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Effect of wharves on intertidal assemblages on seawalls in Sydney Harbour, Australia

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Abstract

Worldwide, urbanisation has resulted in extensive replacement of natural habitats with man-made habitats. In Sydney Harbour, Australia, approximately half of the natural foreshore has been replaced by seawalls. Many of these have wharves built over part of their length, which could affect intertidal assemblages on seawalls beneath the wharves. This was tested by sampling and comparing assemblages under and not under wharves in Sydney Harbour. Assemblages differed between the two habitats, with greater cover of macro-algae and abundance of grazing molluscs on seawalls without a wharf and, to a lesser extent, greater cover of sessile invertebrates on seawalls under a wharf. There was, however, considerable spatial variability among locations in composition of assemblages and the species dominating differences between the two habitats. The impact of multiple artificial structures in close proximity and the variability among apparently homogeneous artificial habitats must be considered for the management of urbanised estuaries.

Keywords: Algae; Artificial habitats; Coastal structures; Grazing molluscs; Sessile invertebrates
Shading; Sydney Harbour; Temperature; Urbanisation

1. Introduction

Urbanisation of coastal waters has resulted in proliferation of a variety of different artificial marine structures (e.g. pontoons, pilings and seawalls), each supporting different assemblages (Connell & Glasby, 1999; Glasby & Connell, 1999). Seawalls are among the most common marine habitat within urbanised estuaries and bays (Davis, Levin & Walther, 2002; Chapman, 2003), but often have other types of artificial structures built in close proximity, such as wharves (Blockley & Chapman, In press). These structures might influence the assemblage living on the seawall by increasing or decreasing abundances or covers of different species.

The sections of seawalls under wharves are potentially subject to different environmental conditions (e.g. light, temperature, rain and wind) to those in the open. Wharves, jetties and similar structures have been found to reduce the growth of seagrasses (Short & Burdick, 1996; Burdick & Short, 1999) and density of salt marsh plants (Sanger, Holland & Gainey, 2004). The effect of wharves and jetties on assemblages living on other artificial habitats has also been examined in subtidal habitats (e.g. for pilings), with reductions in the cover and types of algae in shaded areas and an increase in sessile invertebrates (Glasby, 1999a; 1999b). The effect of wharves on intertidal hard substrata has not, however, received much attention. This is an important consideration because wharves are most profuse in areas that are already urbanised and so are most likely to be built in association with other artificial structures, frequently seawalls (Blockley & Chapman, In press).

This study was done in Sydney Harbour, Australia, where most wharves are built over parts of the extensive network of seawalls. Sections of seawalls that were either shaded or unshaded by wharves were predicted to have different assemblages and covers or abundances of individual taxa would differ between shaded or unshaded seawalls. Specifically, it was predicted that; (1) the cover of algae would be greater on unshaded seawalls where there is more light (e.g. Clark, Edwards & Foster, 2004), (2) grazing invertebrates would be more abundant on unshaded seawalls because this

is where their food source was predicted to be greater and (3) sessile invertebrates would have greater cover on shaded seawalls because they would not have to compete for space with algae, nor be dislodged by mobile invertebrates and might be benefited by the presence of a wharf (e.g. reduction of thermal stress and desiccation). It was also predicted that these patterns would be spatially and temporal consistent throughout Sydney Harbour.

2. Methods

This study was done at seven locations in Sydney Harbour: Athol Bay, Cremorne Point, Rushcutters Bay, Hermit Point, Parriwi Head, Little Manly Point and Quarantine Station (Figure 1). All locations had seawalls with adjacent sections either with or without wharves. At each location, one section of seawall, approximately 5 m wide, under a wharf and one not under a wharf were sampled. Despite considerable variability in the design of wharves in this study, each 5 m section under a wharf was completely in shade and at least 1 m from the edge of the wharf. For each section, ten replicate 20 x 25 cm quadrats were sampled at the mid- (0.9 - 1.1 m above chart datum) and low-tidal (0.6 - 0.8 m above chart datum) heights. Percentage cover of all algae and sessile invertebrates were measured and all mobile invertebrates counted. Where possible, without destructive sampling, organisms were identified to species. Where complexes were formed, so that individual species could not be distinguished (e.g. some of the small foliose algae and sponges), these were assigned to broad groups (e.g. mixture of sponges referred to as “orange sponge”). Sampling was repeated four times; in March, June, October, 2003 and February, 2004. Even though the same sections of seawall were sampled each time, these times are far enough apart to provide independent data (Underwood & Chapman, 1998; Bulleri, Chapman & Underwood, 2005). Replicates were sampled randomly across the wall each time, so quadrats were not fixed. At the low-tidal height, only six of the locations were sampled because the lower shore of Parriwi Head was buried by a sand bank after the first sampling.

Environmental conditions on seawalls under or not under wharves were measured, with incident light on the wall and the surface temperature of the substratum the two variables recorded. These variables were considered to most likely differ between seawalls under or not under a wharf and are known to be important in structuring assemblages. The amount of incident light has a strong influence on the growth and survival of algae (Glasby, 1999a; Goldberg & Foster 2002; Clark et al., 2004) and recruitment of invertebrates (Pomeroy & Reiner, 1942; Saunders & Connell, 2001). Incident light was measured (in Lux) using a light meter placed at 10 random areas on seawalls under or not under wharves at each of the 7 locations. Sampling was repeated 5 times each month from April, 2003 until March, 2004.

Surface temperature of the substratum has been closely linked to the body temperature of many sessile invertebrates (Wetzel, 2002) and is an important indirect measure of thermal stress. The surface temperature of the seawall was also recorded for each habitat and location using an infra-red electronic thermometer. This measures the temperature of the surface of the substratum directly and is unaffected by air temperature or whether or not the device is in the sun. As for incident light, 10 random areas were sampled in each habitat for each of the 7 locations, with sampling repeated 5 times each month for a year.

All measurements of light and temperature throughout the sampling period were collected at approximately the same time of day and during low tide. It was not possible to collect incident light data during high tide and it would not have made sense to collect thermal data when organisms were immersed. During high tide, the surface temperature would have been controlled by water temperature and would not have differed between shaded and unshaded seawalls. For each month, there were 50 replicate measures of surface temperature and incident light collected for each habitat and location. These were averaged to give a mean monthly value. Collection of continuous data was not feasible with the resources available over such a large number of sites. There are also many restrictions on what can be attached to seawalls, being publically or privately owned structures.

The assemblages were compared using PERMANOVA (Anderson, 2001). Matrices of

dissimilarity among samples were calculated using the Bray-Curtis dissimilarity coefficient (Bray & Curtis, 1957). The method of permutation used for all analyses was the permutation of residuals under a full model because this gives the best power and accurate Type 1 error while being reasonably quick (Anderson & Legendre, 1999). Each of the 4 times of sampling was treated as an independent test of the hypothesis that difference between assemblages on seawalls shaded or unshaded by wharves was general to all locations, while in separate analyses each of the 7 locations were used as independent tests of the hypothesis that patterns would be temporally consistent. The data were visualised with nMDS ordinations (Clarke, 1993). Analyses of variance tested hypotheses that covers or abundances of taxa differed between the two habitats (fixed, orthogonal), among locations (random, orthogonal) and through time (random, orthogonal) for algae, mobile invertebrates and sessile invertebrates. Generally, it was found that heterogeneous variances for percentage covers could not be stabilised by transformation and so analyses were done on untransformed data with a more conservative significance level (see tables). ANOVA is, however, robust to heterogeneity of variance and non-normal data and so is an appropriate analytical technique (Underwood, 1999).

3. Results

3.1. Comparisons among assemblages

In general, at each time, the assemblages of the two habitats plotted apart on the nMDS graph for each location (Figure 2). Despite some pattern of grouping by habitat, particularly at times 1 and 4, there was a great deal of overlap between habitats shown in the plots among locations (i.e. some points representing assemblages on shaded seawalls plotted close to the cluster of points representing those on unshaded seawalls from different locations (Figure 2)).

There was a significant interaction of Location and Habitat for the mid- and low-tidal heights for the analyses of each time (Table 1a). Therefore, the hypothesis that the patterns of difference would be general to all locations was rejected, although *a posteriori* pairwise

comparisons showed that these habitats were always different for each location. This result is supported by the Bray-Curtis dissimilarities, which show that the dissimilarity between habitats is much greater than the average dissimilarity within each habitat for both tidal heights (Table 2). The dissimilarity among locations for each habitat is also large, supporting the lack of generality of the pattern among locations (hence the variability in Figure 2). Furthermore, the variability among locations for seawalls under wharves was greater than for seawalls not under a wharf at the mid-tidal height, but similar at the low tidal height (Table 2).

The analyses of each location separately across all times gave interactions between time and habitat for both heights in each location (Table 1b) showing that patterns of difference changed through time. Nevertheless, the plot for each location shows strong separation between habitats across all times indicating differences between the habitats remained large (Figure 3). The temporal changes, illustrated in the nMDS plots, did not show a consistent pattern among locations or between habitats.

3.2. Comparisons of individual taxa

Despite no general pattern of difference between habitats for whole assemblages, it was evident that there were consistent patterns for individual taxa among locations at the mid- (Table 3, Figure 4) and low-tidal height (Table 4, Figure 5). The encrusting alga, *Hildenbrandia rubra* was the dominant alga at the mid-tidal height (Figure 4a), while the turf, *Corallina officinalis* or foliose green algae, formed by complex patches of *Enteromorpha intestinalis*, *Ulva lactuca*, *Cladophora* sp., *Chaetomorpha* sp. and *Bryopsis* sp., dominated the low-tidal height (Figure 5a). *Hildenbrandia rubra* showed Time x Location and Location x Habitat interactions (Table 3a) while the low-shore algae had significant Time x Location x Habitat interactions (Table 4a). Despite this, the general patterns did not vary much among times, as shown by *Hildenbrandia rubra* (Figure 4a). For this reason and for the sake of brevity, only one time is shown to illustrate patterns for the other two alga (Figure 5a). There were large differences in cover among locations and the difference between

habitats was only significant at some times and locations, but there was a strong pattern of greater cover on seawalls not under wharves (Figure 4a & 5a). Binomial tests indicated that, despite the lack of significant differences at some locations or times, the general pattern was significant (Figure 4a & 5a).

The oyster *Saccostrea glomerata* was the dominant sessile invertebrate at most locations at the mid-tidal height. The mussel *Mytilus galloprovincialis*, the tubeworm *Galeolaria caespitosa*, the barnacles *Tesseropora rosea* and *Tetraclitella purpurascens* and an encrusting orange sponge also had relatively large covers at many locations (Figure 4b). The pattern was similar at the low-tidal height, although *S. glomerata* was not as dominant and the barnacle *Austrobalanus imperator* was also present (Figure 5b). As for the algae, there were significant Time x Location x Habitat interactions for most analyses of cover of sessile invertebrates (Table 3b & 4b). Exceptions were *M. galloprovincialis* at the mid-tidal height and *A. imperator* and *T. rosea* at the low-tidal height, which showed higher-order interactions. Despite this, the patterns were fairly consistent through time, shown for *S. glomerata* and so only one time is presented for the remaining taxa to illustrate the pattern (Figure 4b). There was, however, considerable difference in the covers of the various species among locations.

Covers of *S. glomerata* were most consistent among locations mid-tidally and were significantly greater on seawalls that were not under a wharf (binomial tests, Figure 4b). This is opposite to the pattern predicted. Similarly, mid-tidally *T. rosea* had a greater cover on seawalls not under wharves at many locations, although the general pattern was not significant (Figure 4b). The other sessile invertebrates showed the predicted pattern of greater covers on seawalls under wharves at many, but not all locations, however the difference was still significant (Figure 4b).

The cover of *S. glomerata*, *M. galloprovincialis*, *G. caespitosa*, and *A. imperator* did not differ between habitats significantly at the low-tidal height, although the cover of *A. imperator* was significantly greater on walls under wharves at Athol Bay and Cremorne Point at all times (Table 4b, Figure 5b). *T. rosea* showed a significant pattern, although as for the mid-tidal height, it was

opposite to that predicted (Figure 5b). *T. purpurascens* and orange sponge, however, showed a significant pattern of greater cover on walls under wharves as predicted (Figure 5b).

Of the mobile invertebrates, only *Chiton pelliserpentis* and the limpet, *Siphonaria denticulata* occurred in large enough numbers to be analysed. Analyses showed that each were more abundant on walls not under a wharf, although not significantly at all locations or times (Table 3c, Figure 6). Nevertheless the general pattern was consistent through time (Figure 6). There were many locations with a significantly greater abundance of both species on unshaded seawalls (Table 3c, Figure 6), although, at some times and locations, the opposite was found. Despite this, the predicted pattern of greater abundance of grazing invertebrates was significant (Figure 6).

3.3. Measurements of surface temperature and light on seawalls

The mean surface temperature on walls not under wharves was greater than on walls under wharves at each location (Figure 7). Nevertheless, the magnitude of the difference between the two habitats was not consistent among locations (e.g. the difference between the two habitats at Athol Bay was relatively small, while the difference at Hermit Point was much larger). There was also a difference in range of mean temperatures among locations (e.g. the seawall not under a wharf at Rushcutters Bay had a maximum temperature of approximately 28° C, while the same habitat at Cremorne Point was about 23° C).

Despite the mean surface temperature on seawalls not under wharves being greater than that on walls under wharves, the magnitude of the difference in temperature between habitats changed through time. The greatest difference was in the Austral summer months (December through to February), when the greatest mean surface temperatures were recorded.

The change in mean light, measured in Lux, on seawalls shows some similarity to the pattern seen for mean temperature (Figure 8). Incident light was, as would be expected, greater on seawalls not under wharves at all locations and at all times. There was considerable variability among locations in the magnitude of difference between the two habitats, as well as the range of

values recorded and a great deal of variability through time. Unlike temperature, there was no easily discernible pattern for the temporal variability of the light. There did not appear to be a consistent pattern among locations or in relation to seasonal change.

Discussion

In the current study, algae were virtually absent from walls under wharves and there was considerable covers of algae, such as *Corallina officinalis* and foliose green algae (e.g. *Enteromorpha intestinalis*), on unshaded seawalls. Shade can be important in structuring assemblages and has been shown to have important effects on the growth and survival of terrestrial plants (Weih & Karlsson, 1987; Valladares & Pearcy, 1997; Sans, Escarré, Lepart, & Hopkins, 2002), marine algae (Glasby, 1999b; Goldberg & Foster, 2002; Clark et al, 2004) seagrasses (Burdick & Short, 1999) and saltmarsh (Sanger et al., 2004). Animals on intertidal shores have also been shown to be affected by shading, with greater recruitment or survival where there is shade (Denley & Underwood, 1979; Harper & Williams, 2001). Shading alone may, therefore, explain the absence of algae and the greater cover of most species of sessile invertebrates under wharves in the present study, although this can not be concluded categorically without manipulative experiments.

Unlike many other sessile invertebrates in this study, the barnacle *T. rosea* had greater cover on unshaded walls. Denley & Underwood (1979) found that *T. rosea* would settle on unshaded and shaded shores, but survived better in the sun. The oyster *S. glomerata*, one of the dominant space occupiers, also had greater cover on unshaded walls. Bulleri et al. (2005) found that *S. glomerata* was able to dominate space on seawalls in Sydney Harbour, although the pattern was variable among locations. Beds of *S. glomerata* can be quite thick, providing oysters with protection from environmental extremes (e.g. thermal stress) in a similar way to the presence of a wharf. The lesser cover of other sessile invertebrates on unshaded seawalls may also have meant that oysters had less competition for space and so were able to maintain greater covers than on shaded seawalls.

The present study has shown that there is less incident light reaching seawalls with wharves compared to sections without wharves. Glasby (1999b) found that the degree of shading may be important in structuring assemblages of epibiota on subtidal pier pilings, with similar results as in the present study. The amount of shade can also influence the surface temperature of rocky intertidal areas, with unshaded areas having much greater surface temperatures than adjacent shaded areas during low-tide leading to physiological affects (e.g. greater mortality through desiccation or thermal stress (Garrity, 1984; Harper & Williams, 2001)). The provision of shade can ameliorate thermal stress and increase recruitment and survival (Denley & Underwood, 1979; Williams, 1994; Bertness, Leonard, Levine, & Bruno, 1999). According to Helmuth and Hofmann (2001), however, it is extreme temperature events (extremes of heat and cold) rather than the mean temperature that causes physiological stress. The design of the experiment was unlikely to capture temperature extremes because it unavoidably involved “snap-shot” measurements. The data collected does give a good indication that these extreme high temperatures would occur on unshaded seawalls, where surface temperature was always greater, whereas wharves would buffer seawalls beneath them from these events.

Recruitment of algae and invertebrates to seawalls has been shown to be affected by wharves, which shade the wall directly under them (Blockley & Chapman, In press). The greater cover of most sessile animals in the lower light conditions under wharves might represent a negative phototactic response at the time of settlement (e.g. Pomerat & Reiner, 1942; Wisely, 1959). O'Donnell (1984) showed that *G. caespitosa* recruit in greater numbers to shaded habitats, possibly explaining the patterns in the current study. Algae has also been shown to have greater recruitment to unshaded habitats (Goldberg & Foster, 2002; Clark et al, 2004). It is, therefore, possible that the patterns found in the present study are determined at the time of recruitment rather than by post-recruitment processes.

Despite support for patterns of difference between assemblages on seawalls under or not under wharves, there was great variability among locations and to, a lesser extent, among times.

Large-scale spatial (at the scale of km) and temporal differences in intertidal assemblages are a feature of the rocky shores of New South Wales, Australia (Dakin, Bennett, & Pope, 1948; Underwood & Chapman, 1998; Benkendorff & Davis, 2002). However, seawalls, unlike rocky shore, are homogeneous structures and so would be predicted to be less variability among locations. Previous research on seawalls in Sydney Harbour by Bulleri et al. (2005) has, however, shown that the variability of assemblages on seawalls can be as great as, or greater than that found on rocky shores among locations. Although Bulleri et al. (2005) found that the taxa responsible for patterns on seawalls varied among locations, general patterns were consistent for each location. This is similar to the present study, with assemblages consistently differing between the shaded and unshaded seawalls at each location, but species responsible for patterns differing, resulting in the overall variability among locations. In their study, Bulleri et al. (2005) only examined three locations and did not directly compare among locations. The present study has therefore expanded on this by examining a greater number of locations, comparing among locations and studying a common, yet so far largely ignored, artificial habitat, that is seawalls under wharves.

One explanation for the large-scale spatial variability is that the orientation and position within the harbour of seawalls differed among locations, such that physical conditions on the seawalls could have varied among locations. Seawalls that faced north, for example, would be subject to more direct sunlight than those facing south, resulting in greater surface temperatures. This is evident in the measures of incident light and surface temperature of unshaded seawalls (e.g. Hermit Point and Quarantine Station, north facing wall, compared to Cremorne Point and Athol Bay, south facing wall). In locations where seawalls were oriented towards the sun, the difference in temperature between shaded and unshaded seawalls would be expected to be greater than where seawalls were not oriented towards the sun. In the present study, the difference in temperature between shaded and unshaded sections of seawall that faced north, towards the sun, was up to 10°C, while the difference between habitats for south facing walls was less than 5°C. This could explain some of this dissimilarity in the composition of assemblages among locations.

Urbanised waterways are heavily impacted by anthropogenic activity, with many sources of disturbance (Kullenberg, 2001; Vallega, 2001; Kennish, 2002). The multiple impacts of artificial structures built on, or in the vicinity of, other artificial structures and the additive effects of their associated impacts has generally been overlooked in studies of disturbance ecology. Although this study did not examine how the assemblages associated with two different types of artificial structures (i.e. seawalls and wharves) differed from those on natural shores, previous studies have shown that assemblages differ between seawalls and natural shores (Chapman & Bulleri, 2003; Chapman, 2003; Bulleri et al., 2005). The present study has shown that the presence of another structure (wharves) can further alter assemblages on seawalls. Whether the difference to assemblages on seawalls caused by the presence of wharves translates to making assemblages more or less different from those on natural shores is an area of further study.

The potential of wharves to provide or alter habitats for marine organisms needs to consider the possible positive effects against negative impacts. The presence of a wharf not only means that the composition of assemblages or relative covers or abundances of taxa differs from adjacent unshaded seawalls, but also results in assemblages that are more variable at small and large spatial scales. The shaded surfaces may act as substitutes for microhabitats that are missing from seawalls, as well as adding to the amount and variety of habitats because of structures, such as pilings, associated with wharves. The negative impacts on surrounding habitats and the fact that the assemblages on these structures do not necessarily represent natural assemblages must, however, be considered. If seawalls with wharves do not support assemblages that are representative of those on natural shores, then they cannot necessarily be said to have a positive impact, regardless of increasing local diversity. This is an important issue if, as Cole, Glasby & Holloway (2005) suggest, we attempt to apply ecological theories from the study of natural shores to the management of artificial structures.

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Table 1. Results from analyses by non-parametric MANOVA on assemblages on sections of seawall under or not under wharves (a) among locations for each time of sampling and (b) through time at each location, at mid-and low-tidal heights. 5000 permutation of residuals were used for all analyses. NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

(a)

Mid-tidal height

Source	df	<i>F</i> Time 1	<i>F</i> Time 2	<i>F</i> Time 3	<i>F</i> Time 4
Location = L	6	-	-	-	-
Habitat = H	1	-	-	-	-
L x H	6	23.84***	18.23***	15.14***	14.28***
Residual	126				

Low-tidal height

Source	df	<i>F</i> Time 1	<i>F</i> Time 2	<i>F</i> Time 3	<i>F</i> Time 4
Location	5	-	-	-	-
Habitat	1	-	-	-	-
L x H	5	12.10***	10.98***	10.03***	11.13***
Residual	119				

(b)

Mid-tidal Height

Source	df	<i>F</i> Athol Bay	<i>F</i> Cremorne Point	<i>F</i> Rushcutters Bay	<i>F</i> Hermit Point	<i>F</i> Parriwi Head	<i>F</i> Little Manly Pt	<i>F</i> Quarantine Station
Time = T	3	-	-	-	-	-	-	-
Habitat = H	1	-	-	-	-	-	-	-
T x H	3	3.54***	11.07***	5.14***	6.75***	4.71***	2.64**	3.53***
Residual	72							

Low-tidal Height

Source	df	<i>F</i> Athol Bay	<i>F</i> Cremorne Point	<i>F</i> Rushcutters Bay	<i>F</i> Hermit Point	<i>F</i> Little Manly Pt	<i>F</i> Quarantine Station
Time	3						
Habitat	1						
T x H	3	3.18 ***	2.80 ***	7.55 ***	8.39 ***	6.66***	5.98***
Residual	72						

Table 2. Average Bray-Curtis dissimilarities within and among locations for each habitat and between the two habitats at each time for mid- and low-tidal height. W= Wharf and NW = No-wharf habitats.

Mid-tidal height

	WHARF		Between W/NW	NO-WHARF	
	Within	Among		Within	Among
Time 1	41.2	75.9	71.4	23.1	64.0
Time 2	41.5	80.2	74.4	29.3	60.6
Time 3	44.5	82.9	72.6	27.2	50.5
Time 4	48.0	85.2	79.6	36.9	60.4

Low-tidal height

	WHARF		Between W/NW	NO-WHARF	
	Within	Among		Within	Among
Time 1	58.6	85.0	90.1	38.5	79.2
Time 2	54.4	85.4	78.0	44.7	87.5
Time 3	61.0	87.3	88.5	45.5	79.3
Time 4	52.7	83.9	83.3	48.5	82.7

Table 3. Analyses of individual taxa of (a) algae, (b) sessile invertebrates and (c) mobile invertebrates on sections of seawall under or not under wharves at the mid-tidal height.

(a)		<i>H. rubra</i>	
Source	df	MS	<i>F</i>
Time = T	3	178.1	
Location = L	6	3767.1	
Habitat = H	1	10386.8	
T x L	18	281.8	2.7 *
T x H	3	85.4	0.4 NS
L x H	6	3333.0	14.1 *
T x L x H	18	237.1	2.3 NS
Residual	504	104.3	
Transformation	None		
Cochran's test	**		

(b)		<i>S. glomerata</i>		<i>M. galloprovincialis</i>		<i>G. caespitosa</i>		<i>T. rosea</i>	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time = T	3	2795.5		42.8		1767.6		35.8	
Location = L	6	49571.3		1469.9		6301.4		2151.8	
Habitat = H	1	207587.9		1980.2		13519.5		192.5	
T x L	18	1481.0		29.2	1.2 NS	646.6		18.9	
T x H	3	927.3		68.4	1.2 NS	1823.2		224.1	
L x H	6	13918.3		1329.2	22.6 *	11220.4		82.1	
T x L x H	18	1683.8	5.9 *	58.9	2.4 NS	730.0	4.14 *	199.9	5.1 *
Residual	504	286.0		25.0		176.2		39.0	
Transformation	None			None		None		None	
Cochran's test	*			**		**		**	

		<i>T. purpurascens</i>		Orange sponge	
Source	df	MS	<i>F</i>	MS	<i>F</i>
Time	3	441.0		26.0	
Location	6	13137.8		124.3	
Habitat	1	40683.8		536.3	
T x L	18	243.7		18.5	
T x H	3	639.4		27.2	
L x H	6	10876.1		113.6	
T x L x H	18	313.8	3.2 *	18.6	3.2 *
Residual	504	97.5		5.9	
Transformation	None			None	
Cochran's test	**			**	

(c)		<i>C. pelliserpentis</i>		<i>S. denticulata</i>	
Source	df	MS	<i>F</i>	MS	<i>F</i>
Time	3	3.5		1.3	
Location	6	9.1		2.0	
Habitat	1	11.4		11.8	
T x L	18	1.3		0.5	
T x H	3	2.8		0.2	
L x H	6	7.1		5.9	
T x L x H	18	1.2	5.4 ***	0.8	2.9 ***
Residual	504	0.2		0.3	
Transformation	Ln(X + 1)			Ln(X + 1)	
Cochran's test	NS			NS	

Where analyses showed significant interactions, *F*-ratios are not given for main effects and lower order interactions because these cannot be logically interpreted. NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ except where Cochran's test was significant (for *C* with $P < 0.05$, * = $P < 0.01$, ** = $P < 0.001$; for *C* with $P < 0.01$, * = $P < 0.001$)

Table 4. Analyses of individual taxa of (a) algae and (b) sessile invertebrates on sections of seawall under or not under wharves at the low-tidal height.

(a)		<i>C. officinalis</i>		Foliose green algae	
Source	df	MS	F	MS	F
Time = T	3	4468.2		4.2	
Location = L	5	10590.6		13.3	
Habitat = H	1	76329.8		44.7	
T x L	15	1163.2		3.9	
T x H	3	4446.4		7.5	
L x H	5	10518.0		5.5	
T x L x H	15	1164.7	6.5 *	2.7	7.1 *
Residual	432	179.4		0.4	
Transformation		None		None	
Cochran's test		**		**	

(b)		<i>S. glomerata</i>		<i>M. galloprovincialis</i>		<i>G. caespitosa</i>		<i>A. imperator</i>	
Source	df	MS	F	MS	F	MS	F	MS	F
Time = T	3	2129.6		721.5		977.9		56.8	
Location = L	5	10070.7		698.2		3987.7		450.1	10.6 *
Habitat = H	1	8535.0		286.8		1117.3		763.4	
T x L	15	2270.7		756.4		415.9		^P 35.9	
T x H	3	6362.0		799.4		58.1		71.6	1.7 NS
L x H	5	7786.4		969.5		2347.6		299.7	7.1 *
T x L x H	15	2610.3	10.1 *	736.1	41.9 *	316.0	2.6 *	^P 45.8	
Residual	432	259.3		17.6		122.0		42.6	
Pooled	462							42.5	
Transformation		None		None		None		None	
Cochran's test		**		**		**		**	

		<i>T. rosea</i>		<i>T. purpurascens</i>		Orange sponge	
Source	df	MS	F	MS	F	MS	F
Time	3	110.4		12.4		45.2	
Location	5	809.5		1252.6		6107.6	
Habitat	1	145.8		3370.8		18710.1	
T x L	15	109.8	4.3 *	285.4		258.2	
T x H	3	18.0	0.7 NS	10.3		107.1	
L x H	5	105.7	4.1 *	1084.2		4437.5	
T x L x H	15	^P 19.5		289.2	7.9 *	364.3	3.2 *
Residual	432	25.9		74.4		113.5	
Pooled	447	25.7					
Transformation		None		None		None	
Cochran's test		**		**		**	

^P indicates pooling ($P > 0.25$). Where analyses showed significant interactions, F -ratios are not given for main effects and lower order interactions because these cannot be logically interpreted. Because Cochran's test was significant ($P < 0.01$) a conservative significance level was used was used NS = $P > 0.01$, * = $P < 0.001$

Figure captions

Figure 1. Map of field sites within Sydney Harbour, Australia

Figure 2. nMDS ordination of centroids of assemblages on seawalls under wharves (filled shapes) or not under wharves (empty shapes) at each location: Athol Bay (circle); Cremorne Point (square); Rushcutters Bay (downward triangle); Hermit Point (upward triangle); Parriwi Head (diamond); Little Manly Point (small circle); Quarantine Station (small square). Each sampling times and height is graphed separately.

Figure 3. nMDS ordination of centroids of assemblages on seawalls under wharves (circles) or not under wharves (squares) through time (1-4) for selected locations as examples of general patterns at the mid- and low-tidal heights.

Figure 4. Mean (+SE) percentage cover of algae and sessile invertebrates on seawalls under (shaded) or not under (hashed) wharves at the mid-tidal height. Only one time is shown to illustrate general patterns, except for *H. rubra* and *S. glomerata*. A = Athol Bay; C = Cremorne Point; R = Rushcutters Bay; H = Hermit Point; P = Parriwi Head; M = Little Manly Point; Q = Quarantine Station. Text in bold indicate number of times the mean was greater under a wharf (W) or where there was no wharf (NW), with number of these that were significantly greater, from SNK tests, given in brackets. *P* values (with number of comparisons in subscript) are from binomial tests of means.

Figure 5. Mean (+SE) percentage cover of algae and sessile invertebrates on seawalls under (shaded) or not under (hashed) wharves at the low-tidal height. Only one time is shown to illustrate general patterns. A = Athol Bay; C = Cremorne Point; R = Rushcutters Bay; H = Hermit Point; M =

Little Manly Point; Q = Quarantine Station. Text in bold indicate number of times the mean was greater under a wharf (W) or where there was no wharf (NW), with number of these that were significantly greater, from SNK tests, given in brackets. *P* values (with number of comparisons in subscript) are from binomial tests of means.

Figure 6. Mean (+SE) abundance of mobile invertebrates on seawalls under (shaded) or not under (hashed) wharves at the mid-tidal height. A = Athol Bay; C = Cremorne Point; R = Rushcutters Bay; H = Hermit Point; P = Parriwi Head; M = Little Manly Point; Q = Quarantine Station. Text in bold indicate number of times the mean was greater under a wharf (W) or where there was no wharf (NW), with number of these that were significantly greater, from SNK tests, given in brackets. *P* values (with number of comparisons in subscript) are from binomial tests of means.

Figure 7. Mean surface temperature ($\pm$ S.E.) of seawalls under (circle, solid line) or not under (triangle, hashed line) wharves at each location from April 2003 until March 2004.

Figure 8. Mean light (Lux) on seawalls under (circle, solid line) or not under (triangle, hashed line) wharves at each location from April 2003 until March 2004.

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Fig. 4

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