Two invaders achieve higher densities in reserves

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ABSTRACT

1. Invasive species threaten marine biodiversity on a global scale.

2. To test whether marine reserves provide resistance to invading species, the abundance of two conspicuous invaders, a seaweed and an oyster, were measured inside marine reserves and in comparable areas outside reserves in north-western Washington State.

3. Densities of both invaders were significantly higher in marine reserves than in comparable unprotected areas outside reserves. Although the causal mechanisms have not yet been identified, differential rates of human harvest do not appear to be responsible for the patterns observed.

4. It is provisionally suggested that physical or biological aspects of the reserves themselves may directly or indirectly facilitate biological invasion.
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KEY WORDS: marine reserves; exotic species; biological invasion; *Crassostrea*; *Sargassum*

INTRODUCTION

Invasive species are widely recognized as important agents of global change (Vitousek *et al.*, 1997; Dukes and Mooney, 1999; Mack *et al.*, 2000). At their worst, invasive species are known to compete with and prey on native species (Mack *et al.*, 2000), hybridize with natives (Simberloff, 2001), alter natural disturbance regimes (Mack and D'Antonio, 1998) and dominate nitrogen and carbon cycles (Hall *et al.*, 2003). Moreover, recent evidence suggests that, once established, non-indigenous species can facilitate the establishment of subsequent invaders in a synergistic fashion (Levin *et al.*, 2002). As a result of these and other effects, non-indigenous species are a leading cause of biodiversity loss worldwide (Wilson, 1992; Vitousek *et al.*, 1996; Richter *et al.*, 1997; Wilcove *et al.*, 1998). Invaders pose serious problems for the management of native species and restoration of native ecosystems. Consequently, invasion biology has become a key area of ecological research, with a proliferation of recent studies addressing the topic. Despite this, growing numbers of new invaders and increasing rates of introduction have elevated the threat of

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invasion throughout ecosystems worldwide (Perrings *et al.*, 2002). This trend is likely to continue into the foreseeable future.

Some communities appear to be more resistant to invasion than others (Levine and D'Antonio, 1999; Stachowicz *et al.*, 1999; 2002; Naeem *et al.*, 2000; Kennedy *et al.*, 2002; Stohlgren *et al.*, 2002, 2003). However, a great deal of uncertainty regarding site- and community-specific resistance to invasion remains. For example, issues of both temporal and spatial scale have led to conflicting results in experimental versus correlational studies (D'Antonio *et al.*, 2004). Consequently, predictive capacity remains low and management decisions are often made on an ad hoc basis, even in relatively well-studied terrestrial systems.

The effect of reserves and protected areas on the success of invaders generally is not known. While terrestrial reserves often are highly invaded (Usher, 1988; MacDonald *et al.*, 1989), they tend to be substantially less invaded than areas outside reserves (Lonsdale, 1999). We know far less about the frequency and fate of invaders in marine reserves and protected areas, but it is apparent that marine reserves are not immune to biological invasion (Lawson *et al.*, 2004; Byers, 2005).

In the San Juan Archipelago of north-western Washington State, two conspicuous invaders (*Sargassum muticum* (Yendo) Fensholt and *Crassostrea gigas* (Thunberg 1793)) have increased in abundance and spread to new areas during the past decade. *S. muticum* was introduced to the region as a hitch-hiker in oyster shipments from the early or middle part of the last century (Scagel, 1956). The species has slowly expanded its distribution since that time. *C. gigas* was introduced from Japan early in the twentieth century and now dominates the commercial oyster industry in Washington State (Gordon *et al.*, 2001). Both *S. muticum* and *C. gigas* are perennials with lifespans exceeding several years; the two species differ considerably in nearly all other aspects of their life histories. Despite these differences, both have invaded other nearshore ecosystems in the Pacific and Atlantic Oceans, and both are known to displace native organisms and modify habitats, especially where they occur at high densities (Orensanz *et al.*, 2002; Britton-Simmons, 2004).

Field observations made by the authors over the past decade indicate that *S. muticum* and *C. gigas* recently have spread to marine reserves and to other sites in the San Juan Archipelago. Much of this spread has occurred since 1997. These observations motivated a census of *S. muticum* and *C. gigas* in reserves and in comparable areas outside reserves to determine whether a reserve effect could be detected. Protection provided to native populations within reserves might confer a detectable degree of resistance to invasion by either or both of these two non-native species. If this were the case, densities of *S. muticum* or *C. gigas* would be expected to be lower within reserves than in areas outside reserves.

METHODS

Reserves

Six regulatory research reserves (Point Caution, Point George, Yellow Island, Low Island, Argyle Lagoon and False Bay; Figure 1) were established in 1990 by the Washington Department of Fish and Wildlife to preserve native biological diversity, support scientific research and serve as undisturbed reference sites for areas not protected from extraction of biological resources (Murray, 1998). Accordingly, recreational and commercial removal of all species other than salmon and herring is prohibited within the reserves and terrestrial access is limited, although research is allowed with permission. The reserves vary in size, but all are comparatively small. The largest reserve (Point Caution) encompasses about 4 km of shoreline and the adjacent waters to 457 m offshore. The biological communities within these reserves are characteristic of the region, dominated by native species, and unimpacted by shoreline development other than low-density home-building (Klinger, unpublished data). Importantly, all reserve sites were relatively pristine at the time they were established; none have been highly disturbed or modified since then; and none are
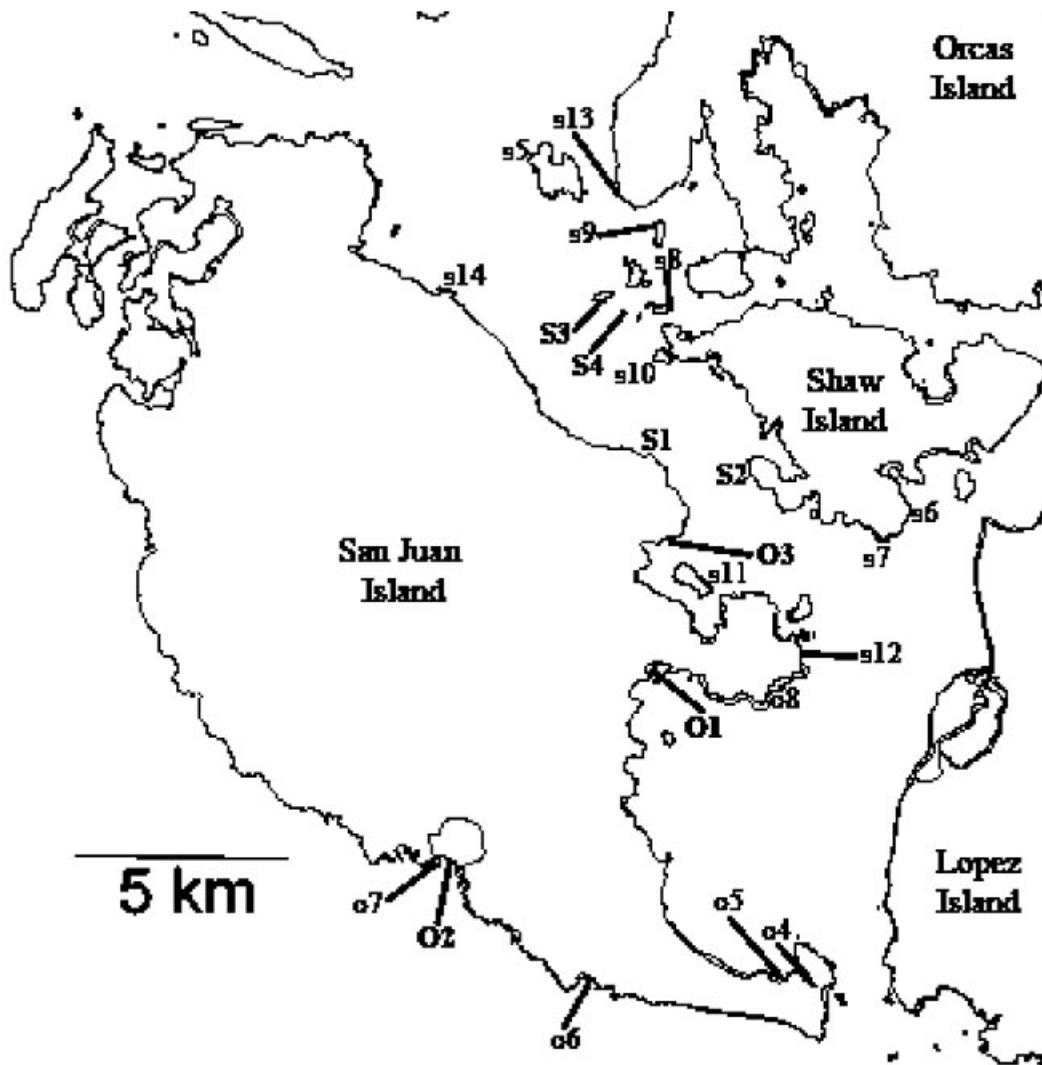
Figure 1. Study site locations in the San Juan Archipelago, Washington, USA. **S** = *Sargassum muticum* reserve site; s = *S.muticum* reference site. **O** = oyster reserve site; o = oyster reference site. Numerical order of site codes is arbitrary. See Tables 1 and 2 for corresponding place names and coordinates.

restoration or remediation sites. The establishment of these reserves pre-dates by several years the expansion of *S. muticum* and *C. gigas* into the sites.

Sargassum muticum

Four subtidal reserves and 10 subtidal sites outside reserves were sampled in June, 2002 for the presence and abundance of *S. muticum* (Table 1). To prevent bias in site selection, sample sites within and outside reserves were randomly chosen from a larger, predetermined pool of suitable sites. Suitable sites were defined as those containing physical habitat known to be appropriate for the recruitment and growth of *S. muticum* (Britton-Simmons, 2003), specifically, flat to moderately sloping rocky substrate, including cobble,

Table 1. Coordinates for reserve and reference sites sampled for presence and abundance of *Sargassum muticum*, and corresponding site codes used in Figure 1

Reserve site	Figure 1 code	Latitude	Longitude
Point Caution			
(San Juan Channel)	S1	48°33.720′ N	123°00.993′ W
Point George	S2	48°33.549′ N	122°59.306′ W
Yellow Island	S3	48°35.476′ N	123°01.867′ W
Low Island	S4	48°35.350′ N	123°01.585′ W
Reference site	Figure 1 code	Latitude	Longitude
Jones Island	s5	48°37.059′ N	123°03.280′ W
Squaw Reef	s6	48°33.032′ N	122°56.535′ W
Snag Point	s7	48°32.778′ N	122°56.954′ W
Cliff Island	s8	48°35.484′ N	123°00.728′ W
Reef Island	s9	48°35.711′ N	123°01.534′ W
So. Neck Point	s10	48°34.822′ N	123°01.023′ W
Brown Island	s11	48°32.216′ N	122°59.195′ W
Seal Cove	s12	48°31.547′ N	122°58.310′ W
Steep Point	s13	48°36.649′ N	123°01.604′ W
Mineral Point	s14	48°35.563′ N	123°04.645′ W

boulders, bedrock, or some combination of these, at depths of about 2 m below Mean Lower Low Water (MLLW). The presence of *S. muticum* was not a criterion for determining suitability. Suitable sites were identified by conducting snorkel surveys at (approximately) 50-m intervals along the full length of shoreline within each reserve, yielding a pool of three to six suitable sample sites within each reserve, from which a single sample site per reserve was then randomly chosen.

Outside reserves, a pool of 21 potential reference sites was identified using the same criteria and procedures described above. These reference sites were interspersed with the reserves, spanning a total distance of 9 km from north to south; adjacent sites were separated by a minimum distance of 0.8 km to avoid spatial overlap between replicate sites. The physical habitats and biological communities within the reference sites were highly similar to those in the reserve sites. Ultimately, 10 sites were randomly selected from this pool for use as reference sites.

Density and age class of *S. muticum* within each reserve and reference site were measured by sampling 10 randomly chosen 50×50 cm ($0.25 \, \text{m}^2$) plots along a 30 m transect. The total area sampled per site was identical ($2.5 \, \text{m}^2$ within both reserve and reference sites). The distance between plots along each transect ranged from 50 cm to 6 m. All sampling was conducted at a depth of 2 m below MLLW. Analysis of variance was used to test for differences in density of *S. muticum* between reserve and reference sites.

Crassostrea gigas

Three intertidal reserves and five reference sites on southern San Juan Island were sampled in July and August, 2001, for the presence and abundance of *C. gigas* (Figure 1 and Table 2). Because access to intertidal areas is restricted by private ownership in Washington State, a paired-sample design that required access to relatively few reference sites was used. In this design, each intertidal reserve was paired with one or two unprotected reference sites for purposes of comparison. Each reserve and its paired reference site(s) were selected a priori for similarity of physical attributes, including exposure, substrate type, and relief.

Within each site, sampling was restricted to areas of intertidal bedrock suitable for oyster settlement and growth. Oyster densities were estimated by counting all living oysters in large polygons up to $120 \, \text{m}^2$. The

Table 2. Coordinates for reserve and reference sites sampled for presence and abundance of *Crassostrea gigas*, and corresponding site codes used in Figure 1; paired reserve and reference sites are indicated

Reserve site	Figure 1 code	Latitude	Longitude	
Argyle Lagoon	O1	48°31.175′ N	123°00.768′ W	
False Bay	O2	48°29.433′ N	123°03.983′ W	
Point Caution				
(Beverton Cove)	O3	48°32.772′ N	123°00.780′ W	

Reference site	Figure 1 code	Latitude	Longitude	Paired reserve site
Fish Creek	o4	48°27.748′ N	122°58.198′ W	Argyle Lagoon
Third Lagoon	o5	48°27.761′ N	122°58.307′ W	Argyle Lagoon
Eagle Cove	o6	48°27.781′ N	123°01.966′ W	False Bay
Kanaka Bay	o7	48°29.380′ N	123°04.221′ W	False Bay
Pear Point	o8	48°31.110′ N	122°59.588′ W	Point Caution

size and shape of each polygon was determined by the size and shape of the rocky area being sampled. This method maximized the spatial extent of sampling on rocky substrates while avoiding interspersed areas of unconsolidated sediments and gravel. Within the same polygons, the first 100 living oysters (minimum sample size) were measured along their longest axis to provide an estimate of size–frequency distribution, except at Kanaka Bay and Eagle Cove, where all living oysters were sampled and fewer than 100 were found ($N = 70$ and 35, respectively).

Analysis of variance was used to test for differences in oyster density between reserve and reference sites. Size–frequency distributions were used to determine whether individuals originated from a single settlement event, or whether there was evidence of repeated recruitment over multiple years.

RESULTS

S. muticum was present in all four subtidal reserves and in seven of 10 sites outside reserves. *S. muticum* was significantly more abundant in reserves than in reference sites ($P = 0.05$; Figure 2). Large, reproductive adults were found at all sites where *S. muticum* was present. New recruits (< 1 yr old) and juveniles (1–2 yr old) were found in two of four reserves and three of seven reference sites, indicating that the presence of this species at these sites was not due to an isolated recruitment event. Although recruits and juveniles generally were less numerous than adults, recruits comprised 70% of the individuals counted in one reserve.

Crassostrea gigas was present in all three intertidal reserves and all five reference sites sampled; densities were significantly higher within reserves than outside them ($P = 0.05$; Figure 2). Multiple size (and by extension, age) classes were present (Figure 3), indicating that oysters have recruited repeatedly to these sites. All sites but one contained new recruits (< 30 mm), as well as intermediate-sized (50–100 mm) and large oysters (> 150 mm) two or more years old. A *post hoc* test of oyster densities among reference sites showed no significant difference between oyster densities at public-access sites where oysters may be harvested and at privately owned sites where owners report no human harvest of oysters (ANOVA, $P = 0.46$).

DISCUSSION

Marine reserves in the San Juan Archipelago were found to contain higher densities of two very different invaders, a subtidal seaweed and an intertidal oyster, than comparable unprotected areas outside reserves.
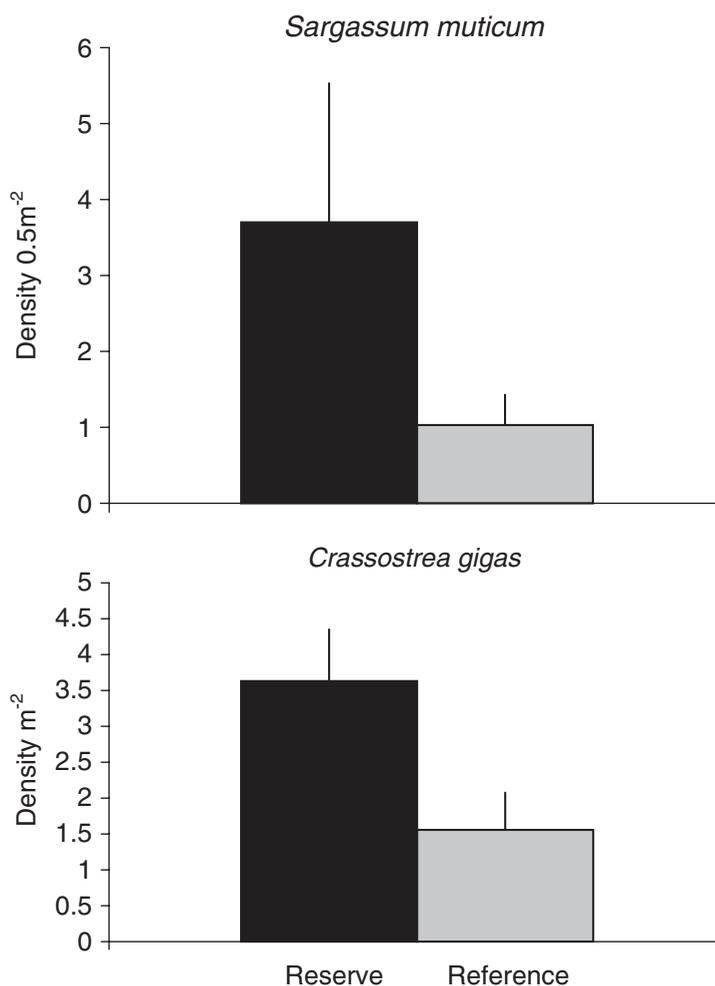
Figure 2. Average densities of non-indigenous species in reserves and reference sites. *Sargassum muticum* (upper panel): $N_{(reserve)} = 4$; $N_{(refrence)} = 10$. *Crassostrea gigas* (lower panel): $N_{(reserve)} = 3$; $N_{(reference)} = 5$. Differences between reserve and reference sites are significant (ANOVA, $P = 0.05$) for both species.

Populations of both species appeared to be viable within the reserves, based on abundance and on age structure inferred from size–frequency distributions. Size–frequency distributions of both *S. muticum* and *C. gigas* indicate that multiple recruitment events have occurred since the initial invasion of these sites, and the relatively high proportion of small size classes observed at some sites indicates that successful recruitment is continuing. These findings suggest either that the communities within these reserves are less resistant to invasion, or that intrinsic characteristic(s) of these reserve sites facilitate invasion by these two non-native species.

Several mechanisms could render reserves or their constituent communities more vulnerable to invasion than comparable unprotected sites. For example, restrictions on human harvest inside reserves could protect invaders from exploitation, producing higher densities within reserves. However, differences in human harvest do not appear to explain our results. *S. muticum* is not harvested anywhere in the archipelago. *C. gigas* occasionally is harvested locally for food, but this harvest occurs
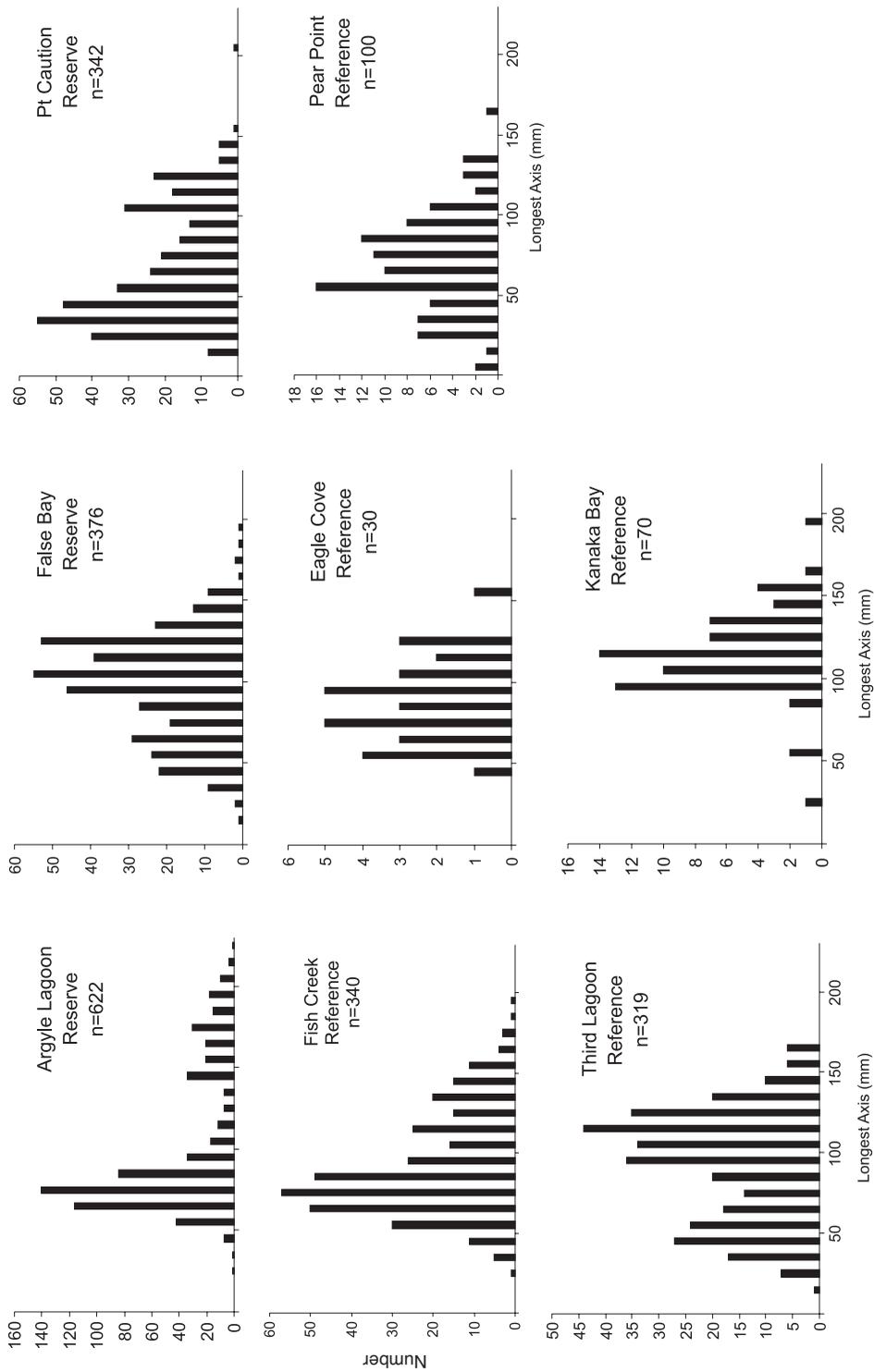
Figure 3. Size class–frequency distributions for *Crassostrea gigas* in reserve and paired reference sites in 2001. Individual size was measured as the longest axis of each shell. Top panel in each column corresponds to reserve site; lower panels in each column correspond to paired reference sites. Note differences in scale of *y*-axes.

almost exclusively in soft-sediment habitats where oysters are easily removed from the substratum (T. Klinger and D.K. Padilla, pers. obs.). Among the sites studied, oyster 'scars' (persistent remnant shells left behind when oysters are removed from rocky substrates) were rare, and were no more numerous inside reserves than at reference sites. Among living oysters, densities within reference sites did not differ between public-access sites where harvest is allowed and privately owned sites where the landowners do not, by their own admission, harvest oysters. These lines of evidence collectively indicate that differences in oyster densities between reserve and reference sites are not due to differences in the human harvest of oysters.

A second mechanism by which reserves might facilitate invasion is through altered trophic interactions. However, the direct effects of grazing or predation on *S. muticum* and *C. gigas* do not appear to explain the results reported here. Fish or invertebrate grazers that can regulate the abundance of adult *S. muticum* are unknown in this region and elsewhere. The Japanese oyster drill, *Ceratostoma inornatum*, which is predatory on *C. gigas* and which might be capable of regulating oyster populations, has never been recorded in repeated censuses of these study sites (Klinger, unpublished data), nor is it known to be present elsewhere in the archipelago. The indirect effects of altered trophic interactions on invasion success are more difficult to assess, and the findings reported here cannot be used to address the role of indirect trophic interactions in facilitating these invasions.

Species richness itself has been demonstrated to increase invasion rates in marine epibenthic communities by increasing the frequency of bare space (via mortality) and by increasing opportunities for associations with other preferred species (Dunstan and Johnson, 2004). However, there are no data at present to support this hypothesis for these sites, and other work (Stachowicz *et al.*, 2002) suggests that an opposite correlation between invasion and species richness would be expected.

Abiotic characteristics of these sites that are unrelated to their reserve status could render them favourable for establishment and spread of these two species. The reserves studied were designated for regulatory protection based on ownership of adjacent tidelands or uplands (Murray, 1998), rather than on physical, biological, oceanographic or ecosystem attributes. Although coarse physical attributes (exposure, substrate type, relief) appeared similar between reference and reserve sites, it is possible that other attributes (for example, temperature, nutrient availability or rates of propagule supply) favoured the establishment of *S. muticum* and *C. gigas* in reserves relative to surrounding sites. Elsewhere in the San Juan Archipelago, physical habitat structure has been demonstrated to mediate biotic resistance to invasion by the Asian clam, *Nuttallia obcurata*, leading to site-specific physical controls on invasion success and associated impacts (Byers, 2002). Other physical attributes (low salinity, high temperature and restricted circulation) appear to be responsible for the spread of the invasive barnacle, *Elminius modestus,* through a marine reserve in Ireland (Lawson *et al.*, 2004). If physical attributes that facilitate invasion are more frequent within reserves than outside them, then reserves are likely to be invaded more frequently than other sites.

It is important to recognize that invasion of marine reserves can be influenced both by characteristics intrinsic to individual sites and by those resulting directly from reserve status. Furthermore, processes that facilitate or inhibit invasion are likely to operate at different spatial scales (Stohlgren *et al.*, 1999). Whereas biotic interactions, such as the trophic interactions described above, are likely to operate on relatively small spatial scales, intrinsic processes such as propagule supply may operate on larger spatial scales (Levine, 2000). The net effect on the invasion process will depend on the magnitude of individual effects as well as their tendency to favour or inhibit invasions. For example, biotic interactions operating at a small scale could make species-rich reserve communities more resistant to invasion, but this effect might be overwhelmed by high rates of propagule supply characteristic of a particular site, yielding a net tendency towards invasion in that locale (Levine, 2000).

The generality of these findings cannot yet be evaluated. That two very different species — a subtidal alga and an intertidal mollusc — both were more abundant inside reserves than outside them lends

weight to these observations and suggests that these findings may have relevance beyond these two taxa at these six sites. If so, then elements of marine reserve design and management must address the potential problem of invasion facilitation. For example, high rates of larval delivery and exchange, both usually considered beneficial design attributes (Roberts, 1997; Allison *et al.*, 1998; Gaines *et al.*, 2003; Roberts *et al.*, 2003), have the potential to intensify propagule pressure and increase the vulnerability of marine reserves to biological invasion. Reserve sites chosen to maximize larval delivery will accumulate larvae of native and non-native species indiscriminately, thereby potentially facilitating invasion, and linkages between multiple reserves will facilitate spread if one or more sites becomes invaded by non-native species.

Similarly, site choice based on environmental factors (light, temperature, nutrients, exposure, substrate) favourable for native species could simultaneously enhance the survivorship and reproduction of non-native species once they have become established. Indirect effects of protection, for example the restoration of trophic relationships dominated by upper-level predators, could inadvertently favour the establishment or survivorship of invasive species. Clearly, managers should seek to enhance resistance to invasion and reduce facilitation of invasion to the maximum extent possible under specific management plans. This requires that factors that promote resistance to and facilitation of invasion can be identified and their modes of action within nearshore communities understood.

More generally, a better understanding of the mechanisms driving successful biological invasion is required for the development of effective management strategies. The patterns of invasion reported here and elsewhere are indicative of the potential for invasion of marine reserves, but on their own they provide insufficient basis for policy decisions and management actions. The mechanisms underlying biological invasion of reserves are likely to vary by site, region and invader, and this variability adds substantial complexity to management considerations.

However, once the mechanisms that account for successful invasion of reserves are understood, managers and policy makers can address directly the threats posed by biological invasion of marine reserves. For example, the likelihood of biological invasion and the risk to management objectives can be estimated prior to reserve designation or during development of management plans. Acceptable levels of risk can be determined, and management plans that allow immediate, appropriate response to invasions that exceed acceptable levels can be formulated. Potential management responses include limited or targeted removals, full eradication or biological control of invasive species. However, none of these alternatives is likely to be entirely successful or benign. Removals can cause serious disturbance, which in turn can facilitate further invasion or cause other undesirable effects; and the history of biological control is replete with examples of serious unintended effects (Louda *et al.*, 1997). This is a dilemma that managers of terrestrial reserves have long been faced with, for example, in the control of invasive species in parks and wilderness areas (Westman *et al.*, 1990). Managers of marine reserves must incorporate invasion risk into the planning process in order to maximize the benefits of reserves to the protection of nearshore biodiversity. Additionally, the necessity of baseline and long-term monitoring programmes within marine reserves must be recognized. The temporal comparisons that led to findings presented in this study would have been impossible in the absence of observations made prior to reserve designation, and could have been strengthened by the existence of quantitative baseline data for each reserve.

Marine reserves offer a promising management tool for protection of native marine biodiversity, but on their own they do not afford protection against biological invasion, which threatens to erode gains in biodiversity conservation made through the establishment of reserves. The success of marine reserves as a management tool to protect native marine biodiversity depends on development of risk-averse strategies to address biological invasion. Failure to address the root causes and potential negative impacts of invasive species in marine reserves will compromise the effectiveness of reserves in maintaining native species diversity, reduce their long-term utility as a management tool and hinder the development of appropriate policies to remedy this important problem.

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