasive is somewhat counteracted by the universal reprieve from fishing for all species within MPA boundaries (as discussed in Byers 2005). As the demographic superiority of the invasive species increases, increasing reserve size will make the reserve paradox effects predicted here more pronounced even if the invasive species is fished. Similarly, these results are qualitatively robust for many combinations of parameter values; the trade-off between competitive strength and demographic characteristics generally results in more scenarios of invasive coexistence than invader exclusion.
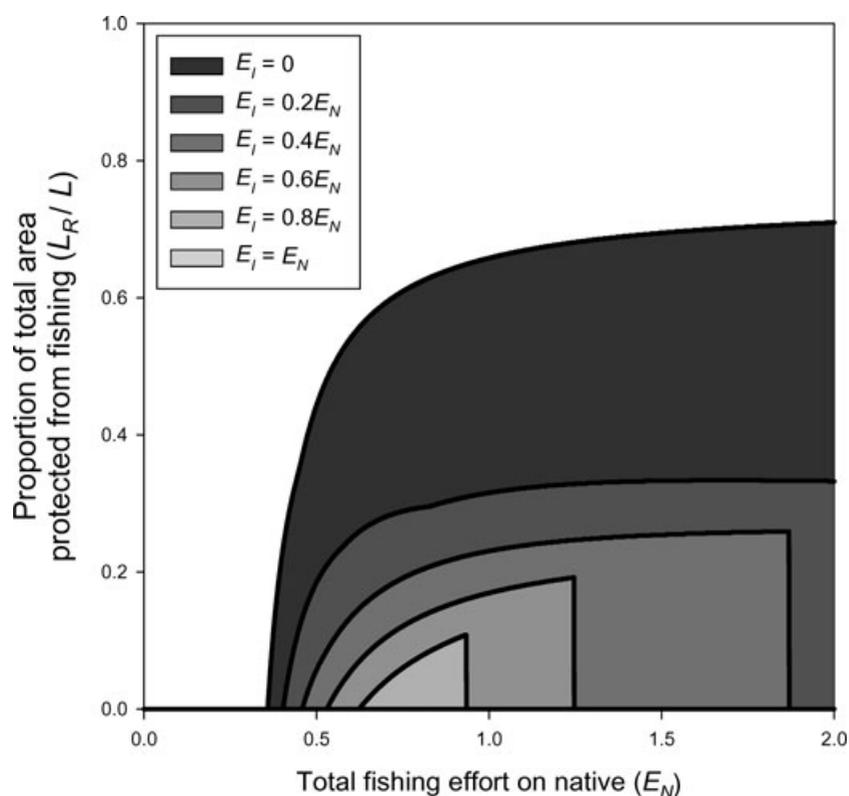
Figure 4 Persistence of the invasive species as a function of its total fishing effort (E_I) relative to the total fishing effort on the native (E_N) and the proportion of total area protected from fishing (L_R/L). For a given level of fishing effort on the invasive (E_I), the invasive species can persist in the shaded region below each curve, but is unable to invade when it is targeted at the same level as the invasive (i.e., when $E_I = E_N$). Parameter values are the same as those used in Figure 3B unless otherwise indicated.

Conclusions

Marine reserves provide blanket protection for numerous species within their boundaries but a growing number of multispecies studies make it clear that the regional persistence and abundance of targeted species will depend on changes in survivorship, fecundity, and movement rates of both target and non-target species, and in the trophic interactions between them. Marine reserves aim to shift fishing effort and are therefore likely to increase the spatial complexity of food web interactions; as such, it should be anticipated rather than unforeseen that both targeted and non-targeted species will be affected by the implementation of MPAs. We have shown that in the presence of fishing, the effect of marine protected areas on biodiversity can be complex and needs to be considered carefully. In some cases, an MPA will make the community more susceptible to invasion by introduced species, with concomitant negative long-term effects on the ecosystem. In light of this study, we advocate that MPA planning and monitoring should include explicit protocols for ecosystem-wide assessments, with particular attention to changes in invasive species presence, trophic structure, and community interactions. Particular attention needs to be paid to monitoring invasive species both inside and outside reserves since heavy fishing of invasive species outside MPAs may be an effective and important part of their control (Figure 4).

The "reserve paradox" we identify deserves further study and in general, greater attention needs to be paid to the community-level consequences of different fisheries management options (Guichard *et al.* 2004). Our efforts are an important step in this direction and these results illustrate the essential need to identify potential community-wide advantages and shortcomings of spatial management. Current modeling and empirical efforts primarily focus on single species and are narrow in scope, and therefore limit our ability to assess direct and indirect effects of MPAs outside their boundaries and regionally. However, there are emerging theories that reserves may cause undesirable effects, such as selective pressure on dispersal (Baskett *et al.* 2007b), or in the case studied here, increasing regional susceptibility to bioinvasions.

The issues raised here have also been raised in the context of terrestrial systems (Gascon *et al.* 2000; Parrish *et al.* 2003), where development and general human activities including agriculture may increase the likelihood of invasive species gaining a foothold. The interplay between preserving native or desirable biota while minimizing the number and impact of invasive species is a

much more general and broader question (Shea & Chesson 2002; Didham *et al.* 2005; MacDougall & Turkington 2005). Thus, the important issues raised here about the role of human activities in increasing spatial heterogeneity are likely to have impacts not only in the marine realm, but in much broader contexts as well.

Acknowledgments

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