Performance of invasive species within marine reserves

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Abstract

Conservation of biodiversity is a major aim of marine reserves; however their effect on non-native invasive species, a major threat to biodiversity globally, is not widely known. Marine reserves could resist invasive species due to enhanced native diversity and biomass that heightens biotic resistance. Or invasive species could be enhanced by reserves by at least three mechanisms, including protection from harvesting, increased fishing pressure outside reserves facilitating invasions at a regional scale and increasing the exposure of reserves to more potential invaders, and increased propagule pressure from human visitation. We exhaustively searched the literature and found 13 cases that contained quantitative data on invasive species inside and outside marine reserves. In no cases did reserves resist invasive species. Of the seven cases where reserves were established prior to the arrival of the invasive species, five had no effect on the invasive species and two enhanced invasive species. Of the six cases where reserves were established in areas that had pre-existing invasive species, two had no effect on the invasive species and four enhanced the invasive species. These results suggest that while invasive species do equally well or better within marine reserves, too few data are currently available to draw broad, general conclusions regarding the effects of marine reserves on invasive species. Management plans for marine reserves rarely include guidelines for preventing or managing invasive species. If the trends we have detected here are supported by future studies, invasive species should be a priority for management of marine reserves.

Introduction

In terrestrial reserves invasive species have long been documented, absorbing substantial portions of management budgets for control and prevention efforts (Usher 1988; Westman 1990; Pimentel et al. 2005; Allen et al 2009). In the marine environment, reserves have only recently become a favored management option for conservation (Lubchenco et al. 2003). Like their terrestrial counterparts, marine reserves can effectively protect ecosystems from the effects of harvesting, but their ability to protect against other threats, such as pollution and invasive species, may be more limited (Simberloff 2000). In fact, marine invasive species are abundant (Bax et al. 2003); however, few studies (e.g. Simberloff 2000; Byers 2005; Klinger et al. 2006; Kellner and Hastings 2009) have discussed the extent or potential consequences of invasive species in marine reserves.

There are several mechanisms by which marine reserves could affect invasive species that lead to opposing predictions of their overall influence (Fig. 1). On one hand, marine reserves may limit invasive species. Marine reserves usually support a greater number of species than non-protected areas (Lester et al. 2009) and the higher biomass and species diversity within a reserve may limit the successful establishment and proliferation of invasive species whose success often stems from unused resources (Davis et al. 2000; Stachowicz et al. 2002). For example, at least at small spatial scales (settlement tiles), species-rich communities sometimes appear to withstand the establishment of invasive species (Fig. 1; Elton 1958; Stachowicz et al. 1999, 2002), leading to speculation that reserves may better resist invasion by non-native species (Kellner and Hastings 2009). However, the hypothesis that species richness confers “invasion resistance” is often not supported on larger spatial scales (Byers and Noonburg 2003; Stohlgren et al. 2003; Fridley et al. 2007), including marine reserves, which in some cases have been documented to contain greater densities of invasive species than non-protected areas (e.g. Byers 2005; Klinger et al. 2006). While it could be argued that the addition of a new species may increase local diversity, it has been found that the introduction of a new species does not compensate for loss of native biodiversity (although this finding may be scale-dependent; Worm et al. 2006).

On the other hand, marine reserves may enhance invasive species. Marine reserves, particularly those created to protect areas of natural beauty, can be a drawcard for tourists (Edgar et al. 2010). If they attract higher rates of visitation this could promote the introduction of invasive species through increased disturbance and vectors (e.g., boat anchors, SCUBA equipment, bilge water, hull fouling) and subsequent dispersal of propagules (Lonsdale 1999; Minchinton and Bertness 2003; West et al. 2007; Britton-Simmons and Abbott 2008; Clark and Johnston 2009). Additionally, unlike terrestrial protected areas, most marine reserves are not managed to control invasive species within their boundaries. For invasive species that are harvested (recreationally or commercially), marine reserves may, ironically, act as a refuge from harvesting, resulting in the invasive species being more prevalent inside, than outside, the reserve

(Byers 2005; Klinger et al. 2006). Another mechanism that may lead to a greater performance of invaders in reserves is higher diversity and abundance of predators and parasites that reduce the dominance and competitive abilities of potential native competitors (predator mediated competition; Liu and Stiling 2006). Additionally, it has been hypothesized that protection from fishing may facilitate the establishment of invasive species within a region by creating conditions for invasive species to establish (Kellner and Hastings 2009). By banning harvesting within reserves, fishing effort within the region is concentrated into smaller areas outside the reserve boundaries, increasing the fishing intensity per unit area (Byers and Noonburg 2007; Kellner and Hastings 2009). Concentrating fishing effort creates areas where densities of native species are reduced, which may increase the availability of resources and reduce interspecific competition (Kellner and Hastings 2009), creating an opportunity for non-native species to establish in a new region (Daskalov et al. 2007). Although inside the reserve the biomass at the highest trophic levels should remain intact maintaining biotic resistance, the presence of the reserve increases the ability of invasive species to establish at a regional level (Kellner and Hastings 2009). Additionally the reserves themselves may be more vulnerable compared to before the reserve was created because the establishment of new invasive species within a region may expose reserves to a greater abundance and diversity of potential invaders that are now established in the region (Kellner and Hastings 2009). This mechanism results in more invasive species overall in a region; however, at a smaller scale there would still likely be fewer invasive species inside reserves than outside due to stronger biotic resistance inside.

Finally, it is possible that marine reserves may have no effect on the persistence of invasive species. Many invasive species have dispersal mechanisms that would allow them to easily distribute across marine reserve boundaries, and if post-recruitment processes (e.g. predation, competition for resources or space) are not different between reserve and non-reserve locations, then there is unlikely to be a reserve effect.

In this study we conducted a systematic review of the literature to determine: 1) if marine reserves reduce, enhance or have no influence on the likelihood of successful colonization of invasive species; 2) if the implementation of a reserve affects the prevalence of existing invasive species.

Methods

General approach

We systematically searched the peer-reviewed literature in ISI Web of Science (covering 1898 to June 2010). Articles returned by the searches were indexed according to the invasive species studied, the geographic location of the study, the year the species was first detected, the year the no-take reserve was established, the response variable measured (e.g. abundance, biomass), whether the invasive species is harvested, and the invasive species' performance in the reserve relative to control areas. We verified the location of the reserve, its no-take status, and the year it was established using the MPA Global database (Wood 2007). To be included in our analysis, studies needed to have quantitative measures of occurrence of the invasive species (e.g. abundance, relative abundance or biomass,) inside and outside (i.e. in control areas) of one or more marine reserves. The marine reserves needed to be zoned as 'no-take' (i.e. all extractive activities prohibited) to be included. There was one exception where studies of intertidal bivalves and an alga from the San Juan Islands, USA, (Byers 2005; Klinger et al. 2006) were included even though limited degrees of fishing for salmon and herring were permitted (Klinger et al. 2006). The performance of a species within a marine reserve was categorized as:

- enhanced - invasive species that were more prevalent inside than outside reserves,
- resisted - species absent from, or less prevalent inside than outside reserves, or
- neutral - species that had similar patterns of occurrence, or showed no consistent pattern inside and outside reserves.

Literature search strategies

We first paired the search terms "introduced species", "invasive species", "NIS", "exotic", "non-native", "non-indigenous species", "nonindigenous species", "alien species", "introduction", and "foreign species" with every possible combination of "marine park", "marine protected area", "marine reserve", "no-take marine", and "MPA". This search produced 336 papers on invasive species in marine reserves, resulting in six case studies. We then searched by a combination of species name for the 15 most common invasive species mentioned in the first set of papers (Online Resource 1), and the previously mentioned five search terms for marine reserves. This search expanded on the previous search by capturing papers listing only species names, and not if a species was invasive in that area. This search identified an additional two case studies.

Studies of invasive species undertaken incidentally in marine reserves but without a focus on reserves were unlikely to have been identified using our previous search strategies. We therefore undertook a detailed geographic search of countries occurring in 11 key regions (Online Resource 2). We searched the International Union for

Conservation of Nature (IUCN) Global Invasive Species Database for invasive marine species that occurred in each country within each of the 11 regions. If a country bordered more than one region (e.g. Canada was included in both the west and east coast of North America regions), then the appropriate state/province that occurred in each region was searched instead of the country. It was important to search countries bordering more than one region separately as different invasive species occur in each region (e.g. *Spartina alterniflora* is native on the east coast of North America, but invasive on the west coast). Then we searched each species and location combination within ISI Web of Science to determine the species/location combinations with the greatest number of publications. Species that returned more than 30 papers for that region were included in regional searches (4-7 species per region). In the Caribbean, South America, southeastern Africa, Asia, Australia, New Zealand and Hawai'i, all invasive species occurring in the IUCN Global Invasive Species Database for that region were used, as there were few invasive species with greater than 30 studies. Studies were then searched for quantitative data on the occurrence of invasive species at two or more locations, where at least one of the locations could have been a reserve. In suitable papers, we searched study locations in the MPA Global database to determine if studies took place within reserves. Where necessary, authors were contacted to verify if studies were conducted within no-take reserves. Pelagic species were excluded, as they are likely to have short residence times in reserves as adults. We identified a further five case studies with this search strategy.

Case studies were divided into two categories: 1) reserves that were established before the invasive species was introduced, and 2) reserves that were established in areas where invasive species were already detected. If statistical comparisons of the occurrence of invasive species inside and outside reserves were not reported, we extracted relevant data and tested for differences inside and outside reserves. The statistical analyses and evidence used to categorize the effect of the reserve on the invasive species for each case study are presented in Table 1. Where statistical tests were possible but showed no significant difference inside and outside reserves, we calculated the statistical power of the test to detect differences. Power was calculated using G*Power v3 with alpha set at 0.05 and the effect size calculated using the mean and standard deviation of each group. The effect sizes therefore reflected the differences between means inside and outside reserves found in the study as opposed to us setting a standard consistent across the studies. Thus, effect sizes varied among studies, but were typically large (e.g. mean inside reserve > 25% different to outside; Online Resource 3). Two case studies (*H. stipulacea* from St. Lucia and Dominica) only had one reserve and one non-reserve location and therefore did not have enough data for formal statistical analysis (see Table 1). Our search revealed only 13 studies that met our strict criteria. A formal meta-analysis was not, therefore, possible but trends in the data were described.

Results

Our search through more than 13 000 papers found 13 cases from 8 papers containing quantitative data on invasive species inside and outside marine reserves. In no cases did reserves resist invasive species. Where reserves were established before the invasive species was introduced, there were five cases where reserves exhibited neutral effects on invasive species and two cases where reserves enhanced invasive species (Table 2). The first of these latter two cases was the sponge *Chalinula nematifera* which, in a survey of 150 locations (9 reserve and 141 non-reserve) along the west coast of Mexico, occurred only in two reserves and none of the 141 non-reserve locations (Avila and Carballo 2009). The second case was the alga *Undaria pinnatifida* in Tinderbox Reserve in Tasmania, Australia, where the alga had an average of 10% cover in spring 2001 (the first year the species was detected in the area) but was absent in 2 adjacent control sites (Barrett et al. 2009). For marine reserves that were established after an invasive species had been established, there were two cases where marine reserves had neutral effects on invasive species and four cases where marine reserves enhanced invasive species (Table 3). Of the four cases where marine reserves enhanced invasive species, two of these species were harvested (both bivalves, *Crassostera gigas* and *Venerupis philippinarum*) and two were not harvested (the barnacle *Elminius modestus* and the alga *Sargassum muticum*). Estimates of statistical power in neutral cases established that power of tests to detect differences inside and outside reserves was low (all values < 0.32; Table 1); this low power, even at relatively large effect sizes, reflects the small sample size used in many tests of reserve effects.

Discussion

Our results must be interpreted cautiously because of the limited sample size, but they do indicate that marine reserves do not resist invasive species, nor does the implementation of a reserve reduce the persistence of existing invasive species. Indeed reserves appear to have little influence on invasive species as seven of the 13 cases showed no effect of protection. In all cases, however, the statistical power to detect a difference, should one have existed, was low. In areas where reserves were established after the invasive species was introduced, there were more cases where the invasive species performed better within reserves. This observation applied to some species that were harvested (*Crassostrea gigas*, *Venerupis philippinarum*) and, therefore, benefited from the cessation of harvesting once the marine reserve was established (Byers 2005; Klinger et al. 2006). Two of the other positively influenced species (*S. muticum* and *E. modestus*) are not harvested themselves, but likely benefited by commonly living as epibionts on the harvested non-native oyster *C. gigas* (Klinger et al. 2006; Witte et al. 2010). The other species that were positively affected presumably benefited because many species generally perform better within marine reserves (Lester et al. 2009), and the same factors promoting the abundance of native species might also have aided the invasive species.

The limited studies available suggest that invasive species are often abundant and co-occur with other invasive species inside reserves (Byers 2005; Klinger et al. 2006; Abdulla et al. 2008). Indeed, even isolated or reasonably pristine reserves hosted multiple invasive species (PMNM 2008). It is important to acknowledge that there is often spatial and taxonomic bias in reporting the occurrence of invasive species (Ruiz et al. 2000); therefore, given that many marine reserves are the subjects of research it may be more likely that there are a higher number of invasive species reported in marine reserves than unprotected areas. However, any such bias would most likely affect data on the occurrence or presence/absence of invaders as opposed to the pairwise comparisons of the relative performance of invasive species inside versus outside of reserves that we focused on here. From a conservation perspective what remains as a potentially troubling issue is that the presence of invasive species may facilitate the colonization of subsequent invasive species (i.e. invasion meltdown; Simberloff and Von Holle 1999). Because a primary goal of many marine reserves is to maintain high biodiversity, their conservation value is potentially undermined since invasive species may ultimately reduce biodiversity (Carlton 1999; Bax et al. 2003).

Any relationship between reserve status and invasion success may be very complex. This relationship is likely to be a function of the attributes of the reserve (e.g. habitat, location, size, and age of the reserve) and the dynamics within the reserve (e.g. condition of the native community, disturbance regime, magnitude of invasion pressure). However, we need a much larger data set than is currently available to tease out the impact of each of these factors.

Even with our exhaustive review, we found very few empirical comparisons of invasive species between marine reserves and appropriate control areas. Additionally, of the 13 case studies included in this paper there were six different response variables measured: percent cover (4 case studies), biomass (2), CPUE (2), density (2), average maximum abundance (1), and presence/absence (1). The most rigorous approach to testing our hypothesis would be to undertake a formal meta-analysis but the paucity of data and the diversity of response variables measured in the case studies made a formal meta-analysis impracticable (see Harrison 2011). There were only two studies representing five case studies (Byers 2005; Klinger et al. 2006), of the 13 000 we searched, that explicitly examined the role of marine reserves on invasive species, which serves to highlight a critical need for more research on invasive species in marine reserves. It is also worth noting that there was a non-random geographic distribution of the case studies that we found. There were no case studies from Africa, South America, or Asia. While invasive species are identified in these regions, and marine reserves are present, there were fewer studies to interrogate from these regions.

Control, detection, and eradication of invasive species are a common priority issue for management of terrestrial reserves (Thomas 1988; Usher 1988; Macdonald et al. 1989; Westman 1990). For example, >3700 non-native plant species have been catalogued within US National Parks (Allen et al. 2009). However, in the marine realm, non-native species have received little attention in reserve planning processes. In some marine reserves the occurrence of invasive species has been quantified (deRivera et al. 2005; Abdulla et al. 2008) yet these studies have not led to substantive changes to the ways in which those reserves are managed. Indeed, the role of invasive species (Simberloff 2000) and potential consequences to the effectiveness of marine reserves in maintaining biodiversity (Kellner and Hastings 2009) are rarely considered in reserve planning. While there has been some discussion among scientists of incorporating management of invasive species into management plans for marine reserves (Wasson et al. 2002), there are very few practical examples of this being done. The management plan for Papahānaumokuākea Marine National Monument in Hawai'i (PMNM 2008) is unique in its comprehensive management strategies for invasive species. For example, they have implemented strict quarantine and inspection protocols for vessels and equipment entering the marine reserve. Furthermore, they have developed an invasive species action plan to detect, control, and eradicate (where possible) invasive species occurring within the marine reserve. We acknowledge that the reserve's extreme isolation (200 km from the nearest populated island, Kaua'i) may create a unique opportunity to incorporate strict vessel and gear inspection. However, it is important that all reserves incorporate strategies to limit the introduction of invasive species and manage existing invasive species as part of the reserve planning process.

In summary, it is surprising how little is known about the extent and performance of invasive species in marine reserves compared to their terrestrial counterparts. We

encourage scientists to undertake quantitative and rigorous studies of invasive species by sampling invasive species inside marine reserves and at appropriate control areas, and replicating their studies through time. If the trend of marine reserves exerting positive effects on invasive species continues to be supported by future studies, invasive species should be a priority for management of marine reserves, much as they already are in terrestrial reserves.

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Figure Legend

Figure 1. Theoretical pathways by which marine reserves resist or enhance invasive species.

Figure 1.

Table 1: Summary of analyses used to determine performance of invasive species in marine reserves. Effect size is calculated from the differences in the means and standard deviations in control and reserve locations, as determined using G*Power. Performance in reserves is defined as: Resisted (-); Neutral (0); Enhanced (+).

Performance in reserve	Species	Reserve Location	Objective	Test of effect	Reference
-	none				
0	<i>Carcinus maenas</i> (crab)	Maria Island – Tasmania, Australia	To compare CPUE of <i>C. maenas</i> in several locations along the east coast of Tasmania, South Australia, Victoria, and southern New South Wales.	Since both reserve and control locations were present only in Tasmania, only data from Tasmania were analyzed (1 reserve and 10 control locations (excluding Hobart area)). 1-sample t-test, $p = 0.240$, Power = 0.32, Effect size = 0.40	Thresher et al. 2003
0	<i>Carcinus maenas</i> (crab)	Redwood Shores and Elkhorn Slough – California, USA	To compare <i>C. maenas</i> CPUE along the coast of California (northern to central California).	Two reserves and 9 control locations were surveyed. t-test, $p = 0.587$, Power = 0.06, Effect size = 0.04	Grosholz & Ruiz 1995
0	<i>Halophila stipulacea</i> (seagrass)	Cabritas National Park – Dominica	To map distributions of invasive seagrass and other habitats.	Percentage covers in the reserve (20%), and control site (22%) were similar but since only one data point was available for the marine reserve and control, no statistical analysis was undertaken.	Willette & Ambrose 2009, Steiner & Willette 2010

0	<i>Halophila stipulacea</i> (seagrass)	Anse la Raye Marine Reserve Management Area – St Lucia	To map distributions of invasive seagrass.	<i>H. stipulacea</i> covered 0.006% of the reserve and an average of 0.018% across two control areas. Due to the invasion occurring very recently and the small total area covered by the seagrass, the reserve was determined to have had no effect on the invasion.	Willette & Ambrose 2009
0	<i>Mya arenaria</i> (bivalve)	Argyle Lagoon, British Camp Historical Site and Shaw Island – San Juan Islands, Washington, USA	To compare the density and biomass of 4 species of bivalves (3 invasive, 1 native) at 3 reserves and 11 control sites.	t-test, $p = 0.744$, Power = 0.09, Effect size = 0.23	Byers 2005
0	<i>Nuttallia obscurata</i> (bivalve)	Argyle Lagoon, British Camp Historical Site and Shaw Island – San Juan Islands, Washington, USA	To compare the density and biomass of 4 species of bivalves (3 invasive, 1 native) at 3 reserves and 11 control sites.	t-test, $p = 0.318$, Power = 0.18, Effect size = 0.53	Byers 2005
0	<i>Undaria</i>	Maria Island,	To compare fish and	The analysis was based on mean percent	Barrett et al. 2009

	<i>pinnatifida</i> (alga)	Tasmania, Australia	macroalgal communities inside versus outside marine reserves in Tasmania, Australia	cover (values were extracted from figures) of <i>U. pinnatifida</i> averaged across 6 replicate sampling sites within Maria Island Reserve and at 6 control sites outside reserve. Test compared average % cover inside vs outside reserves over 6 years. t-test, $p = 0.497$, Power = 0.12, Effect size = 0.30	
+	<i>Chalinula</i> <i>nematifera</i> (sponge)	Isla Isabel National Park and Cabo Pulmo – Mexico	To survey 150 locations (9 reserves, 141 non-reserves) along the west coast of Mexico for the invasive sponge <i>Chalinula</i> .	Test of effect: The sponge occurred in 2 of the 150 locations and both were within reserves. The probability of the sponge occurring within the two reserves by chance was calculated as follows: $(9 \times 150) \times (8 \times 149) \rightarrow p = 0.0097$.	Avila & Carballo 2009
+	<i>Crassostera</i> <i>gigas</i> (bivalve)	Point Caution, Argyle Lagoon and False Bay – San Juan Islands, USA	To compare densities of <i>C. gigas</i> at 3 reserves and 5 control sites.	ANOVA, $p = 0.05$	Klinger et al. 2006
+	<i>Elminius</i> <i>modestus</i> (barnacle)	Lough Hyne Marine Nature Reserve – Ireland	Objective: to compare the abundance and vertical distribution	Test of effect: Average of maximum abundance of <i>E. modestus</i> inside reserves was 1800 barnacles m^{-2} , compared with 75 barnacles m^{-2} in control sites.	Lawson et al. 2004

			of multiple species of barnacle at 11 sites within the marine reserve and 6 sites outside the reserve.		
+	<i>Sargassum muticum</i> (alga)	Point Caution, Point George, Yellow Island, Low Island, Argyle Lagoon and False Bay – San Juan Islands, USA	To compare abundances of <i>S. muticum</i> in 4 reserves and 10 control sites.	ANOVA, $p = 0.05$	Klinger et al. 2006
+	<i>Undaria pinnatifida</i> (alga)	Tinderbox – Tasmania, Australia	To compare fish and macroalgal communities inside versus outside marine reserves in Tasmania, Australia	Although <i>U. pinnatifida</i> has been present in Tasmania since 1988, it did not occur in Tinderbox Reserve or nearby control areas until spring 2001. Therefore, Tinderbox Reserve was analyzed as a separate case study (from Maria Island) as the reserve was established before the species was introduced. Average 10% cover at 2 locations in reserve, absent at 2 control locations. Insufficient data available for a statistical test.	Barrett et al. 2009
+	<i>Venerupis philippinarum</i>	Argyle Lagoon, British Camp	Objective: to compare the density	Test of effect: density (t-test, $p = 0.0085$) and biomass ($t = -3.43$, $p = 0.0075$)	Byers 2005

(bivalve)	Historical Site and Shaw Island – San Juan Islands, Washington, USA	and biomass of 4 species of bivalves (3 invasive, 1 native) at 3 reserves and 11 control sites
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Table 2. Performance of invasive species in marine reserves, where reserves were established before the invasive species were introduced. Resisted (-); Neutral (0); Enhanced (+)

Performance in reserve	Invasive species	Harvested?	Time detected	Study years	Native range	Reserve location (Year established)	Reference
-	none						
0	<i>Carcinus maenas</i>	no	1993	1996-2000	Western Europe, Western Africa	Maria Island (1991) Australia	Thresher et al. 2003
0	<i>Carcinus maenas</i>	no	1989 ^b , 1993 ^c	1993-1994	Western Europe, Western Africa	Redwood Shores State Marine Park (1976), Elkhorn Slough (1979), USA	Grosholz & Ruiz 1995
0	<i>Halophila stipulacea</i>	no	2000s	2007-2008	Indian Ocean	Cabrits National Park (1980), Dominica	Willette & Ambrose 2009
0	<i>Halophila stipulacea</i>	no	2000s	2007	Indian Ocean	Anse la Raye Marine Reserve Management Area (1987), St. Lucia	Willette & Ambrose 2009
0	<i>Nuttallia obscurata</i>	no	1991 ^a	2000	Northern Asia (Japan, Korea)	British Camp (1977), Argyle Lagoon (1990), Shaw Island (1990), USA	Byers 2005

+	<i>Chalinula nematifera</i>	no	2003	1999-2007	Indo-Pacific	Isla Isabel National Park (1980), Cabo Pulmo (1995), Mexico	Avila & Caballo 2009
+	<i>Undaria pinnatifida</i>	not in this region	2001	1992-2002	Eastern Asia (Japan, China, Korea)	Tinderbox (1991), USA	Barrett et al. 2009

^aFirst report from Pacific Northwest, on Vancouver Island. Anecdotally reported in San Juan Islands between 1996-1998.

^bFirst report from San Francisco Bay

^cFirst report from Monterey Bay

Table 3. Performance in marine reserves, where marine reserves were established after the invasive species were introduced. Resisted (-); Neutral (0); Enhanced (+)

Performance in reserve	Invasive species	Harvested?	Year detected	Study years	Native range	Reserve location (Year established)	Reference
-	none						
0	<i>Mya arenaria</i>	not in this region	late 1800s	2000	Atlantic coast North America	British Camp Historical Site (1977), Argyle Lagoon (1990), Shaw Island (1990), USA	Byers 2005
0	<i>Undaria pinnatifida</i>	not in this region	1988	1992-2002	Eastern Asia (Japan, China, Korea)	Maria Island (1991), Australia	Barrett et al. 2009
+	<i>Crassostera gigas</i>	yes	early 1900s	2001	Japan	Point Caution, Argyle Lagoon, False Bay (1990), USA	Klinger et al 2006
+	<i>Elminius modestus</i>	no	1956	2001	New Zealand, southern Australia	Lough Hyne Marine Nature Reserve (1981),	Lawson et al. 2004

Invasive species in marine reserves

Ireland

+	<i>Sargassum muticum</i>	no	late 1800s	2002	Eastern Asia (Japan, China, Korea)	Point Caution, Point George, Yellow Island, Low Island, Argyle Lagoon, False Bay (1990), USA	Klinger et al. 2006
+	<i>Venerupis phillppinarum</i>	yes	1930s	2000	Japan	British Camp Historical Site (1977), Argyle Lagoon (1990), Shaw Island (1990), USA	Byers 2005

Online Resource 1 — Species used in taxonomic search

Common name	Scientific name
Asian date mussel	<i>Musculista senhousia</i>
Asian mitten crab	<i>Eriocheir sinensis</i>
European green crab	<i>Carcinus maenas</i>
Fan worm	<i>Euchore limnicola</i>
Feather algae	<i>Caulerpa taxifolia</i>
Grape algae	<i>Caulerpa racemosa</i>
<i>Halophila</i> seagrass	<i>Halophila stipulacea</i>
Japanese kelp	<i>Undaria pinnatifida</i>
New Zealand screwshell	<i>Maoricolpus roseus</i>
North Pacific sea star	<i>Asterias amurensis</i>
Pacific lionfish	<i>Pterois volitans</i>
Pacific oyster	<i>Crassostrea gigas</i>
Strap weed	<i>Caulerpa filiformis</i>
Venus clam	<i>Ruditapes largillierti</i>
Wire weed	<i>Sargassum muticum</i>

Online Resource 2 — Geographic search terms

North America – West Coast

Location search terms	Invasive species search terms
Alaska	<i>Carcinus maenas</i>
Baja California	<i>Caulerpa taxifolia</i>
British Columbia	<i>Crassostrea gigas</i>
California	<i>Mytilus galloprovincialis</i>
Oregon	<i>Spartina alterniflora</i>
Washington	<i>Undaria pinnatifida</i>
	<i>Zostera japonica</i>

North America – East Coast

Location search terms	Invasive species search terms
Alabama	<i>Carcinus maenas</i>
Campeche	<i>Codium fragile</i> ssp. <i>tomentosoides</i> *
Connecticut	<i>Perna perna</i>
Delaware	<i>Pterois volitans</i>
Florida	
Georgia	
Louisiana	
Maine	
Maryland	
Massachusetts	
Mississippi	
New Brunswick	
New Hampshire	
New Jersey	
New York	
Newfoundland	
North Carolina	
Nova Scotia	
Quebec	
Quintana Roo	
Rhode Island	
South Carolina	
Tabasco	
Tamaulipas	
Texas	
Virginia	
Yucatan	

* Note the name has changed to *Codium fragile* spp. *fragile*, but we have used *Codium fragile* ssp. *tomentosoides* in our search given that this the term used in the literature.

Northern Europe

Location search terms	Invasive species search terms
Belgium	<i>Crassostrea gigas</i>
Denmark	<i>Mya arenaria</i>
England	<i>Mytilopsis leucophaeata</i>
Estonia	<i>Mytilus galloprovincialis</i>
Finland	<i>Sargassum muticum</i>
Germany	<i>Spartina alterniflora</i>
Ireland	<i>Urosalpinx cinerea</i>
Latvia	
Lithuania	
Netherlands	
Norway	
Poland	
Scotland	
Sweden	
Wales	

Mediterranean Sea

Location search terms	Invasive species search terms
Albania	<i>Caulerpa</i>
Algeria	<i>Crassostrea gigas</i>
Bosnia and Herzegovina	<i>Mya arenaria</i>
Croatia	<i>Sargassum muticum</i>
Cyprus	<i>Undaria pinnatifida</i>
Egypt	
France	
Greece	
Israel	
Italy	
Libya	
Malta	
Monaco	
Montenegro	
Morocco	

Slovenia

Spain

Syria

Tunisia

Turkey

Eastern Africa

Location search terms	Invasive species search terms
Comoros	<i>Carcinus maenas</i>
Kenya	<i>Codium fragile</i> ssp. <i>tomentosoides</i>
Madagascar	<i>Crassostrea gigas</i>
Mauritius	<i>Kappaphycus</i> spp
Mayotte	<i>Musculista senhousia</i>
Mozambique	<i>Mytilus galloprovincialis</i>
Reunion	
Seychelles	
South Africa	
Tanzania	
Zanzibar	
Africa	

Asia

Location search terms	Invasive species search terms
Bangladesh	<i>Carcinus maenas</i>
Cambodia	<i>Crassostrea gigas</i>
China	<i>Kappaphycus</i> spp.
East Timor	<i>Mytilopsis sallei</i>
Hong Kong	<i>Ostrea edulis</i>
India	<i>Spartina alterniflora</i>
Indonesia	<i>Styela plicata</i>
Japan	
Malaysia	
Myanmar (Burma)	
North Korea	
Palau	
Philippines	
Singapore	
South Korea	
Sri Lanka	
Taiwan	
Thailand	
Vietnam	

Australia

Location search terms	Invasive species search terms
Australia	<i>Acanthogobius flavimanus</i>
Queensland	<i>Allita succinea</i>
New South Wales	<i>Ascidella aspersa</i>
Victoria	<i>Asterias amurensis</i>
Tasmania	<i>Carcinus maenas</i>
Northern Territory	<i>Caulerpa taxifolia</i>
	<i>Codium fragile</i> ssp. <i>tomentosoides</i>
	<i>Crassostrea gigas</i>
	<i>Musculista senhousia</i>
	<i>Mya arenaria</i>
	<i>Mytilus galloprovincialis</i>
	<i>Ostrea edulis</i>
	<i>Perna viridis</i>
	<i>Sabella spallanzanii</i>
	<i>Spartina alterniflora</i>
	<i>Styela clava</i>
	<i>Styela plicata</i>
	<i>Undaria pinnatifida</i>

New Zealand

Location search terms	Invasive species search terms
New Zealand	<i>Charybdis japonica</i>
	<i>Codium fragile</i> ssp. <i>tomentosoides</i>
	<i>Crassostrea gigas</i>
	<i>Musculista senhousia</i>
	<i>Ostrea edulis</i>
	<i>Spartina alterniflora</i>
	<i>Styela clava</i>
	<i>Undaria pinnatifida</i>

Hawai'i

Location search terms	Invasive species search terms
Hawai'i	<i>Acanthophora spicifera</i>
	<i>Carijoa riisei</i>
	<i>Chthamalus proteus</i>
	<i>Gracilaria salicornia</i>
	<i>Hypnea musciformis</i>
	<i>Kappaphycus</i> spp.
	<i>Lutjanus kasmira</i>
	<i>Mycale grandis</i>
	<i>Mytilus galloprovincialis</i>

South America

Location search terms	Invasive species search terms
Argentina	<i>Charybdis hellerii</i>
Brazil	<i>Codium fragile</i> ssp. <i>tomentosoides</i>
Chile	<i>Crassostrea gigas</i>
Colombia	<i>Geukensia demissa</i>
Ecuador	<i>Perna viridis</i>
French Guyana	<i>Rapana venosa</i>
Galapagos Islands	<i>Tubastraea coccinea</i>
Guyana	
Peru	
Suriname	
Uruguay	
Venezuela	

Caribbean

Location search terms	Invasive species search terms
Anguilla	<i>Charybdis hellerii</i>
Antigua and Barbuda	<i>Halophila stipulacea</i>
Aruba	<i>Perna viridis</i>
Barbados	<i>Pterois volitans</i>
Belize	<i>Tubastraea coccinea</i>
British Virgin Islands	
Caribbean	
Cayman Islands	
Costa Rica	
Cuba	
Dominica	
Dominican Republic	
Grenada	
Guadeloupe	
Guatemala	
Honduras	
Jamaica	
Martinique	
Montserrat	
Netherlands Antilles	
Nicaragua	
Panama	
Puerto Rico	
Republic of Haiti	

St Kitts and Nevis
St Lucia
St Vincent and the Grenadines
The Bahamas
Trinidad and Tobago
Turks and Caicos
Virgin Islands
West Indies

Online Resource 3 – Notes on analysis and interpretation of case studies

Halophila stipulacea* (seagrass)*Location:** Anse la Raye Marine Reserve Management Area – St Lucia**Reference:** Willette and Ambrose 2009, personal communication with author**Comments:**

- *H. stipulacea* covered 50m² in total across 3 bays in St Lucia.
- The author reported via personal communication that *Halophila stipulacea* covered approximately 4m² the marine reserve
- Remaining 46m² of *Halophila stipulacea* occurred at two nearby non-reserve areas.
- Google Earth was used to measure the total area of the reserve and control areas, which then enabled calculation of the percent cover at each location.

Nuttallia obscurata* (bivalve)*Location:** Argyle Lagoon, British Camp Historical Site and Shaw Island – San Juan Islands, Washington, USA**Reference:** Byers 2005**Comments:**

- Reserves in San Juan Island permit limited recreational salmon (10 months/year, 2 fish/person/day) and herring fishing. Commercial harvest of salmon is prohibited.
- Study took place in intertidal areas, unlikely to be influenced by small amounts of fishing
- Fishing effort within reserves is minimal (Klinger personal communication)

Carcinus maenas* (crab)*Location:** Maria Island – Tasmania, Australia**Reference:** Thresher et al. 2003**Comments:**

- Since both reserve and control locations were present only in Tasmania, only this state was included in the analysis.
- Only locations along the east coast of Tasmania (excluding the Hobart area) were used as control locations

Table 2. Mean number of crabs per trap at sites on the east coast of Tasmania.

Location	Blackman Bay	Little Swanport	Henersons Lagoon	Maria Island	Georges Bay
Control	1.1	22.5	43.7		21.8
Reserve				10.6	

Unnamed control sites	0	31.6	6.7	15.6	18	2
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Carcinus maenas* (crab)*Location:** Redwood Shores and Elkhorn Slough – California, USA**Reference:** Grosholz and Ruiz 1995Table 3. Average catch per trap of *Carcinus* in northern California.

Location	Control	Reserves
Eureka (Humboldt Bay)	0	
Fort Bragg (Noyo River)	0	
Gualala (Gualala River)	0	
Salt Point (Gerstle Cove)	0	
Bodega Harbor	0.565	
Tomales Bay	0.33	
Bolinas Lagoon (Kent Island)	0	
Drakes Estero (Johnson Oyster)	1.5	
SF Bay (Redwood Shores)		1
Pillar Point	0	
Monterey Bay (Elkhorn Slough)		0

Undaria pinnatifida* (alga)*Location:** Tinderbox – Tasmania, Australia**Reference:** Barrett et al. 2009**Comments:**

- Although *Undaria* has been present in Tasmania since 1988, it did not occur in Tinderbox Reserve or nearby control areas until spring 2001 (as determined from data within this paper).
- The mean percent cover of *Undaria* was averaged across 2 sites within the reserve and at 2 control sites.

Chalinula nematifera* (sponge)*Location:** Isla Isabel National Park and Cabo Pulmo – Mexico**Reference:** Avila and Carballo 2009**Comments:**

- The reserves have different levels of zoning, but the author confirmed that they sampled in no-take areas only.

Undaria pinnatifida* (alga)*Location:** Maria Island, Tasmania, Australia**Reference:** Barrett et al. 2009**Comments:**

- *Undaria* is an annual species with greatest biomass in spring (September); therefore we only included spring values in our analysis.
- Values were extracted from figures

Table 4: Mean percent cover of *Undaria* averaged across replicate sampling sites within Maria Island Reserve and at control sites outside reserve.

Year	1992	1993	1997	1999	2000	2001
Control	1	5.5	2	1	0.5	0.5
Reserve	0	0.5	7	1.5	2.5	3

***Mya arenaria* (bivalve)**

Location: Argyle Lagoon, British Camp Historical Site and Shaw Island – San Juan Islands, Washington, USA

Reference: Byers 2005

Comments:

- For addition information on reserves see *Nuttallia*.

***Sargassum muticum* (alga)**

Location: Point Caution, Point George, Yellow Island, Low Island, Argyle Lagoon and False Bay – San Juan Islands, USA

Comments:

- For addition information on reserves see *Nuttallia*.

***Crassostera gigas* (bivalve)**

Location: Point Caution, Point George, Yellow Island, Low Island, Argyle Lagoon and False Bay – San Juan Islands, USA

Reference: Klinger et al. 2006

Comments:

- For addition information on reserves see *Nuttallia*.

***Venerupis philippinarum* (bivalve)**

Location: Argyle Lagoon, British Camp Historical Site and Shaw Island – San Juan Islands, Washington, USA

Reference: Byers 2005

Comments:

- For addition information on reserves see *Nuttallia*.

***Elminius modestus* (barnacle)**

Location: Lough Hyne Marine Nature Reserve – Ireland

Reference: Lawson et al 2004

Comments:

- No statistical comparison of densities inside and outside reserves was reported but the authors stated that “*E. modestus* was by far the most dominant species inside the Lough Hyne (reserve area) in terms of abundances at each site and distribution around the Lough.”
- Values for average of maximum abundance we extracted from kite plots