



# Differential patterns of distribution of limpets on intertidal seawalls: experimental investigation of the roles of recruitment, survival and competition

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**ABSTRACT:** On artificial surfaces (seawalls) in Sydney Harbour (Australia), local biodiversity of grazers differs between sandstone and concrete constructions because limpets *Siphonaria denticulata* are more abundant on sandstone, while *Patelloida latistrigata* are more abundant on concrete walls. Competition between siphonarian and patellid limpets is unstudied on artificial structures, although the limpets are common and are known to compete in natural habitats. We tested hypotheses that the substratum (concrete or sandstone), intra- and/or interspecific competition, or a combination of factors, influence recruitment, survival, rates of grazing, or the quantity and types of algal food to explain the observed patterns. Such analyses enable better understanding of the processes influencing diversity. Both species recruited more to concrete than to sandstone plates. *S. denticulata* recruited more in the presence of conspecifics and slightly less in the presence of *P. latistrigata*. Results varied between locations and experiments, but each species survived better on concrete, which had more macro- and micro-algal food. Increased densities of *P. latistrigata* reduced survival of conspecifics and of *S. denticulata*. *S. denticulata* had no effect on survival of *P. latistrigata*, but reduced amounts of macro-algae. *P. latistrigata* did not affect macro-algae. Initially, there were more micro-algae on concrete and a minor effect of large densities of *S. denticulata*. After 95 d, differences between habitats decreased and *P. latistrigata* were more strongly associated with reduced amounts of micro-algae. Neither substratum, density, nor mix of limpets affected rates of grazing. Thus, interspecific interactions were similar to predictions from knowledge of natural habitats, despite the different characteristics of artificial habitats and the reduced intertidal area available for grazing. Recruitment and competition were important in explaining different densities of these limpets on sandstone and concrete walls. Increasing urbanization requires more experimental tests to identify how well current theories of intertidal ecology and of the processes maintaining local biodiversity can apply to artificial shorelines.

**KEY WORDS:** Artificial structures · Habitat · Competition · Grazing · Intertidal · Limpets

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## INTRODUCTION

Increasing urbanization raises many concerns about sustainability of biodiversity in terrestrial (Laurie 1979, Breuste et al. 1998, McIntyre 2000) and marine (Suchanek 1994, Smith et al. 2000) habitats. Despite many definitions of biodiversity (May 1994), it is often esti-

mated as numbers and types of species in an area, usually by sampling, or from compiled lists of species. Counts of species do not, however, provide information about variability in distributions and abundances of species due to environmental changes or biological processes. Yet, ecological interactions among species, e.g. between resources and consumers or competitors

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and between organisms and the environment, determine sustainability of diversity in the long term, because these processes largely determine patterns of abundance of individual species. The focus of the present study is to investigate the ecological processes that maintain biodiversity in artificial settings.

There has been growing awareness of changes to shorelines due to urbanization, especially along estuarine shores (e.g. Attrill et al. 1999, Glasby & Connell 1999, Moschella et al. 2005, Marzinelli et al. 2009). For example, more than 70% of the shoreline of San Diego Bay, California (Davis et al. 2002) and approximately 50% of the shoreline of Sydney Harbour, Australia (Chapman 2003) is artificial, mainly composed of seawalls. Seawalls and similar infrastructure are built to prevent erosion and for commercial, residential, or recreational purposes. They replace natural intertidal or subtidal rocky and sedimentary shores, potentially disrupting connectivity among populations (Bulleri & Airoldi 2005), providing stepping stones or corridors for spread of invasive species (Bulleri et al. 2006), and affecting assemblages in adjacent habitats (Goodsell et al. 2007). Environmental impacts of 'armouring' of shores are likely to worsen with climatic change, due to rising sea levels and increased frequency of storms, requiring more artificial protection of coastlines.

Seawalls in Sydney Harbour provide intertidal habitat, but do not support natural assemblages (Chapman & Bulleri 2003, Bulleri et al. 2005). Common species on rocky shores may be found at unnatural densities or are absent from seawalls (Chapman 2003, 2006, Moreira et al. 2006, Jackson et al. 2008). The most abundant grazing animals on seawalls are limpets, which are major components of assemblages on natural intertidal shores, structuring algal and faunal assemblages (Branch 1981, Hawkins & Hartnoll 1983, Underwood et al. 1983). There is currently no information about how interactions among these grazers might differ on vertical seawalls that compress distributions of intertidal species, nor how changes to these interactions might determine differences between assemblages on walls compared to natural shores.

Intertidal areas on most natural shores in New South Wales (NSW) are extensive wave-cut platforms with abundant space for the large diversity of grazers. On natural shores, small limpets *Patelloida latistrigata* and *Siphonaria denticulata* are usually found in different areas, with the latter more abundant lower on the shore (Creese & Underwood 1982). *P. latistrigata* are outcompeted by the larger *Cellana tramoserica* and the former are mainly found in refuges among barnacles (Creese 1982), where they feed on micro-algae and, to a lesser extent, germlings of macro-algae (Jernakoff 1985). *C. tramoserica* also outcompete *S. dentic-*

*ulata*, but intraspecific competition generally reduces densities of *C. tramoserica* before they can eliminate *S. denticulata* locally (Creese & Underwood 1982). If macro-algae develop, *S. denticulata* can persist, feeding on these larger plants which are not food for *C. tramoserica*.

On intertidal seawalls in Sydney Harbour, *Patelloida latistrigata* and *Siphonaria denticulata* are generally more abundant than on natural shores, although there is great variation from place to place (Bulleri et al. 2005). These species are also found in close proximity because of the small intertidal range on vertical walls. Moreira (2006) documented differences in abundances between different types of walls. *P. latistrigata* were more abundant on concrete than on sandstone seawalls; *S. denticulata* showed the opposite pattern. Differences in relative abundances on different types of walls and the restricted area over which animals may forage could therefore change or intensify interactions between these species from those found on natural shores.

Differences in local biodiversity are a direct consequence of any differences in relative abundances of species (including being absent versus present) in different areas or on different substrata. Understanding how diversity is controlled or maintained is more likely if the processes regulating different relative abundances are themselves understood. In this study, a number of models that might explain differences in abundances of *Patelloida latistrigata* and *Siphonaria denticulata* between concrete and sandstone seawalls were examined using a manipulative field experiment. The models tested were that differences in abundance between the 2 species on concrete and sandstone walls were due to differential recruitment and/or survival of adults, each of which may be mediated by the substratum itself, by the presence of the other species and/or by a combination of both factors. Specific hypotheses examined were: (1) *P. latistrigata* will recruit more to concrete and *S. denticulata* will show the opposite pattern, irrespective of the species present; (2) each species will recruit more to plates where the other species is absent, irrespective of substratum; (3) recruitment will be influenced by the substratum and by the species present; (4) adult *P. latistrigata* will survive better on concrete and *S. denticulata* better on sandstone, irrespective of the presence of the other species; (5) each species will survive better on plates where the other species is absent, irrespective of the substratum; (6) survival of adults of each species will differ according to the combination of substratum and species present.

Densities of limpets on intertidal shores in NSW are strongly influenced by availability of food (Underwood et al. 1983). *Patelloida latistrigata* and

*Siphonaria denticulata* usually consume different types of algae, the former mostly eating micro-algae and the latter eating macro-algae (Creese 1982, Creese & Underwood 1982). Interspecific interference competition might alter the rates at which different species forage. Thus, survival of these limpets on different surfaces in the presence of the other species might be related to availability of food, or the rates at which food is consumed. These models were examined by testing the following hypotheses: (7) there will be different quantity/types of algae on concrete and sandstone plates, irrespective of the species present; (8) algae will differ according to the species present, but not the substratum; (9) a combination of substratum and species will determine the quantity/types of algae; (10) rates of grazing will differ between concrete and sandstone, irrespective of the species present; (11) grazing rates will differ according to the species present, but not the substratum; (12) grazing will be influenced by the substratum and species present.

## MATERIALS AND METHODS

Sandstone and concrete seawalls are generally located in different parts of the harbour and are thus subjected to different environmental conditions, have different extant assemblages, are of different ages and so forth. There are also many restrictions about attaching experimental structures, such as cages, onto some seawalls in the harbour, so experiments were done using concrete and sandstone plates attached to 2 intertidal sandstone walls where *Siphonaria denticulata* were abundant. Each wall also had an adjacent (within 10 m) concrete wall where *Patelloida latistrigata* were present in reasonably large densities, but attaching any structures to the concrete walls was not permitted.

A total of 20 concrete and 20 sandstone plates (20 × 20 cm) were attached to each of 2 intertidal seawalls, at Careening Cove (CC) and Cremorne Point (CP) in Sydney Harbour (Fig. 1A). Four sandstone or concrete plates, arranged in random order, were attached to each of 10 frames, which were then screwed onto the walls at mid-tidal height, which is the range naturally occupied by these limpets on these seawalls (Fig. 1B). Each plate was surrounded by a fence (5 mm mesh) to prevent limpets from moving off or onto the plates.

The sampling protocol is given in Fig. 2. The plates were deployed 28 d prior to limpets being added to ensure that an algal film had developed (e.g. MacLulich 1986). Adult limpets were added to the plates on Day 0 (Start 1). Sizes of limpets were: *Siphonaria denticulata*, 9.3 to 16.6 mm; *Patelloida latistrigata*, 8.9 to 15.5 mm. The deployed limpets were thus larger than recruits (<4 mm) and estimates of mortality were not confused by recruitment. Mortality of these adults in some treatments was relatively rapid, so the original numbers of limpets were re-established 16 (Start 2) and 81 d (Start 3) from Day 0 by adding new limpets to those surviving. At each time, limpets were deployed in 5 treatments: (A) 12Sd: *S. denticulata* at mean natural density found on sandstone walls (12 per plate, i.e. 12 per 400 cm<sup>2</sup>); (B) 9Pl: *P. latistrigata* at mean natural density on concrete walls (9 per plate). These densities were slightly larger than those given by Moreira (2006) to allow some initial mortality in response to any disturbance associated with the transplan-

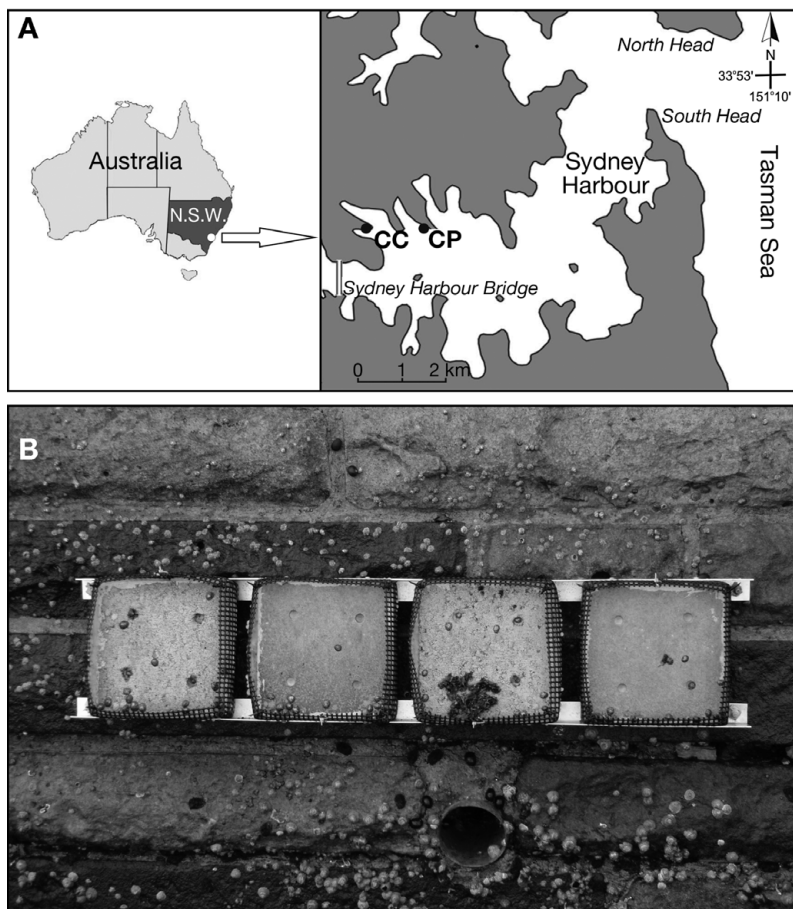


Fig. 1. (A) Study sites in Sydney Harbour (Australia) and (B) method of attachment of plates onto the walls

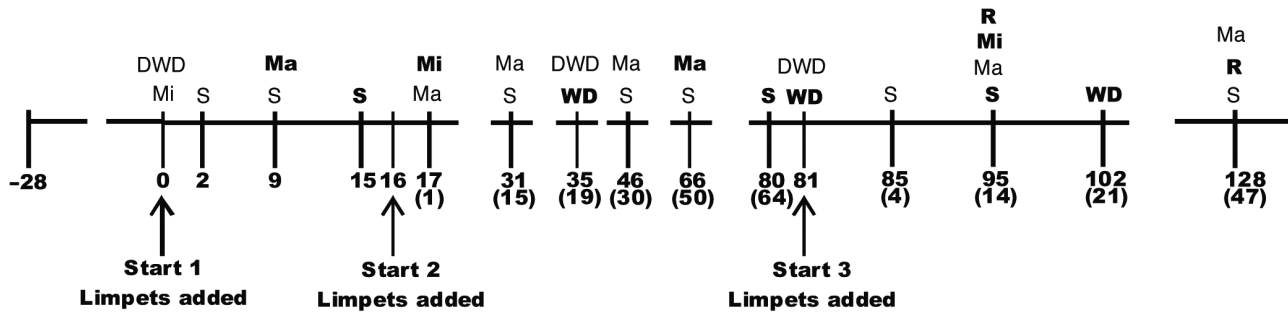


Fig. 2. Chronological sequence (days after starting the experiments on Day 0) showing times of measurement of survival (S), recruitment (R), quantity and types of micro-algae (Mi) and macro-algae (Ma) and amount of grazing (DWD: deployment of wax discs; WD: collection of wax discs). Data collected at times marked in **bold** were analysed. Numbers in parentheses show the days after the original numbers of limpets were re-established during Starts 2 & 3 of the experiments. Breaks in the time-line are periods of no activity

tation. To distinguish between effects of intra- and interspecific competition (Underwood 1986, 1992), there were 3 further treatments: (C) 12Sd + 9Pl (or 9Pl + 12Sd, depending upon the focal species): 12 *S. denticulata* plus 9 *P. latistrigata*; (D) 21Sd and (E) 21Pl: 21 *S. denticulata* or 21 *P. latistrigata*, respectively. The limpets were deployed randomly amongst the experimental treatments and marked with non-toxic nail polish. Survival was measured at irregular intervals after each start (Fig. 2). Recruitment was measured twice towards the end of the experiment, after 95 d and again after 128 d. Recruits were not removed between these 2 sampling periods.

During the experiment, a cover of green filamentous and foliose algae developed towards the lower edges (i.e. lower on the wall) of some plates, particularly the concrete plates. This cover was sampled from digital photos of each plate *in situ* at irregular intervals throughout the experiment (Fig. 2), using a grid of 100 regular points placed over each photo.

Micro-algae were sampled prior to and at irregular intervals after deployment of the limpets (Fig. 2). The plates were removed from the wall for a period of about 1 h. There was no apparent disturbance to the limpets, which were immobile and firmly attached during low tide. The amounts of chlorophyll *a* (chl *a*) were measured using colour-infrared imagery (Murphy et al. 2004) with a 3-CCD colour-infrared (CIR) camera (Geospatial Systems), which measures light at green (525 to 575 nm), red (645 to 689 nm) and near-infrared (NIR; 758 to 833 nm) wavelengths. The images were converted to reflectance values using a calibration panel (30% Spectralon; Labsphere). A ratio of red and near-infrared reflectances (NIR/red) is indicative of the amount of chl *a* on the substratum (Murphy et al. 2006). Because concrete and sandstone had different spectral properties, the relationships between chl *a* and NIR/red ratio were derived for each substratum using linear regressions to convert ratio values into amounts of chlorophyll:

Concrete:

$$\text{Chl } a \text{ (}\mu\text{g cm}^{-2}\text{)} = 2.6221 \times (\text{NIR/red}) - 2.8956 \quad (1)$$

Sandstone:

$$\text{Chl } a \text{ (}\mu\text{g cm}^{-2}\text{)} = 2.2823 \times (\text{NIR/red}) - 2.519 \quad (2)$$

The types of micro-algae present were determined using spectrometry (Murphy et al. 2005a). Reflectance spectra (350 to 1050 nm) were recorded from the surface of each plate using a field spectrometer (Field-Spec Pro Analytical Spectral Devices), with spectra taken from 3 random locations on each plate from a height of 12 cm using a 25° field-of-view fibreoptic. Each spectrum thus recorded an area of approximately 22 cm<sup>2</sup>. Prior to each spectrum being recorded, a calibration spectrum was recorded from a white reference panel (~99% Spectralon). Derivative analysis was used to enhance subtle absorption features and to separate overlapping absorptions (Murphy et al. 2005a). Reflectance data were converted to pseudo-absorbance units and fourth-derivative spectra (Bidigare et al. 1989) calculated using a combined smoothing and differentiation technique, with a 24 nm smoothing window (Savitzky & Golay 1964, Steinier et al. 1972). Absorptions by different pigments were identified as separate peaks and the absorption by each pigment extracted from each spectrum as the maximal derivative value for each peak above the zero-baseline. Derivative reflectance increased with increasing amounts of pigment. Absorptions associated with different pigments were identified in the spectra from published wavelengths of absorption by pigments *in vivo* (Murphy et al. 2005b), specifically: carotenoids (~546 nm), phyco-erythrocyanin (~575 nm), chlorophyll *c* (chl *c*) (~640 nm), chlorophyll *b* (chl *b*) (~650 nm) and chl *a* (~680 nm).

To test hypotheses about rates of grazing, 4 wax discs (12 mm diam.) were inserted into each plate (see Thompson et al. 1997 for details) and the radular marks of *Patelloida latistrigata* and *Siphonaria denticulata*

scored after deployment for different periods of time, after 35 d, again after 46 d and again after 21 d (Fig. 2). Although individual radular marks were identified, they frequently obscured those below, making counts difficult. Therefore, each wax disc was divided into 8 sectors and the numbers of sectors containing radular marks of each species recorded.

## RESULTS

### Recruitment

Because very small *Siphonaria denticulata* are difficult to distinguish from other species of *Siphonaria* in the field, all small (<2 mm) *Siphonaria* were counted *in situ* and a random sample of >50 individuals was collected for later identification in the laboratory. More than 90% of these were juvenile *S. denticulata*; the others were mostly *S. virgulata*. Recruits of *Siphonaria* were therefore considered to be *S. denticulata*.

More *Siphonaria denticulata* recruited than did *Patelloida latistrigata*, with most recruitment of *S. denticulata* at CC. After 128 d, over all 40 plates, there was a total of 701 recruits, but only 69 at CP. At CC (Fig. 3), there were more recruits on concrete (420) than on sandstone (281;  $\chi^2 = 27.6$ ,  $p < 10^{-6}$ ), which does not support Hypothesis 1. There was also substantially more recruitment onto plates with adult *S. denticulata* (a total of 622 on treatments 12Sd, 21Sd and 12Sd + 9PI) than to treatments without (a total of 79 on treatments 9PI, 21PI), providing support for Hypothesis 3. To make comparisons using the same number of plates, recruitment of *S. denticulata* to 12Sd and 21Sd was compared to recruitment to 9PI and 21PI;  $\chi^2 = 235.6$ ,  $p < 10^{-54}$ . There was also significantly less difference between

recruitment on concrete than on sandstone on plates with *S. denticulata* than was the case on plates without these limpets (Fig. 3;  $\chi^2 = 81.1$ ,  $p < 10^{-18}$ ). In support of Hypothesis 2, the presence of *P. latistrigata* did, however, reduce recruitment by *S. denticulata*; there were 306 recruits on treatment 12Sd and only 179 on 12Sd + 9PI. At CP, Hypotheses 1 & 2 were again not supported — there were more recruits on concrete (42) than on sandstone (27) and more with (52) than without (17) *S. denticulata*, but no influence of *P. latistrigata* (20 recruits on treatment 12Sd and 22 on treatment 12Sd + 9PI). Probably because there were fewer recruits at this location, these differences were not significant in  $\chi^2$  tests. Only 9 recruits of *P. latistrigata* were found, but, in support of Hypothesis 1, 8 of these were on concrete plates (binomial test;  $p < 0.05$ ).

### Survival

The proportional survival of the deployed limpets of each species was analysed separately using a 3 factor analysis of variance (ANOVA) for each of 3 times: 15 d after Start 1 (Time 1), 64 d after Start 2 (Time 2) and 14 d after Start 3 (Time 3), just prior to resetting the original densities each time. Although the experiment was continued for 128 d, very few *Patelloida latistrigata* were found alive at CP at this time in any treatment, which compromised examination of any interactions between *P. latistrigata* and *Siphonaria denticulata*. Therefore, this time of sampling was not analysed.

Significantly more *Patelloida latistrigata* survived on concrete than on sandstone plates at Times 1 & 2 (Table 1). At Time 3, there was no significant difference, but a similar trend was observed. These results are consistent with Hypothesis 4. There was no signifi-

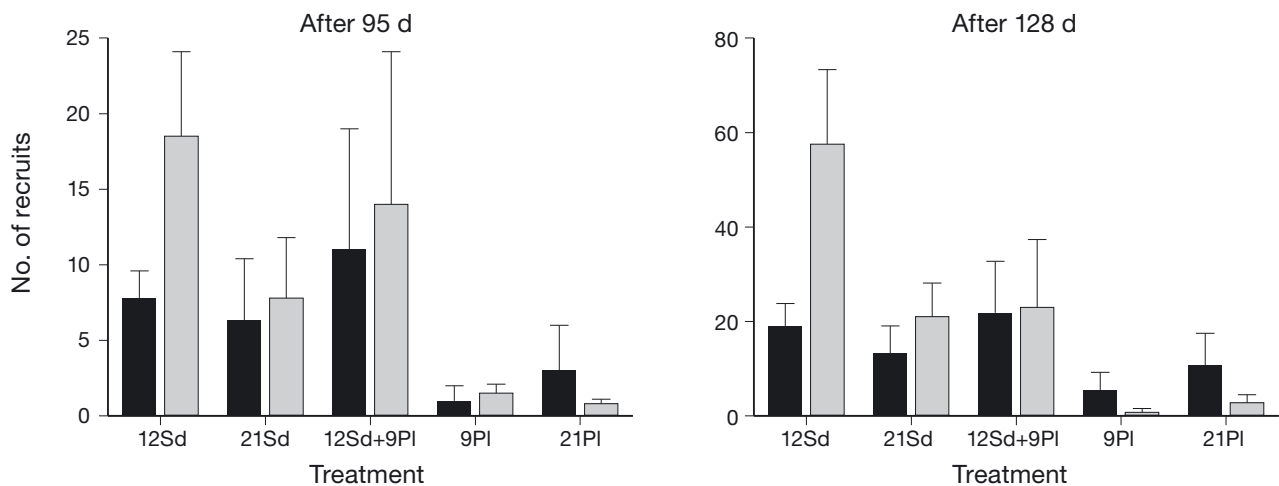


Fig. 3. Mean ( $\pm$ SE;  $n = 4$ ) recruitment of *Siphonaria denticulata* for each experimental treatment (see 'Materials and methods' for treatments) at Careening Cove after 95 and 128 d; black bars: sandstone plates; grey bars: concrete plates

Table 1. Analyses of proportions of surviving *Patelloida latistrigata* on sandstone and concrete plates (substratum, fixed factor) at Careening Cove and Cremorne Point (locations, random factor) in 3 treatments (9Pl, 21Pl and 9Pl + 12Sd, fixed factor; Treatments B, E and C, respectively, as described in 'Materials and Methods'); Time 1: 15 d after Start 1, Time 2: 64 days after Start 2, Time 3: 14 days after Start 3 (details in 'Materials and Methods'). L: location; S: substratum; T: treatment. <sup>ns</sup>p > 0.05, \*p < 0.05, \*\*p < 0.01

Source	df	Time 1		Time 2		Time 3	
		MS	F	MS	F	MS	F
L	1	0.04	0.81 <sup>b</sup>	0.14	6.06 <sup>*b</sup>	3.86	164.43 <sup>**a</sup>
S	1	0.38	7.28 <sup>*b</sup>	0.12	5.07 <sup>*b</sup>	0.03	0.64
T	2	0.24	2.00	0.02	0.43	0.06	1.10
L × S	1	0.00	0.01 <sup>a</sup>	0.02	0.65 <sup>a</sup>	0.04	1.81 <sup>a</sup>
L × T	2	0.12	2.24 <sup>b</sup>	0.05	1.91 <sup>b</sup>	0.05	2.23 <sup>a</sup>
S × T	2	0.02	0.33 <sup>b</sup>	0.00	0.02 <sup>b</sup>	0.02	0.65 <sup>a</sup>
L × S × T	2	0.02	0.36	0.00	0.18	0.01	0.41
Residual	36	0.06		0.03		0.02	
Cochran's test (C)		0.24 <sup>ns</sup>		0.16 <sup>ns</sup>		0.21 <sup>ns</sup>	

**Student-Newman-Keuls (SNK) tests, mean (SE):**  
Time 1 (Concrete) 0.58 (0.05) > (Sandstone) 0.36 (0.05)  
Time 2 (Concrete) 0.37 (0.03) > (Sandstone) 0.27 (0.03)

**Tested against:**  
<sup>a</sup>Pooled Residual and L × S × T  
<sup>b</sup>Pooled Residual, L × S × T and L × S

though again this was not always significant (Table 2). Adding *P. latistrigata* always caused greater mortality of *S. denticulata* than was caused by adding more *S. denticulata*. These results are in agreement with Hypothesis 5.

### Amounts and types of algae

Prior to deploying the limpets, many concrete plates had developed a layer of *Enteromorpha* spp., Ulvales and Cladophorales (with fronds up to 1.5 cm long) along the lower third of the plate, which persisted throughout the experiment. This result is in agreement with Hypothesis 8, but only for macro-algae. There was little cover on the upper parts of the plates, so percentage covers of macro-algae were estimated from the digital photos separately for the upper

cant effect of treatment on survival of *P. latistrigata*, with large variability among plates.

Because of the large amount of variability among plates, the data were tested further by pooling survivors of *Patelloida latistrigata* across replicate plates. There were no significant interactions among locations, substrata and treatments (3 factor  $\chi^2$  test, p > 0.05), nor between substrata and treatments (2 factor  $\chi^2$  test, p > 0.05) when data from the 2 locations were pooled. There was a trend for fewer survivors on each substratum where densities were larger, i.e. 21 versus 9 *P. latistrigata*, although this was not always significant, and there was only a small difference on sandstone at Time 3. There was no consistent effect on survival of *P. latistrigata* due to adding *Siphonaria denticulata* (compare 9Pl with 9Pl + 12Sd in Table 2), rejecting Hypothesis 5.

Significantly more *Siphonaria denticulata* survived on concrete than on sandstone plates at each time (Table 3), which is the opposite prediction to that in Hypothesis 4 for this species. Survival of *S. denticulata* differed significantly among treatments at Times 2 & 3, but Student-Newman-Keuls (SNK) tests failed to identify differences among means. The data were therefore further tested using  $\chi^2$  tests (Table 2). Again, there were no significant interactions between locations, substrata and treatments, nor substrata and treatments ( $\chi^2$  tests, p > 0.05). Except for Time 1 on concrete, adding *S. denticulata* (21Sd versus 12Sd) or *Patelloida latistrigata* (12Sd + 9Pl versus 12Sd) decreased survival of *S. denticulata*, al-

Table 2.  $\chi^2$  tests of numbers of surviving limpets in each treatment at Times 1, 2 & 3 (see Table 1 for explanations); data are numbers (proportions) surviving, summed over 5 replicate plates and 2 locations. \*p < 0.05, \*\*p < 0.01

	Treatments			$\chi^2$
	9Pl	21Pl	9Pl + 12Sd	
<b><i>Patelloida latistrigata</i></b>				
Concrete				
Time 1	57 (0.63)	86 (0.41)	61 (0.68)	20.45**
Time 2	38 (0.42)	71 (0.34)	32 (0.36)	1.31
Time 3	59 (0.65)	107 (0.51)	61 (0.68)	7.76*
Sandstone				
Time 1	42 (0.47)	61 (0.29)	39 (0.43)	9.48*
Time 2	28 (0.31)	53 (0.25)	23 (0.26)	0.67
Time 3	51 (0.57)	113 (0.54)	54 (0.60)	0.83
Total no. at start	90	210	90	
	Treatments			$\chi^2$
	12Sd	21Sd	12Sd + 9Pl	
<b><i>Siphonaria denticulata</i></b>				
Concrete				
Time 1	110 (0.92)	200 (0.95)	97 (0.81)	5.63
Time 2	103 (0.86)	162 (0.77)	88 (0.73)	5.94
Time 3	112 (0.93)	179 (0.85)	101 (0.84)	3.64
Sandstone				
Time 1	98 (0.82)	139 (0.66)	76 (0.63)	10.55**
Time 2	88 (0.73)	128 (0.61)	61 (0.51)	10.75**
Time 3	106 (0.88)	166 (0.79)	89 (0.74)	5.64
Total no. at start	120	210	120	

Table 3. Analyses of proportions of surviving *Siphonaria denticulata* on sandstone and concrete plates. See Table 1 for details of experimental design and abbreviations. <sup>ns</sup>p > 0.05, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001

Source	df	Time 1		Time 2		Time 3	
		MS	F	MS	F	MS	F
L	1	0.03	0.37 <sup>c</sup>	0.00	0.10 <sup>c</sup>	0.18	13.87*** <sup>c</sup>
S	1	0.30	4.50** <sup>c</sup>	0.29	8.25*** <sup>c</sup>	0.06	4.70** <sup>c</sup>
T	2	0.11	1.61 <sup>c</sup>	0.16	4.46** <sup>c</sup>	0.05	3.88** <sup>c</sup>
L × S	1	0.02	0.34 <sup>a</sup>	0.02	0.45 <sup>a</sup>	0.02	1.28 <sup>a</sup>
L × T	2	0.02	0.27 <sup>b</sup>	0.02	0.66 <sup>b</sup>	0.00	0.08 <sup>b</sup>
S × T	2	0.01	0.13 <sup>c</sup>	0.00	0.11 <sup>c</sup>	0.00	0.24 <sup>c</sup>
L × S × T	2	0.01	0.16	0.00	0.11	0.01	0.11
Residual	36	0.07		0.04		0.01	
Cochran's test (C)		0.26 <sup>ns</sup>		0.21 <sup>ns</sup>		0.31 <sup>ns</sup>	

**SNK tests, mean (SE):**  
Time 1 (Concrete) 0.86 (0.04) > (Sandstone) 0.70 (0.04)  
Time 2 (Concrete) 0.78 (0.03) > (Sandstone) 0.62 (0.05)  
Treatments No significant differences among means identified by SNK  
Time 3 (Concrete) 0.87 (0.02) > (Sandstone) 0.80 (0.03)  
Treatments No significant differences among means identified by SNK

**Tested against:**  
<sup>a</sup>Pooled Residual and L × S × T  
<sup>b</sup>Pooled Residual, L × S × T and L × S  
<sup>c</sup>Pooled Residual, L × S × T, L × S and L × T

and lower 40% of each plate. Data were analysed 9 and 66 d after limpets were deployed the first time. Because data from the upper and lower surfaces of the same plate are not independent, 2 randomly selected plates of each treatment were analysed for the upper surface and 2 different plates for the lower surface. Substratum, treatment and height were fixed factors, location was a random factor.

After 9 d, there was no difference between the 2 locations, nor significant interactions between locations and any other factor (all p values > 0.25). There was, how-

ever, a significant interaction among substrata, treatments and heights on the plate ( $F_{4,40} = 7.04$ ,  $p < 0.05$ ). There was zero cover on all upper levels, very little cover on the lower level on the sandstone plates and no differences among treatments (Fig. 4). On concrete plates, there was significantly less cover on the lower 40% of those plates with 12 or 21 *Siphonaria denticulata* compared to those plates with only *Patelloida latistrigata*. Where *P. latistrigata* were present without *S. denticulata* (9PI), there was significantly more cover on the lower than on the upper 40% of concrete plates (Fig. 4). Although data were not collected from the upper and lower 40% of the plates prior to deployment of the limpets, treatments were assigned to plates randomly and there is no reason to expect that, prior to the limpets being deployed, there would have been any difference in macro-algal cover between plates allocated to treatments with or without *S. denticulata*.

After 66 d, a similar pattern was found—a significant interaction among substrata, treatments and heights on the plate ( $F_{4,40} = 15.81$ ,  $p < 0.001$ ) and no difference between locations. Patterns among substrata, treatments and heights were similar to those found after 9 d (Fig. 4).

The amounts and small-scale spatial variation of micro-algae were estimated using measures of chl a from the top halves of the plates (due to the cover of macro-algae on the lower parts of concrete plates) from the CIR camera images. To test the hypothesis

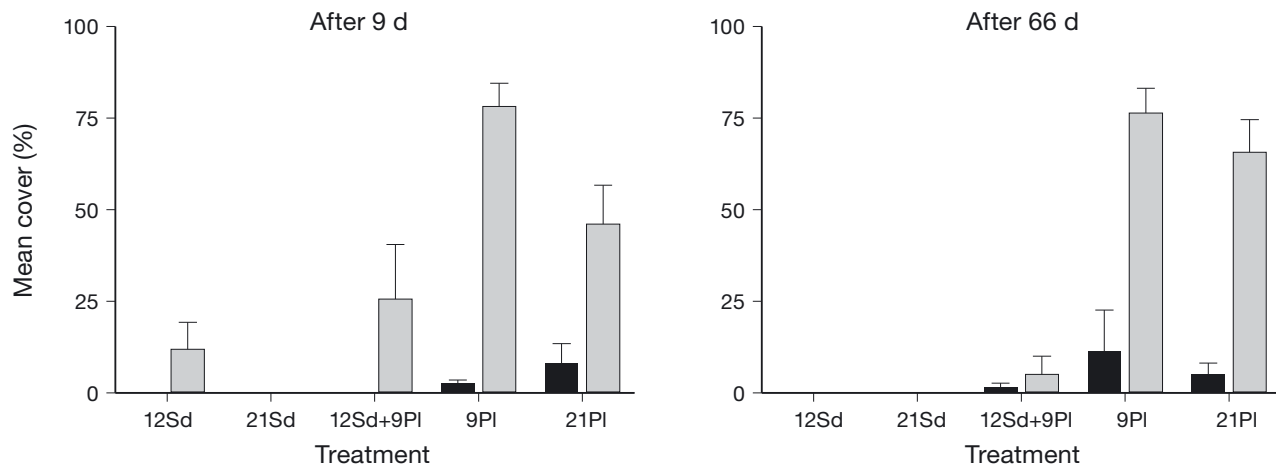


Fig. 4. Mean ( $\pm$ SE;  $n = 4$ ) % cover of ephemeral green macro-algae on the lower parts of concrete and sandstone plates after 9 or 66 d for each experimental treatment (see 'Materials and methods' for treatment descriptions); data averaged across locations; black bars: sandstone plates; grey bars: concrete plates

that the amount and/or spatial variance in biomass of micro-algae was affected by location, substratum or treatment, the biomass of chlorophyll ( $\mu\text{g cm}^{-2}$ ) in the upper 40% of each plate was derived from areas extracted from each image, in a nested design incorporating 4 spatial scales, with 2 levels of each scale. There were 2 independent sets of data incorporating a large scale (i.e. sampled 12 cm apart), a medium scale (4 cm apart) and a small scale (2 cm apart), with 2 replicate areas of  $0.25 \text{ cm}^2$  placed 1 cm apart. Care was taken to ensure that measures were only taken over areas with no erect macro-algae.

These data were analysed for locations (random factor), substrata (fixed factor) and treatment (fixed factor), with plates nested inside the interaction and the large, medium and small scales nested in plates. Data were analysed for 2 time periods, 17 and 95 d after the start of the experiment (Fig. 2). After 17 d, there was significant small-scale variation in the amount of chlorophyll at scales of 2 and 4 cm and among replicate plates and a significant interaction between locations and substrata (Table 4). Supporting Hypothesis 7, there was significantly more chlorophyll on concrete than on sandstone at CC (Table 4). At CP, a similar pat-

tern was found, but the difference was not significant (SNK test,  $p > 0.05$ ). Treatments did not differ significantly, but there was less chlorophyll in the treatment with large than in the treatment with small densities of *Siphonaria denticulata* (mean  $\pm$  SE: 21Sd =  $0.20 \pm 0.02$ ; 12 Sd =  $0.40 \pm 0.07 \mu\text{g cm}^{-2}$ ), which is, at least, consistent with Hypothesis 8. This difference was not found for *Patelloida latistrigata* (21Pl =  $0.28 \pm 0.04$ ; 9Pl =  $0.29 \pm 0.03 \mu\text{g cm}^{-2}$ ).

After 95 d, variation at scales of 2 and 4 cm, among replicate plates and the interaction among locations and substrata was again significant (Table 4). Micro-algae were more abundant overall, with smaller differences between locations and substrata, although at CP, abundance was significantly greater on sandstone than on concrete plates (Table 4), so Hypothesis 7 (differences between substrata) is supported. At CC, a similar pattern was found, but the difference was not significant (SNK test,  $p > 0.05$ ). Treatments differed significantly, with significantly less chlorophyll with densities of 21 *Patelloida latistrigata* ( $0.97 \pm 0.02 \mu\text{g cm}^{-2}$ ) than in the other treatments, which ranged from  $1.16 \pm 0.03 \mu\text{g cm}^{-2}$  for the 12 *Siphonaria denticulata* with 9 *P. latistrigata* to  $1.56 \pm 0.04 \mu\text{g cm}^{-2}$  for 12 *S. denticulata* alone. These outcomes partially support Hypothesis 8.

Because of the large amounts of small-scale variability in the biomass of chlorophyll and the different modes of feeding of the 2 species, the hypothesis that the scales of spatial variation in chlorophyll differs between substrata and treatments was tested by extracting the components of variation from the mean square (MS) values for 12, 4, 2 cm and the residual for each plate separately (Underwood 1997) and analysing each of these in ANOVAs with locations (random), substrata and treatments (fixed;  $n = 4$ ).

At neither time were there any significant differences among any factors for variation at the scale of 12 cm, but significant differences between substrata were found for 4 cm (Time 1), 2 cm (Time 1), significant interaction with locations (at Time 2) and the residual variance (both times). Consistent with the prediction (Hypothesis 7) that micro-algal assemblages would differ between substrata, there was more variability (i.e. spatial patchiness) in the biomass of micro-algae on concrete than on sandstone in all cases, except for the 4 cm scale at CC at Time 2, where the trend

Table 4. Analyses of biomasses of micro-algae ( $\mu\text{g cm}^{-2}$ ) estimated from the colour-infrared (CIR) camera on sandstone and concrete plates (substratum, fixed factor) at Careening Cove (CC) and Cremorne Point (CP) (locations, random factor) in 5 treatments (9Pl, 21Pl, 9Pl + 12Sd, 12Sd and 21Sd, fixed factor; Treatments B, E, C, A, D, respectively, as described in 'Materials and methods'), for 3 spatial scales of variation within each plate (large, medium, or small; see 'Results — Amounts and types of algae' for details); Time 1: 17 d and Time 2: 95 d after Start 1. P: plate; G: large; M: medium; D: small. See Table 1 for other abbreviations. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Source	df	Time 1		Time 2	
		MS	F	MS	F
L	1	40.0	20.17***	0.4	0.19
S	1	56.2	3.01	17.8	1.22
T	4	1.4	0.43	13.1	6.28**
L $\times$ S	1	18.6	9.41***	14.6	7.02**
L $\times$ T	4	3.3	1.68	2.0	0.95
S $\times$ T	4	1.5	0.48	1.4	0.69
L $\times$ S $\times$ T	4	3.2	1.61	2.0	0.94
P(L $\times$ S $\times$ T)	60	2.0	4.11***	2.1	7.44***
G(P(L $\times$ S $\times$ T))	80	0.5	1.12	0.3	1.10
M(G(P(L $\times$ S $\times$ T)))	160	0.4	2.18***	0.3	1.62***
D(M(G(P(L $\times$ S $\times$ T))))	320	0.2	1.29**	0.2	1.60***
Residual	640	0.2		0.1	

**SNK tests, mean (SE):**

Time 1	CC	(Sandstone) 0.13 (0.01) < (Concrete) 0.79 (0.06)
	CP	(Sandstone) 0.01 (0.00) = (Concrete) 0.19 (0.01)
Time 2	CC	(Sandstone) 1.29 (0.02) = (Concrete) 1.27 (0.03)
	CP	(Sandstone) 1.47 (0.04) > (Concrete) 1.02 (0.03)

**Tested against:**  
<sup>a</sup>Plates after elimination of L  $\times$  S  $\times$  T, L  $\times$  T and S  $\times$  T



was similar, but not significant. There were no differences among treatments except for the residual variation at Time 2, where SNK tests failed to identify which treatments differed. It is not possible to interpret such results as supporting Hypotheses 8 or 9.

The data from the spectrometer were also analysed 17 and 95 d from the start of the experiment to identify whether there were differences in the relative abundances of the different pigments according to location, substratum, or treatment. Because of large differences in the biomass of chlorophyll between the locations and substrata, the estimates of carotenoids (determined from the peak at ~546 nm), phyco-erythrocyanin (~575 nm), chlorophyll *c* (chl *c*; ~640 nm) and chlorophyll *b* (chl *b*; ~650 nm) were standardized according to the overall amount of chlorophyll, by dividing each value by the value of chl *a* (~680 nm) for that spectrum. These data were averaged to give one measure per plate and analysed as a multivariate data set using PERMANOVA (Anderson 2001) for each location separately, with substratum orthogonal to treatment (each a fixed factor) on standardized Euclidean distances, with 999 permutations of the reduced model.

After 17 d, there were no differences in the suite of pigments at CC (all  $p > 0.05$ ), but at CP the relative amounts of the different pigments differed between sandstone and concrete (at  $p < 0.01$ ), which, for this

site, is consistent with Hypothesis 7. After 95 d, the pigments differed among substrata at CC ( $p < 0.01$ ) and CP ( $p < 0.01$ ; Fig. 5A). There was relatively more phyco-erythrocyanin and chl *b* on concrete and more chl *c* on sandstone (illustrated for CP, Time 2 in Fig. 5B).

At CP after 95 d, the data did not support Hypotheses 8 or 9; there was a difference among treatments ( $p < 0.05$ ), but post-hoc pair-wise tests failed to find significant differences between any pairs of treatments. Similarly, there were no clear patterns in relative amounts of the different pigments according to the species present or their densities (Fig. 5C).

### Rates of grazing

Because of the large cover of macro-algae on the lower 40% of the concrete plates, the discs used to measure grazing were separated into those placed on the higher 40% of each plate and those placed on the lower 40% of each plate, with 2 plates randomly assigned to each height (to maintain independence of data). Because the number of limpets deployed and survivorship varied among plates, the number of segments scratched was standardised to the mean number of limpets (each species separately) per plate, calculated from the numbers present when the discs were

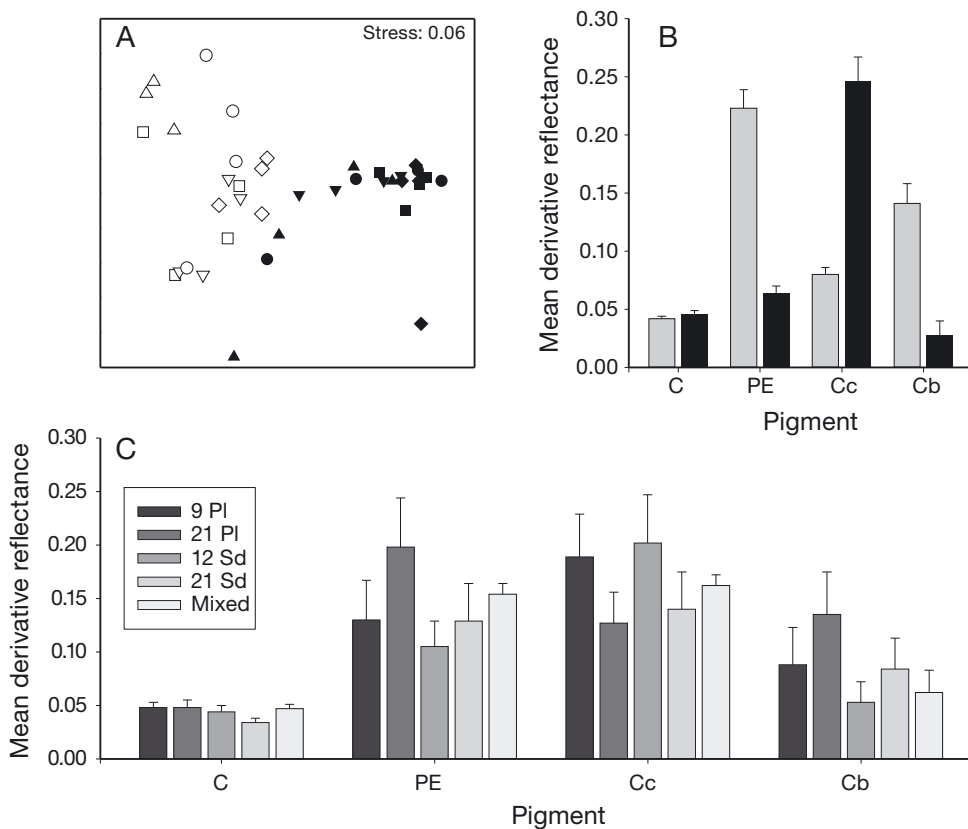


Fig. 5. (A) nMDS plot of derivative reflectance from 4 spectral pigment bands, corrected for biomass of chlorophyll *a* (chl *a*) for Cremorne Point, 95 d after the start of the experiment; ■, □, 12 *Siphonaria denticulata*; ▲, △, 21 *S. denticulata*; ▼, ▽, 9 *Patelloida latistrigata*; ●, ○, 21 *P. latistrigata*; ◆, ◇, 12 *S. denticulata* and 9 *P. latistrigata* (see 'Materials and methods' for treatments); black symbols: sandstone plates; white symbols: concrete plates; (B) mean ( $\pm$ SE;  $n = 20$ ) derivative reflectance (unitless) for each pigment band (C = carotenoids; PE = phyco-erythrocyanin; Cc = chlorophyll *c*; Cb = chlorophyll *b*) for concrete (grey bars) and sandstone (black bars) averaged across treatments; (C) mean ( $\pm$ SE;  $n = 8$ ) derivative reflectance for each pigment band for each treatment (details in key), averaged across substrata

deployed and the numbers present when the discs were collected.

The wax discs were collected 35 (Time 1), 46 (Time 2) and 21 d (Time 3) after they were deployed (Fig. 2). The numbers of sectors grazed by each species were analysed using ANOVAs for each species separately, with location (random; 2 levels), substratum (fixed; 2 levels), treatment (fixed; 3 levels per species), height on the plate (fixed; 2 levels), 2 plates nested inside the combination of all factors;  $n = 2$  discs per plate (Tables 5 & 6).

Differences among locations, substrata, treatments and heights on the shore in the amounts of grazing by *Siphonaria denticulata* were inconsistent among the 3 different times (Table 5). There was no consistent support for Hypothesis 10, because there were few significant differences in comparisons between sandstone and concrete plates (Table 5) and there were no general trends among treatments, nor between locations. For example, although there was less grazing per individual where there were 21 *S. denticulata* than where there were 12 *S. denticulata* in 14 of the 24 comparisons (i.e. 2 locations  $\times$  2 substrata  $\times$  2 heights  $\times$  3 times), the opposite occurred in the other 10 comparisons. Similarly, in contrast to Hypothesis 11 (that grazing would be affected by substratum and the species of grazers present), adding *Patelloida latistrigata* to *S. denticulata* had no consistent effect on rates of grazing of *S. denticulata*. Of the 24 comparisons of grazing by 12 *S. denticulata* plus 9 *P. latistrigata* versus 12 *S. denticulata* alone, 15 showed more grazing when the *S. denticulata* were alone, but 9 showed more grazing when the *S. denticulata* were with *P. latistrigata*. Despite there being so few significant differences in multiple comparisons, there was a tendency for less grazing on the upper than the lower parts of the plates, but this was not consistent among substrata, treatments, nor locations (Table 5).

There were similarly no general patterns among the 3 replicate deployments in rates of grazing by *Patelloida latistrigata* between locations, sub-

Table 5. Analyses of the numbers of sectors per wax disc grazed per individual *Siphonaria denticulata* at CC and CP (locations, random factor) on sandstone and concrete plates (substratum, fixed factor) in 3 treatments (12Pl, 21Sd and 12Sd + 9Pl, fixed factor; treatments A, D and C, respectively, as described in 'Materials and Methods') at 2 vertical heights (high, low) on each plate, with 2 plates selected randomly per combination of factors;  $n = 2$  discs per plate; Time 1: 35 d after 1st deployment; Time 2: 46 d after 2nd deployment; and Time 3: 21 d after 3rd deployment of discs. H: height. See Tables 1 & 4 for other abbreviations. <sup>ns</sup> $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Source	df	Time 1		Time 2		Time 3	
		MS	F	MS	F	MS	F
L	1	0.94	20.88 <sup>c***</sup>	3.39	56.91 <sup>f***</sup>	0.61	8.36 <sup>h**</sup>
S	1	0.24	0.67	0.01	0.01	0.58	8.02 <sup>h**</sup>
T	2	0.29	6.40 <sup>**</sup>	0.57	1.28	0.60	3.05
H	1	0.48	6.82	0.71	11.90 <sup>f**</sup>	2.90	18.97
L $\times$ S	1	0.37	8.34 <sup>c**</sup>	0.68	11.08 <sup>e**</sup>	0.08	1.23 <sup>g</sup>
L $\times$ T	2	0.06	1.44 <sup>c</sup>	0.45	7.26 <sup>e**</sup>	0.20	2.72 <sup>g</sup>
L $\times$ H	1	0.07	1.62 <sup>c</sup>	0.00	0.00 <sup>e</sup>	0.15	2.12 <sup>g</sup>
S $\times$ T	2	0.11	2.56 <sup>c</sup>	0.07	1.11 <sup>e</sup>	0.21	2.92 <sup>g</sup>
S $\times$ H	1	0.07	0.09	0.04	0.15	0.01	0.14 <sup>g</sup>
T $\times$ H	2	0.04	0.27	0.00	0.04	0.08	1.07 <sup>g</sup>
L $\times$ S $\times$ T	2	0.04	0.88 <sup>b</sup>	0.03	0.59 <sup>d</sup>	0.03	0.32 <sup>d</sup>
L $\times$ S $\times$ H	1	0.07	1.59 <sup>b</sup>	0.29	4.41 <sup>d*</sup>	0.00	0.04 <sup>d</sup>
L $\times$ T $\times$ H	2	0.14	3.27 <sup>b</sup>	0.10	1.59 <sup>d</sup>	0.02	0.26 <sup>d</sup>
S $\times$ T $\times$ H	2	0.06	0.28 <sup>b</sup>	0.04	0.60 <sup>d</sup>	0.06	0.68 <sup>d</sup>
L $\times$ S $\times$ T $\times$ H	2	0.05	1.13 <sup>a</sup>	0.08	1.25	0.07	0.87
P(L $\times$ S $\times$ T $\times$ H)	24	0.04	1.21	0.07	3.63 <sup>***</sup>	0.08	3.07 <sup>***</sup>
Residual	48	0.04		0.02		0.03	
Cochran's test (C)		0.18 <sup>ns</sup>		0.27 <sup>*</sup>		0.16 <sup>ns</sup>	
<b>SNK tests, mean (SE):</b>							
Time 1 L $\times$ H $\times$ S							
CC	High	(21Sd) 0.29 (0.06)	<	(12Sd) 0.46 (0.10)	<	(12Sd + 9Pl) 0.44 (0.09)	
	Low	(21Sd) 0.39 (0.04)	<	(12Sd) 0.64 (0.07)	=	(12Sd + 9Pl) 0.75 (0.01)	
CP	High	(21Sd) 0.19 (0.07)	=	(12Sd) 0.16 (0.06)	<	(12Sd + 9Pl) 0.40 (0.08)	
	Low	(21Sd) 0.29 (0.04)	<	(12Sd) 0.43 (0.11)	=	(12Sd + 9Pl) 0.30 (0.11)	
<i>All comparisons between heights non-significant, except</i>							
CC	12Sd + 9Pl	(High) 0.40 (0.08)	<	(Low) 0.75 (0.01)			
CP	12Sd	(High) 0.15 (0.06)	<	(Low) 0.43 (0.11)			
Time 2 L $\times$ H $\times$ S							
CC	High	(Sandstone) 0.68 (0.05)	>	(Concrete) 0.46 (0.08)			
	Low	(Sandstone) 0.78 (0.09)	=	(Concrete) 0.70 (0.06)			
CP	High	(Sandstone) 0.02 (0.02)	<	(Concrete) 0.37 (0.06)			
	Low	(Sandstone) 0.35 (0.08)	=	(Concrete) 0.38 (0.09)			
Time 2 L $\times$ T							
CC		(21Sd) 0.38 (0.05)	<	(12Sd) 0.72 (0.02)	=	(12Sd + 9Pl) 0.87 (0.05)	
CP		(21Sd) 0.26 (0.05)	=	(12Sd) 0.28 (0.08)	=	(12Sd + 9Pl) 0.30 (0.08)	
Time 3 S							
		(Sandstone) 0.36 (0.04)	<	(Concrete) 0.52 (0.05)			
<b>Tested against:</b>							
<sup>a</sup> Pooled Residual and P(L $\times$ S $\times$ T $\times$ H)							
<sup>b</sup> Pooled Residual, P(L $\times$ S $\times$ T $\times$ H) and L $\times$ S $\times$ T $\times$ H							
<sup>c</sup> Pooled Residual, P(L $\times$ S $\times$ T $\times$ H), L $\times$ S $\times$ T $\times$ H and L $\times$ S $\times$ T							
<sup>d</sup> Pooled P(L $\times$ S $\times$ T $\times$ H) and L $\times$ S $\times$ T $\times$ H							
<sup>e</sup> Pooled P(L $\times$ S $\times$ T $\times$ H), L $\times$ S $\times$ T $\times$ H and L $\times$ S $\times$ T							
<sup>f</sup> Pooled P(L $\times$ S $\times$ T $\times$ H), L $\times$ S $\times$ T $\times$ H, L $\times$ S $\times$ T and L $\times$ H							
<sup>g</sup> Pooled P(L $\times$ S $\times$ T $\times$ H), L $\times$ S $\times$ T $\times$ H, L $\times$ T $\times$ H, L $\times$ S $\times$ H and L $\times$ S $\times$ T							
<sup>h</sup> Pooled P(L $\times$ S $\times$ T $\times$ H), L $\times$ S $\times$ T $\times$ H, L $\times$ T $\times$ H, L $\times$ S $\times$ H, L $\times$ S $\times$ T and L $\times$ S							

Table 6. Analyses of the numbers of sectors per wax disc grazed per individual *Patelloida latistrigata* at CC and CP (locations, random factor) on sandstone and concrete plates (substratum, fixed factor) in 3 treatments (9Pl, 21Pl, and 9Pl + 12Sd, fixed factor; Treatments B, E and C, respectively, as described in 'Materials and methods') at 2 vertical heights (high, low) on each plate, with 2 plates selected randomly per combination of factors; n = 2 discs per plate; Time 1: 35 d after 1st deployment; Time 2: 46 d after 2nd deployment; and Time 3: 21 d after 3rd deployment of wax discs. See Tables 1, 4 & 5 for other abbreviations. <sup>ns</sup>p > 0.05, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001

Source	df	Time 1		Time 2		Time 3	
		MS	F	MS	F	MS	F
L	1	1.78	13.82 <sup>c***</sup>	0.23	2.11 <sup>c</sup>	2.73	65.86 <sup>e***</sup>
S	1	0.01	0.04	0.25	2.28 <sup>c</sup>	0.33	1.02
T	2	0.72	5.61 <sup>c***</sup>	0.31	2.87 <sup>c</sup>	0.01	0.36 <sup>e</sup>
H	1	1.75	13.61 <sup>c***</sup>	0.39	3.54 <sup>c</sup>	0.71	1.24
L × S	1	0.36	2.63 <sup>b</sup>	0.00	0.02 <sup>b</sup>	0.32	7.73 <sup>d**</sup>
L × T	2	0.05	0.36 <sup>b</sup>	0.06	0.49 <sup>b</sup>	0.00	0.04 <sup>d</sup>
L × H	1	0.00	0.01 <sup>b</sup>	0.04	0.34 <sup>b</sup>	0.57	12.79 <sup>d**</sup>
S × T	2	0.10	0.75 <sup>b</sup>	0.01	0.04 <sup>b</sup>	0.01	0.26 <sup>d</sup>
S × H	1	0.13	0.97 <sup>b</sup>	0.57	4.74 <sup>b*</sup>	0.41	1.01
T × H	2	0.02	0.12 <sup>b</sup>	0.03	0.24 <sup>b</sup>	0.06	0.56
L × S × T	2	0.04	0.29 <sup>a</sup>	0.19	1.64 <sup>a</sup>	0.01	0.26
L × S × H	1	0.09	0.28 <sup>a</sup>	0.00	0.00 <sup>a</sup>	0.47	8.65 <sup>**</sup>
L × T × H	2	0.03	0.21 <sup>a</sup>	0.15	1.31 <sup>a</sup>	0.10	2.09
S × T × H	2	0.11	0.62 <sup>a</sup>	0.15	1.27 <sup>a</sup>	0.09	0.99
L × S × T × H	2	0.18	1.17	0.13	1.09	0.09	1.90
P(L × S × T × H)	24	0.15	2.75 <sup>**</sup>	0.12	0.81	0.05	1.49
Residual	48	0.06		0.14			
Cochran's test (C)		0.40 <sup>**</sup>		0.15 <sup>ns</sup>		0.40 <sup>**</sup>	

**SNK tests, mean (SE):**

Time 1

T (21Pl) 0.27 (0.04) < (9Pl) 0.50 (0.06) < (9Pl + 12Sd) 0.55 (0.08)

H (High) 0.30 (0.05) < (Low) 0.58 (0.05)

Time 2 S × H

High (Concrete) 0.39 (0.07) > (Sandstone) 0.13 (0.04)

Low (Concrete) 0.36 (0.08) = (Sandstone) 0.41 (0.08)

Concrete (High) 0.39 (0.07) = (Low) 0.36 (0.08)

Sandstone (High) 0.13 (0.04) < (Low) 0.41 (0.08)

Time 3 L × S × H

CC (Concrete) 0.01 (0.01) = (Sandstone) 0.01 (0.01)

CP (Concrete) 0.23 (0.05) > (Sandstone) 0.46 (0.09)

CC (High) 0.00 (0.00) = (Low) 0.02 (0.01)

CP (High) 0.18 (0.04) < (Low) 0.51 (0.09)

**Tested against:**

<sup>a</sup>Pooled P(L × S × T × H) and L × S × T × H

<sup>b</sup>Pooled P(L × S × T × H), L × S × T × H, L × T × H, L × S × H and L × S × T

<sup>c</sup>Pooled P(L × S × T × H), L × S × T × H, L × T × H, L × S × H, L × S × T, L × T and L × H

<sup>d</sup>Pooled P(L × S × T × H) and L × S × T

<sup>e</sup>Pooled P(L × S × T × H), L × S × T and L × T

strata, treatments, or heights (Table 6). For example, contrary to Hypothesis 10, there was no consistent effect of substratum, which varied inconsistently according to the location (Time 3) or the height at which the limpets were grazing (Time 2). Treatments only differed significantly in the first deployment, when the mean number of sectors grazed per individual was smaller for the treatment with 21 *P. latistrigata* than for those with 9 *P. latistrigata*, irrespective of the presence

or absence of *Siphonaria denticulata*. These outcomes provide partial support for Hypothesis 11, but reject Hypothesis 12. This could have been due to an experimental artefact, because all sectors were grazed on many plates. Therefore, standardizing by dividing by the number of snails artificially lowered the rate of grazing in the large density treatment. This did not occur in the other deployments where the discs were recovered before they were so extensively grazed and the pattern found at Time 1 did not occur. As for *S. denticulata*, the limpets tended to graze more lower than higher on the plates on both substrata, but differences were not always significant (Table 6). There was no indication that *S. denticulata* or increased densities of *P. latistrigata* changed whereabouts on the plates the limpets fed.

## DISCUSSION

In NSW, there are many species of interacting intertidal grazers and an extremely diverse assemblage (Dakin 1953, Stephenson & Stephenson 1972). Despite many papers in recent years documenting patterns of assemblages on seawalls, few have compared ecological interactions among animals between artificial and natural shores. Bulleri et al. (2004) showed grazing by *Cellana tramoserica* on walls differed from that on natural shores in NSW, which could have major impacts on assemblages because of its strong interactions with other species (Underwood et al. 1983, Underwood 1984, 1985). Intertidal shores in NSW are generally extensive wave-cut platforms, so interactions among grazers might be expected to be stronger on seawalls

where the intertidal area is reduced and species are crowded into a limited area.

*Siphonaria denticulata* have greater densities on many sandstone seawalls in Sydney Harbour than on natural shores. *Patelloida latistrigata* are more common on concrete than on sandstone walls. *S. denticulata* graze on fronds of macro-algae and do not remove algal propagules as do patellid or acmaeid limpets, such as *P. latistrigata* (Underwood & Jernakoff 1981).

Thus, micro-algal food may persist in the presence of large densities of *S. denticulata*. Patellid limpets, in contrast, remove nearly all algal spores and many species outcompete siphonarian limpets, although they seldom cause local extinctions because of strong intraspecific competition (Creese & Underwood 1982, Ortega 1985, Lasiak & White 1993). Thus, changes in competitive interactions, types or amounts of food, or differences in recruitment might explain the pattern of greater densities of *S. denticulata* on sandstone walls and greater densities of *P. latistrigata* on concrete walls.

Unfortunately, too few *Patelloida latistrigata* recruited during the experiment for detailed analysis, although all but one recruited onto concrete. Thus, recruitment may explain larger densities of *P. latistrigata* on concrete walls. What caused this is not known, although some gastropods settle in response to biofilms (Kay 2002), which may differ between substrata. Concrete is also a strong inducer to settlement of oysters, irrespective of biofilm (Anderson 1996). There were too few data to be able to test whether *Siphonaria denticulata* affected recruitment of *P. latistrigata*.

Recruitment of *Siphonaria denticulata* was more complex. They recruited more to concrete than to sandstone, although adults are more abundant on sandstone. Recruitment increased in the presence of conspecifics (Kay 2002, Zhao & Qian 2002), but decreased in the presence of *Patelloida latistrigata*. Adult limpets can reduce densities of juveniles by bull-dozing (Underwood et al. 1983), or, as described for *Patella longicosta*, by ejecting juveniles from territories (Branch 1975). For interactions between recruits and adults to explain the observed patterns of abundance of *S. denticulata*, *P. latistrigata* must have a stronger negative effect on small *S. denticulata* than do adult *S. denticulata*, possibly because they feed by scraping the substratum. *S. denticulata* may move over recruits without much damage. Unravelling this requires focused experiments about settlement and mortality of settlers on both surfaces in the presence/absence of each species.

Adults of each species survived better on concrete, although each was affected by adult *Patelloida latistrigata*. Increased densities of *P. latistrigata* reduced conspecific survival, as on natural shores (Creese 1982). They also decreased survival of *Siphonaria denticulata*, as shown for other patellid and siphonarian limpets (e.g. Underwood & Jernakoff 1981, Creese & Underwood 1982, Lasiak & White 1993). This may have been due to removal of food or interference when feeding. Thus, if densities of *P. latistrigata* increase on concrete walls due to recruitment, their presence might further reduce any *S. denticulata* that survive settlement on these surfaces. The smaller rates of recruitment of *P. latistrigata* to sandstone might mean

that they never reach large enough densities to affect recruiting *S. denticulata* on these surfaces.

*Siphonaria denticulata* did not affect mortality of *Patelloida latistrigata*, as shown for other species (Creese & Underwood 1982, Ortega 1985), but in contrast to the interaction between *Siphonaria concinna* and *Cellana capensis* (Lasiak & White 1993). Thus, the presence of adult *S. denticulata* is unlikely to explain patterns of abundance of either species between sandstone and concrete seawalls. In general, the competitive interactions on seawalls reflect what occurs on natural shores, even though intra- and interspecific competition were expected to be more severe on walls due to the limited number of refuges and the small amount of intertidal habitat.

Interactions between limpets and their resources are complex, including interference competition (Stimson 1970), defence of 'gardens' (Stimson 1970, Wright 1982) and removal of resources (Dayton 1971, Branch 1975, Underwood 1978, 1984). Because *Patelloida latistrigata* and *Siphonaria denticulata* exploit different algal resources, patterns of development of micro- and macro-algae were examined to determine whether these could explain the patterns of the adult limpets. Ephemeral macro-algae, which are eaten by *S. denticulata*, developed as a thick band on the lower halves of the concrete plates. These algae are not particularly common on well-established sandstone or concrete seawalls (Bulleri et al. 2005, Moreira 2006), where oysters and tubeworms are major components of the assemblages (Moreira 2006). Ephemeral algae commonly colonize new, damp surfaces (Bacchiocchi & Aioldi 2003) or areas with few grazers (Pinn et al. 2005). They rapidly colonize newly built seawalls in Sydney Harbour, but usually low on the shore (M. G. Chapman pers. obs.). The concrete plates may have retained more water during low tide than did the sandstone plates, remaining damp like low-shore areas. There was a smaller cover of macro-algae where there were larger densities of *S. denticulata*, indicating that these limpets were exploiting this resource, as would be predicted from their known ecology. Increased survival of *S. denticulata* on concrete may therefore be, in part, due to concrete having more macro-algae, even though there was no evidence of intraspecific competition on either surface.

Amounts of macro-algae were not influenced by densities of *Patelloida latistrigata*, despite the fact that this species can eat macro-algae (Jernakoff 1985). The reduced amounts of space for development of the micro-algal assemblage due to space occupied by macro-algae did not alter either intra- or interspecific effects of this limpet. Micro-algae were also more abundant on concrete plates, although differences between surfaces decreased with longer periods of de-

ployment. Where large amounts of macro-algae cover the substratum on natural shores, they inhibit recruitment of *P. latistrigata* and survival of this and other limpets (Underwood et al. 1983). This was, however, not shown here, where both species survived better and *P. latistrigata* recruited more where there were greater covers of macro-algae. Thus, the development of ephemeral macro-algal assemblages cannot explain the patterns of *Siphonaria denticulata* reported by Moreira (2006).

Amounts of micro-algae were reduced by large densities of *Patelloida latistrigata*, as predicted from patterns shown on natural shores. *Siphonaria denticulata*, again as predicted from their known ecology, had no major effects on micro-algae. The composition of the micro-algal assemblage and its spatial variation differed between the 2 substrata, but this was not affected by the types or numbers of limpets present.

It was surprising that there was no clear pattern in grazing activities of the 2 species. Given that *Siphonaria denticulata* eat macro-algae, it would have been expected to find more grazing by *S. denticulata* on lower parts of the plates. In contrast, *Patelloida latistrigata* would have been expected to graze more on the upper parts of plates, where macro-algae were sparse and there was more access to areas covered by micro-algae. Where *P. latistrigata* were numerous, because they consume micro-algae, including early stages of development of macro-algae, *S. denticulata* should have been even more likely to feed on lower parts of plates where their food was more abundant. In fact, there were no influences of either species on the other, in terms of where they fed. If anything, each species tended to forage more on lower parts of plates, but that cannot be explained by known aspects of their ecology on natural substrata.

There was more phyco-erythrocyanin and chl *b* on concrete and more chl *c* on sandstone plates, which suggests relatively more green micro-algae and cyanobacteria on concrete and relatively more diatoms on sandstone. Increased amounts of green micro-algae on concrete may, at least in part, be due to increased numbers of sporelings of the ephemeral macro-algae that developed on this substratum. Although cyanobacteria may have limited value as food for grazers, Nagarkar et al. (2004) found that epilithic cyanobacteria can be superior as food over other micro-algae, in terms of their protein, calorific content and, sometimes, carbohydrates. Thus, increased amounts of micro-algae, plus their composition, may have explained greater survival of each species on concrete.

The assemblage of micro-algae was, however, not affected by the mix of limpets, which is surprising considering their different modes of feeding. There was more small-scale patchiness of micro-algae on concrete than

on sandstone, possibly due to the substratum, or to differences in the ways the species grazed on the different surfaces. Little is known about the complex causes of small-scale patchiness of abundances of micro-algae on intertidal rocky shores, although grazing by different species can cause differences in amounts (Underwood & Murphy 2008) and types (Murphy & Underwood 2006) of micro-flora present. Variations in abundances and types of micro-algae due to grazing are at spatial scales of mm to cm and have not been detectable until the development of methods over recent years to measure micro-algae *in situ* at the relevant small scales. Differences in such an important food resource may have important implications for the suite of species that can persist in the long-term on artificial structures, but have, as yet, received little attention. Because the procedures used here measure light reflected vertically from the surface, it is not possible to measure amounts of micro-algae on the vertical surfaces of seawalls, except on experimental surfaces that could be moved to a horizontal position for sampling. So, no comparisons were made between seawalls and natural shores.

Thus, the material used to build artificial structures may influence rates of recruitment, the amounts and types of food resources, or the quality of habitat due to the lack of many macro-habitats (Moreira et al. 2006, Chapman & Blockley 2009). Here, 2 species of limpets that have complex competitive interactions with numerous other species on natural shores showed similar complex interactions on plates attached to vertical seawalls, which varied according to the material of the plate. Despite our predictions, competition was not very great on seawalls, possibly because of adequate food. The results here cannot fully explain the patterns of distribution reported by Moreira (2006), perhaps because these interactions are more complex than originally thought, or other differences between substrata that were not investigated here, or because the concrete in the plates used here differed from that used to build walls, or because more time is needed to establish the relationships that led to the originally observed patterns.

Whatever is demonstrated by more complete analyses when they become available, several important points are demonstrated by the experiments described here. Processes were more complex and predicted interactions less clear than had been anticipated. This is important for developing useful frameworks for identifying and managing the core ecological processes that must be maintained to ensure maintenance of local patterns of biodiversity. Because grazing is such an important controlling process for many intertidal species (reviewed by Branch 1981, Hawkins & Hartnoll 1983, Underwood 1985, 1992), it is one of the key processes to understand. The extent to which

knowledge about such a well-studied topic succeeded or failed to provide appropriate predictions for artificial habitats is instructive. It demonstrates that care will particularly be needed where the processes in natural habitats are less well-known or less amenable to experimental development of theory. Future increased needs of conservation of biodiversity in man-made habitats require more tests of the applicability of extant ecological knowledge and theories to increasingly stressed and altered shorelines.

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