8 Are the Marine Biotas of Island Ecosystems More Vulnerable to Invasion?

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8.1 Introduction

New Zealand's native marine ecosystems are facing challenges from more than 130 nonindigenous species (NIS) which have become established in New Zealand's coastal waters in the past 200 years (Cranfield et al. 1998). The Asian date mussel *Musculista senhousia*, the smooth cord grass *Spartina alterniflora*, and the Japanese kelp *Undaria pinnatifida* have substantially modified habitats, changing their suitability for native species. Others, such as the Pacific oyster (*Crassostrea gigas*) and Pacific salmon (*Oncorhynchus tshawytscha*), now form the basis of valued industries and are actively cultured. Most NIS (~96 %) have arrived accidentally, on the hulls or in the ballast of ocean-going ships (Cranfield et al. 1998). A dependence on maritime trade, together with changes in the diversity of our major trading partners and global increases in the number, size and speed of ocean-going vessels, means that the influx of foreign species is likely to continue in the future (Ruiz et al. 2000).

The susceptibility of island biotas to invaders has been a central theme in invasion biology, with the changes wrought to New Zealand's terrestrial and freshwater ecosystems featuring prominently in most international reviews of the subject (e.g. Elton 1958; Simberloff 1995; Williamson 1996). Despite differences between marine and terrestrial ecosystems, Ruiz et al. (1997) predicted that the effects of marine invaders would also be greatest on small islands which have large numbers of endemic marine species. The long ocean distances between New Zealand and continental neighbours mean that its marine plants and animals have evolved in relative isolation from other coastal assemblages and, in many ways, are as distinctive as its terrestrial biota (Dell 1968; Towns and Ballantine 1993). In this chapter, we review current ideas about the susceptibility of island biotas to invasion, and discuss their application to the marine environments of New Zealand and other oceanic islands.

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8.2 Island Bioinvasion Theory

The success of NIS on islands has been attributed to a variety of evolutionary and ecological causes. Central to most explanations has been the generally smaller pool of native species and, consequently, limited competition for relatively abundant resources (Elton 1958). Both the "maladaptation" and the "empty niche" hypotheses have since been challenged. Simberloff (1995) noted that island species are not always poorer competitors than their mainland counterparts and that resources on islands were typically never underutilized. The success of island invaders, therefore, is not necessarily because there are fewer native species present on islands, but because entire ways of living (i.e. functional groups) may be absent, allowing particular types of invaders to flourish (Simberloff 1995).

Contemporary treatments of "niche opportunity" define the conditions which promote invasions as a combination of available resources (such as food and space), lack of natural enemies, and suitable environmental conditions (Williamson 1996; Shea and Chesson 2002). A community's susceptibility to invasion is not a static or permanent attribute (Davis et al. 2000), resulting in a dynamic definition of an "available niche". Frequent inoculations of a particular species ("propagule pressure") enhance the chance that its arrival will coincide with suitable conditions for establishment. Species which have a strong association with human transport pathways will generally have greater odds of success (Wonham et al. 2000). Similarly, species with physiological attributes or life-history characteristics which allow establishment under a greater range of conditions, such as broad habitat tolerances and high reproductive potential, should be more successful invaders than less adaptable species.

8.3 Are Marine Biotas of Islands More Invaded?

8.3.1 Number of Nonindigenous Species in Various Regions

Carlton (1987) analysed available data on the distribution of NIS in the Pacific and noted that Hawai'i, the Pacific coast of North America, and Australasia (including New Zealand) appeared to be major recipients of introduced species, whereas the Pacific coast of Asia and the south-western Pacific were major source regions. Like many other countries, New Zealand has only recently begun to document the extent of invasions in its coastal environments. Inventories of marine NIS, similar to that compiled for New Zealand by Cranfield et al. (1998), have been developed for (at least) parts of Australia, the USA, UK, Mediterranean Sea, North Sea, Black Sea, and Baltic Sea (see Table 8.1). In

Table 8.1 Numbers of non-indigenous marine species reported from coastal regions

Oceans and seas	Fishes	Molluscs	Barnacles	Macroalgae	Sponges	Decapods	Bryozoans	Total
New Zealand[a]	3	22	18	21	9	6	19	130
Hawai'ian Islands[b]	20	53	4	24	23	16	16	343
Guam[c]	6	14	2	?	5	5	3	85
United Kingdom[d]	1	13	3	15	1	3	3	79
North Sea[e]	0	11	4	20	0	4	2	80
BalticSea[f]	29	12	1	7	?	6	1	101
Black Sea[g]	7	7	2	2	0	4	0	53
Mediterranean Sea[h]	55	75	?	61	?	33	?	>300
Bays and harbours								
Pearl Harbour (Hawai'i)[i]	4	15	4	1	5	5	8	69
Kane'ohe Bay (Hawai'i)[j]	12	23	4	6	11	4	12	82
Apra Harbour (Guam)[k]	?	?	?	?	?	?	?	46
Port Phillip Bay (Australia)[l]	4	7	1	16	6	2	23	99
San Francisco Bay (USA)[m]	6	27	2	6	5	7	11	212
Venice Lagoon (Italy)[n]	?	7	?	8	?	3	2	30

[a] Cranfield et al. (1998)
[b] Eldredge and Carlton (2002)
[c] Paulay et al. (2002)
[d] Minchin and Eno (2002)
[e] Reise et al. (1999, 2002)
[f] Leppäkoski et al. (2002)
[g] Gomoiu et al. (2002)
[h] Galil (2000)
[i] Coles et al. (1999a)
[j] Coles et al. (2002)
[k] Coles and Eldredge (2002)
[l] Hewitt et al. (1999)
[m] Cohen and Carlton (1995)
[n] Occhipinti Ambrogi (2000)

most cases, these encompass both historical (since biological records were first kept) and more recent introductions.

The number of NIS known to have established in New Zealand waters is markedly higher than that recognized from the North Sea, Black Sea or UK (Table 8.1). Similarly, recent studies in the Hawai'ian Islands have recorded almost as many nonindigenous marine species as have been recorded from the whole of mainland USA (Table 8.1; Eldredge and Carlton 2002). Around 298 nonindigenous invertebrates and algae, and 100 species of fish have so far been reported from the coastal waters of the continental USA (Ruiz et al. 2000). A reliable comparison of the rates of invasion in the marine biotas of island and mainland areas is not yet possible, however, because the methods used to compile lists of NIS, the geographic scales of consideration, and the taxonomic criteria used vary widely among the published studies (Ruiz et al. 2000). In some cases (e.g. Cranfield et al. 1998; Reise et al. 2002), the lists were compiled solely from published records and museum specimens. Others were developed using a combination of historical records and targeted field studies (e.g. Coles et al. 1999a, b).

In Australia, standardized sampling techniques have been used to determine the extent of invasions in major shipping ports throughout the country. Results reveal a trend towards greater numbers of nonindigenous species in southern temperate environments than in tropical ports (Hewitt 2002). The southern marine ecosystems of Australia are relatively isolated from other temperate environments, and contain a large proportion of endemic species. However, the southern ports of Australia also have a longer history of settlement than does tropical Australia, and the latitudinal trend may simply reflect a longer history and quantity of supply of NIS to southern Australia, rather than any inherent difference in susceptibility to invasion (Hewitt 2002).

8.3.2 Problem of Cryptogenic Species

"Cryptogenic" species (i.e. species which are not demonstrably introduced or indigenous) can comprise up to 30 % of some coastal marine assemblages (Ruiz et al. 2000). Their prevalence creates an uncertain regulatory environment for managers of marine pests, since eradication and control measures are usually not sanctioned against native species. This was highlighted recently by two pest alerts in New Zealand in which decisions about remedial action revolved around the geographic origins of the species.

Chaetopterus sp.: a Pesky Worm

In 1997, commercial scallop fishers in north-eastern New Zealand reported catching large numbers of a parchment tubeworm which was clogging dredges and reducing catch efficiency. The worm, a species of polychaete in the genus *Chaetopterus*, has since been found along the eastern coast of northern New Zealand. Its tubes formed dense aggregations (>120 individuals per 0.02 m^2) up to 2 m in diameter and 25 cm deep, and it colonized a wide variety of habitats including rocky reef and soft sediment substrates from the shallow intertidal to depths>60 m (Tricklebank et al. 2001). Museum collections suggest that isolated individuals may have been present in New Zealand during the 1960s, but these specimens were poorly preserved and not formally identified at the time. The complex and confusing taxonomy of this group (most species are inadequately described) and the poor condition of museum specimens has meant that it has not been possible to determine whether the species is indigenous to New Zealand or is introduced. A similar, unidentified species of *Chaetopterus* has become abundant in Kane'ohe Bay and Pearl Harbour, Hawai'i, since the 1970s where it is also regarded as cryptogenic (DeFelice et al. 2001).

Didemnum vexillum sp. nov.: a Worrying Ascidian

In 2001, the Harbourmaster of a small coastal harbour in north-eastern New Zealand reported an unusual growth which blanketed wharf piles and some boats in the harbour. Subsequent surveys showed it to be a previously undescribed colonial ascidian in the genus *Didemnum* (Kott 2002). The species was subsequently recorded in Tauranga, and on a barge in Picton Harbour which had been relocated from Tauranga. Because of its habit of overgrowing other fouling species, discovery of the ascidian in the Marlborough Sounds raised alarm bells with the Greenshell™ mussel industry. There is no evidence that *Didemnun vexillum* sp. nov. has been introduced to New Zealand and, because it has not been described elsewhere, it is currently assumed to be a native species which underwent a sudden, unusual bloom in abundance (Kott 2002).

8.4 Are the Marine Biotas of Islands Less Diverse?

Elton (1958) considered that islands contained a smaller pool of species than was present in comparable areas of continental landmasses, and therefore provided greater opportunity for invaders. The relationship between species richness and invasibility has received little consideration in marine environments. A recent experimental study (Stachowicz et al. 2002) showed that invaders of space-limited marine invertebrate communities tend to be more successful when the native assemblage has low species richness. At the small scale at which the experiments were done (10x10 cm tiles), the mechanism for this success appeared to be the greater temporal stability in resource (open space) utilization by diverse assemblages, thereby providing less opportunity for an invader to establish. Whether similar mechanisms apply in different types of marine assemblages or at the larger, biogeographic scales relevant to island bioinvasion theory is still unclear. However, patterns of species distribution and diversity in the oceans are complex and still poorly understood (Warwick 1996), in part because the description of biogeographic patterns is contingent upon the state of taxonomy and systematics – both of which are patchy for marine biotas (Gordon 2001). Also, because most biological surveys of marine environments commenced centuries after ships began traversing the globe, many species which are currently considered "cosmopolitan" or even "native" could well have been spread throughout the world before any records were made (Ruiz et al. 2000).

Biodiversity gradients for coastal marine species tend to occur as a mosaic at a wide range of spatial scales, and reflect the geological history of the shoreline as well as contemporary and historical biogeographic barriers to dispersal (Myers 1997; Hooper et al. 2002; Roberts et al. 2002). This can mean that, for particular groups of organisms, variation in species richness can be greater within a continent than between mainland and island biotas. Some islands also have particularly rich marine floras and faunas. For example, southern Australia and New Zealand have rich marine macroalgal floras and bryozoan assemblages. Hawai'i and French Polynesia have particularly rich crab faunas. Conversely, estuaries of continental north-eastern America, and the Baltic, Black and eastern Mediterranean seas, which have relatively large numbers of NIS, are known to have quite depauperate native biotas (see Cohen and Carlton 1998; Galil 2000). Currently, there is little direct evidence that marine biotas of oceanic islands are, on average, less speciose than comparable areas of continental shoreline.

8.5 Insularity and Niche Opportunity

The unique evolutionary history of New Zealand's coastal marine biota has resulted in both missing and functionally distinctive groups of species. Compared with other temperate coastlines, for example, New Zealand has a relatively depauperate crab fauna (Dell 1968), with around 63 species of crab (McLay 1988) – about two-thirds as many as South Australia (93), and less than one-fifth the number of species found in Japan (>337). Most genera (82 %) are represented by only a single species (typical of isolated biotas), with a large percentage of endemic species (53 %). Dell (1968) suggested that many of the niches which are filled by crabs elsewhere appear to be occupied by other organisms or are filled by only a single species in New Zealand.

The recent establishment in Auckland of the large (max. carapace width~110 mm) estuarine swimming crab *Charybdis japonica*, a native of northern Asia, supports the view that New Zealand niches are underrepresented for some groups (Webber 2001). Large portunid (swimming) crabs are important predators of benthic invertebrates in most temperate and subtropical estuarine environments (e.g. *Portunus pelagicus* in temperate Australia; *Callinectes sapidus* on the Atlantic coast of North and South America; various species of *Charybdis* and *Thalamita* in northern Asia). There was no comparable species assemblage in New Zealand estuaries, where native swimming crabs are typically much smaller (e.g. *Nectocarcinus antarcticus*, max. carapace width~87 mm; *Liocarcinus corrugatus*, max. width~26 mm) or are uncommon in estuarine habitats (e.g. *Ovalipes catharus*; McLay 1988). If *C. japonica* becomes more widespread and abundant, then it could have large impacts on native estuarine invertebrate assemblages.

Similarly, the composition of New Zealand's algal assemblage is quite different from those of temperate environments in the Northern Hemisphere. For example, New Zealand has many indigenous species of large brown algae (Phaeophyta) in the order Fucales (31 species from 10 indigenous genera), but comparatively few kelps from the order Laminariales (six species from three indigenous genera). Members of the Fucales are distinctive in that the mature plants (sporophytes) develop directly from settled gametes after fertilization, whereas laminarian kelps have two alternating life-history phases – the large kelp stage, which is the sporophyte generation, and a microscopic gametophyte generation, which functions somewhat like the seed bank of terrestrial angiosperms. Most Fucalean species are perennial, occupy the coastal shallow subtidal zone, and many are fertile in winter. Comparatively few species occur in intertidal habitats in New Zealand. All three of the New Zealand laminarian genera also occur in upper subtidal habitats, and none are intertidal in distribution.

The invasive Japanese kelp *Undaria pinnatifida*, which appeared in New Zealand in 1987 (Hay 1990), is a laminarian alga. Its gametophyte stage is able to tolerate relatively high temperatures, allowing it to penetrate higher on the shoreline than many native fucalean or laminarian species (Dieck 1993). *Undaria* has spread to shorelines throughout southern and eastern New Zealand where it reaches maximal abundance in low intertidal areas and shallow subtidal habitats to around 3 m, extending to depths of 18 m. *Undaria* grows on both sheltered and open coastlines, in clear seas or in highly turbid estuarine waters, on natural substrates or in a wide range of artificial habitats including ropes, buoys, boat hulls, and concrete retaining walls (Hay and Villouta 1993). None of the indigenous laminarian kelps or fucalean species is able to occupy a similarly broad range of substrates or conditions.

Although niche opportunity may explain the success of *Undaria* and *Charybdis* in New Zealand, there are other plausible explanations. *Undaria* has also established adventive populations in regions with diverse laminarian floras, such as on the coasts of Argentina, California, France (both Atlantic and Mediterranean coasts), Spain, and Italy. Its success worldwide may reflect both its high reproductive output and broad habitat tolerances, features which have been selected for during decades of mariculture in Korea, Japan, and China (Hay and Villouta 1993).

Nonindigenous swimming crabs have also invaded elsewhere. *Charybdis helleri*, a close relative of *C. japonica*, recently established populations in Colombia, Cuba, Venezuela, Florida and Brazil, regions which have rich native faunas of swimming crabs (Dineen et al. 2001). Along the Brazilian coast where *C. helleri* has spread, there are up to 20 species of portunid crab, at least four of which occupy similar habitats (Mantelatto and Garcia 2001). The success of *C. helleri* in the Western Atlantic has been attributed to several life-history traits, including a relatively long larval life, short generation time, and the ability of females to store sperm and produce multiple broods from a single insemination. The expanding global range of *C. hell*eri may reflect the tendency for pre-moult and moulting crabs to seek shelter in the crevices of ocean-going ships. In 2000, a single specimen of *C. helleri* was recovered from the sea chest of a fishing vessel which was hauled up for maintenance in Nelson, in New Zealand's South Island (Dodgshun and Coutts 2002).

Marine invaders exhibit considerable variability in resource use (Grosholz and Ruiz 1996). Some, like *Undaria* and *Charybdis*, use distinctly different resources from native species in their introduced range (Lohrer et al. 2000; Byers 2002), others compete directly with native counterparts (Byers and Goldwasser 2001), while still others use different resources in different parts of their introduced range (Grosholz and Ruiz 1996). It is unlikely, therefore, that "empty niche" concepts alone will explain geographic variation in the success of marine invaders.

8.6 Are Marine Species of Islands Poor Competitors?

If island species were poorer competitors than continental species, we should expect that mainland species fail less often when introduced to islands than do island species when introduced to continental areas (Simberloff 1995). Though there are few data to test this hypothesis directly, it is notable that some of the most successful marine introductions have been of island (Japanese) species (e.g. oysters and algae) which were transported to the Americas, Europe and Australia for mariculture. A least 45 NIS have established permanent populations as a result of introductions for fisheries or aquaculture on the mainland coast of the USA (Ruiz et al. 2000). In contrast, only five species appear to have persisted in Hawai'i, although at least 18 marine species have been introduced deliberately for fisheries (Coles et al. 1999a, b; Eldredge and Carlton 2002). Similarly, there have been concerted attempts over the last 50 years to introduce a range of aquatic plants and animals to the Pacific

Islands for the purposes of aquaculture or fisheries (Eldredge 1994). More than 100 different species, including at least 38 marine organisms, have been deliberately transported to the islands (excluding Hawai'i), and most have failed. At least 50 % of the marine species either did not establish wild populations or their status in the introduced environment is unknown (45 %), presumably indicating that they are (at best) uncommon.

In New Zealand, deliberate introductions of marine species have also met with limited success. During the late 1800s, attempts were made to establish wild populations of the European herring (*Clupea harengus*), turbot (*Scophthalmus maximus*), lobster (*Homarus gammarus*), European cancer crab (*Cancer pagurus*), Pacific salmon, and three species of cord grass (*Spartina*). Only the Pacific salmon, and cord grass gained a lasting foothold (Cranfield et al. 1998). Many of these attempts appear to have failed because the original stock suffered high mortality during shipment, and relatively few individuals were actually released into the wild. Nevertheless, between 1908 and 1914, around $1x10^6$ lobster (*H. gammarus*) larvae and $12x10^6$ crab (*C. pagurus*) larvae were liberated from hatchery facilities in Dunedin (Thomson 1922). Neither established successfully in New Zealand waters.

No endemic marine species from Hawai'i are known to have established in other parts of the world (Carlton 1987), but a number of endemic New Zealand marine species have been successfully transported elsewhere. During the 1920s, crates of New Zealand oysters (*Tiostrea chilensis*) were shipped alive submerged in water to Tasmania, Australia (Cranfield et al. 1998). At least nine other native New Zealand species (*Astrostole scabra*, *Patiriella regularis*, *Neilo australis*, *Venerupis* (*Paphirus*) *largillierti*, *Maoricolpus roseus*, *Cancer novaezelandiae*, *Halicarcinus innominatus*, *Petrolisthes elongatus*, *Chiton* (*Amaurochiton*) *glaucas*) are thought to have accompanied these shipments and subsequently became established there. However, most have not spread far from the point of introduction, with one notable exception, the New Zealand screw shell, *Maoricolpus roseus*, which occurs in vast beds in northern Bass Strait, south-eastern Australia. This area contains among the most diverse native marine soft-sediment assemblages anywhere in the world (Gray et al. 1998). *Maoricolpus* has also spread to the coasts of eastern Tasmania, Victoria and New South Wales. Other New Zealand species have been recorded elsewhere in Australia (e.g. green mussel, *Perna canaliculus* – Tasmania and South Australia; flat oyster, *Tiostrea chilensis* – Victoria; isopod, *Eurylana arcuata* – New South Wales and South Australia; fish, *Fosterygion varium* – Tasmania; fish, *F. lapillum* – Victoria), the USA (e.g. isopod, *Sphaeroma quoyana*; sea slug, *Philine auriformis*), the UK (barnacle, *Elminius modestus*; flat oyster, *Tiostrea chilensis*), and Europe (macroalga, *Asparagopsis armata*, also a native of Western Australia; amphipod, *Corophium sextonae*; Gosliner 1995; Cranfield et al. 1998; Lockett and Gomon 2001; Reise et al. 2002). The relatively high number of native New Zealand species which have been successfully exported (mostly unintentionally) to other regions of the world is disproportionate to the country's size and importance as a shipping nation, and argues against the idea that island species are necessarily poor competitors.

8.7 Do NIS Have Greater Impacts in Island Environments?

Native species with restricted geographic ranges (such as those occurring on islands) are thought to be more prone to extinction simply because an invader can affect a larger proportion of the total population (Parker et al. 1999). Intuitively, this should also hold true for marine populations, despite the high dispersal capabilities commonly assumed for marine species. Indeed, recent ecological, biogeographic and genetic studies have challenged conventional ideas about the "openness" of marine populations by showing that population subdivision, narrow endemism, and small range sizes are more common than previously suspected (Myers 1997; Benzie 1998; Hooper et al. 2002). In New Zealand, up to 90 % of the known species of marine molluscs, 66 % of shallow water amphipods, 95 % of sponges, 60 % of crabs, 60 % of bryozoans, 35 % of macroalgae and 28 % of reef fishes are endemic (Towns and Ballantine 1993; Myers 1997; Francis and Nelson 2003). The geographic range sizes of many of these species are extremely small. For example, several of the small islands within the New Zealand archipelago, such as the Three Kings (484 ha), Chatham (97,244 ha), Snares (333 ha) and Antipodes (2,095 ha) islands, contain species endemic to individual islands (Nelson 1994). Other isolated island groups such as the Marquesas, Mauritius, Easter Island, Society Islands, St. Helena, Ascension Island and the Galápagos Islands also support many marine species whose distribution is restricted to the island chain (Norse 1993; Roberts et al. 2002). Analogously, movement of tectonic plates and dynamic discontinuities in ocean currents have, over evolutionary time, created sharp barriers to dispersal which limit the range of marine species on continental coastlines. We predict that the impacts of invasions will be most severe in regions where many species have relatively restricted ranges, and that these will not necessarily be confined to oceanic islands. Importantly, the review by Roberts et al. (2002) covered only a few marine groups, these being relatively large and well studied. We expect that other marine groups, many of which have poorer dispersal capabilities than those examined by Roberts et al. (2002), will also contain high numbers of species with very restricted ranges.

Marine invaders are capable of a variety of ecological effects, the most cited of which tend to be competition for resources, habitat alteration, and trophic interactions (predation and herbivory) with native species (Parker et al. 1999; Ruiz et al. 1999). Much information on impacts, however, is anecdotal and relatively few studies have measured the three fundamental dimensions which determine the total impact of an invader: its range, abundance, and per capita impact in the introduced range (Parker et al. 1999). A comparison of the vulnerability of island and continental biotas also requires (at least) contrasting the per capita effects of invaders in each setting independently of the invader's range and abundance. There are few examples of such studies, in part because they are methodologically challenging. Creese et al. (1997) and Crooks (1998) determined the effects of habitat alteration by dense mats of the exotic bivalve *Musculista senhousia* in Auckland, New Zealand, and San Diego, USA respectively. In the New Zealand study, species richness and total abundance of macroinvertebrates were generally lower inside the mats than in adjacent control areas (Creese et al. 1997). Suspension-feeding bivalves were most affected, with an 87 % reduction in average densities inside the mats at one site. In contrast, Crooks (1998) found that macrofaunal densities and species richness were typically greater inside than outside the mats. Although the contrasting impacts found in these two studies could be interpreted as evidence for a regional difference in the effects of *M. senhousia*, a more parsimonious explanation is that they represent different points on a spectrum of possible outcomes in each country. The composition of marine soft-sediment assemblages varies widely in space and time, resulting in localized and idiosyncratic effects of an invader. Greater spatial replication of the observations could have revealed a range of effects of *M. senhousia* mats in each country. Indeed, of the two sites sampled by Creese et al. (1997), one exhibited a deleterious effect of the mats on macrofauna, whereas no significant changes in invertebrate richness or abundance were found at the other. Demonstrating regional differences in the per capita effects of an invader requires tests which show variation between island and continental ecosystems is greater than that within each ecosystem.

8.8 Is Propagule Pressure to Islands Greater than to Mainland Areas?

Many successful marine invaders have strong associations with human transport vectors, and have repeatedly been transported by ships around the globe. Their success outside their native range may be related as much to the frequency with which they are transported ("propagule pressure") as to the susceptibility of recipient ecological assemblages ("niche availability"). Although small island states such as New Zealand, Hawai'i and the Marianas are heavily dependent on maritime trade (Nawadra and Gilbert 2002), they receive comparatively little of the world's shipping traffic. The majority of international shipping occurs within and between continental Europe, North America and East Asia. The International Maritime Organization estimates that around $3x10^9$–$5x10^9$ m^3 of ballast water is transferred internationally each year (2000–2005) from more than 45,000 commercial cargo vessels (Carlton 2001;

GloBallast 2005). Each cubic metre of ballast water can contain up to 1,000 marine organisms from as many as 16 taxa (Smith et al. 1999). Compliance records kept by the New Zealand Ministry of Fisheries show that at least 2.8x10^6 m^3 of ballast water was discharged in New Zealand in 1999 from ca. 2,000 international vessel movements (Inglis 2001). This is twice the volume discharged into the Port of Melbourne, Australia, each year (1.2x10^6 m^3; Walters 1996), but about half the amount discharged within the State of Victoria, Australia (5.8x10^6 m^3; Walters 1996), and less than one-fifth of the volume of ballast discharged into the port of New Orleans, USA, annually (~13.5x10^6 m^3; Smith et al. 1999).

Ballast water discharged into New Zealand ports is currently sourced from more than 23 different countries, but the majority comes from the temperate northwest Pacific (Japan, China, Hong Kong, Taiwan, South Korea, 71 %) and Australia (29 %; Inglis 2001). Most of the recent arrivals of NIS to New Zealand also come from these two regions. Since 1960, at least three species of crab, three macroalgae, five species of mollusc, one bryozoan, and one species of fish have arrived in New Zealand from the north-western Pacific (Cranfield et al. 1998). In Hawai'i, the main source regions for NIS appear to be the western and central Indo-Pacific (Eldredge and Carlton 2002), reflecting wartime shipping during the 1940s. Most ballast water entering Hawai'i is now sourced from the west coast of North and Central America, but large numbers of fishing boats, which do not discharge ballast, still enter the islands from Asia (Godwin and Eldredge 2001).

8.9 Conclusions

Nonindigenous species invasions are transforming coastal marine ecosystems throughout the world. While the initial results are alarming, the current status of marine taxonomy, systematics and biogeography do not allow the true extent of the problem, or regional variations in the prevalence and impacts of introduced marine species, to be determined clearly. We have attempted to show why conventional explanations for the susceptibility of island biotas to invasions are not currently amenable to tests in marine environments and, indeed, may not be applicable. The case studies which we have reviewed make it clear that marine invaders can have severe impacts on the ecology of both island and continental biotas. We found no evidence that native marine biotas of islands are any more or less susceptible to invasion, or that they are more severely affected by them, than is the case for continental biotas. Many of these hypotheses await more rigorous treatment as more data become available.

As in other ecosystems, we expect the effects of marine invaders to be of greatest consequence for those native species which have highly restricted distributions and limited capacity to expand their range, and for local populations which are not replenished by recruitment from outside infested areas.

Successful establishment by an NIS outside its natural range is a highly probabilistic outcome which depends upon the coincidence between delivery of the species to the new location and suitable conditions for establishment, including the absence of enemies and the availability of resources. Both the supply characteristics (i.e. propagule pressure) and opportunity for establishment (i.e. niche opportunity) are likely to be highly variable in space and time in marine systems. Although there are few data on rates of transport, the geographic origins of invaders in different parts of the world reflect the predominant shipping routes into each region (Carlton 1996). Species with habitat preferences (e.g. Wonham et al. 2000), environmental tolerances, or life-history strategies which predispose them to transport by human vectors are likely to reach new locations more often than are other organisms.

The composition of marine assemblages and ecological interactions within them are strongly influenced by the rate of supply of new recruits and the frequency of resource-releasing disturbances (Underwood and Fairweather 1989). We believe, therefore, that the most profitable studies of invasion success will be those which vary supply characteristics in combination with resource availability. By shifting the theoretical emphasis away from considering invasion resistance as a static function of species diversity to a more dynamic consideration of resource utilization and availability, we should gain a better understanding of how the frequency of invasion is influenced by temporal and spatial variability in the host environment.

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