

Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions?

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Abstract We identified different distributions of marine nonindigenous species (NIS) and native species on some artificial structures versus natural reefs and using experimental manipulations, revealed some possible causal mechanisms. In well-established subtidal assemblages, numbers of NIS were 1.5–2.5 times greater on pontoons or pilings than on rocky reefs, despite the local species pool of natives being up to 2.5 times greater than that of NIS. Conversely, on reefs

and seawalls, numbers of native species were up to three times greater than numbers of NIS. Differential recruitment to different positions and types of surfaces appeared to influence distribution patterns. NIS recruited well to most surfaces, particularly concrete surfaces near the surface of the water, whilst natives occurred infrequently on wooden surfaces. The position of rocky reefs and seawalls close to the shore and to the seabed appeared to make them favourable for the recruitment of natives, but this positioning alone does not hinder the recruitment of NIS. We argue that pontoons and pilings represent beachheads (i.e. entry points for invasion) for many nonindigenous epibiota and so enhance the spread and establishment of NIS in estuaries. Habitat creation in estuaries may, therefore, be a serious threat to native biodiversity.

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Introduction

Habitat destruction and introductions of nonindigenous species (NIS) are believed to be two of the greatest threats to native biodiversity (Gray 1997; Sala et al. 2000) and in coastal marine habitats these threats are coincident. Estuarine habitats are under increasing risk from invasion (Cohen and Carlton 1998; Ruiz et al. 2000), due in large part to alterations of donor and recipient habitats, and because increased shipping has changed the linkages between biotic provinces (Carlton 1996; Grosholz 2002). Simultaneously, estuarine habitats are becoming more urbanised, in many instances creating hard surfaces in regions where none existed previously (Ruiz et al. 1997; Bacchiocchi and Airoldi 2003). These new surfaces are typically associated with shipping and aquaculture; both of which are often

linked with the transfer of marine NIS (Carlton 1996; Hewitt et al. 2004).

Biological invasions can be categorised broadly into three stages: arrival, establishment and diffusion (Carlton 1987). Considerable research on marine invasions has focused on the arrival of NIS, in particular, accidental introductions of invertebrates and algae via ballast water (Carlton 1985; Ruiz et al. 1997), ships' hulls (Carlton 1987; Hewitt et al. 2004), or sea chests (Coutts et al. 2003). Processes of establishment of marine NIS have also been well studied, especially the roles that native species diversity (Stachowicz et al. 1999; Dunstan and Johnson 2004) and disturbances (Cohen and Carlton 1998; Ruiz et al. 1999) play in modulating invasions. In comparison, little is known about the diffusion or small-scale spread of marine NIS after they have invaded a region (Grosholz and Ruiz 1996), despite this being a critical component of marine invasions (Wasson et al. 2001).

Artificial structures have long been known to be colonised, or fouled, by nonindigenous epibiota (algae and sessile invertebrates). Indeed, the association with such structures is one criterion for categorising a species as nonindigenous (Chapman 1988; Chapman and Carlton 1991). Bulleri and Airoidi (2005) recently found that the invasive alga *Codium fragile tomentosoides* was prevalent on artificial breakwalls and they argued that these structures help the alga invade and spread. No study has, however, specifically examined habitat use by natives versus NIS on artificial and natural habitats. Such a test for discrepancies in habitat use is an essential first step in an investigation of the role that artificial structures might play in the dispersal of epibiota (Underwood et al. 2000). Because space is often a limiting resource for epibiota (Jackson 1977; Russ 1982), the provision of new surfaces in the form of artificial structures could enhance the recruitment of epibiota, particularly early successional species. In this way, artificial structures may represent beachheads (sensu Simberloff 1997) for newly arrived marine NIS, and form the base from which further invasion can occur.

Here we re-analyse data from studies done in Sydney Harbour, Australia, to evaluate the patterns of distribution of native and nonindigenous epibiota in established subtidal assemblages. We test the hypotheses that there are (1) more NIS than native species on artificial structures, and more native species than NIS on rocky reefs, and (2) more NIS on artificial structures than on nearby natural rocky reefs, and more natives on rocky reefs than on artificial structures. We also utilise manipulative experiments to test hypotheses about the role that recruitment might play in explaining these patterns. Specifically, we separated the effects of posi-

tion (relative to the shore, the seabed and the surface of the water) from composition of the surface, and also examined the effects of movement on recruitment of natives versus NIS. The studies described here were done initially to test more general hypotheses about sessile assemblages growing on different types of structures, but at the time little information about the native or nonindigenous status of the species was available.

Materials and methods

Studies were done in Sydney Harbour, Australia, and focused primarily on epibiota growing on shallow subtidal vertical surfaces. Sydney Harbour is a commercial port and also has many recreational marinas and naval facilities. There are extensive intertidal and subtidal rocky reefs throughout the harbour, most of which are comprised of sandstone. Except where otherwise indicated, all sites were >8 km from commercial shipping berths. The same sites were used for studies 1, 3 and 4 and sites for other studies were within a few kilometres. Sites were in sheltered locations and were not exposed to oceanic swell, or strong tidal currents.

Species of epibiota were classified as introduced or native based on a variety of criteria loosely following Chapman and Carlton (1991) (S1). These criteria included disjunct regional and global distributions, recognised invasion history and published record of native region, and recognised phyletic relatedness or greater molecular affinities with species from other biotic provinces. The presence or affinity with artificial or human-modified structures was not used in this study as a criterion for classification. Presence/absence data were used for all analyses and cryptogenic species (those of uncertain origin; Carlton 1996) were not included. This resulted in a small number of species being used for some analyses.

All comparisons concerned the numbers of species, not numbers of individuals. First, numbers of NIS or native species per replicate were compared among different treatments. Second, the frequency of occurrence of natives versus NIS was compared for each treatment using χ^2 tests of goodness of fit. The latter comparison combined information on the number of species (NIS or native) and the number of replicates in which those species occurred and related this to what would be expected by chance given the available species pool. Separate comparisons were done for each site where species pools differed among sites. Percentage cover data for individual taxa were not used here for formal comparisons of NIS versus natives because different growth forms of species in the two categories

would confuse any interpretation of results. Results of multivariate and univariate analyses of percentage cover data for abundant species can be found in the publications referred to in the methods below.

Reef versus seawalls, pilings and pontoons

Using data from photographic samples (15×15 cm, $n = 5$ per surface per site), epibiota on various artificial structures was compared to that on natural vertical sandstone rocky reefs at two sites associated with recreational boats (Connell and Glasby 1999). Sites were 1 km apart and situated in Middle Harbour, the northern arm of Sydney Harbour. The artificial structures sampled were sandstone brick seawalls, fibreglass or concrete pontoons, concrete pilings, and wooden pilings with bark or stripped of bark. At each site, the different surfaces were situated within 5–10 m of each other, but pontoons and pilings were always closer to docked boats than were rocky reefs. Samples were taken at a depth of approximately 0.2 m below Mean Low Water Springs, or in the case of pontoons, 0.2 m below the water surface.

Reef versus seawalls and reef versus wooden pilings

A much larger study (Holloway unpublished data), involving in situ sampling by divers rather than photographic sampling, was used to further investigate the distribution of NIS and natives among reefs, seawalls and pilings. The presence of species was recorded in 20×25 cm quadrats at depths of approximately 1–2 m below Mean Low Water Springs. Compositions of epibiotic assemblages were compared between vertical sandstone reefs and nearby sandstone seawalls at each of three sites ($n = 60$ quadrats per surface per site). Also, epibiotic assemblages were compared among vertical reefs, horizontal reefs and wooden pilings without bark at an additional three sites ($n = 38$ quadrats per surface per site). Sites were dispersed throughout Sydney Harbour and ranged from 1 to 8 km from commercial shipping berths. The different hard substrata were typically within 10 m of each other at each site. Pilings were associated with jetties used for commercial ferries operating within Sydney Harbour and so were occasionally closer to docked boats than were rocky reefs.

Effects of position on recruitment of NIS and natives

One possible cause for any differences between assemblages on pontoons and reefs is the different position of each structure in the estuary. Reefs and retaining walls were situated close to the shore and close to the seabed

because all reefs were low profile, without extensive vertical walls. In contrast, samples on pontoons and pilings were up to 5 m from the seabed and from the shore, and pontoons floated near the water surface. We tested whether these differences in position might influence patterns of settlement and/or post-settlement processes of NIS versus natives. Compressed concrete panels were attached to the two different structures and recruitment (defined as settlement and growth of species to the point that they are visible at the time of sampling; Butler 1986) was measured after 30 weeks. At each of three sites, five replicate 15×15 cm panels were attached vertically to floating pontoons 25 cm below the water surface and to rocky reefs at a depth of 1.5 m below Mean Low Water Springs (Glasby and Connell 2001). Pontoons were ~5 m seaward of the reefs. Assemblages that developed on the panels were sampled under the microscope, thereby enabling more detailed searches and identifications than in the first study. Even so, various taxa, particularly sponges, were classified as cryptogenic.

Effects of surface composition on recruitment of NIS and natives

Patterns of distribution of epibiota may be influenced by the type of surface they colonise (Pomeroy and Weiss 1946; McGuinness 1989). The reefs sampled in the previous studies were sandstone, pontoons were either concrete or fibreglass, and pilings were composed of concrete or wood. Effects of surface composition on the recruitment of nonindigenous or native species were investigated by sampling epibiota on vertical 15×15 cm panels ($n = 5$) made of sandstone, concrete or wood. The experiment was set up at three sites, approximately 200 m apart, which were within hundreds of metres of the sites used for the first study. To remove any effects of position, all panels were attached to rocky reefs by aluminium beams that had been drilled into the reef at a depth of 1.5 m below Mean Low Water Springs (Glasby 2000). Replicate panels were separated by distances of 1–5 m at each site and submerged for 30 weeks.

Effects of movement on recruitment of NIS and natives

Differences in numbers of natives and NIS on pontoons and reefs, and the fact that NIS are often transported on the hulls of vessels, led us to test the hypothesis that increasing movement of a surface, and hence increased water flow over the surface, would result in greater recruitment of NIS. The experiment was done at two sites, 3 km apart, in Sydney Harbour. Both sites were naval bases, but they were not docking areas for large

vessels. Sandstone panels (15 × 15 cm; $n = 5$) were deployed such that some did not move (fixed panels), others moved up and down (moving panels), and a third set rotated (rotating panels) (Glasby 2001). All panels were vertical and attached to aluminium beams. The beams of fixed panels were attached to concrete blocks. Beams of moving panels were suspended between two metal stakes with ropes going from either end of the beam to a float such that the panels moved up and down and backwards and forwards, much like a pontoon. The beam of rotating panels was anchored to a metal stake via a central rope and swivel, and was suspended by a float attached via ropes to either end of the beam. The panels therefore moved in most directions and rotated according to prevailing currents, mimicking to some extent the movement of the hull of a vessel. Importantly, however, all panels were at depths of 2–3 m below Mean Low Water Springs rather than at the surface and were positioned over sandy sediments approximately 10 m from shoreline rocky reef. Panels were deployed for 29 weeks at each site and the experiment was repeated twice. Water flow around each panel was estimated by measuring the dissolution of plaster clods (Glasby 2001).

Results

Reef versus seawalls, pilings and pontoons

There were significant differences in the numbers of natives and NIS on different surfaces (Fig. 1; $F = 12.0$, $P < 0.001$). Post-hoc comparisons did not produce a clear result among all surfaces, but the greatest number of NIS occurred on concrete or fibreglass pontoons,

and the least on seawalls and reefs. Conversely, the greatest number of native species occurred on reefs, followed by seawalls (Fig. 1).

The frequency of occurrence of natives and NIS on all pontoons and pilings were significantly different from what would be expected by chance given the species pool (fibreglass pontoons: $\chi^2 = 7.4$, $P < 0.01$; concrete pontoons: $\chi^2 = 5.0$, $P < 0.05$; concrete pilings: $\chi^2 = 7.4$, $P < 0.01$; wooden barked pilings: $\chi^2 = 5.5$, $P < 0.05$; wooden pilings without bark: $\chi^2 = 4.6$, $P < 0.05$). That is, NIS occurred more frequently on pilings and pontoons than would be expected by chance, and vice versa for natives. No significant pattern was detected on seawalls ($\chi^2 = 3.2$, $P > 0.05$), whilst on rocky reefs natives occurred significantly more often than would be expected by chance ($\chi^2 = 4.2$, $P < 0.05$).

The most prevalent NIS were the serpulid polychaete *Hydroides elegans* and the bryozoan *Watersipora subtorquata* which were present on all surfaces, the solitary ascidian *Styela plicata* (found only on pilings and reefs) and the brown alga *Dictyota dichotoma* (on concrete pilings and pontoons). The most prevalent native species included the red alga *Corallina officinalis* which occurred on all surfaces, barnacles (*Balanus trigonus*, *Amphibalanus variegatus*, not found on seawalls) and the brown alga *Sargassum* sp. which was not present on pilings. Many of the cryptogenic species, which occurred on all surfaces, were green, brown or red filamentous algae.

Reef versus seawalls and reef versus wooden pilings

There were no significant differences in the numbers of NIS or natives between seawalls and vertical reefs at any site ($F = 2.93$, $P > 0.05$; Fig. 2a). At one site, the

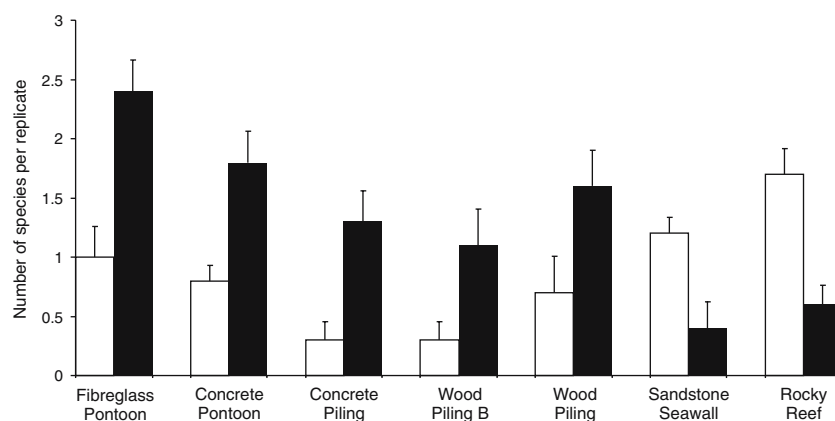


Fig. 1 Mean (\pm SE) number of native species (white) and NIS (black) per replicate in established assemblages on artificial structures and on natural sandstone rocky reefs. Artificial structures are: fibreglass pontoons, concrete pontoons, concrete pilings,

wooden pilings with bark, wooden pilings stripped of bark, sandstone brick seawalls. Data from five replicates at each of two sites have been pooled

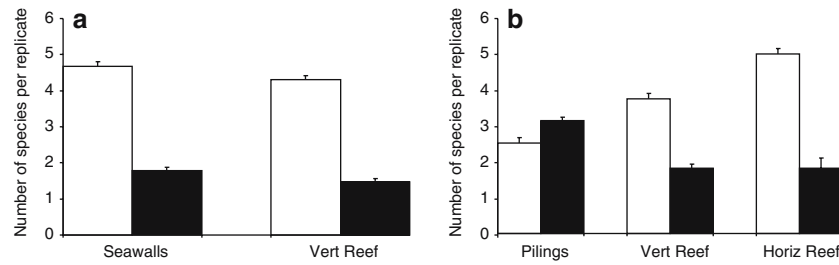


Fig. 2 Mean (\pm SE) number of native species (white) and NIS (black) per replicate in established assemblages on **a** artificial sandstone seawalls and vertical sandstone reef and **b** wooden

pilings, vertical reef and horizontal reef. Data from three sites have been combined (different sites for each study)

frequency of occurrence of natives on seawalls and on rocky reefs was significantly greater than would be expected by chance ($\chi^2 = 17.0$, $P < 0.001$ and $\chi^2 = 24.2$, $P < 0.001$, respectively). At the other two sites, no such pattern existed.

When comparing reefs of different orientations to vertical wooden pilings, at each site, the most natives occurred on horizontal reefs and the fewest on wooden pilings, whilst the greatest number of NIS was on pilings ($F = 6.7$, $P < 0.001$; Fig. 2b). The frequency of occurrence of NIS on pilings was significantly greater than would be expected by chance at all three sites ($\chi^2 = 36.0$, 44.9, 14.6; $P < 0.001$ for each). Conversely, natives occurred significantly more frequently than NIS on vertical reefs at two of three sites ($\chi^2 = 11.9$, $P < 0.001$; $\chi^2 = 4.8$, $P < 0.05$; $\chi^2 = 2.8$, $P > 0.10$) and on horizontal reefs at each site ($\chi^2 = 6.2$, $P < 0.05$; $\chi^2 = 34.5$, $P < 0.001$; $\chi^2 = 9.5$, $P < 0.01$).

Various native species were found commonly on reefs but rarely on pilings, including the algae *Sargassum* sp. and *Corallina officinalis*, the bivalve *Anomia* sp. and the ascidian *Botrylloides perspecum*. Some of the most common natives on vertical reefs were also prevalent on pilings, such as the bryozoans *Beania magellanica* and *Fenestrulina mutabilis*, the red alga *Rhodymenia* sp. and the kelp *Ecklonia radiata*. The most prevalent introduced species were the bryozoans *Bugula stolonifera*, *Tricellaria catalinensis* (primarily on vertical reefs) and *Schizoporella errata* (primarily on pilings) and the brown alga *Dictyota dichotoma* (reefs and pilings). Cryptogenic species were found on all surfaces and the most common were spirorbid and serpulid polychaetes, green and red filamentous algae, sponges, the ascidian *Botrylloides leachi* and the bryozoan *Bugula flabellata*, the latter being particularly common on pilings.

Effects of position

Results of this recruitment study were similar to those of the first study of established assemblages in that significantly more natives recruited to panels on reefs

than to panels on pontoons ($F = 10.2$, $P < 0.01$; Fig. 3). In contrast to the study of established assemblages, similar numbers of NIS recruited to reef panels and pontoon panels at two sites (Fig. 3) and at the third site, more NIS recruited to reef panels. Native species occurred significantly less frequently on pontoon panels than expected by chance ($\chi^2 = 14.2$, $P < 0.001$ across all three sites) whereas the distribution of natives and NIS on reef panels was as would be expected given the species pool ($\chi^2 = 1.6$, $P > 0.20$).

The most prevalent introduced species recruiting to panels were serpulid polychaetes and bryozoans (on reefs and pontoons) and the ascidian *Styela plicata*, the mussel *Mytilus galloprovincialis* and the brown alga *Dictyota dichotoma* (most commonly on pontoons). The most prevalent native species that recruited to reef and pontoon panels were the barnacles *Balanus trigonus* and *Amphibalanus variegatus*, the sponge *Leucandra* sp. and the brown alga *Feldmania* sp. The native oyster *Saccostrea glomerata*, the brown alga *Sphacelaria rigidula* and the red alga *Hypnea* sp. were also common on reef panels, but rare on pontoon panels. The native algae *Laurencia* sp. and *Rhodymenia* sp. were common on pontoon panels, but rare on reef

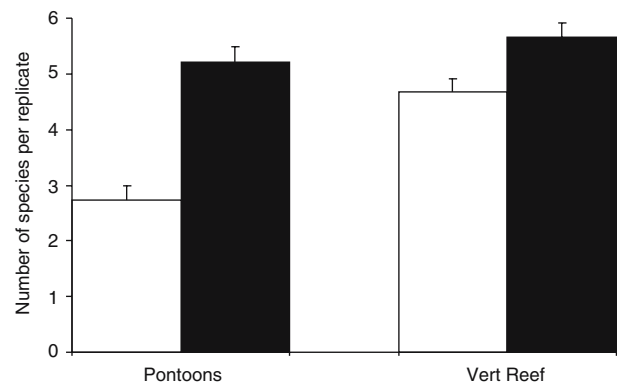


Fig. 3 Mean number (\pm SE) of native species (white) and NIS (black) that recruited to concrete settlement panels attached subtidally to rocky reefs or pontoons for 30 weeks. Data from three sites have been combined but different patterns occurred at some sites (see text)

panels. Cryptogenic species included spirorbid polychaetes (primarily reef panels), red filamentous algae (reef and pontoon panels) and the ascidian *Diplosoma listerianum* (primarily pontoon panels).

Effects of surface composition

The recruitment of NIS was greatest on concrete surfaces ($F = 4.1$, $P < 0.02$), with no difference between sandstone and wooden panels (Fig. 4). The fewest native species recruited to wooden panels. On concrete and wooden panels, significantly more NIS occurred than would be expected given the species pool ($\chi^2 = 8.3$, 7.9 , respectively, $P < 0.01$ for each). But on sandstone panels, the frequency of occurrence of NIS and natives was not significantly different from what would be expected by chance ($\chi^2 = 2.5$, $P > 0.11$ across both sites).

The most prevalent NIS were the polychaetes *Hydroides elegans* and *H. ezoensis* and the bryozoans *Conopeum seurati*, *Cryptosula pallasiana* and *Watersipora subtorquata*, which were found on all types of panels. *Schizoporella errata* was typically found on concrete panels whilst *Bugula neritina* was primarily on concrete or wooden panels. Native species that were common on all panels were the barnacle *A. variegatus*, the sponge *Leucandra* sp. and the brown alga *Sphacelaria rigidula*. *Rhodymenia* sp. was a native alga that was very common on sandstone panels. Cryptogenic species that were present on most panels were spirorbid polychaetes, the ascidian *Diplosoma listerianum*, and red and green filamentous algae.

Effects of movement

Numbers of NIS per panel increased with increasing movement of the surface, with significantly more NIS

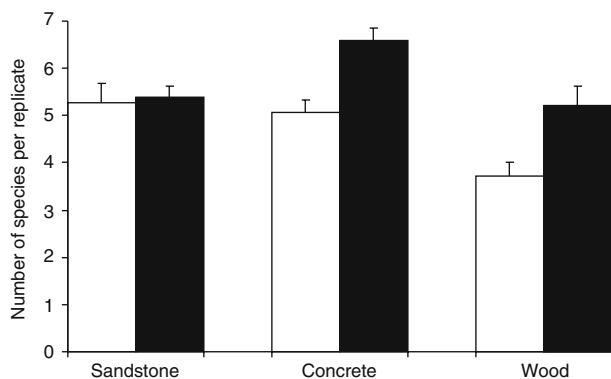


Fig. 4 Mean number (\pm SE) of native species (white) and NIS (black) that recruited to sandstone, concrete or wooden settlement panels deployed subtidally on rocky reefs for 30 weeks. Data from three sites were not significantly different and have been combined here

recruiting to rotating sandstone panels than to fixed or moving panels ($F = 6.4$, $P < 0.003$; Fig. 5). There was a non-significant trend for the most native species to recruit to fixed panels (Fig. 5). However, only at one site on fixed panels was the frequency of occurrence of natives greater than would be expected by chance ($\chi^2 = 6.0$, $P < 0.05$). No such pattern existed for other treatments at either site. Water flow was significantly greater around rotating panels than around fixed or moving panels (Glasby 2001).

Of the common NIS, *Hydroides elegans*, *Ulva lactuca*, *Colpomenia sinuosa* and *Watersipora subtorquata* were prevalent on fixed, moving and rotating panels. *Dictyota dichotoma* and *Styela plicata* were most prevalent on rotating panels. The natives *Balanus trigonus*, *Amphibalanus variegatus*, *Sphacelaria rigidula* and *Leucandra* sp. were prevalent on all types of panels. Some algal species tended to be more prevalent on fixed panels than on moving or rotating panels, in particular *Ecklonia radiata* and *Laurencia* sp. The most prevalent cryptogenic species included red filamentous algae (Ceramiales), sponges, spirorbid polychaetes, and on rotating and moving panels, the ascidian *Diplosoma listerianum*.

Discussion

Remarkably consistent results emerged from these five studies despite the fact that they were different in timing and methodologies. In established assemblages (studies 1 and 2), NIS were more common than were native species on pontoons and on pilings, and they occurred more frequently on these structures than would be expected by chance given the available species

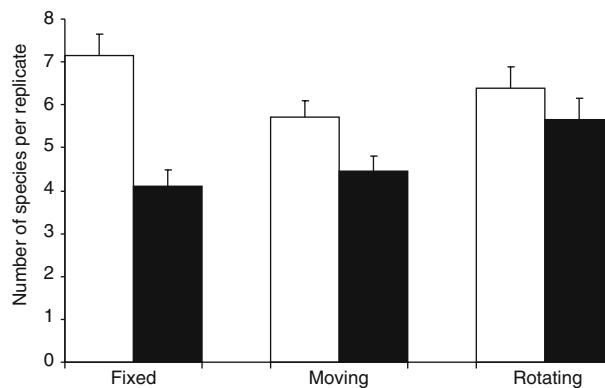


Fig. 5 Mean number (\pm SE) of native species (white) and NIS (black) sampled on sandstone settlement panels that did not move (fixed), moved up and down (moving) or rotated and orientated parallel to currents (rotating). Panels were deployed twice for 29 weeks at two sites and times and sites have been combined in this graph

pool. Pilings and pontoons also had more NIS on them than did nearby rocky reefs and there was some indication that pontoons may be better habitats for NIS than are pilings. Moreover, native species were more common in established assemblages on reefs and sandstone seawalls than in assemblages on pontoons and pilings.

By manipulating position independently of surface material, we demonstrated that the position of pontoons, floating and about 5 m from the shore, is more conducive to the recruitment of NIS than natives. Notably, colonial ascidians, which include many invasive species, have been found to recruit in largest numbers at shallow depths on floating docks (Hurlbut 1991). The position of reefs close to the seabed and the shore was equally favourable for the recruitment of natives and NIS. This latter result is of concern because it suggests that if gaps were created in native assemblages on reefs, then NIS could invade and potentially affect native habitats—matching classic theories of invasibility (Elton 1958) and recent experiments with invasive bryozoans (Clark and Johnston 2005). Surface composition also influenced the recruitment of NIS and natives. To add to the concerns mentioned above, sandstone surfaces appeared as good for the recruitment of NIS as they were for natives, meaning that neither position nor surface type will limit the recruitment of NIS to sandstone reefs. Furthermore, more NIS than natives recruited to concrete surfaces, whilst recruitment of natives to wooden surfaces was significantly less than to sandstone or concrete. Coe (1932) also reported that settlement of many epibiotic species was greater on concrete than on wooden panels. Thus, the combined effects of position and surface composition are likely to explain, at least in part, the greater numbers of NIS than natives on pontoons and pilings compared to reefs. Additional studies are needed to test whether the recruitment of NIS to reefs might be influenced by proximity to artificial structures.

The effects of increasing movement of panels did not influence the recruitment of NIS to the extent predicted. On most surfaces, the frequency of occurrence of natives and NIS was as would be expected given the species pool. There was, however, some indication that native epibiota tended to recruit disproportionately to fixed sandstone panels rather than to panels that moved, although many native algae and barnacles also recruited to moving surfaces with high water flow. Future studies will need to utilise multifactorial experiments to identify how the factors identified here, and others such as shading and possibly predation and age of the surface, interact to influence patterns of distribution of NIS and native species. This may be best done on a species-by-species basis rather than lumping

together all NIS or all natives. Certainly one limitation of our studies was that many species were classified as cryptogenic and so were not used in analyses. Because of this, and due to difficulties with identifications, some taxa such as sponges were under-represented in our analyses.

There were few commonalities among our studies in terms of the species causing the observed patterns, possibly because the studies were done at different times of the year and in different years. It was rarely possible to attribute any patterns to particular species, but some patterns were apparent. For example, the introduced ascidian *Styela plicata* and the introduced alga *Dictyota dichotoma* were most common on pontoons and pilings in the first study, recruited more commonly to panels attached to pontoons than to reef panels and also recruited in largest numbers to panels that rotated. Thus increasing movement of the surface and water flow, which is typically high around curved pilings (Abelson and Denny 1997), may favour the recruitment of these species onto artificial structures. Algae such as *Laurencia* sp. and *Rhodymenia* sp. did not recruit to wooden panels and recruited most commonly to fixed panels, which could explain why these species were not prevalent on wooden pilings, or moving pontoons. The native algae *Sargassum* sp. and *Corallina officinalis* were typically prevalent on reefs, but not on artificial structures. Although it was rare that these species recruited to panels, *C. officinalis* recruited equally to fixed, moving and rotating panels. Thus, the degree of movement of the surface was unlikely to account for *C. officinalis* being rare on artificial structures, and this pattern may instead be related to light intensity.

Various introduced encrusting bryozoans including *Watersipora subtorquata* and *Schizoporella errata* were found more often in established assemblages on pontoons, pilings or seawalls than in established assemblages on reefs. However, in all our recruitment studies, these species were equally prevalent on all surfaces and in all positions. The prevalence of these bryozoans on artificial structures and settlement panels was probably due to the fact that they are early successional species (Vail and Wass 1981; Floerl et al. 2004) and so quickly colonise new surfaces. Moreover, nonindigenous bryozoans can themselves provide surfaces for the recruitment of other NIS (Simberloff and Von Holle 1999; Floerl et al. 2004). The propensity for NIS such as *S. errata* and *S. plicata* to cover large areas and then slough off surfaces (Sutherland 1978), thereby exposing space, may also contribute to the maintenance of assemblages of NIS on artificial structures.

Despite being fast occupiers of space and producing large numbers of recruits, many fouling organisms such as bryozoans and colonial ascidians have a restricted invasive potential due to their limited natural dispersal (Keough and Chernoff 1987; Todd 1998; Shanks et al. 2003). It is likely that the provision of structures such as pontoons and pilings has enhanced the dispersal of these species in a step-wise manner (Glasby and Connell 1999), and enabled them to become highly effective invaders of estuaries. Habitats created by pontoons and pilings are likely to enhance the establishment of viable populations of epibiota (Carlton 1996; Kolar and Lodge 2001), thereby making a successful invasion more probable (Wonham et al. 2000).

It will be difficult to determine the extent to which NIS might invade assemblages on reefs in the absence of artificial structures. The most obvious test would be to compare abundances of NIS on reefs in estuaries with artificial structures to those on reefs in estuaries without artificial structures. But such a test is likely to be confounded by the amount of boating in each estuary because artificial structures are generally associated with commercial shipping or recreational boating, both of which are likely sources of NIS. Interestingly, Cohen et al. (2005) reported that numbers of NIS (epibiota and soft sediment infauna) did not differ between port and non-port areas in southern California, but this result may have been influenced by the fact that the majority of their samples were taken from artificial structures. Also, Wasson et al. (2005) found more NIS in estuaries than on the open coast, possibly because artificial structures were sampled only in the estuaries.

Pontoons and pilings therefore provide unique subtidal habitats that are poorly utilised by some native species (see also Paulay et al. 2002; Lambert 2002, 2003 for data on ascidians) and pontoons seem particularly favourable habitats for many NIS. We concur with Simberloff's (1997) suggestion that prevalence of invasive species may not be related only to how disturbed is an environment, but also to the extent that novel, human-produced habitats are available. Because non-indigenous epibiota also have the propensity to colonise nearby reefs, the creation of artificial structures in estuaries could be a threat to native biodiversity. That is, habitat creation, in addition to the commonly cited mechanism of habitat destruction, may be an indirect threat to native species. Further studies, replicated at different times of the year and using other suites of NIS and native species, are needed to test the consistency of our results and some of the ideas presented here. It would also be instructive to compare the patterns of distribution for species native to Sydney Harbour to those in places where the same species are introduced.

Most importantly, experimental studies are needed to examine the effects of NIS on naturally-occurring epibiotic assemblages and whether particular types of artificial structures may be less suitable for NIS and more suitable for natives. These will be important areas of research if we are to understand and ameliorate the spread and potential impacts of invasive species in waterways.

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