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Chapter 5

How Anthropogenic Activities Affect the Establishment and Spread of Non- Indigenous Species Post-Arrival

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HOW ANTHROPOGENIC ACTIVITIES AFFECT THE ESTABLISHMENT AND SPREAD OF NON-INDIGENOUS SPECIES POST-ARRIVAL

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When humans transport a species to a location outside its native range, multiple biotic and abiotic factors influence its post-arrival establishment and spread. Abiotic factors such as disturbance and environmental conditions determine the suitability of the new environment for an invader, as well as influence resource availability and ecological succession. Biotic processes such as competition, facilitation, predation and disease can either limit or promote invasion, as can emergent community-level traits such as species diversity. Synergies arise when the abiotic and biotic factors controlling invasion success are themselves influenced by anthropogenic activities, such as those associated with coastal urbanization and industrialization. Here we present a review of the major anthropogenic activities that affect the success of non-indigenous species (NIS) post-arrival. We prioritize the factors in terms of their ecological and evolutionary importance, and present potential management actions to reduce NIS success post-arrival. Evidence-based management has the potential to mitigate anthropogenic activities that enhance invasion success. High priority management actions include: 1) the removal, or containment, of legacy contaminants and reduction of new inputs to reduce the competitive advantage that some invaders have in contaminated environments, 2) the redesign of artificial structures to reduce colonization by NIS through eco-engineering, selection of construction materials and the 'seeding' of structures with native species to provide a priority advantage, 3) the management of dominant regional transport pathways to ensure that the risk of transporting NIS via our increasingly complex transport networks is minimized and 4) the protection and maintenance of biotic resilience in the form of intact living habitats and endemic diversity. Further research is required to advance our understanding of the role of anthropogenic activities in driving post-arrival success of NIS. Such work is vital for developing responsive and mechanistic management plans and ultimately for reducing the impacts of marine invasive species.

Introduction

The invasion of natural ecosystems by non-indigenous species (NIS) is one of the greatest threats to native biodiversity (Wilcove et al. 1998, Butchart et al. 2010). Although only a small proportion of NIS artificially transported to new regions establish, spread and cause impacts (Williamson et al. 1986, Suarez et al. 2005, Blackburn et al. 2011), successful invasions have had a wide range of effects on native biota. The post-arrival establishment of NIS is strongly influenced by a number of biotic and abiotic factors (Theoharides & Dukes 2007, Forrest et al. 2009). For example, ecological interactions such as competition, facilitation, predation or disease and environmental factors such as temperature and salinity may produce synergies that allow ecological dominance of NIS (Castilla et al. 2004). Species traits, such as predatory avoidance or growth rate, can sometimes be linked to the success of NIS over natives (Van Kleunen et al. 2010, McKnight et al. 2016). Abiotic influences such as disturbance can regulate resource availability, which may in turn affect invasibility (Davis et al. 2000, Airoldi & Bulleri 2011). Therefore, understanding biotic and abiotic factors that govern the survival and success of NIS and their populations post-arrival is key. In addition, it is important to have a good understanding of major anthropogenic factors that interact with these factors and ultimately shape the success of NIS post-arrival. In particular, anthropogenic factors associated with urbanization and industrialization are key for improving our understanding of post-arrival NIS success (Figure 1). Anthropogenic activities on land and in the ocean change physico-chemical parameters of marine habitats, such as water and sediment quality, directly influencing NIS. However, many NIS have wide tolerances to environmental conditions (Dukes & Mooney 1999, Sorte et al. 2010, Zerebecki & Sorte 2011, Rius et al. 2014b) and to highly toxic chemicals

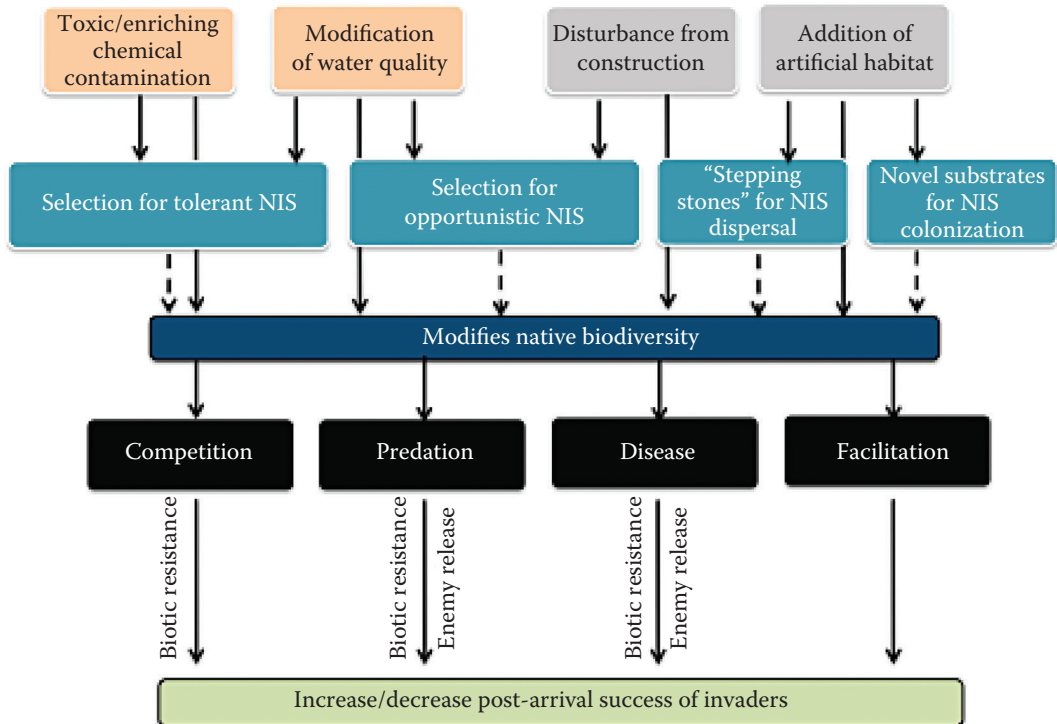


Figure 1 Chemical (orange) and physical (grey) disturbances from human activities that influence the post-arrival success of invaders. Effects of disturbance on NIS can be direct (dark green) or indirect (blue), and can affect associated biotic processes (black). Direct interactions are illustrated by an unbroken line; indirect interactions are illustrated by a broken line.

such as copper biocides (Prentis et al. 2008, Piola et al. 2009). Hence, anthropogenic activities that promote extreme environmental conditions might provide a post-arrival advantage for NIS.

The global increase in anthropogenic activities has resulted in previously-undisturbed marine and estuarine environments being transformed into habitats with artificial features such as pontoons, jetties, breakwaters, boating marinas and commercial ports (Dugan et al. 2011). The physical characteristics of artificial structures tend to differ markedly from that of natural systems (Airoldi et al. 2005, 2009, Airoldi & Beck 2007), creating environmental novelty and newly available artificial habitat (Glasby & Connell 1999). Urban sprawl into our waterways and the construction of vessel infrastructure also results in hydrological modifications that reduce flow and increase silt, nutrient and contaminant retention (Johnston et al. 2011, Rivero et al. 2013).

Human-assisted regional translocation of species can increase connectivity, overcoming barriers to natural dispersal and facilitating the post-establishment spread of NIS, with patterns and rates of spread being very different from those achieved via natural dispersal (Buchan & Padilla 1999, Ruiz & Carlton 2003). Intraregional transport increases propagule pressure of NIS (Zabin et al. 2014). Such transport patterns are likely to increase the frequency of propagule arrival, which is correlated with NIS success in both theoretical (Leung et al. 2004) and experimental studies (Clark & Johnston 2009, Hedge et al. 2012).

Vectors that initially transport a species beyond its native range have been the focus of NIS science and management for decades (Carlton 1985, Ruiz et al. 1997, Hewitt & Campbell 2008, Davidson et al. 2010). After a marine non-indigenous species has arrived, less attention and resources are allocated to its management as removal or control is automatically deemed too expensive or logistically impossible. If we pay more attention to the factors affecting NIS success post-arrival in a new region we can identify the biotic and abiotic conditions that will be important for the likelihood of a species' establishment and spread. For example, more information is needed to understand how human activities influence species traits that promote biological invasions. Such factors may be more amenable to management and more effective than attempts at direct eradication via physical removal or chemical/biological control.

In this paper, we explore the anthropogenic factors that influence the successful establishment and spread of introduced species in the marine environment, post-arrival (Figure 1). We first provide an overview of the major anthropogenic influences to marine environments and describe how they may affect NIS. We separate these factors into four major categories of change: chemical and physical changes to environments, changes to connectivity and changes to the biological aspects of recipient environments. Finally, we highlight areas in which there is potential for effective management of NIS post-arrival.

Chemical alteration of recipient environments

Contamination and changes to water quality

The intense and extensive development by humans across the planet has subjected much of the world's biological diversity to frequent chemical changes, which are often concentrated in urban and industrial areas (Grimm et al. 2008). Human activity is reliant on access to freshwater and trade such that it becomes concentrated around waterways. These activities inevitably release contaminants into water bodies and result in other modifications to physico-chemical conditions. As a consequence, estuaries in particular have been highly impacted by chemical change related to agriculture, industrialization and urbanization, with almost all estuaries suffering some degree of impact (Lotze et al. 2006). An example is fertilizer runoff into waterways; fertilizer use is already responsible for the eutrophication and formation of 'deadzones' in many of the world's coastal waterways (Rabalais et al. 2010); global nitrogen and phosphorous effluent is predicted to increase between 150–180% between the years 2000–2150 (Marchal et al. 2011, Alexandratos &

ANTHROPOGENIC ACTIVITIES AFFECT POST-ARRIVAL SUCCESS OF NIS

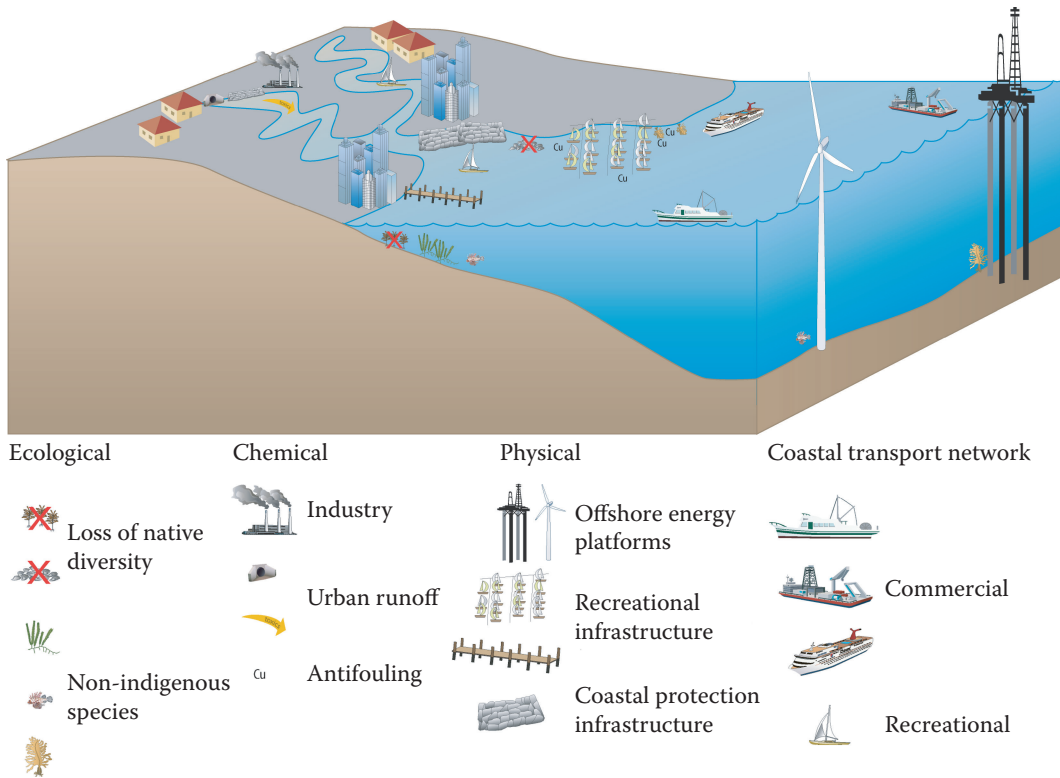


Figure 2 Anthropogenic factors influencing the establishment and spread of NIS include chemical and physical alterations of habitat, which interact with ecological traits and processes, as well as coastal transport networks. The introduction of chemicals from industrial and urban runoff and vessel antifouling paint may facilitate metal-tolerant NIS and reduce native biodiversity. Increasing coastal development adds novel habitat such as recreational infrastructure (e.g. marinas and jetties) and coastal protection infrastructure (e.g. sea walls) for colonization by NIS, and creates stepping-stones for their spread. These structures are linked by busy coastal transport networks, such as commercial and recreational vessel movements or aquaculture operations, which can act as vectors for NIS for inter- and intraregional spread.

Bruinsma 2012). Important chemical stressors include toxic contaminants (e.g. metals) (Birch 2000, Rodríguez-Obeso et al. 2007, Burton & Johnston 2010) and enriching contaminants (e.g. nutrients) (Statham 2012) (Figure 2).

Chemical stressors that are released into waterways impact the ecological composition and function of important habitats (Johnston & Roberts 2009, Burton & Johnston 2010). Metals are known to have toxic effects on aquatic taxa, including increased mortality (Tranum et al. 2004, Martínez-Lladó et al. 2007), reduced reproductive potential (Alquezar et al. 2006, Simpson & Spadaro 2011) and other sublethal effects (Fleeger et al. 2003). Nutrients such as dissolved nitrogen and phosphorus can also have community-wide effects, with high levels resulting in a community composed of very high densities of a few tolerant opportunistic species (Pearson & Rosenberg 1978). However, in contrast to toxic contaminants, such nutrients initially have an enriching effect, increasing the richness and abundance of primary producers with consequences at higher trophic levels (Tewfik et al. 2005, Smith et al. 2006, Elser et al. 2007, McKinley & Johnston 2010, Clark et al. 2015).

Environmental suitability is now acknowledged as a strong predictor of invasion success, and consideration of the role of chemical parameters has generally emphasized natural environmental variables such as dissolved oxygen (DO), pH, salinity and temperature (Williamson et al. 1986, Blackburn & Duncan 2001). There has been less consideration of how anthropogenic modifications

to environmental conditions may influence the establishment and spread of NIS. Locations where NIS are often introduced are low flow, high retention sites (naturally or by construction) (Floerl & Inglis 2003, Rivero et al. 2013) and therefore also locations of high contaminant retention (Dafforn et al. 2008, Johnston et al. 2011). Where the transport process for NIS is environmentally stressful (e.g. copper-coated vessel hull), it is likely that selection for environmentally tolerant (particularly to copper) NIS will take place (McKenzie et al 2012). This will lead to greater success of NIS in anthropogenically-modified habitats.

Toxic and enriching contaminants aid post-arrival success of NIS

The addition of toxic contaminants is perhaps the least intuitive reason for increasing NIS success, but is the area in which we have the strongest experimental and mensurative data to support the hypothesis. The mechanism is relatively simple and relies on selection for toxicant tolerance in NIS (Piola & Johnston 2009, McKenzie et al. 2012). Elevated concentrations of metals, for example, are highly toxic to many marine organisms (Hall et al. 1998), but some organisms have evolved effective detoxification and avoidance mechanisms and are considered to be superior in their ability to withstand exposures to these toxicants (Johnston 2011).

The majority of marine NIS are transported in ballast water or as hull-fouling organisms (Ruiz et al. 1997, 2000, Hewitt 2002, Godwin 2003, Clarke Murray et al. 2011) and both of these transport mechanisms are highly contaminated with metals (Alzieu et al. 1986, Claisse & Alzieu 1993, Schiff et al. 2004, Warnken et al. 2004, Piola et al. 2009, Dafforn et al. 2011). Hulls are contaminated because they are often coated in toxic antifouling paints containing metal-based biocides, and ballast water tanks are sometimes antifouled and often corroding internally (Tamburri et al. 2005). The transport process may therefore select for metal tolerance, and the major contaminants in ports and harbours are metals (Piola et al. 2009). Metal tolerance has now been observed in a wide range of marine organisms including polychaetes, bryozoans, algae, amphipods and barnacles (reviewed by Johnston 2011, Pineda et al. 2012). Hence, shipping selects for metal-tolerant species, then delivers them to metal-contaminated locations (Piola & Johnston 2008a). This gives NIS arrivals a competitive advantage over local native species that may not have developed tolerance. However, it should be noted that native species can also adapt or become tolerant and there is potential for toxicant tolerance to be a useful risk-identifier for predicting future NIS (Dafforn et al. 2009a). Some studies have observed that assemblages switch from native-dominated to NIS-dominated when exposed to a small strip of antifouling paint (Piola & Johnston 2008a) – an effect as relevant in small marinas as it is in large working ports (Dafforn et al. 2009a). Interestingly, large-scale surveys of selected NIS are now finding that these species possess higher tolerance to metals in more polluted environments than in pristine habitats (Clark et al., unpublished data), and it would appear that NIS have the ability to lose tolerance (which can be costly to fitness) when spreading from contaminated to clean systems (Piola & Johnston 2006).

The addition of nutrients to a system is an example of the addition of resources, and is therefore more readily understood as a mechanism for increasing the success of NIS (Davis et al. 2000). Many high-impact NIS are ‘weedy’ (reviewed by Sutherland 2004) with an ‘r-type’ life-history strategy (Ruiz & Hewitt 2002, Hänfling et al. 2011) so they are therefore capable of dominating in high-resource environments. This has been demonstrated for land-based weeds (Grime 1977, Dukes 2001) – more research is required for marine species, but disturbance that renews resources is certainly a facilitator (Clark & Johnston 2009, 2011, Airolidi & Bulleri 2011). Humans elevate nutrients in nearshore areas via run-off from agricultural and urbanized areas and through the release of sewage (Figure 2). Nutrients may be limiting in marine systems and hence anthropogenically-modified waterways may be more productive than natural systems (Nixon et al. 1986, 2001). Productivity increases may result from large changes in community composition (Duarte 1995). Productivity increases will occur up until thresholds are exceeded and excessive eutrophication

takes place, reducing water quality and causing oxygen depletion as has happened in much of the Baltic Sea (Carstensen et al. 2014). Thresholds and tipping points will differ for each habitat and each NIS and are therefore difficult to predict without extensive monitoring. Up until such tipping points are reached, the system is increasingly susceptible to fast-growing weedy species that are able to rapidly take advantage of excess primary and secondary food sources (Clark et al. 2015). Non-indigenous species are often considered ‘weedy’ species and examples of this are the fast-growing invasive *Caulerpa* macroalgal species (Williams & Smith 2007) and harmful microalgae, which have a tendency to bloom in high-nutrient conditions (Hallegraeff & Gollasch 2006).

Changes in water quality and hydrological regimes

Due to a paucity of empirical studies, it is difficult to generalize the response of NIS to anthropogenic modifications of water quality *per se*. Where our activities push these parameters beyond natural realms of variability, we might expect that modifications will benefit species with wide environmental tolerances. Species that benefit are unlikely to be the resident native species that have evolved under historical conditions and will be disadvantaged by changed environmental or biological regimes. Water quality modifications may also be of concern if they represent a change in natural habitat or a uniformity of conditions that, as a result, drives biotic homogenization (McKinney & Lockwood 1999). Anthropogenic modifications of hydrological regimes will likely increase in the future as inland waterway transport is predicted to rise and there will be a greater need for expansion and new canal developments to support this trade (Galil et al. 2007, 2015). These modifications in hydrological regimes are likely to occur together with an increase in available suitable habitat for colonization by NIS. Increasing drought will drive water extractions from river sources, with associated impacts further downstream in estuaries. The interaction of water-usage practices and climate change anomalies has the potential to create invasion windows. For example, the co-occurrence of increased freshwater extraction and increased drought severity is thought to have created saline conditions in San Francisco estuary that benefitted a non-indigenous zooplankton species (Winder et al. 2011). Anthropogenic activities and associated stressors tend to be a common problem and may establish a particular set of conditions that are replicated in harbours around the globe (Halpern et al. 2008, Knights et al. 2013, Pearson et al. 2016). NIS are transported from multiple locations, but it is possible that these locations may have similar water quality conditions because they are busy ports or marinas, usually characterized by low flow, high turbidity, low DO and high nutrient conditions. These situations can create environments that suit a set of species representing ‘harbour-tolerant’ conditions as described in Floerl et al. (2009a).

Regime shifts associated with climate change may lead to the exacerbation of hydrological regime change and impacts on water quality (Delpla et al. 2009, Whitehead et al. 2009). It is inherently difficult to make predictions in complex ecological systems, but climate change will change the nature of basic chemical interactions. Increasing temperature and pH both have the potential to increase the availability of toxic contaminants (Schiedek et al. 2007, Sokolova & Lannig 2008, Nikinmaa 2013) as does increasing storm activity, which resuspends contaminated sediments (Eggleton & Thomas 2004). With temperature increases, we might also expect increases in primary productivity and an increased frequency of eutrophic events and hypoxia (Rabalais et al. 2009, Moss et al. 2011, O’Neil et al. 2012).

Physical alteration of recipient environments

Estuarine, coastal and offshore development

The estuarine environment faces increasing pressure from encroaching urban and industrial developments (Figure 2). Historically, the majority of human settlement has occurred within 100 km of

the coast (Bulleri 2006, Firth et al. 2016) and, despite these areas being at most risk from climate change events, this trend continues (McGranahan et al. 2007). World population growth is projected to increase from 7.2 to 9.6 billion in 2050 (Gerland et al. 2014) and resource demand will result in increased exploitation of the marine environment. For example, some areas of Europe have lost 50–80% of coastal wetlands and seagrasses to development to support urban activities (reviewed by Airoldi & Beck 2007). Anthropogenic habitat modification also extends beyond the coastal zone as world population growth has driven the search for new energy sources off shore (Asif & Muneer 2007). The discovery of new oil and gas reserves, such as those in the Arctic region, will result in the continued construction of near and offshore production platforms (Asif & Muneer 2007). Over 7500 offshore oil and gas platforms had been constructed worldwide as of 2003 (Hamzah 2003, Parente et al. 2006). Similarly, renewable energy is moving off shore with the construction of marine wind farms (Kennedy 2005, Punt et al. 2009). To exploit renewable energy sources, several thousand turbines will be constructed in wind farm clusters along the European Atlantic coast (Kennedy 2005) and, presumably, other global locations (Firth et al. 2016). Offshore energy platforms may appear relatively isolated, but they are linked to coastal areas by vessel movements (e.g. maintenance) and therefore can act as sinks or sources of NIS propagules (Yeo et al. 2009, Sammarco et al. 2010, Adams et al. 2014). Furthermore, the decommissioning of offshore installations may remove the structures that support NIS or leave behind permanent structures for NIS that are no longer maintained or monitored (Schroeder & Love 2004, Page et al. 2006, Macreadie et al. 2011). Underwater pipelines have received less attention in relation to their potential impacts, but they connect offshore energy infrastructure with coastal zones and introduce other novel structures to the marine environment that may be colonized by NIS or facilitate their spread (Feary et al. 2011).

Habitat modification often involves the addition of structures that may increase or replace existing natural habitat (Glasby & Connell 1999). Common structures added to coastal zones include sea walls, break walls and groynes constructed to protect urban coastal zones and maritime vessels (Mineur et al. 2012). Marinas and ports are often protected by break walls and infrastructure within these areas includes pilings and pontoons to support vessel berthing. Furthermore, vessel transport is supported by hydrological modifications including the construction of canals and other waterways. Similarly, offshore energy platforms, while built above the waterline, require extensive underwater scaffolding (Wilson & Elliott 2009). Comparisons of artificial structures and natural habitats have revealed distinct differences in the assemblages able to colonize and persist on them (Connell & Glasby 1999, Glasby 1999a, Glasby & Connell 1999, Atilla et al. 2003, Chapman & Bulleri 2003, Bulleri & Chapman 2004, 2010, Firth et al. 2016). Differences between anthropogenic and natural hard-substratum habitats arise due to their physical characteristics, including substratum composition and microhabitats (Anderson & Underwood 1994, Glasby 2000, Chapman & Bulleri 2003, Chapman 2011, Firth et al. 2013, 2014, Browne & Chapman 2014), age (Perkol-Finkel et al. 2005, Pinn et al. 2005, Burt et al. 2011), orientation or incline (Connell 1999, Glasby & Connell 2001, Saunders & Connell 2001, Knott et al. 2004, Langhamer et al. 2009, Chapman & Underwood 2011, Firth et al. 2015), predation levels (Clynick et al. 2007, Nydam & Stachowicz 2007), illumination levels (Glasby 1999b, Shafer 1999, Marzinelli et al. 2011, Davies et al. 2014), disturbance levels (Airoldi & Bulleri 2011) and movement (Holloway & Connell 2002, Perkol-Finkel et al. 2008, Shenkar et al. 2008, Dafforn et al. 2009b). The increasing transformation of natural to urbanized coastlines has promoted the establishment and spread of NIS (Bulleri & Airoldi 2005, Bulleri et al. 2006, Airoldi et al. 2015).

Artificial structures aid establishment and dispersal of NIS

The addition of artificial structures in close proximity may provide ‘stepping stones’ for NIS (Glasby & Connell 1999, Coutts & Forrest 2007) (Figure 2), providing ‘corridors’ for their spread and dispersal (Bulleri & Airoldi 2005, Airoldi et al. 2015). Propagules released from one structure have

a higher chance of making it to other structures where the presence of NIS is often higher than in surrounding natural habitats (often sedimentary, Airoidi et al. 2015). The large amount of artificial structures in ports and harbours provides suitable habitat in close proximity to key vectors, such as commercial and recreational vessels (Bulleri & Airoidi 2005) (Figure 2). Some invasive fouling NIS exhibit preferences for shallow floating artificial structures (Lambert & Lambert 1998, Glasby et al. 2007, Dafforn et al. 2009b), potentially because they present a similar surface to a vessel hull with respect to movement and depth (Neves et al. 2007). Such artificial habitats unprecedentedly provide downward-facing surfaces, which are uncommon in natural ecosystems (Miller & Etter 2008). Thus, certain species that were present in low abundance in nature are now thriving in these new environments. Research on larval phototaxis and geotaxis of ascidians (arguably one of the most important marine groups in terms of NIS) (Zhan et al. 2015), found that some globally-distributed species show settlement preference for downward surfaces (Svane & Dolmer 1995, Rius et al. 2010). In addition, studies have shown that recruitment of fouling species are enhanced within proximity to a pier (Hedge & Johnston 2012) and shading (Miller & Etter 2008). Moreover, the design of ports and marinas can disrupt tidal flushing and result in vastly local increased recruitment rates (Floerl & Inglis 2003, Johnston et al. 2011, Toh et al. 2016), but also increase regional connectivity by creating a network of substrata away from initial invader entry points (Knights et al., 2016). As a result, the characteristics of marinas increase retention of NIS propagules and provide a substratum for their establishment (Vaselli et al. 2008). This effect has been so strong that association with artificial structures has been used as a criterion for classifying species as non-indigenous (Chapman & Carlton 1991). Even temporary or removable infrastructure, such as slow-moving barges and drilling rigs, can cause changes to the local habitat. During their period of operation, these floating structures provide a hard substratum for colonization of NIS, often surrounded by soft-sediment habitats (Sheehy & Vik 2010). Invasive corals of the genus *Tubastraea* have, in recent years, colonized an ever-increasing proportion of oil-production infrastructure off the coasts of Brazil and southern USA (Sammarco et al. 2010, 2012, 2014, Costa et al. 2014). Hydrological modifications have also been implicated in the spread of NIS. For example, canals and waterways provide links between distant areas that would otherwise be isolated (Galil et al. 2007, Bishop et al. 2017). The increased addition of artificial structures into coastal areas and hydrological modifications that link isolated waterways provide NIS with 'stepping stones', networks and 'dispersal corridors', respectively (Glasby & Connell 1999, Bulleri & Airoidi 2005, Coutts & Forrest 2007).

The increasing intensity of storms and rising sea levels associated with climate change are likely to increase the need for artificial coastal defences to be constructed on a global scale (Nicholls & Mimura 1998, Moschella et al. 2005, FitzGerald et al. 2008). At the same time, climate change has created environmental conditions that have facilitated significant range expansion of various species (Barry et al. 1995, Hawkins et al. 2009, Ling et al. 2009, Mieszkowska et al. 2014, Rius et al. 2014a). Therefore, increased connectivity from networks of hard structures, together with climate change, may additively enhance the spread of NIS by providing habitat for colonization in areas opened up by warming temperatures (Ware et al. 2014, Firth et al. 2016). In addition to warming, there is a growing number of studies reporting more frequent extreme weather conditions (e.g. significantly larger differences between minimum and maximum seawater conditions, Wernberg et al. 2011, 2012, 2013), which facilitates the success of species with broader thermal ranges (Rius et al. 2014a).

In addition to increasing energy demands over the next decades, an increased demand for protein will result in a considerable expansion of the global aquaculture industry (FAO 2012). This will involve the construction of larger and denser aggregations of fin and shellfish farms in coastal regions that provide extensive artificial habitats to NIS (Fitridge et al. 2012). Another example is the Norwegian salmon farming industry that currently operates ~ 700 coastal farms, each comprising approximately 50,000 m² of artificial habitat (Bloecher et al. 2015), and is predicted to grow five-fold by 2050 (Olafsen 2012). Aquaculture facilities are a major vector of NIS (Voisin et al. 2005, Fitridge et al. 2012, Aldred & Clare 2014), not only because they intentionally introduce NIS to be

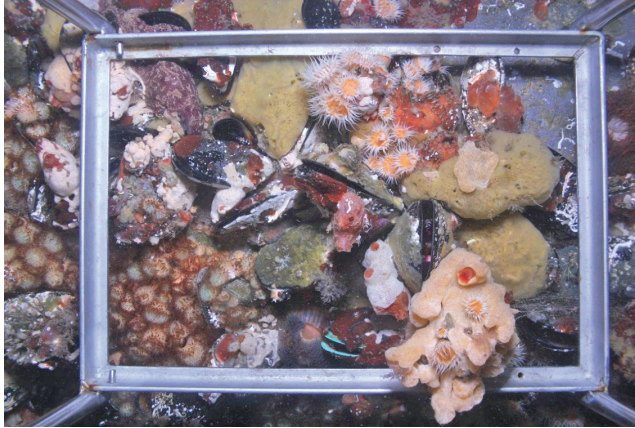


Figure 3 Extensive fouling of a salmon farm pontoon supports a diverse community of non-indigenous species, including the invasive ascidian, *Didemnum vexillum*. The development of dense aquaculture farming regions can facilitate the human-assisted spread of NIS and disease pathogens via the provision of stepping-stone habitats and a complex transport network. (Photo: Javier Atalah, Cawthron Institute)

farmed, but because they unintentionally transport associated organisms that may establish and spread in the new range (Rosa et al. 2013, Woodin et al. 2014, Grosholz et al. 2015) (Figure 3). Once the farmed or associated species grow, they release propagules that will settle both in the aquaculture facilities and elsewhere. After the initial introduction in the 1970s of the Mediterranean mussel, *Mytilus galloprovincialis*, for farming in South Africa, this species spread more than 2000 km, where it now dominates extensive sections of the rocky intertidal zone (Rius et al. 2011). In addition, the presence of aquaculture facilities has provided new artificial substrata where other NIS that coexist with the farmed NIS can thrive (Rius et al. 2011). Research has shown that such coexistence can allow persistence over long periods, which means that aquaculture facilities act as incubators for multiple NIS. Another problem associated with aquaculture facilities is the accidental release of the non-indigenous farmed stock (Schröder & De Leaniz 2011), such as the case of fish farms in Chile (Soto et al. 2001, 2006, Soto & Norambuena 2004). Finally, the development of dense aquaculture farming regions can facilitate the human-assisted spread of NIS and disease pathogens via the provision of stepping-stone habitats for natural dispersal and a complex transport network (Murray et al. 2002, Morrisey et al. 2011) (Figure 4).

Connectivity: coastal transport networks

Commercial and recreational vectors

Once established, the spread of marine NIS is often facilitated through the presence of extensive transport networks associated with coastal shipping, boating and aquaculture. Urbanized coastlines are characterized by the presence of commercial ports, boating marinas, ferry terminals and other infrastructure that are associated with a wide range of vectors, including merchant ships, cruise liners, naval vessels, car and passenger ferries, water taxis, recreational yachts, dredges, barges and others (Figure 2). Movements of these vectors occur at local (e.g. car ferries, water taxis, service vessels), regional or national scales (e.g. merchant or recreational vessels). Domestic transport networks can be complex. For example, New Zealand's recreational vessel network comprises > 500 distinct voyage routes among 36 of the country's main marina facilities, and involves > 8000 marina-to-marina voyages per year. In addition, there are ~ 7200 annual movements of large commercial vessels between New Zealand's commercial ports that occur via > 300 voyage routes (Floerl

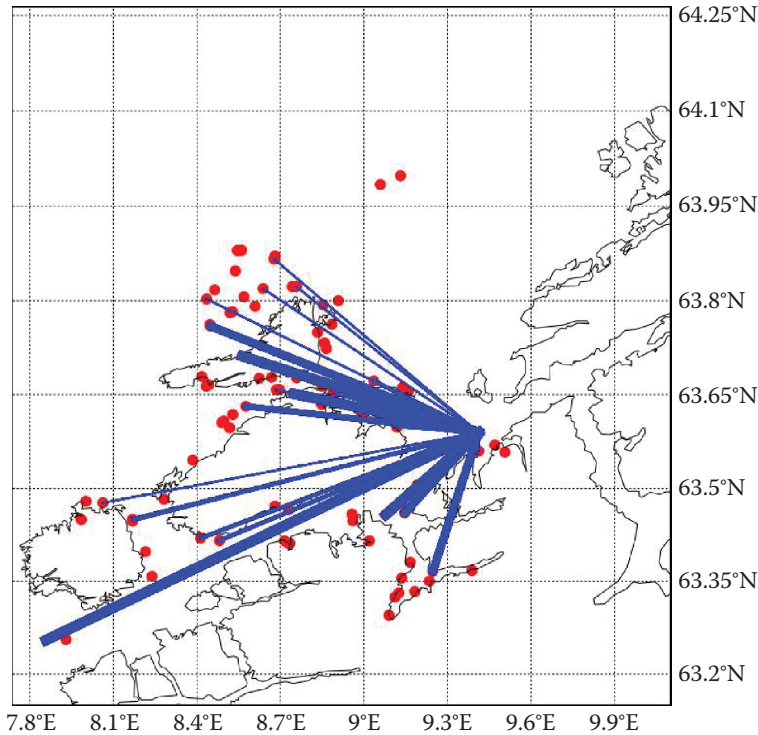


Figure 4 Annual ‘connectivity’ of a single Norwegian salmon farm in a network of 90 salmon farms on the coast of mid-Norway. The thickness of blue lines indicates the strength of connectivity. Vessel movements were tracked using automatic identification system (AIS) data (Floerl unpublished data).

et al. 2009a, Hayden et al. 2009). Many recreational, cruise, aquaculture and fishing vessels also regularly move between coastal centres and a wide range of relatively pristine natural coastal environments (Wasson et al. 2001, Gust et al. 2008, Zabin et al. 2014). For example, in 2013, a subset of 90 commercial salmon farms along the coast of Trøndelag, Norway, was visited by a total of 204 different vessels, including well-boats and feed, cleaning and service vessels (Figure 3). Individual farms received up to 400 visits from up to 57 different vessels, and farm-to-farm voyages of contractor vessels connected individual farms with up to 20 other farms (Floerl 2014). Human-assisted translocation can overcome barriers to natural dispersal and result in patterns and rates of spread very different from those achieved via natural dispersal (Buchan & Padilla 1999, Ruiz & Carlton 2003, Seebens et al. 2013) (Figure 4).

*Coastal transport networks facilitate transport
of NIS at local, regional and domestic scales*

Transport of NIS via movements of vessels and other mobile submerged infrastructure predominantly occurs via biofouling on submerged surfaces or in internal ballast water (Drake & Lodge 2007, Hewitt & Campbell 2008). International conventions and guidelines to regulate shipping pathways are in development or already operational (IMO 2005, 2011b), but the domestic risk associated with both of these transportation modes remains largely unmanaged by most coastal nations. For example, Simkanin et al. (2009) established that approximately 27% (~ 6 million metric tons) of ballast water discharged at commercial ports on the west coast of the USA originates from other west coast ports, which can facilitate the translocation of organisms among regional ports. Similarly, domestic vessel

movements in the USA and New Zealand (to name two examples) are likely to transport biofouling species between ports or from ports to remote natural environments (Floerl et al. 2009b, Zabin et al. 2014). Dispersal of biofouling species can be facilitated by all types of vessels and mobile infrastructure. The greatest risk is often attributed to vessels that spend extended periods (weeks to months) at their destinations, such as many recreational vessels, towed barges and inactive commercial vessels (Apte et al. 2000, Davidson et al. 2008, Floerl & Coutts 2009). However, Schimanski (2015) recently showed that the export of recruits from a local larval pool via vessel movements can occur following residency periods of a single day. Recreational vessels are implicated in the domestic spread of NIS in North America (Wasson et al. 2001, Davidson et al. 2008, Clarke Murray et al. 2011, Zabin et al. 2014), Europe (Fletcher & Farrell 1999, Dupont et al. 2010) and New Zealand (Goldstien et al. 2010). There is also evidence of commercial vessels acting as domestic transport vectors. For example, the translocation of a dumb barge from New Zealand's North Island to the South Island has facilitated the dispersal of the invasive ascidian, *Didemnum vexillum*, from its probable founder population into the heart of the country's aquaculture growing region 500 km further south, where it established highly prolific populations (Coutts & Forrest 2007, Forrest et al. 2013). Regional movements of leased marina pontoons and transfers of aquaculture stock between growing regions have also been identified as potential dispersal vectors of NIS (Forrest & Blakemore 2006, Gust et al. 2008).

The spread of NIS is determined by myriad factors that are not all well understood and that are likely to differ between species and environmental contexts. For example, there are known relationships between propagule pressure and colonization success (Hedge & Johnston 2012) and between aspects (size, gene pool, etc.) of founder populations and longer-term persistence (Simberloff & Gibbons 2004). The modes of anthropogenic transport described above can enhance the post-establishment success of marine NIS in several ways. First, they can facilitate the establishment of further regional satellite populations whose cumulative spread and impact can be greater and far more difficult to manage than that of a single invasive population (Moody & Mack 1988). Second, some elements of coastal transport networks, such as container vessel movements, involve repeat voyages or loops (Kaluza et al. 2010). These can facilitate recurring introductions of propagules to established NIS populations, which may enhance resilience and adaptive capacity of such populations to disturbance or environmental change (Carlton & Hodder 1995, Prentis et al. 2008, Hedge et al. 2012). Third, repeat introductions can also help small populations overcome Allee effects and become self-sustaining (Drake & Lodge 2006) thereby increasing invasion risk. Finally, the transport of biofouling species on vessels can select for individuals that are particularly robust (e.g. environmentally tolerant, Piola & Johnston 2008a). Vessels with particular voyage profiles, such as frequent short-distance voyages, may facilitate transport of recruits that are able to produce viable offspring for release in vessels' future destinations (Schimanski 2015).

There is mounting evidence that both recreational vessels and commercial shipping allow the translocation of genotypes around the world. Many studies show little genetic differentiation among distant populations found within a species' introduced range (Tepolt et al. 2009, Rius et al. 2012, Ordóñez et al. 2013), indicating the presence of population connectivity both at regional and global scales. Although genetic bottlenecks can have deleterious effects on recently-established introduced populations (Roman & Darling 2007), the majority of marine genetic studies support the idea that introduced populations have high levels of genetic diversity as a result of recurrent introductions from multiple and diverse sources (Rius et al. 2015). Human-assisted global reshuffling of genotypes may have evolutionary consequences for species and assemblages in both introduced and native ranges (Olden et al. 2004, Hudson et al. 2016). Human activities fundamentally alter evolutionary trajectories that have been shaped by millions of years. For example, both artificial transport of species and climate change facilitate contacts of previously isolated genotypes, which unprecedentedly increases hybridization rates (Rius & Darling 2014, Vallejo-Marin & Hiscock, 2016). However, more research is needed to understand how human activities are affecting species ranges of both native and NIS.

Ecological, physiological and genetic alteration of recipient environments

When a NIS interacts with the receiving community, a gradient of possible outcomes can be expected. The first one is ecological dominance by the NIS, in which the absence of natural competitors and predators (the so-called ‘enemy release hypothesis’, Keane & Crawley 2002) facilitates NIS success. Another possibility is that a NIS becomes established in the new area but that the receiving community limits its success (i.e. biotic containment, Stachowicz et al. 2002a, Levine et al. 2004, Simkanin et al. 2013). Finally, biotic resistance or the ability of resident species to resist newcomers may prevent the establishment of NIS. Human activities have the potential to modify each of these processes and thereby influence the success of NIS post-arrival.

Loss of species diversity and changes in community interactions

One of the most studied but debated forms of community-level biotic resistance is that attributable to species diversity (Elton 1958). Species diversity is thought to affect biotic resistance through two main mechanisms: the sampling effect and species complementarity. The sampling effect refers to the probability that a community will contain one or more dominant species (e.g. superior competitors or predators) that are particularly effective in repelling invaders (Huston 1997). Dominant species may create habitat for many subordinate species, which increases species diversity and inhibits the establishment of new arrivals. Species complementarity, or resource partitioning, refers to differential resource use between species (Schoener 1974, Tilman 1997). A higher number of species can often utilize a larger proportion of the resource base, which reduces invasibility by leaving fewer unused resources available to invaders (Davis et al. 2000).

Experimental studies have shown that diverse communities can ‘overyield’, where they are more productive and use more resources than would be expected by the sum of component species (Hector et al. 2002). Species complementarity can also occur temporally, when diversity buffers the effects of temporary species loss (Levine 2000). This was observed in a marine system where the primary space-occupiers (colonial ascidians) underwent boom-and-bust cycles at different times of the year, and diverse communities tended to contain species in each boom-phase (Stachowicz et al. 1999). These experimental studies demonstrate effects of species diversity on invasibility at local scales, but there is debate over its importance at larger scales (Fridley et al. 2007, Clark & Johnston 2011, Clark et al. 2013).

Competition between species within trophic levels is an important process in many marine communities (Branch 1984), and represents a key form of biotic resistance. Classic ecological theory identifies three main types of competition (interference, exploitative and apparent), which include both direct and indirect mechanisms (Fellers 1987). Examples of these in hard-substratum marine systems are overgrowth interactions between neighbours (interference, Russ 1982) and competition for resources such as food and space (exploitative, Buss 1990), both of which can act to resist post-establishment invasion (Kimbrow et al. 2013). Apparent competition is that mediated by a predator or herbivore and is more difficult to study, but has been implicated as a mechanism influencing the invasion success of some terrestrial plants (Dangremond et al. 2010, Combs et al. 2011).

The importance of competition shaping community composition is context-dependent (Firth et al. 2009, Klein et al. 2011) and is regulated by resources and stress levels (McQuaid et al. 2015), so is variable across space and time. It is less important in early successional or highly disturbed communities where resources are abundant, but becomes increasingly important as communities develop and resources become scarce (Parrish & Bazzaz 1982, Dohn et al. 2013). The degree of niche partitioning also influences the importance of competition, since divergent resource use between species diminishes the frequency and/or intensity of competitive interactions. There is some evidence for latitudinal trends in the intensity of competition (Barnes 2002), which may contribute

to differences in the invasibility of latitudinal regions (Freestone & Osman 2011, Freestone et al. 2011, 2013).

Increased disturbance, for example by human activities that chemically or physically alter the environment, typically increases species turnover and the amount of available resources (Davis et al. 2000, Clark & Johnston 2005) (Figure 1). This reduces the importance of competition in structuring communities, and advantages species with r-selected traits and/or tolerance to disturbance. Many NIS are relatively successful in disturbed environments by their virtue of high dispersal (particularly in association with human transport vectors), rapid reproduction and wide environmental tolerance (Piola & Johnston 2008b) (Figure 1). Byers (2002) argued that anthropogenic disturbances create environmental conditions that favour NIS, removing the advantages of pre-adaptation that would normally be held by natives.

The loss of native species or a reduction in their abundance can compromise species interactions that would otherwise provide biotic resistance. Fewer species reduces the scope for species complementarity and the probability that communities will contain dominant taxa (i.e. the sampling effect). Stress that reduces the fitness of native species may weaken biotic resistance by decreasing the intensity of competition, or by altering the outcome of competitive interactions (Liancourt et al. 2005). Conversely, positive interactions (facilitation) between invaders can exacerbate their impacts, spread and subsequent invasions—a phenomenon known as ‘invasional meltdown’ (Simberloff & Von Holle 1999, Grosholz 2005) (Figure 1). An example in hard-substratum marine fauna is when habitat-forming invaders (e.g. the colonial bryozoan, *Watersipora subtorquata*) provide secondary substratum for other invaders (Floerl et al. 2004), sometimes on antifouling-painted surfaces that would otherwise be uninhabitable by non-tolerant invaders. Facilitative interactions can also occur between native and NIS. Most evidence of this comes from studies on terrestrial and freshwater ecosystems, but some marine examples exist (see review by Rodriguez 2006). Facilitative effects are often transitory (Holloway & Keough 2002) or dependent on environmental conditions (Maestre et al. 2009, Rius & McQuaid 2009, Holmgren & Scheffer 2010). Overall positive and negative ecological interactions affect levels of biodiversity, which ultimately influence the success of NIS.

Impacts of human activities on biotic resistance are spatially variable, as some habitats are dominated by taxa that are particularly susceptible to environmental change. For example, areas with more stable environments (e.g. subtidal reefs or deep-sea sediments) are more likely to contain species less able to adapt to or tolerate change, relative to areas with fluctuating conditions (e.g. tidal rock pools or shallow estuaries) (Levin & Lubchenco 2008). Change in biotic resistance may also be temporally variable, as species can approach their physiological limits during seasonal extremes (Durrant et al. 2013). These fluctuations in natural stress might interact with human stressors to create periods of heightened vulnerability to invasion.

Loss of top-down control or ‘enemy release’

Predation or herbivory is a third type of ecological interaction that, in the context of biological invasions, is referred to as top-down control (McEnvoy & Coombs 1999). Non-indigenous marine invertebrates can be prey for some native fish or grazing invertebrates (e.g. echinoderms), and likewise non-indigenous fish can be prey for larger native fish or higher-order predators. The importance of this to marine bioinvasions is difficult to gauge since predation rates on many lower trophic levels are not often well understood. Some evidence exists from studies that describe predation of early life-history stages of marine epifaunal taxa (both native and/or NIS) as a key determinant of the development of benthic communities (Osman & Whitlatch 1995, 2004, Rius et al. 2014b). Soft-bodied marine invertebrates (e.g. solitary and colonial ascidians) may be more prone to predation than those with hard outer shells, so the susceptibility of invertebrate invaders to top-down control can be influenced by their morphology (Lavender et al. 2014), the natural predators present (e.g. specialist versus generalist) and other competitors (Russ 1980, 1982, Osman & Whitlatch 2004).

Chemical defences can also inhibit predation upon fish (Snyder & Burgess 2007) and marine invertebrates (Bakus 1981, Pawlik 1993, Teo & Ryland 1994), and herbivory upon algae (Steinberg 1986, Hay & Fenical 1988), providing some invaders with relative immunity to top-down control (Lagesa et al. 2006, Enge et al. Chapter 6 in this volume).

The ‘enemy release hypothesis’ refers to situations when the invader has partial or complete immunity from predation in its new range, and can lead to the proliferation and dominance of the invader (Keane & Crawley 2002) (Figure 1). Most examples of the enemy release hypothesis come from terrestrial studies (Colautti et al. 2004, Liu & Stiling 2006), but there is some evidence from the marine environment (Torchin et al. 2003, Blakeslee et al. 2009, 2012). A laboratory study compared the preference of a sea urchin for feeding upon native versus exotic ascidians, and found that the urchin preferred the native prey (Simoncini & Miller 2007). Another study found that even though Hawaiian herbivores grazed introduced algae in preference to native algae, the intensity of herbivory was lower there than in the invaders’ native range (Vermeij et al. 2009). Field studies have highlighted that besides a relative immunity to predation, invaded communities dominated by NIS may benefit native predators by providing previously unavailable resources (Branch & Steffani 2004, Rius et al. 2009). Torchin et al. (2003) highlighted the importance of escape from parasites in the success of some exotic marine invertebrates, since parasites are known to reduce growth, survival and natality (Torchin et al. 2002). For example, infection of the native mussel, *Perna perna*, in South Africa by trematodes was found to reduce growth and adductor muscle strength, and increase water loss compared to the uninfected non-indigenous mussel, *Mytilus galloprovincialis* (Calvo-Ugarteburu & McQuaid 1998). While not top-down control, this appears to be another important form of enemy release in marine systems. Enemy release can accelerate invasion events that were initiated or facilitated by the anthropogenic factors mentioned in other sections of this chapter.

Managing anthropogenic factors to reduce the establishment and spread of NIS

Our existing insights of how humans can influence the post-arrival success of NIS by altering physical, chemical and biological parameters of the environment, or by facilitating dispersal, provide us with a wide range of options for reducing invasion risk. These are briefly discussed here and summarized in Table 1.

Ecological interactions, such as biotic resistance or containment, occur across and within trophic groups, as well as at multiple levels of biological organization and life-history stages (Kimbrow et al. 2013). Human activities can impair biotic resistance to post-establishment spread of NIS by reducing the types, extent or magnitude of species diversity, community interactions and top-down control (Figure 1). At local or regional scales, for example, diversity loss can result from anthropogenic stressors such as contamination providing an advantage to non-indigenous species (Piola & Johnston 2008b). Physical modifications of habitats due to increasing coastal development can result in species removal and the loss of native species that might otherwise provide a barrier to invasion (Dafforn et al. 2015). Fishing practices that remove apex predators can reduce top-down control on marine communities and might also facilitate invasion at lower trophic levels (Baum & Worm 2009, reviewed by Johnson et al. 2011). At larger scales, human-induced climate change is modifying natural ranges of species (Ling et al. 2009) and may be increasing the rate of biotic homogenization (Stachowicz et al. 2002b, Olden et al. 2004).

The way we manage and conserve the diversity and integrity of native species assemblages will affect their ability to repel NIS now and in the future. Specifically, it will be important to conserve the native attributes of systems such that natural mechanisms of biotic resistance can operate most efficiently. For example, conserving native diversity will facilitate synergistic mechanisms of biotic resistance (e.g. species complementarity and indirect interactions) that would be virtually

Table 1 Summary of mechanisms for establishment and spread of NIS, likely impacts and suggestions for effective management

Establishment and/or dispersal vector	Likely impacts	Management suggestions
Reduced biotic resistance	Changes in species diversity, competitive interactions and top-down control	<ul style="list-style-type: none"> • Conserve native biodiversity (e.g. with marine sanctuaries) • Understand interactions between stressors • Protect natural predators for top-down control • Monitor key native species
Contamination, eutrophication and changes to water quality	Selection for tolerant species, selection for fast-growing species, freeing of resources for NIS	<ul style="list-style-type: none"> • Improve flushing in marinas to reduce water retention • Use of non-toxic antifouling paints • Remediate contaminated sediments to avoid resuspension of toxicants • Manage storm water runoff
Addition of artificial structures	Introduction of artificial hard substratum, invasion stepping stone	<ul style="list-style-type: none"> • Shift from hard defence structures to natural coastal protection • Design structures to conserve natural habitat complexity and reduced shading • Use fixed rather than floating structures
Commercial and recreational transport networks	Translocation of NIS via fouling on hulls or equipment, and in ballast water	<ul style="list-style-type: none"> • Pathway management • Domestic ballast water management • Improved ability for hull treatment

impossible to artificially engineer. Reducing the input of contaminants to receiving environments and removing historical legacies of toxicants would go some way to support native species resistance (Piola et al. 2009). For example, there has been evidence of macrofaunal recovery following the ban on tributyltin in antifouling paints (Smith et al. 2008, Langston et al. 2015). Similarly, the removal of organic contaminants associated with a fish farm resulted in positive changes to native ecological structure and function over time (Macleod et al. 2008). Broad conservation of processes that maintain strong ecological interactions will provide the most comprehensive protection against a wide range of possible scenarios.

The increased addition of artificial structures to coastal environments aids the establishment and dispersal of NIS. Where artificial structures are used for protection and defence (e.g. groynes, breakwaters, sea walls), the establishment of natural coastal protection would reduce these risks. For example, the addition of buffer zones for the landward extension of coastal vegetation (e.g. mangroves) would provide more natural protection from storms and storm surges (Hoang Tri et al. 1998, Kelly & Adger 2000, Costanza et al. 2008). Where coastal defence structures are needed, improving the design of artificial structures would go some way to reducing post-arrival success of NIS if structures matched the complexity of natural habitats (Atilla et al. 2005), shading was reduced to encourage native algal assemblage growth (Dafforn et al. 2012) and developments such as ports and marinas were designed to improve flushing and reduce retention rate for invasive propagules (Floerl & Inglis 2003, Vaselli et al. 2008). Future management strategies should take into account the potential for shallow moving structures to enhance invader dominance, and strongly consider using fixed structures to reduce opportunities for invaders (Dafforn et al. 2009b).

Physical changes that increase connectivity of habitats are a primary cause for invader spread. Canals have been implicated in invader spread (e.g. Suez and Panama canals) linking regions that would have otherwise been isolated by a natural barrier. The design of locks and weirs within such canals, combined with effective water or hull treatment technology, could help to reduce the transport of viable species between naturally isolated waterbodies (Galil et al. 2007, 2015). Upstream hydrological modifications should take into consideration the potential for changes to environmental conditions downstream that might enhance abiotic conditions for invaders (Winder et al. 2011).

A reduction in the risk of post-establishment spread via human transport mechanisms can also be achieved via the development and implementation of effective pathway management measures. Such initiatives may involve the setting of hygiene requirements or movement restrictions for vessels or infrastructure (e.g. aquaculture equipment) of particular types or origin to minimize their risk of translocating NIS (see discussions in Sinner et al. 2013, Inglis et al. 2014). One recent example of such measures is the Craft Risk Management Standard developed by the New Zealand government to limit the arrival and spread of non-indigenous biofouling species via overseas vessels (MPI 2014). Similar regional efforts are required to control domestic spread, and are being developed by several New Zealand regional jurisdictions (Sinner et al. 2013). To be effective and feasible, such measures need to be evidence-based and underpinned by effective prevention, inspection/surveillance and treatment technologies, industry codes of practice, incentivized schemes and educational measures (Floerl et al. 2016).

Longer-term international strategies for reducing risk include the implementation of widely-adopted, best-practice ballast water treatment and hull maintenance regimes that reduce biofouling (Hewitt & Campbell 2007, Tamelander et al. 2010) (Figure 5) and the development of more effective risk-based screening tools for border clearance. Genetic tools, including environmental DNA, are providing improved strategies for early detection, which can enable a faster and more effective detection and response to species invasions (Jerde et al. 2011, Zaiko et al. 2016). A sustained reduction in the overall per-vector risk of facilitating species transfers will be associated with long-term benefits for biosecurity (Drake and Lodge 2004). This is reflected in current international measures made for commercial ships (e.g. IMO 2011a) but needs to be better and more effectively implemented at domestic scales and across the range of anthropogenic transport mechanisms (Williams et al. 2013).

Multiple stressors (biological, chemical or physical) can impose additive or synergistic effects on ecosystems. Ameliorating as many stressors as possible will bolster the ability of ecosystems to deal with the remainder, and identifying important interactions between stressors may also help in prioritizing their management (Crain et al. 2008). Marine protected areas (MPAs), where certain human activities are restricted or forbidden, are one such tool with which to conserve the natural attributes of systems, and thereby biotic resistance. MPAs harbour natural predators that impose top-down control (Shears & Babcock 2002), and have the potential to conserve diversity and strong competitors within trophic levels to minimize excess resource availability (Baskett et al. 2007). Further understanding of species interactions most important to biotic resistance would be



Figure 5 Propeller of a domestic vessel fouled by the invasive ascidian, *Ciona robusta*. Longer-term strategies for reducing invasion risk include the implementation of widely-adopted, best-practice hull maintenance regimes that reduce fouling. (Photo: Javier Atalah, Cawthron Institute)

useful, allowing us to monitor key species and predict when and where biotic resistance is likely to be compromised.

Much research has focused on the vectors that initially transport a species beyond its native range (Carlton 1985, Ruiz et al. 1997, Hewitt & Campbell 2008, Davidson et al. 2010). However, it is clear that human activities have the potential to increase invader success through multiple stages of the invasion process (Williamson et al. 1986, Piola et al. 2009). Anthropogenic activities that increase the survival, establishment, proliferation and secondary spread of marine NIS post-arrival in a new region require greater management attention and research focus if we are to prevent the gradual homogenization of the world's coastal biota.

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