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Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities

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ABSTRACT

Anthropogenic disturbance is considered a risk factor in the establishment of non-indigenous species (NIS); however, few studies have investigated the role of anthropogenic disturbance in facilitating the establishment and spread of NIS in marine environments. A baseline survey of native and NIS was undertaken in conjunction with a manipulative experiment to determine the effect that heavy metal pollution had on the diversity and invasibility of marine hard-substrate assemblages. The study was repeated at two sites in each of two harbours in New South Wales, Australia. The survey sampled a total of 47 sessile invertebrate taxa, of which 15 (32%) were identified as native, 19 (40%) as NIS, and 13 (28%) as cryptogenic. Increasing pollution exposure decreased native species diversity at all study sites by between 33% and 50%. In contrast, there was no significant change in the numbers of NIS. Percentage cover was used as a measure of spatial dominance, with increased pollution exposure leading to increased NIS dominance across all sites. At three of the four study sites, assemblages that had previously been dominated by natives changed to become either extensively dominated by NIS or equally occupied by native and NIS alike. No single native or NIS was repeatedly responsible for the observed changes in native species diversity or NIS dominance at all sites. Rather, the observed effects of pollution were driven by a diverse range of taxa and species. These findings have important implications for both the way we assess pollution impacts, and for the management of NIS. When monitoring the response of assemblages to pollution, it is not sufficient to simply assess changes in community diversity. Rather, it is important to distinguish native from NIS components since both are expected to respond differently. In order to successfully manage current NIS, we first need to address levels of pollution within recipient systems in an effort to bolster the resilience of native communities to invasion.

Keywords

Anthropogenic disturbance, biological invasions, native diversity, non-indigenous species (NIS), pollution, sessile invertebrate community.

INTRODUCTION

Non-indigenous species (NIS) pose a significant threat to the health and productivity of marine ecosystems, through reductions in native diversity, predation, habitat alteration, and competition for resources (Mack *et al.*, 2000). Observational studies that research the distribution of exotics have identified anthropogenic disturbance as a key factor in facilitating invasion of NIS (Celesti-Grapow *et al.*, 2006). In the marine environment, estuaries and bays are the habitats simultaneously most exposed to invasive propagules (Ruiz *et al.*, 1997) and most prone to anthropogenic disturbance (Hall *et al.*, 1998). The extent to which these two factors interact in facilitating successful invasion remains unclear. Is the increasing occurrence of NIS within estuaries and harbours primarily a result of increased inoculation rates (from a combination of vectors such as shipping, fishing and aquaculture), or are NIS better able to take advantage of increasingly disturbed environments? This uncertainty highlights the urgent need for studies that not only record observed patterns of invasives in natural systems, but simultaneously examine the contributory mechanisms driving these patterns. Only through such studies can we hope to provide useful information to inform invasive species management.

Anthropogenic disturbances can change community dynamics and facilitate the establishment of NIS through a variety of mechanisms. The most common is through increased resource

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availability, either by the introduction of new resources or by decreasing resource-use by resident species (Davis *et al.*, 2000). Space has repeatedly been found to be a primary limiting resource in marine invertebrate assemblages (Dayton, 1980; Paine & Levin, 1981; Connell & Keough, 1985), and anthropogenic disturbance can play a very important role in the creation of available open space within an affected assemblage (Johnston & Keough, 2000; Johnston & Keough, 2002). Anthropogenic disturbance may also facilitate invasion by decreasing diversity in native recipient communities. Species richness may be negatively related to the invasibility of a system (Stachowicz *et al.*, 1999; Naeem *et al.*, 2000; Kennedy *et al.*, 2002), and anthropogenic disturbance events may reduce a system's ability to withstand invasion through the selective removal of sensitive species and taxa. Finally, specific types of anthropogenic disturbance may increase the invasion potential of exposed systems by complimenting inherent characteristics of NIS. For example, it has been shown that certain species and/or populations of NIS have a greater tolerance to heavy metal pollution relative to closely related native species (Piola & Johnston, 2006a,b). This may be a result of antifouling paints acting as a selective force upon transported species. Such NIS may experience a competitive advantage over native species at recipient locations subject to transient or persistent metal pollution.

Much of our current knowledge of NIS and patterns of invasion in marine systems has been garnered from observational studies and community surveys (examples include Cohen & Carlton, 1998; Hewitt *et al.*, 2004). Observational studies alone, however, are insufficient in resolving the causative links between anthropogenic disturbance and the establishment of NIS, since they cannot account for one of the primary factors that affect observed patterns of invasion – variation in propagule supply (as proposed by Ruiz *et al.*, 2000). This problem can only be addressed through the use of manipulative field experiments, that either control the supply of propagules to experimental assemblages across a range of disturbance regimes (e.g. Clark & Johnston, 2005), or manipulate the level of anthropogenic disturbance received by experimental assemblages within specific location(s) (with the assumption that the propagule supply experienced by each experimental unit is relatively uniform within a study location).

Pollution in the form of toxic chemicals is one of the most prevalent anthropogenic disturbances within marine environments worldwide (Luoma, 1996; Preston & Shackelford, 2002). Metal pollution is a major pollution source within estuarine and harbour environments, occurring in the form of antifouling coatings (Warnken *et al.*, 2004), industrial waste (Hall *et al.*, 1998), urban run-off (Pitt, 2002), sewage discharge (Scanes, 1996), and wood preservatives (Weis & Weis, 2002). Given that metal pollution can play a role in both the introduction of pollution-tolerant NIS (Floerl *et al.*, 2004; Piola & Johnston, 2006b) and as a habitat-modifying agent in recipient communities (Weis & Weis, 1996; Johnston *et al.*, 2002), the potential for it to influences NIS establishment is great.

Recent research investigating links between invasion and metal pollution have indicated tolerance to heavy metal toxicants (in particular antifouling coatings) can facilitate the spread of NIS via hull fouling and shipping movements (Floerl *et al.*, 2004). This study addresses the question of whether such resistance constitutes any real benefit to the establishment and community dominance of NIS within recipient locations. Specifically, we conducted a baseline survey to identify the native and NIS components of local hard-substrate sessile invertebrate assemblages, and combined this with manipulative field experiments to determine differences in the abundance and distribution of NIS and native species within assemblages across a range of pollution loads. Many NIS present in this study are likely to have been introduced via hull fouling (Floerl *et al.*, 2004). Given the potential for antifouling paints on boat hulls to exert strong selection for metal tolerance, we predict that native taxa in our system (having not undergone similar selection for metal tolerance) will be more sensitive to metal pollution relative to NIS

MATERIALS AND METHODS

Study sites

Experiments were conducted at two sites within Sydney Harbour and two sites within Botany Bay, New South Wales, Australia (Fig. 1). Sydney Harbour is a highly urbanized harbour that has been an international port since the arrival of Europeans in the 18th century (AMBS, 2002). In the year preceding June 2006, Sydney Harbour received 1045 commercial ship visits, transporting approximately 30 million tonnes of cargo. The harbour is also a major destination for cruise vessels, receiving 91 visits from 22 international passenger liners in 2005–06. Additionally, Sydney Harbour supports two Australian naval bases and is a major destination for international and domestic recreational boating traffic. The experimental study sites within Sydney Harbour were at Woolloomooloo Bay and Bradley's Head (Fig. 1a). Woolloomooloo Bay is a narrow, poorly flushed embayment with a long history of shipping activity, extensive foreshore development, and both a recreational boating marina and naval base and slipway located within 300 m of the experimental site. In contrast, Bradley's Head is open and well flushed, has a foreshore comprised of native bushland, and experiences less direct boating activity relative to Woolloomooloo Bay.

Botany Bay is a large marine-dominated estuary, again subject to extensive commercial and recreation boating traffic. The commercial cargo port of Port Botany on the northern shore of the bay is one of Australia's largest ports, servicing *c.* 60% of Sydney's commercial shipping needs. During the period between June 2005 and June 2006, Port Botany received 1551 ship visits, representing a total cargo movement of over 42 million tonnes. The Caltex oil refinery on the southern shores of the bay also receives a large number of international and domestic bulk carriers every year. In addition to this commercial shipping, the entire bay is heavily trafficked by domestic and international recreational boating craft. Experimental sites were selected at Port Botany and Bare Island (Fig. 1b). At Port Botany the shoreline immediately surrounding the port (where the experimental site was located) has been modified with an artificial revetment wall, which also acts to protect the site from direct oceanic exposure. In contrast,

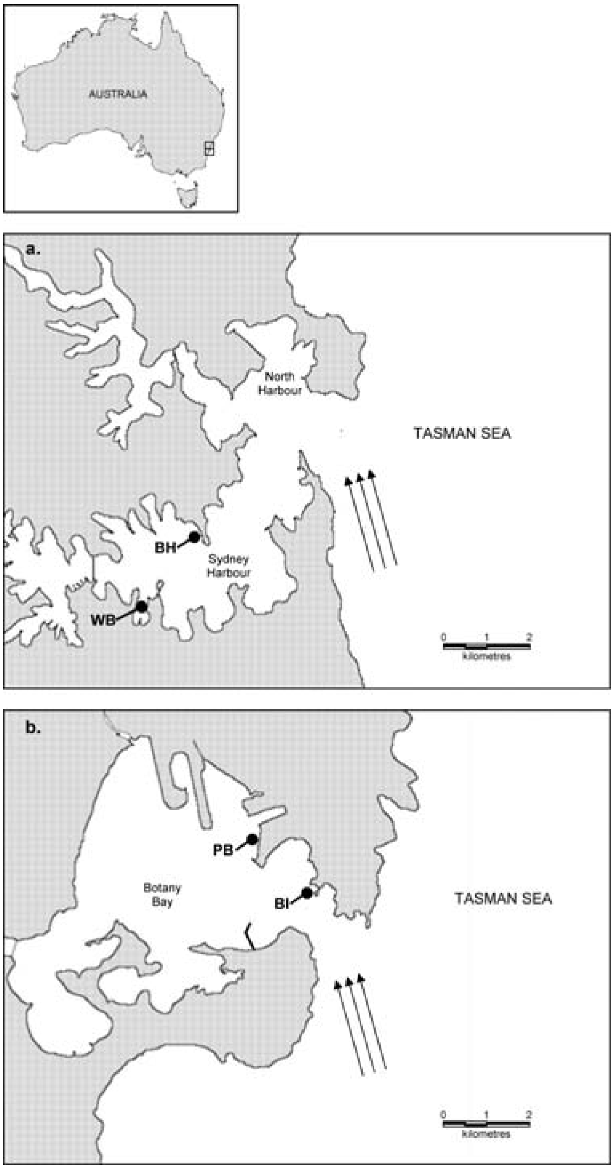
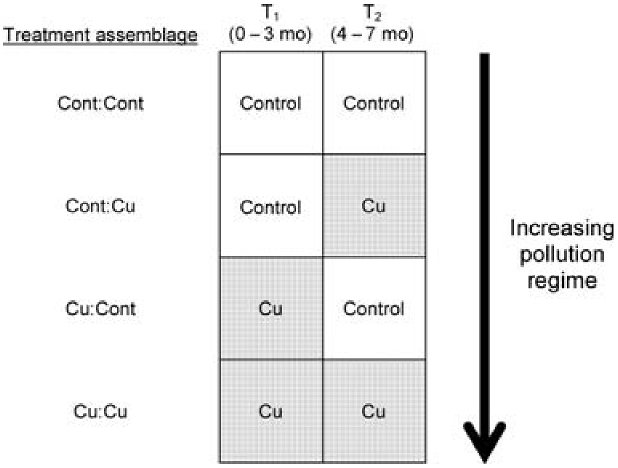


Figure 1 Maps of (a) Sydney Harbour and (b) Botany Bay detailing locations of experimental sites at Bradley's Head (BH), Woolloomooloo Bay (WB), Port Botany (PB), and Bare Island (BI). Arrows indicate the direction of dominant southerly swells entering Sydney Harbour and Botany Bay.

Bare Island is surrounded by natural rocky reef adjacent to a relatively undisturbed intertidal rocky shelf. The Bare Island site receives the greatest oceanic influence of all sites selected, and is also the most exposed, experiencing frequent direct southerly swells (see Fig. 1b).

Experimental comparison of hard substrate assemblages

A manipulative experiment was used to test the effect of heavy metal pollution on the establishment of hard-substrate assemblages. Steel-mesh frames (1.2 × 1.2 m) were deployed at each site, with 24 replicate settlement plates (11 × 11 cm) attached by cable ties acting as experimental settlement surfaces. Hard-substrate organisms have been shown to preferentially recruit to shaded areas (Glasby, 1999), so settlement plates were attached to the underside of the metal frames with the frame constructed such that settlement surfaces were situated approximately 20 cm above the sea floor. The frames were deployed at a depth of 3 m. In the context of this experiment, frames were considered an experimental convenience for the deployment of independently replicated treatment plates, and as such are not considered pseudo-replication. Previous studies employing the use of multiple frames have shown minimal interframe differences relative to observed site differences (Dafforn & Johnston, in review) and as such we did not predict the need for multiple frames as part of this experimental design.



Treatment assemblage	T_1 (0 – 3 mo)	T_2 (4 – 7 mo)
Cont:Cont	Control	Control
Cont:Cu	Control	Cu
Cu:Cont	Cu	Control
Cu:Cu	Cu	Cu

Figure 2 Schematic representation of experimental design indicating the pollution dosing regime received by the four experimental assemblages for the duration of the experiment.

In order to test the effect of duration and timing of heavy metal pollution exposure on hard-substrate assemblage development, experimental settlement plates on each frame were randomly allocated to one of four pollution treatments regimes (Fig. 2). These pollution treatments involved exposing developing assemblages to a heavy metal toxicant (in this case Cu) during their initial period of development (T_1 = 0–3 months) and/or their second period of growth (T_2 = 3–4 months). This method of heavy metal dosing resulted in a gradient of increasing pollution among experimental treatments, ranging from control assemblages that received no pollution (Cont:Cont treatments), assemblages exposed to intermediate pollution, that is exposed during either T_1 or T_2 (Cont:Cu and Cu:Cont treatments) and heavily polluted assemblages exposed for both T_1 and T_2 (Cu:Cu treatment). Previous research indicates that toxicants such as heavy metals have the greatest impact upon the larvae and early life stages of organisms (Connor, 1972; Calabrese *et al.*, 1973; McKim, 1977). As such, the intermediate pollution treatment receiving a Cu dose in the first phase of community development (Cu:Cont treatment) was predicted to be more affected by the pollution treatment than assemblages exposed during the second phase of development (Cont:Cu treatment; Fig. 2).

The Cu treatments were applied by means of Perspex collars that had been treated with two coatings of a copper-based antifouling agent (International® Micron Extra, Akzo Nobel, Arnhem, the Netherlands). Collars were fixed to the perimeter of each pollution-treatment plate at the commencement of the experiment, effectively forming a 2-cm wide border of antifouling paint around the outer edge of each plate. To ensure the assemblages received a continued high dose of copper for the duration of the experiment, the collars were replaced every month. As a procedural control, control plates were fitted with an identical Perspex collars that had not been treated with antifouling paint.

Census of hard-substrate assemblages

After 7 months submergence, all settlement surfaces were retrieved from the field, and photographed and preserved in 7% formalin. To census the assemblages, photographs were viewed on a computer screen, and the percentage cover of taxa estimated based on 50 randomly selected points overlayed over a 7 × 7 cm central portion of the image (excluding the 2.5-cm perimeter occupied by the experimental collars). Additionally, to gauge the total species richness on each plate, each preserved assemblage was examined carefully using a dissecting microscope, to record any species that did not appear in the percentage cover counts.

Organisms were identified to the lowest taxonomic level possible, and assigned a classification status of native species, NIS or cryptogenic species based on available literature and identification records. Native and NIS were categorized as those taxa originating from Australian waters or international geographical regions, respectively, while cryptogenic species consisted of any taxa whose origins are disputed or remain unknown. The baseline survey was based on the control treatment (Cont:Cont) assemblages from each site.

Statistical analysis

For the baseline survey, differences in species richness and community diversity between sites were examined using one-way analysis of variance (ANOVA). Community diversity of each plate was estimated using the Shannon–Weaver index (H'; Shannon & Weaver, 1949). Species richness estimators and species accumulation curves were used to gauge the accuracy of the baseline survey in describing the true numbers of species in field communities (Wyatt *et al.*, 2005). Species richness estimators used were MM Means (based on Michaelis–Menton equation) and Chao2 (Chao, 1987) and were calculated for each site based on 1000 permutations in EstimateS (Colwell & Coddington, 1994). The species richness estimators were compared to the final point reached in species accumulation curves to determine the percentage of species sampled relative to the total number estimated to be present for successively more sites and plates within each site (Table 2).

For the manipulative pollution experiment, multivariate analyses of assemblage composition were performed using PERMANOVA (Anderson, 2005), CAP (Anderson, 2004), and SIMPER (Clark & Gorley, 2001). The diversity and percentage cover of species on experimental assemblages were contrasted among sites and treatments using a three-factor PERMANOVA, where Harbours and pollution treatments were treated as fixed and orthogonal, and Sites random and nested within harbour. CAP ordinations were then used to visualize differences in hard-substrate community composition with respect to sites and pollution treatments. A SIMPER analysis for each site was used for identifying which species primarily account for observed differences in assemblage composition between the two most extreme treatments (Cont:Cont and Cu:Cu). Only taxa that accounted for ≥ 10% dissimilarity were presented for discussion.

Differences in the species richness and percentage cover of native, non-indigenous, and cryptogenic species at individual sites was determined using one-factor ANOVAs. Planned comparisons were carried out on significant results to determine differences between treatments, with all pollution treatments compared against control treatments (Cont:Cont). All data were assessed for normality and homogeneity of variance using residual plots (as per Quinn & Keough, 2002).

RESULTS

Baseline survey

Forty-seven animal taxa were identified across all sites, including barnacles, arborescent and encrusting bryozoans, colonial and solitary ascidians, sponges, spirorbid and serpulid polychaete worms, and cnidarians. Fifteen species (32%) were identified as native, 19 (40%) as non-indigenous, and 13 (28%) as cryptogenic (Table 1).

The average species richness of the communities differed significantly between sites ($F_{3,20} = 3.14, P < 0.05$), with Tukey's post-hoc tests identifying Bare Island as having considerably less species on average per plate than other sites (Fig. 3a). There was, however, no difference in the community diversity (H') between sites ($F_{3,20} = 0.95, P = 0.435$), with approximately the same numbers of species being recorded overall at each site (between 27 and 31; Table 2).

NIS were found at all sites; however, their diversity and distribution varied (Fig. 3a,b). Woolloomooloo Bay was the only site where the average number of NIS found (7.8 ± 0.6) exceeded the number of natives identified (5.3 ± 0.6; Fig. 3a). NIS at this site were also the most conspicuous, occupying three times more space than native species (Fig. 3b). In contrast, Bare Island had the lowest ratio of NIS : Natives (at 0.5) relative to all other sites (at 0.9, 1.5, and 0.7 for Bradley's Head, Woolloomooloo Bay, and Port Botany, respectively; Fig. 3a), and also had the least percentage cover of NIS of any site (Fig. 3b). Bare Island was the only site with any substantial amount of bare space left unoccupied after 7 months (Fig. 3b).

The species richness estimators (MM and Chao2) suggest that the true numbers of species in the entire community, and the native, NIS, and cryptogenic components was generally well described (at between 74% and 100%; Table 2), with the only exception being the poorly resolved cryptogenic component at Port Botany (40%). This outcome is particularly good given the relatively small sample size used ($n = 6$) compared with similar studies (e.g. $n = 20$) used by Wyatt *et al.* (2005).

Table 1 Summary of taxa found during the survey experiment and (where possible) their identification and classification as native (N), non-indigenous (NIS), or cryptogenic (C).

Taxa	Species name	Status	Source
Barnacles	*Balanus trigonus*	N	AMBS (2002)
	Amphibalanus variegates	N	AMBS (2002)
	Balanus amphitrites	NIS	Hewitt *et al.* (2004)
	Tetraclittella purpurascens	N	Jones (1990)
Arborescent bryozoans	*Bugula neritina*	NIS	Hewitt *et al.* (2004)
	Bugula flabellata	NIS	Hewitt *et al.* (2004)
	Bugula stolonifera	NIS	Hewitt *et al.* (2004)
	Tricellaria inopinata	NIS	Hewitt *et al.* (2004)
	Bowerbankia gracilis	NIS	Gordon & Mawatari (1992)
	Scruparia ambigua	NIS	Hewitt *et al.* (2004)
	Crisia sp.	N	AMBS (2002)
	Amathia distans	NIS	Hewitt *et al.* (2004)
Encrusting bryozoan	*Schizoporella errata*	NIS	Hewitt *et al.* (2004)
	Watersipora subtorquata	NIS	Hewitt *et al.* (2004)
	Fenestrulina mutabilis	N	Clark & Johnston (2005)
	Beania magellanica	N	AMBS (2002)
	Celleporaria nodulosa	N	Type description, Busk (1881)
	Microporella sp.	N	Keough & Ross (1999)
	Conopium seurati	NIS	Gordon & Mawatari (1992)
	Rhynchozoon sp.	C	Gordon & Mawatari (1992)
	Tubulipora sp.	C	Bock (1982)
	Lichenopora sp.	N	Bock (1982)
	Cryptosula pallasiana	NIS	Hewitt *et al.* (2004)
	Smittoidea sp.	C	
	Mucropetraliella elleri	N	MacGillivray (1869)
Solitary ascidians	*Styella plicata*	NIS	Hewitt *et al.* (2004)
	Pyura sp.	N	AMBS (2002)
	Ciona intestinalis	NIS	Hewitt *et al.* (2004)
Colonial ascidians	*Diplosoma listerianum*	NIS	Lambert & Lambert (1998)
	Botrylloides leachi	NIS	Hewitt *et al.* (2004)
	Didemnum sp. *A*	C	
	Didemnum sp. *B*	C	
	Unk. colonial ascidian A	C	
Sponges	*Sycon* sp.	C	
	Unk. encrusting sponge A	C	
	Unk. encrusting sponge B	C	
	Halisarca dujardini	NIS	Hewitt *et al.* (2004)
Polychaetes	*Hydroides elegans*	NIS	Hutchings *et al.* (1989)
	Pomatocerus taeniata	N	Wilson *et al.* (2003)
	Salmacina australis	N	Haswell (1884)
	Branchioma sp.	C	Wilson *et al.* (2003)
	Pileolaria sp.	C	Knight-Jones *et al.* (1972)
	Spirobidae sp. A	C	Knight-Jones *et al.* (1972)
Hydroids	*Clytia* sp.	NIS	Hewitt *et al.* (2004)
Mollusca	*Anomia* sp.	N	AMBS (2002)
Cnidarians	*Aurelia* sp.	C	Dawson *et al.* (2005)
	Culcia sp.	N	Edgar (2000)

Manipulative pollution experiment

Multivariate analyses of community composition based on presence/absence identified very strong differences between study sites (PERMANOVA $P < 0.001$). These differences may have obscured the impact of pollution treatments (PERMANOVA $P = 0.07$). The canonical ordination of species richness largely supported this finding, displaying a clear separation between study sites, with the exception of some overlap between Bradley's Head and Bare Island (Fig. 4a).

Multivariate analyses of community composition based on percentage cover yielded similar results to those for presence/

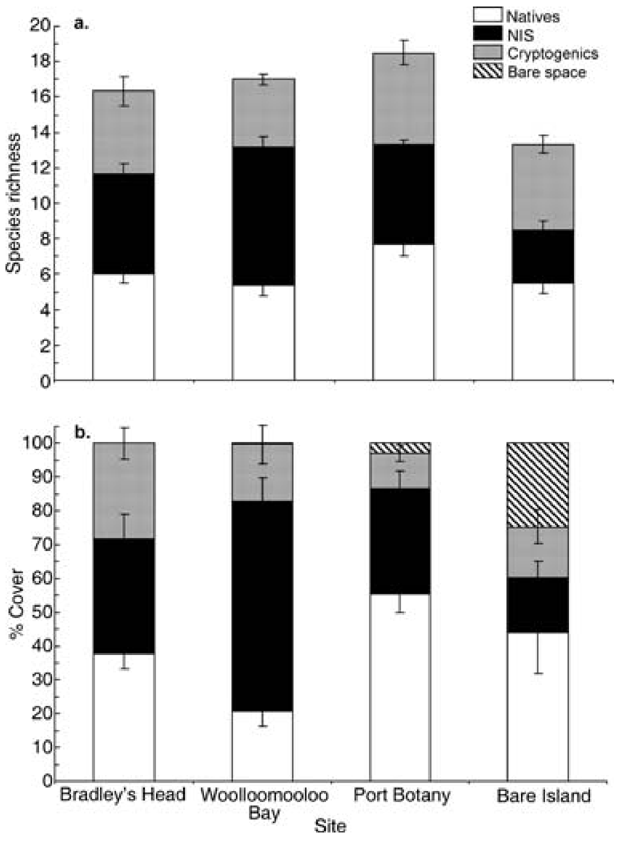


Figure 3 (a) Species richness and (b) percentage area cover at each study site for native, non-indigenous, and cryptogenic species. Percentage cover data includes bare space where applicable. Values represent the mean (± 1 SE).

absence, with clearly defined differences being observed between study sites (PERMANOVA $P < 0.001$, Fig. 4c). A significant interaction was also observed between Site and Treatment (PERMANOVA $P < 0.05$), with planned comparisons indicating some variability among control and pollution-treatment assemblages at several sites.

Individual site analyses

Univariate analyses at the level of site identified distinct effects of pollution on the species richness and percentage cover of NIS and native species. Increased pollution loads significantly reduced the numbers of native species in experimental assemblages at all sites: Bradley's Head ($F_{3,20} = 4.06, P < 0.05$), Woolloomooloo Bay ($F_{3,20} = 4.63, P < 0.05$), Port Botany ($F_{3,20} = 4.33, P < 0.05$), and Bare Island ($F_{3,20} = 3.11, P < 0.05$; Fig. 5a–d). Planned comparisons of pollution treatments against controls (Cont:Cont treatment) revealed that all significant reductions in native species numbers occurred in the two most detrimental pollution treatments, Cu:Cont and Cu:Cu. The primary contributors to the reduction in native species diversity (by ≥ 50%) were varied, and encompassed a range of taxa including barnacles, bryozoans, ascidians, and serpulid polychaete worms (Table 3). This decrease in native species richness contrasted with the observations made for NIS, which showed no significant decline in species numbers despite increasing pollution levels (Fig. 5a–d). There was no change in number of cryptogenics with pollution treatment.

Table 2 Summary of measured species richness and species richness estimates (MM, Michaelas–Menton mean and Chao2) for entire community (All), and the native, NIS, and cryptogenic components. Species richness estimates include a presentation of the percentage of the estimate measured (Total/species richness indicator).

	Measured species richness	Species richness estimates	
Bradley's Head			
All	27	30.55 (88.4)	31.17 (86.6)
Native	10	11.14 (89.8)	12.5 (80.0)
NIS	9	10.29 (87.5)	9 (100.0)
Cryptogenic	8	9.13 (87.6)	8.42 (95.0)
Woolloomooloo			
All	27	30.07 (89.8)	28.39 (95.1)
Native	8	8.86 (90.3)	8 (100.0)
NIS	12	12.89 (93.1)	12.83 (93.5)
Cryptogenic	7	8.46 (82.7)	7 (100.0)
Port Botany			
All	31	34.62 (89.5)	41 (75.6)
Native	10	10.63 (94.1)	10 (100.0)
NIS	9	9.96 (90.4)	9.42 (95.5)
Cryptogenic	12	15.52 (77.3)	30 (40.0)
Bare Island			
All	27	33.69 (80.1)	30.89 (87.4)
Native	11	13.57 (81.1)	13.5 (81.5)
NIS	7	9.53 (73.5)	7.21 (97.1)
Cryptogenic	9	10.84 (83.0)	9.42 (95.5)

Increased pollution loads increased the spatial dominance of NIS. At Bradley's Head and Port Botany, the two highest pollution treatments (Cu:Cont and Cu:Cu) displayed a significant increase in the percentage cover of NIS relative to controls of between 24% and 29%: Bradley's Head ($F_{3,20} = 4.88, P < 0.01$) and Port Botany ($F_{3,20} = 3.13, P < 0.05$; Fig. 6a,c). In the case of Port Botany, this pollution-mediated response resulted in a community shift from an assemblage dominated by natives, to one dominated by NIS (Fig. 6c). Similarly at Bradley's Head, we see a shift from a community where natives and NIS have equal coverage (*c.* 34–37%) to one greatly dominated by NIS (*c.* 60% cover; Fig. 6a). This trend of increased NIS coverage with increasing pollution was repeated at Woolloomooloo and Bare Island sites, with cover of NIS on Cu:Cu treatments greater than those of controls by 6% and 16%, respectively (Fig. 6b,d). The increase in NIS dominance on pollution-treatment assemblages also coincided with a decrease in the cover of native species at three of the four study sites (Bradley's Head, Port Botany, and Bare Island), although this decrease was only significant at Port Botany ($F_{3,20} = 7.28, P < 0.01$; Fig. 6a,c,d). At Bare Island, however, we again see a dramatic community shift from one dominated by native species, to one where native and NIS occupy equal space (Fig. 6c).

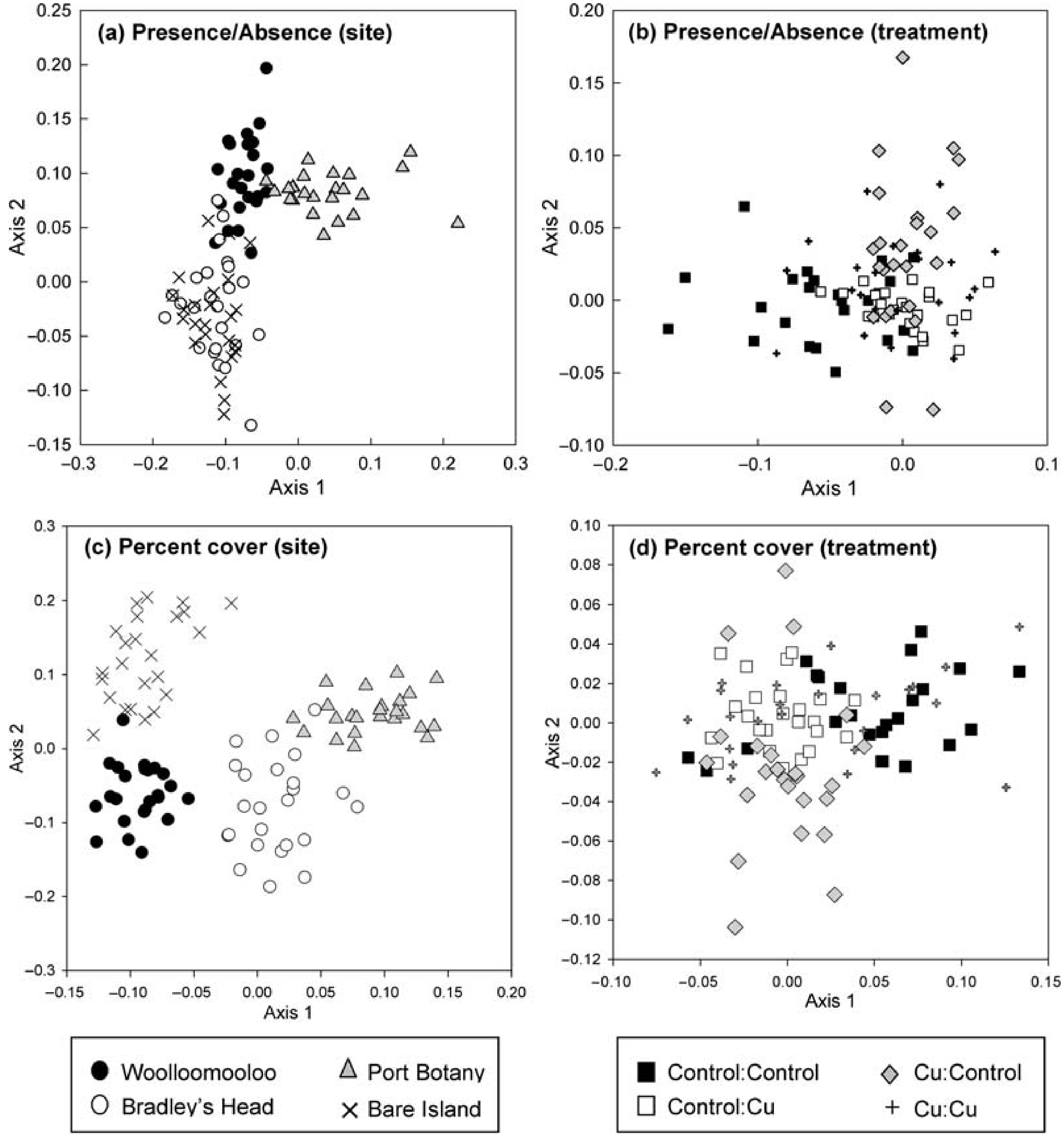


Figure 4 Canonical ordinations of experimental assemblages' showing community composition presented as a factor of (a) site and (b) pollution treatment, and percentage cover of taxa presented as a factor of (c) site and (d) pollution treatment.

Results of the SIMPER analyses to identify which species were primary contributors (by ≥ 10%) to observed changes in assemblage cover between control pollution and treatments confirmed previously observed patterns that pollution increased spatial dominance of NIS and decreased native cover. At Bradley's Head and Woolloomooloo, the introduced bryozoan *Schizoporella errata* was the major contributor to change, with increased cover in polluted assemblages (Table 4). Port Botany communities showed a drastic reduction in the cover of the native bryozoan *Beania magellanica* in Cu-treatment assemblages and a corresponding increase the cover of two introduced colonial ascidians (*Botrylloides leachi*, *Diplosoma listerianum*) and the introduced sponge *Halisarca dujardini* (Table 4). The same pattern was observed at Bare Island, where the cover of a native barnacle (*Balanus trigonus*) and bryozoan (*Celleporaria nodulosa*) decreased in Cu-treatment assemblages, while the NIS ascidian *D. listerianum*

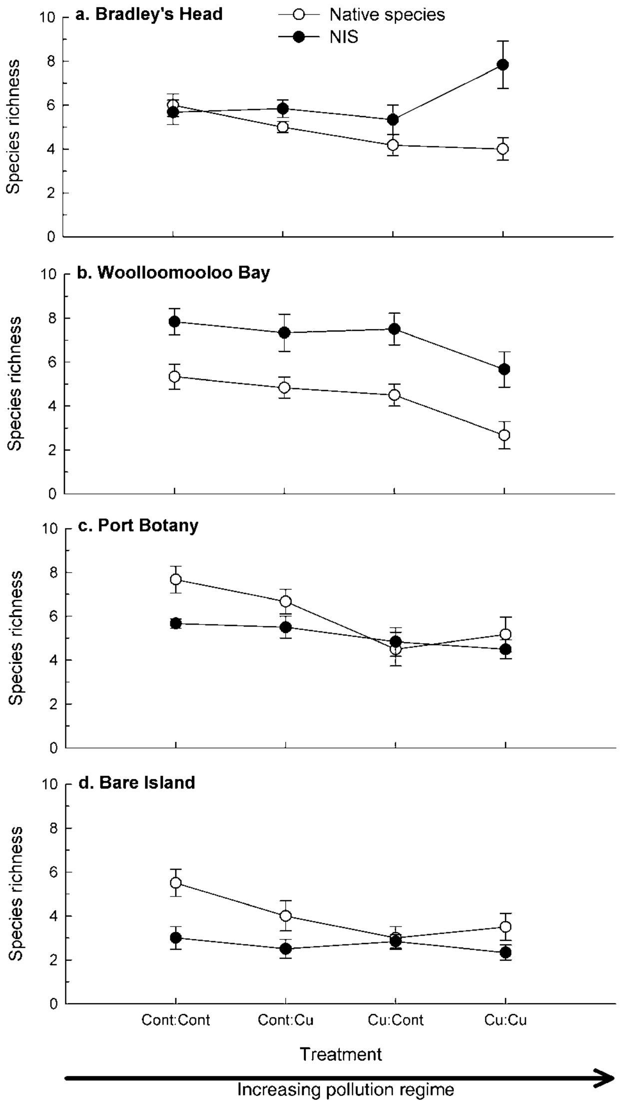


Figure 5 Number of native and non-indigenous species (NIS) observed on control and pollution-treatment assemblage plates at (a) Bradley's Head, (b) Woolloomooloo Bay, (c) Port Botany, and (d) Bare Island, across four pollution regimes. Values represent the mean (± 1 SE).

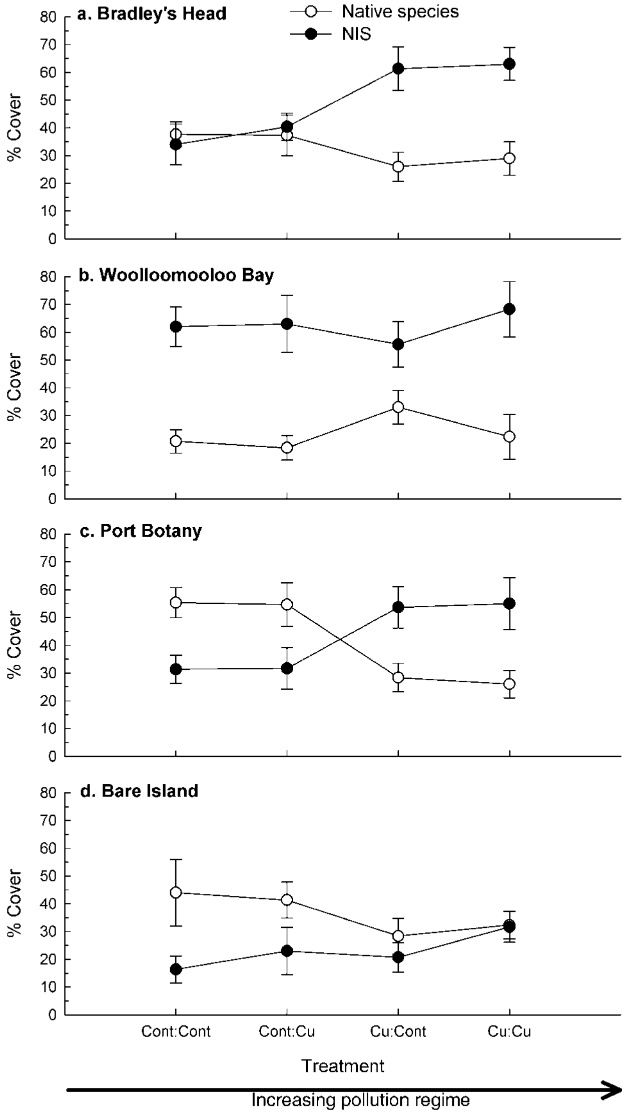


Figure 6 Percentage cover of native, non-indigenous (NIS) and (where applicable) cryptogenic species occupying space on control and pollution-treatment assemblage plates at (a) Bradley's Head, (b) Woolloomooloo Bay, (c) Port Botany, and (d) Bare Island. Values represent the mean (± 1 SE).

increased (Table 4). Interestingly, the percentage cover of bare space in Bare Island assemblages decreased in Cu-treatment communities relative to controls (Table 4). The only major contributor to community change that did not fit the observed pattern of increasing NIS cover/decreasing native cover with pollution was the native serpulid worm *Salmacina australis*, which increased its coverage in pollution assemblages at Woolloomooloo and may indicate a tolerant polychaete population at this site (Table 4).

DISCUSSION

This is one of the first studies to distinguish the effect of pollution on native and non-indigenous species richness and dominance within a marine system (but see Carman *et al.*, 2007). Metal pollution was found to significantly alter the species richness and structure of exposed sessile invertebrate assemblages, resulting in a decline in the numbers of native species at all study locations when subject to an increasing pollution regime. This contrasted with observations for NIS, where pollution had no effect on species richness. Pollution did, however, dramatically increase the spatial dominance of NIS, resulting in fundamental changes to community structure. This research highlights the importance of studies that simultaneously record the occurrence of NIS within native communities, while manipulatively examining the mechanisms facilitating their establishment and distribution.

While there are many studies that examine the effectiveness of antifouling paints by measuring the level of recruitment directly to the surface of the paint (Wisely, 1964; Floerl *et al.*, 2004), there

Table 3 Primary contributors (by ≥ 50%) to the reduction in native species richness observed between control treatment assemblages (Cont:Cont) and the most extreme Cu-pollution treatments assemblages (Cu:Cu) at four study sites in Sydney Harbour and Botany Bay.

Source	Occurrence on Cont:Cont plates (%)	Occurrence on Cu:Cu plates (%)	Overall decrease in occurrence (%)
Bradley's Head			
Amphibalanus variegates	50	0	100
Microporella lunifera	17	0	100
Pomatocerus taeniata	100	33	67
Balanus trigonus	50	17	67
Woolloomooloo			
Microporella lunifera	50	0	100
Beania magellanica	17	0	100
Crisia sp.	100	17	83
Pyura sp.	100	17	83
Fenestrulina mutabilis	50	17	67
Port Botany			
Crisia sp.	83	17	80
Beania magellanica	100	33	67
Pyura sp.	83	33	60
Microporella lunifera	67	33	50
Bare Island			
Amphibalanus variegates	33	0	100
Microporella lunifera	17	0	100
Mucropetraliella elleri	17	0	100
Pomatocerus taeniata	17	0	100
Beania magellanica	67	17	75
Lichenopora sp.	67	33	50

Table 4 Summary of SIMPER analyses performed to identify which native and/or non-indigenous species (NIS) were the primarily contributors (by ≥ 10%) to observed changes in community assemblage percent cover between control treatment assemblages (Cont:Cont) and the most extreme Cu-pollution treatments assemblages (Cu:Cu) at four study sites in Sydney Harbour and Botany Bay. Percentage cover for each species is shown to either (+) increase or (–) decrease with response to pollution.

Source	Status	Percentage of contribution to assemblage change	Direction of change (% cover)
Bradley's Head			
Schizoporella errata	NIS	15	+
Halisarca dujardini	NIS	10	+
Woolloomooloo Bay			
Schizoporella errata	NIS	31	+
Salmacina australis	Native	14	+
Port Botany			
Beania magellanica	Native	28	–
Botrylloides leachi	NIS	11	+
Diplosoma listerianum	NIS	10	+
Halisarca dujardini	NIS	10	+
Bare Island			
Balanus trigonus	Native	17	–
Bare space	–	17	–
Diplosoma listerianum	NIS	12	+
Celleporaria nodulosa	Native	11	–

exist few studies that take advantage of the slow-release properties of these paints to simulate chronic pollution events in adjacent assemblages (but see Johnston & Webb, 2000). The present study successfully employs this technique to dose experimental sessile invertebrate assemblages with a range of heavy metal pollution loads. The mean dissolved Cu flux rates from each experimental treatment collar in this study was calculated to be approximately 310 μg day^{-1} (based on Schiff *et al.*, 2004), which represents a considerable exposure level to each experimental assemblage over the duration of the study (*c.* 65 mg Cu per heavily polluted assemblage, and *c.* 30–37 mg Cu per intermediate pollution treatment). Studies using a similar dosing mechanism (Webb & Keough, 2002) have demonstrated that average monthly dissolved Cu concentrations immediately surrounding such collars are within the range of values actually recorded for chronically polluted ports and estuaries (Moran & Grant, 1989; Srinivasan &

Swain, 2007). We feel confident that this study successfully simulated the impact of a realistic anthropogenic pollution scenario upon sessile invertebrate assemblages.

Anthropogenic pollution has been demonstrated to affect the diversity of organisms in many marine systems (Kennish, 2002; Hooper *et al.*, 2005), with metal pollution in particular being shown to greatly decrease the diversity of sessile and benthic fauna (Rygg, 1985a,b; Moran & Grant, 1989; Medina *et al.*, 2005). To our knowledge, however, the present study is the first to distinguish a specific pollution-mediated reduction in the native species component of a marine community. The absence of a corresponding reduction in NIS with increasing pollution suggests that NIS in this system are differentially tolerant to metal pollution relative to their native counterparts. While the tolerance of NIS to metal pollution has been demonstrated for vessel hull-fouling communities (Floerl *et al.*, 2004) and in laboratory experiments (Piola & Johnston, 2006a), this has not been previously demonstrated in newly formed field populations.

The effect of pollution on the species richness of native assemblages in this study was uniformly negative across all study sites, irrespective of community composition (Fig. 5). The driving mechanism behind the pollution-mediated reduction in native diversity was not the repeated removal of a select few sensitive species, but rather a broad-scale decrease in the number of native species across a range of species and taxa. While some species were consistently removed by the toxicant (e.g. *Microporella lunifera*), no one species was consistently responsible for the decline in native numbers. This finding supports our original prediction that native species in our system would in general be more sensitive to metal pollution relative to NIS, given that they have not undergone selection for metal tolerance experienced by NIS via their likely mode of introduction (hull fouling).

Fluctuating resource availability is a primary factor governing the invasibility of a system (Davis *et al.*, 2000). The removal of native taxa during a pollution disturbance event would likely result in changes to the allocation of system resources (such as space in sessile marine invertebrate assemblages) potentially facilitating the introduction and/or expansion of more tolerant NIS. Most introduced NIS fail to establish in their recipient habitats (Williamson, 1996); however, pollution could potentially provide a ‘leg up’ to tolerant NIS able to function and compete within polluted environments. This may include newly arriving non-indigenous components of vessel hull-fouling assemblages that have been selected for high tolerance to metal pollution (Floerl *et al.*, 2004), or pollution-tolerant NIS already resident within recipient assemblages (for examples, see Piola & Johnston, 2006a).

The majority of NIS identified in this study have previously been recorded in Sydney Harbour (AMBS, 2000; Glasby *et al.*, 2007) and Botany Bay (Pollard & Pethebridge, 2002), with the exception of *Styella plicata*, *Ciona intestinalis*, and *D. listerianum* at Botany Bay, and *H. dujardini* at Botany Bay and Sydney Harbour. Given the long history of international and domestic shipping activity in both these harbours, it seems safe to assume that the NIS observed in this study are well established within the system. Since there was no increase in the species richness of NIS in polluted assemblages, we can assume that pollution did not facilitate any new introductions, but rather provided already resident NIS the opportunity to increase their spatial dominance within the assemblage. A valuable future focus of this research would be to conduct controlled small-scale experiments to examine the effect of pollution on native and NIS dynamics in areas subject to minimal human impact, to determine if pollution exposure aids the establishment of NIS into native assemblages where they are historically absent (or merely minor components). We predict the trends that were observed in this study (i.e. decreasing native diversity with increasing pollution; increased NIS spatial dominance with increasing pollution) would likely be even more pronounced in more pristine environments. Less disturbed pristine environments are likely to hold a greater range of native taxa, comprising both robust species and rare/sensitive species not found in disturbed systems. Given that a strong anthropogenic disturbance event such as pollution is able to remove robust native taxa that are well acclimatized to disturbed environments (as demonstrated by this study), within a pristine system the additional removal of rarer (more sensitive) species should magnify this trend of decreased native species richness. If NIS are absent from an affected system such as this, we predict no dramatic long-term change in community composition since there are no invaders to exploit newly freed resources. If, however, NIS are present in the system, but have previously been prevented from establishing due to native dominance, then their success of establishing post-disturbance will depend primarily on the availability and timing of propagules (Clark & Johnston, 2005).

Findings from this study have important implications for the management and control of NIS in marine protected areas that may be under increasing threat of invasion. For example, some of the key NIS species found to respond favourably to pollution in this study (e.g. *S. errata*, *Conopeum seurati*, *B. leachi*) are among a suite of NIS identified in the World Heritage-listed property of Shark Bay, Australia (Wyatt *et al.*, 2005). *Schizoporella errata* in particular was found to be a major habitat modifying species in this study and occurred at high frequencies in Shark Bay (present in 75% of samples). Hull fouling on recreational vessels was identified as one of the most important vectors of introduction at Shark Bay, so it is possible that at least some of the NIS present there benefit from some degree of metal resistance. Future pollution events at Shark Bay, such as an increase in the number, frequency, and residency times of visiting vessels (Schiff *et al.*, 2004; Warnken *et al.*, 2004) or major ship grounding events (Negri *et al.*, 2002) may result in the further entrenchment of some NIS, resulting in possible major habitat modification and further risk of introductions (Simberloff & Von Holle, 1999).

Increased spatial dominance of NIS associated with an increasing pollution regime was observed at three of the four sites studied (Bradley’s Head, Port Botany, and Bare Island). Not surprisingly this increase was linked with a corresponding decrease in the cover of native species within the assemblage. In all cases, these fluctuations in species dominance resulted in a clear change to community structure that benefited the non-indigenous component. Changes in native assemblage composition such as those observed here can affect the dynamics of a system, resulting in the threat of further invasion (Simberloff & Von Holle, 1999; Stachowicz *et al*., 1999; Stachowicz *et al*., 2002) and/or indirect effects on associated groups of fauna (Perrett *et al*., 2006; White *et al*., 2006).

The only site in this study that did not record an increase in the spatial dominance of NIS with increasing pollution was Woolloomooloo Bay. The baseline survey revealed NIS both outnumber and outcompete natives at Woolloomooloo with the introduction of pollution doing little to change this balance. This is likely a result of the already high background levels of pollution, originating from the nearby marina and naval base and slip yard. Sediment loadings of heavy metals within this bay are reported at 200–300 $\mu g\ g^{-1}$ (Cu), 500–800 $\mu g\ g^{-1}$ (Zn), and $> 400\ \mu g\ g^{-1}$ (Pb) (Birch & Taylor, 1999). These values represent between a 3- and 30-fold increase over similar values recorded at or near our other study sites (Birch & Taylor, 1999; Spooner *et al*., 2003) and are as much as double the recommended values stated in Australian sediment quality guidelines (ANZECC/ARMCANZ, 2000). Based on the patterns observed between pollution and the spatial dominance of NIS at the other experimental sites, high background pollution levels at Woolloomooloo are a likely contributor to the already high dominance of NIS in the system.

Interestingly, Woolloomooloo was also the only site where a native species displayed a similar trend to that observed for NIS, increasing in spatial dominance with increasing pollution regime. A dramatic increase in the cover of the native colonial serpulid *S. australis* was observed in second highest pollution treatment assemblages (Cu:Cont; Fig. 6b). Increased cover of *S. australis* also accounted for 14% of the difference observed between control (Cont:Cont) and highly polluted treatments (Cu:Cu) at this site (Table 4). Metal pollution has been found to increase the densities of some serpulid species through their enhanced ability (as successful early colonizers) to sequester newly created space (Johnston & Keough, 2003). *Salmacina australis* appears to be very effective at utilizing space made available through pollution disturbance, especially in treatments where pollution exposure ceased following an initial dose (treatment Cu:Cont). The fact that this response was not observed in *S. australis* populations from other sites (even though it was present at all locations) may be due to that fact that population densities of this organism were much lower at other sites. Native species subject to selection for metal tolerance may be distributed by vectors such as hull fouling, and *S. australis* appears a potential candidate for export.

With the exception of *S. australis*, pollution had a deleterious effect on the percentage cover of all native species on experimental plates. Furthermore, the recovery of native species numbers or spatial dominance did not improve even after the cessation of pollution exposure. This is evidenced by the continued lower native species richness and NIS spatial dominance in Cu:Cont treatment assemblages at Bradley's Head, Port Botany, and Bare Island that received no metal exposure (for 4 months) following the initial pollution period (of 3 months). Previous research has indicated that pollution can dramatically change community structure in marine hard substrate assemblages, predominantly through the removal of highly competitive species in favour of weedy species, that tend to be good colonizers (Johnston *et al*., 2002). Traits associated with weediness (such as high fecundity and the ability to establish in disturbed areas) have been suggested as characteristics that enhance the invasive success of plant species (Daehler, 2003), and it is possible that these qualities exist in marine hard-substrate invader species also, aiding their establishment and spread.

In order to manage current NIS and prevent fundamental changes to native community structure and dynamics, we may first need to reduce the degree of pollution present within recipient estuaries and harbours, and minimize the risk of future pollution events in currently undisturbed habitats (e.g. Shark Bay, Australia). This will have the effect of improving water quality and the survivorship of potentially sensitive native populations (Medina *et al*., 2005; Smith & Shackley, 2006; Johnston & Clark, in press), while simultaneously reducing the risk of NIS establishment and dominance. Improved water quality could be achieved through the development and adoption of nontoxic antifoulants (e.g. Stupak *et al*., 2003), remediation of contaminated sediments to avoid the risk of toxicant release during resuspension events (Beck, 1996), and/or reducing the risk of ship groundings (Negri *et al*., 2002). Results of this study suggest another solution may be the mooring of long-stay vessels in high flow environments. Traditionally, most recreational vessels are moored in sheltered low flow harbours and embayments, leading to a build up of antifouling biocides and metals (Schiff *et al*., 2004; Warnken *et al*., 2004). This research indicates that the study area with highest water movement (Bare Island) not only had a lower proportion of NIS in baseline survey assemblages (23%) relative to low flow sites (31–46%), but also that pollution had less of an enhancement on the spatial dominance of NIS (*c*. 15% increase) compared to sheltered areas (25–30% increase). This may be due to the more efficient dispersal and removal of pollutants in high energy systems, and/or a result of fewer NIS being adapted to high flow environments. Irrespective of the reason, it remains worthy of consideration as a management strategy. Finally, it must be recognized that pollution may be all that is necessary to establish the dominance of NIS in sessile marine communities.

While the interaction between invasion and disturbance has been the focus of a great deal of ecological research, the specific role that pollution plays in facilitating invasion has been largely overlooked. This research adds an important insight to a growing body of work detailing the specific effects of anthropogenic disturbance on the diversity and distribution of exotic marine species within native habitats.

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