# Patterns of occurrence of grazing molluscs on sandstone and concrete seawalls in Sydney Harbour (Australia)

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## Abstract

Proliferation of artificial structures is a common feature in urbanized environments. In Sydney Harbour (NSW, Australia), much of the coastline is composed of seawalls that have replaced natural habitats, such as rocky shores. Many of these seawalls are made of sandstone blocks or concrete, but the effects of the type of substratum on assemblages living on seawalls has not been documented. Nevertheless, differences in characteristics of substratum have been shown to affect composition and development of intertidal assemblages. Grazing molluscs are important agents in the structuring of intertidal assemblages affecting numbers and distribution of other organisms. This study compares species and numbers of grazing molluscs at midshore levels between concrete and sandstone seawalls across Sydney Harbour. The two habitats supported a similar suite of species, although in different numbers and frequencies of occurrence, particularly higher on the shore. Therefore, concrete and sandstone seawalls provide different habitat for intertidal molluscs depending on tidal height. Experimental work is needed to assess properly the impact of construction of seawalls with different materials on intertidal biodiversity.

**Key words**: artificial habitats, gastropods, intertidal, substratum

## Introduction

The continued growth of human populations and consequent expansion of cities and towns is having a strong impact on natural systems (Carroll *et al*. 2004). Urbanization removes and fragments natural habitats and results in a number of new structures being added to the environment (Glasby and Connell 1999). In coastal areas, artificial structures such as jetties, pilings, pontoons and seawalls are, in many cases, built at the expense of natural shores (Glasby and Connell 1999; Chapman and Bulleri 2003; Bulleri and Chapman 2004). These new structures are made of a variety of materials and differ from natural habitats in terms of composition, orientation, features of the surface and provision of microhabitats (Chapman and Bulleri 2003). As construction of new structures will undoubtedly continue, it is necessary to assess their value as alternative habitats for marine organisms.

Although there is a tendency to build seawalls using the natural rock of the area (sandstone), some seawalls in Sydney Harbour (NSW, Australia) are made of other materials, particularly concrete. In addition, the lack of a common policy among local councils means that collapsed sandstone seawalls are not always repaired or rebuilt with the same original material. Thus, a variety of materials used to build seawalls causes a mix of artificial and natural habitats that make up the fragmented shoreline of Sydney Harbour (Chapman and Bulleri 2003).

Grazing molluscs, such as limpets, snails and chitons are among the most abundant mobile organisms on rocky shores in New South Wales (Underwood 1978; Creese 1981). These animals play a major role in structuring

intertidal assemblages in natural habitats through complex interactions that affect the distribution and abundance of algae and sessile and mobile animals (Underwood 1980; Hawkins and Hartnoll 1983; Petraitis 1987; Anderson and Underwood 1994). Previous work has documented that, although many molluscs found on natural habitats also live on sandstone seawalls (Chapman and Bulleri 2003), some are very sparse on seawalls (Chapman 2003; in press). There are also important differences in behaviour and performance between seawalls and natural rocky shores. For example, some limpets can be found in similar densities on the two habitats, but show differences in grazing behaviour and use of habitat (Bulleri *et al*. 2004), sizes and reproductive output (Moreira *et al*., in press). However, it is not known whether concrete seawalls support similar species and densities of grazing molluscs as sandstone seawalls.

Although sandstone and concrete seawalls in Sydney Harbour are generally vertical or steeply sloping and therefore have a similar intertidal extent (about 2 m), texture and features of exposed surfaces are likely to differ. In addition, sandstone seawalls are made of blocks separated by crevices, which may provide shelter for some intertidal mobile organisms (Chapman 2003). Characteristics of substratum strongly affect numbers and survival of intertidal grazing gastropods (Underwood and Chapman 1992; Williams and Morrit 1995). For example, some limpets and snails retreat to cracks and crevices during low tide to avoid physiological stress (Gray and Hodgson 2004). Furthermore, there are different behavioural responses to small-scale topography between different species (Underwood 1976, 2004). The nature of the substratum may also determine settlement and recruitment of sessile organisms and therefore

the amount of space they occupy (Raimondi 1988; McGuinness 1989; Anderson and Underwood 1994; Bulleri 2005a), which, in turn, may influence the presence and densities of grazing gastropods (Branch 1981; Minchinton and Ross 1999; Steffani and Branch 2003). Thus, if intrinsic characteristics of concrete and sandstone seawalls are different, it can be predicted that numbers and mixes of species of grazing molluscs will differ between these two habitats.

This study aims, therefore, to investigate differences in composition of intertidal assemblages of grazing molluscs between sandstone and concrete seawalls across Sydney Harbour.

## Materials and methods

Study sites and sampling

Five sandstone and five concrete seawalls were sampled across Sydney Harbour between April and May, 2005 (Figure 1). Hereafter, the two different kinds of seawalls (sandstone, concrete) are referred to as habitats. Locations were selected because they had a seawall extensive enough both in length and intertidal extent for the proposed sampling. Locations were separated by distances between hundreds of metres and several kilometres. On each seawall, two heights representing different assemblages of organisms were chosen to examine the assemblages of grazing molluscs: 0.9–1.2 m (high midshore) and 0.6–0.8 m (low midshore). Detailed descriptions of the full suite of sessile and mobile organisms of these assemblages on sandstone seawalls can be found in Chapman (2003) and Chapman and Bulleri (2003). Lowshore levels (< 0.4 m LWST) were not sampled because they were not available in each location and molluscs are sparse at these tidal levels (Chapman, in press). The sampling design did not eliminate potential sources of confounding due to intrinsic characteristics of locations, but was a sensible scheme on the fragmented shoreline of Sydney Harbour (Chapman and Bulleri 2003). Nevertheless, all selected locations have previously been studied in similar studies (Chapman and Bulleri 2003; Bulleri *et al.* 2004, 2005; Chapman, in press) and were chosen because they were located inside Sydney Harbour, sheltered from strong oceanic swell and subjected to similar wave-wash caused by intense maritime traffic.
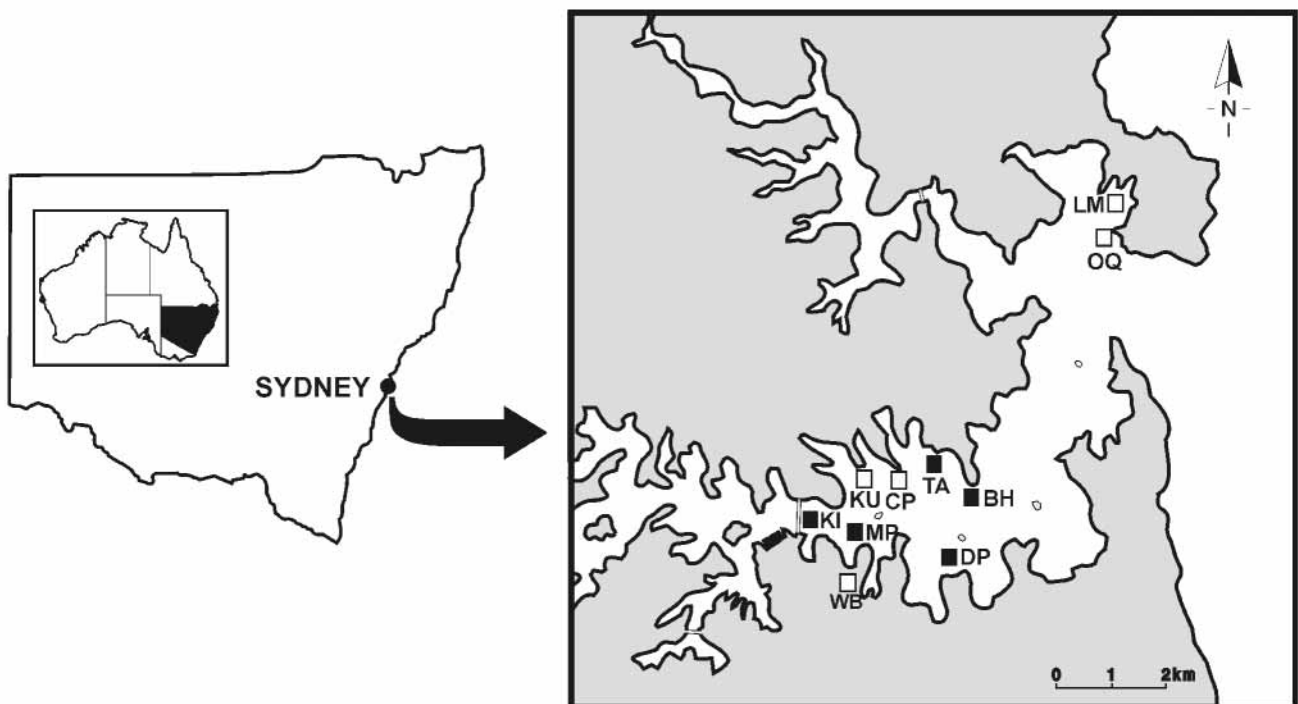


**FIGURE 1**. Study sites in Sydney Harbour, New South Wales, Australia. White squares, concrete seawalls: WB, Woolloomooloo Bay; KU, Kurraba Point; CP, Cremorne Point; OQ, Old Quarantine Station; LM, Little Manly. Black squares, sandstone seawalls: KI, Kirribilli; MP, Mrs Macquarie's Point; TA, Taronga; DP, Darling Point; BH, Bradley's Head.

Two sites, approximately 10 m long and separated by 5–10 m, were selected at each location to measure spatial variation within each seawall. Five replicate quadrats (0.05 m² each) were randomly positioned in each site at each height (Chapman and Bulleri 2003). Quadrats within the same site were separated by at least 50 cm. On sandstone seawalls, quadrats were placed at least 10 cm away from crevices. Grazing molluscs were counted in each quadrat and percentage of cover of sessile organisms and the amount of bare rock as a measure of unoccupied space were estimated from 50 intersection points per quadrat.

Analysis of data

Sessile assemblages and grazing molluscs were compared among habitats separately for each tidal height. Assemblages from different heights were not compared

because tidal heights were selected to represent different assemblages within the same habitat (Chapman and Bulleri 2003). Permutational analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) was used to test the hypothesis that assemblages would differ among habitats. This analysis was done using Bray-Curtis measures of dissimilarity calculated from the full set of untransformed data. Non-metric multidimensional scaling (nMDS) was used to produce a visual representation of the ordination of sites for each tidal height. For nMDS, Bray-Curtis dissimilarities were calculated from data averaged across quadrats producing centroids for sites as replicates. The percentage contribution of each taxon to dissimilarity between and within habitats was calculated using SIMPER (PRIMER; Clarke 1993).

To compare the frequency of occurrence of each species among habitats regardless of actual densities, counts of presence/absence were added across locations for each tidal level and habitat (Chapman, in press). These frequencies were compared through $\chi^2$ contingency tests for all species which gave expected values $\geq 5$ for each cell (Underwood 1997).

Abundances of common taxa were compared among habitats for each tidal level by analysis of variance (three-factor ANOVA), to test for effects of habitat (fixed), location (nested in habitat) and site (nested in habitat and location). Homogeneity of variances was checked using Cochran's test prior to analyses and data were transformed when appropriate. Data were analysed untransformed when homogeneity of variances could not be achieved. ANOVA is a robust analysis despite heterogenous variances when there are many independent replicates and size of samples are equal (Underwood 1997). Nevertheless, a more conservative significance level was used when Cochran's test was significant (see Tables).

## Results

Fourteen molluscan taxa were found, which included one chiton, 11 prosobranch snails and limpets and two pulmonate siphonarian limpets (Table 1). Of these taxa, 11 were present on the two habitats.

**TABLE 1.** Mean number (S.E.) of quadrats per location in which each species of grazing mollusc was found in each habitat at high and low midshore levels.

| Taxon | High midshore | | Low midshore | |
|---|---|---|---|---|
| | Concrete | Sandstone | Concrete | Sandstone |
| **Class Gastropoda** | | | | |
| **Family Nacellidae** | | | | |
| *Cellana tramoserica* (Holten, 1802) | 3.8 (2.0) | 1.2 (0.6) | 0.6 (0.4) | 1.0 (0.5) |
| **Family Lottiidae** | | | | |
| *Notoacmea petterdi* (Tenison-Woods, 1876) | 3.6 (1.4) | 2.4 (0.5) | 0.4 (0.2) | - |
| *Patelloida alticostata* (Angas, 1865) | - | - | 2.2 (0.9) | 5.2 (1.0) |
| *Patelloida latistrigata* (Angas, 1865) | 7.4 (1.7) | 3.0 (0.6) | 3.0 (1.3) | 3.8 (1.5) |
| *Patelloida mimula* (Iredale, 1924) | 2.4 (1.7) | - | 5.4 (0.8) | 2.4 (0.8) |
| *Patelloida mufria* (Hedley, 1915) | - | - | 0.2 (0.2) | - |
| **Family Fissurellidae** | | | | |
| *Montfortula rugosa* (Quoy & Gaimard, 1834) | 0.6 (0.6) | 0.4 (0.4) | 4.2 (1.8) | 4.4 (1.4) |
| **Family Trochidae** | | | | |
| *Austrocochlea porcata* (A. Adams, 1851) | 0.8 (0.8) | - | - | - |
| **Family Littorinidae** | | | | |
| *Littorina unifasciata* Gray, 1826 | 2.4 (1.9) | - | 0.2 (0.2) | - |
| *Bembicium nanum* (Lamarck, 1822) | 4.0 (1.5) | 0.4 (0.2) | 1.4 (1.2) | - |
| **Family Neritidae** | | | | |
| *Nerita atramentosa* Reeve, 1855 | 0.4 (0.2) | 0.2 (0.2) | - | - |
| **Family Siphonariidae** | | | | |
| *Siphonaria denticulata* Quoy & Gaimard, 1833 | 3.2 (0.7) | 9.6 (0.4) | 8.8 (0.8) | 9.6 (0.4) |
| *Siphonaria virgulata* Hedley, 1915 | 3.2 (1.8) | 3.6 (0.7) | 2.2 (1.4) | 1.0 (0.8) |
| **Class Polyplacophora** | | | | |
| **Family Chitonidae** | | | | |
| *Sypharochiton pelliserpentis* (Quoy & Gaimard, 1835) | 2.4 (0.9) | 1.6 (0.8) | 7.8 (1.2) | 7.8 (0.9) |

Multivariate analyses

Cover significantly differed between habitats for high midshore levels (Table 2, Figure 2) and dissimilarities were mainly due to bare space and the oyster, *Saccostrea commercialis* (Iredale & Roughley, 1933) (> 40% dissimilarity each). Thus, cover by oysters was generally greater on concrete seawalls and more unoccupied space was found on sandstone seawalls. Dissimilarities among locations on concrete seawalls were due to differences in space covered by oysters (> 40% dissimilarity). Cover by oysters ranged from 30-70% at Kurraba Point and Woolloomooloo Bay to less than 5% at Little Manly and Cremorne Point. These differences are responsible for the separation among these locations in the nMDS plot (Figure 2). On sandstone seawalls, barnacles and bare space were the main contributors to dissimilarities among locations (> 45% dissimilarity each).

**TABLE 2.** Results of PERMANOVA on untransformed data based on Bray-Curtis dissimilarities, comparing sessile and grazer assemblages at high and low midshore levels (Ha, habitat; Lo, location; Si, site). ns, not significant; ** $p < 0.01$.

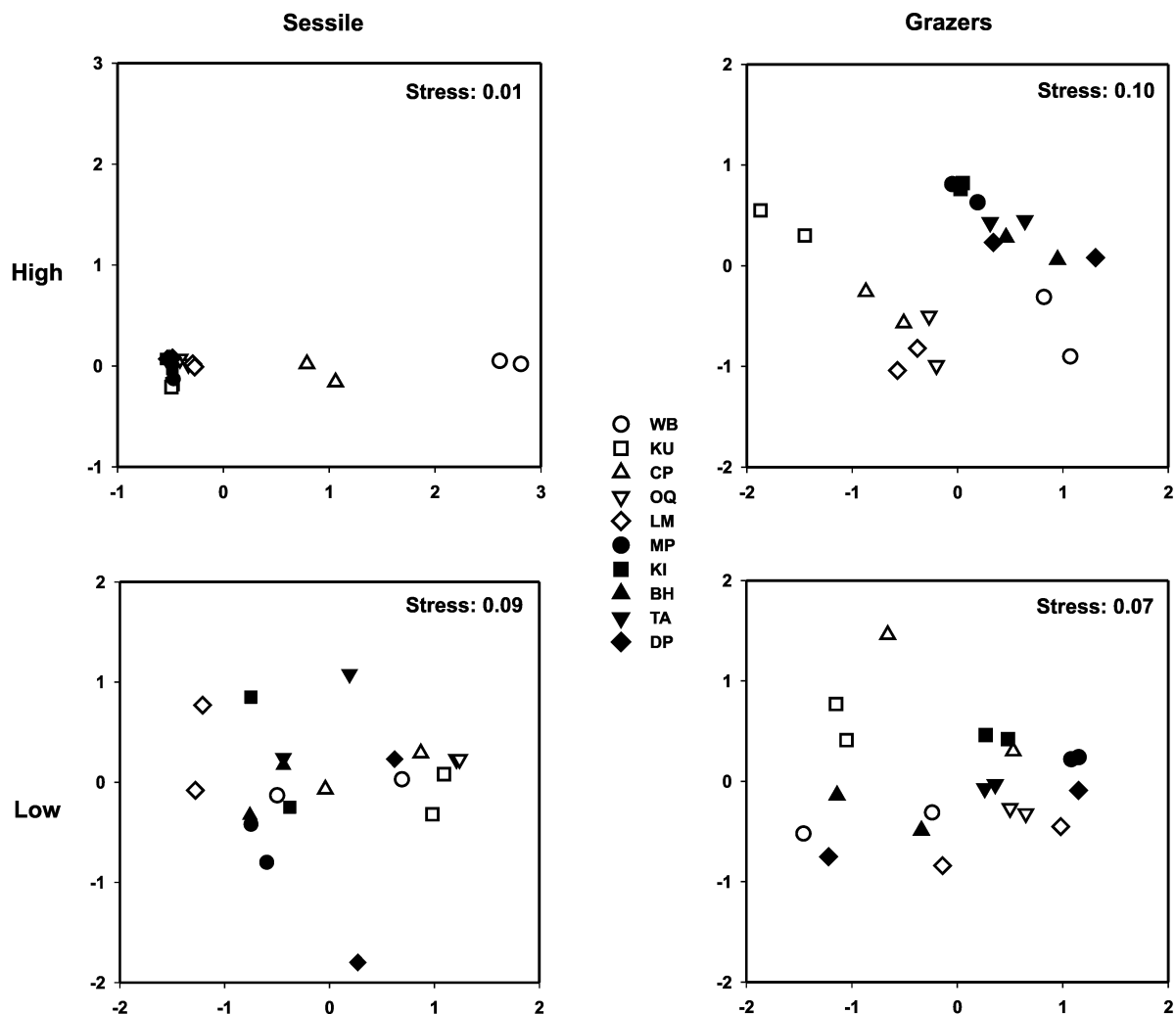|  |  | Sessile | | Grazers | |
| --- | --- | --- | --- | --- | --- |
|  |  | **High** | **Low** | **High** | **Low** |
|  | df | *F* | *F* | *F* | *F* |
| Source |  |  |  |  |  |
| Ha | 1 | 3.06 ** | 0.35 ns | 4.89 ** | 0.92 ns |
| Lo (Ha) | 8 | 68.93 ** | 5.57 ** | 4.95 ** | 5.47 ** |
| Si (Ha, Lo) | 10 | 0.76 ns | 6.65 ** | 3.02 ** | 2.64 ** |
| Residual | 80 |  |  |  |  |
| Total | 99 |  |  |  |  |



**FIGURE 2**. Two-dimensional nMDS plots of centroids comparing assemblages of sessile organisms and grazing molluscs for sites on concrete (white symbols) and sandstone (black symbols) seawalls at high and low midshore levels. Code for locations as in Figure 1.

Assemblages of grazing molluscs were significantly different among habitats at high midshore levels (Table 2, Figure 2) and similar results were obtained when presence/ absence data were analysed (not shown). The main contributors to dissimilarities in molluscan assemblages among habitats for high midshore levels were *Siphonaria*

*denticulata* Quoy & Gaimard, 1833 (44%), *Patelloida latistrigata* (Angas, 1865) (19%) and *Littorina unifasciata* Gray, 1826 (13%). Dissimilarities within habitats were due to *S. denticulata* (84%) on sandstone seawalls, and to *P. latistrigata* (30%), *L. unifasciata* (29%) and *Siphonaria virgulata* Hedley, 1915 (12%) on concrete seawalls.

Average Bray-Curtis dissimilarities among locations within the same habitat for sessile and grazer assemblages were larger on concrete than on sandstone seawalls for high midshore levels and the reverse was found for low midshore levels (Table 3).

**TABLE 3.** Average Bray-Curtis dissimilarities between and within habitats for sessile and grazer assemblages at high and low midshore levels (range for values of dissimilarity among locations are included in brackets).

|  |  | Between habitats | Within habitats | |
|---|---|---|---|---|
|  |  |  | Concrete | Sandstone |
| **Sessile** | **High** | 24.5 | 33.9 (3.2–69.3) | 2.5 (1.0–5.2) |
|  | **Low** | 50.1 | 48.7 (26.8–93.6) | 57.7 (27.7–94.8) |
| **Grazers** | **High** | 75.6 | 67.4 (48.8–88.6) | 38.7 (22.4–69.1) |
|  | **Low** | 55.6 | 44.7 (33.3–66.5) | 68.4 (43.4–96.2) |

Cover of substratum

Substratum was dominated by bare space at high midshore levels in both habitats (> 75%). The remaining space was mostly occupied by the oyster, *S. commercialis*, on concrete seawalls and the barnacle, *Tesseropora rosea* (Krauss, 1848), on sandstone seawalls. The oyster, *S. commercialis*, and the tubeworm, *Galeolaria caespitosa* Lamarck, 1818, occupied much of the available space at low midshore levels (> 65% cover) while the remaining space

was mostly occupied by encrusting algae, barnacles, the mussel, *Mytilus galloprovincialis* Lamarck, 1819 and foliose coralline algae. At low midshore levels, there was, in general, a greater percentage of space covered by oysters on concrete than on sandstone seawalls and the opposite pattern was observed for *G. caespitosa*. These differences in cover of particular taxa were, however, only significant among locations and/or sites within habitats (Tables 4, 5).

**TABLE 4.** ANOVA results comparing percentage cover of substrata by bare space and oysters and abundance of grazing molluscs between habitats at high midshore levels (Ha, habitat; Lo, location; Si, site). When Cochran's test was significant ($p < 0.01$) a more conservative significance level of $p < 0.001$ was used. ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

|  |  | Cover of substrata | | | | Grazing molluscs | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | Bare space | | *S. commercialis* | | *B. nanum* | | *P. latistrigata* | | *S. denticulata* | |
|  | df | MS | F | MS | F | MS | F | MS | F | MS | F |
| Source |  |  |  |  |  |  |  |  |  |  |  |
| Ha | 1 | 3237.6 | 3.59 ns | 3136.0 | 3.06 ns | 12.2 | 4.29 ns | 13.6 | 5.26 ns | 42.1 | 32.84 *** |
| Lo (Ha) | 8 | 900.9 | 61.41 *** | 1023.7 | 99.20 *** | 2.8 | 0.85 ns | 2.6 | 9.04 *** | 1.3 | 3.55 * |
| Si (Ha, Lo) | 10 | 14.7 | 0.77 ns | 10.3 | 0.65 ns | 3.3 | 3.13 ns | 0.3 | 1.29 ns | 0.4 | 1.82 ns |
| Residual | 80 | 19.1 |  | 15.9 |  | 1.1 |  | 0.2 |  | 0.2 |  |
| Total | 99 |  |  |  |  |  |  |  |  |  |  |
| Cochran's test (C) |  | ** |  | ** |  | ** |  | ns |  | ns |  |

**TABLE 5.** ANOVA results comparing percentage cover of substrata by sessile organisms and abundance of grazing molluscs between habitats at low midshore levels (Ha, habitat; Lo, location; Si, site). When Cochran's test was significant ($p < 0.01$) a more conservative significance level of $p < 0.001$ was used. ns, not significant; ** $p < 0.01$; *** $p < 0.001$.

|  |  | Cover of substrata | | | | Grazing molluscs | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | *G. caespitosa* | | *S. commercialis* | | *P. alticostata* | | *S. denticulata* | | *S. pelliserpentis* | |
|  | df | MS | F | MS | F | MS | F | MS | F | MS | F |
| Source |  |  |  |  |  |  |  |  |  |  |  |
| Ha | 1 | 1444.0 | 0.97 ns | 3968.3 | 3.38 ns | 10.9 | 0.60 ns | 1310.4 | 1.97 ns | 43.5 | 0.38 ns |
| Lo (Ha) | 8 | 1484.7 | 2.28 ns | 1174.7 | 2.70 ns | 18.2 | 1.77 ns | 666.4 | 2.29 ns | 113.5 | 56.18 *** |
| Si (Ha, Lo) | 10 | 651.2 | 14.13 *** | 435.4 | 12.79 *** | 10.3 | 3.13 ns | 291.6 | 3.80 *** | 2.0 | 0.24 ns |
| Residual | 80 | 46.1 |  | 34.0 |  | 3.3 |  | 76.7 |  | 8.3 |  |
| Total | 99 |  |  |  |  |  |  |  |  |  |  |
| Cochran's test (C) |  | ns |  | ns |  | ** |  | ** |  | ** |  |

Frequency and numbers of grazing molluscs

The most widespread grazing molluscs across habitats (appearing in at least 30% of quadrats; n = 200) were the limpets, *P. latistrigata*, *Patelloida mimula* (Iredale, 1924), *S. denticulata*, *S. virgulata* and the chiton, *Sypharochiton pelliserpentis* (Quoy & Gaimard, 1835). The snails, *Austrocochlea porcata* (A. Adams, 1851) and *Nerita atramentosa* Reeve, 1855 and the limpet, *Patelloida mufria* (Hedley, 1915), were sparse in the two habitats (< 10% of quadrats). The snail, *L. unifasciata*, was only found at high midshore levels on concrete seawalls although it was observed on sandstone seawalls at higher tidal levels not sampled in this study.

Frequencies of occurrence of molluscs were compared between habitats through $\chi^2$ contingency tests, adding all the counts of presence/absence across locations for each tidal level. At high midshore levels, the limpets, *Cellana tramoserica* (Holten, 1802), *P. latistrigata*, *P. mimula* and the snail, *Bembicium nanum* (Lamarck, 1822), were significantly more frequent on concrete than on sandstone seawalls, while *S. denticulata* showed the opposite pattern (Table 6). At low midshore levels, the limpets, *Patelloida alticostata* (Angas, 1865) and *P. mimula*, were more frequent on sandstone and concrete seawalls, respectively. The limpets, *S. virgulata*, *Notoacmea petterdi* (Tenison-Woods, 1876), *Montfortula rugosa* (Quoy & Gaimard, 1834) and the chiton, *S. pelliserpentis*, did not show significant differences between the two habitats.

**TABLE 6.** Summary of contingency tests for comparisons of frequency of occurrence of grazing molluscs among concrete and sandstone seawalls at high and low midshore levels. Con, concrete; San, sandstone; ns, not significant; ** $p < 0.01$.

|                    | High midshore      | Low midshore       |
|--------------------|--------------------|--------------------|
| *C. tramoserica*   | Con > San (**)     | -                  |
| *N. petterdi*      | Con = San (ns)     | -                  |
| *P. alticostata*   | -                  | San > Con (**)     |
| *P. latistrigata*  | Con > San (**)     | Con = San (ns)     |
| *P. mimula*        | Con > San (**)     | Con > San (**)     |
| *P. mufria*        | -                  | -                  |
| *M. rugosa*        | -                  | Con = San (ns)     |
| *A. porcata*       | -                  | -                  |
| *L. unifasciata*   | Con > San (**)     | -                  |
| *B. nanum*         | Con > San (**)     | -                  |
| *N. atramentosa*   | -                  | -                  |
| *S. denticulata*   | San > Con (**)     | Con = San (ns)     |
| *S. virgulata*     | Con = San (ns)     | Con = San (ns)     |
| *S. pelliserpentis*| Con = San (ns)     | Con = San (ns)     |

Analyses of abundances of widespread species showed significant differences between habitats for *S. denticulata* at high midshore levels (Tables 4, 5). Many of those taxa only

showed significant differences among locations and/or sites. Some species tended, however, to be more abundant in one of the two habitats (Figures 3, 4). At high midshore levels, *B. nanum* and *P. latistrigata* were in general more abundant on concrete than on sandstone seawalls, while *S. denticulata* showed the opposite pattern. For low midshore levels, *P. alticostata*, *S. denticulata* and *S. pelliserpentis* appeared to be more abundant on sandstone seawalls.

## Discussion

This study showed that concrete and sandstone seawalls support a similar suite of species of grazing molluscs. Species commonly found on natural rocky shores were present on the two types of seawall and those considered as rare on sandstone seawalls, such as the snails *A. constricta* and *N. atramentosa* (Bulleri *et al.* 2005), were also sparse on concrete seawalls. Although there was great variability in cover and molluscan assemblages among locations within the same habitat, there were, however, consistent differences in frequencies of occurrence and relative numbers of some common and widespread species between the two habitats at higher tidal levels. This situation suggests that concrete and sandstone seawalls do not provide the same kind of habitat for grazing molluscs.

Differences in assemblages at higher levels on the shore among natural and artificial habitats have been related to differences in the characteristics of substrata whose effects on intertidal organisms are accentuated by the more restrictive environmental conditions at those levels (Bulleri *et al.* 2005). Surfaces of concrete and sandstone seawalls are likely to present differences in texture and complexity because of their different nature, the way in which they are built and different periods of exposure to weathering agents, with sandstone seawalls generally decades older than those made of concrete (Bulleri 2005b). These structural differences may be responsible for potential variations between the two types of seawall in types and availability of microhabitats, algal dynamics, cover of sessile organisms, settlement and recruitment of grazing molluscs, which, in turn, may determine different patterns for these animals between the two habitats.

Microhabitat availability is known to have a great influence in numbers and survival of grazing molluscs. For example, presence of crevices, pits and tidal pools on rocky shores may enhance recruitment and densities of some species (Underwood and Chapman 1992; Delany *et al.* 1998; Underwood 2004). Thus, the sparse presence of *A. constricta* and *N. atramentosa* on each type of seawall may be attributed to the lack of pools and similar structures (Chapman and Bulleri 2003), or microhabitats in which these species can be found on natural rocky shores (Underwood 1976).

One major difference in the structure between the two studied habitats is the regular presence of crevices among blocks in sandstone seawalls. On natural rocky shores, crevices may enhance survival of limpets and chitons by

providing protection against strong wave action, desiccation and predation (Boyle 1970; Levings and Garrity 1983; Harper and Williams 2001). Their importance increases at higher levels on the shore, where the effects of physical stress are accentuated (Moran 1985b). Furthermore, large concentrations of grazers and predators that seek shelter in crevices can have profound influences on the structure of surrounding intertidal assemblages (Menge 1978; Levings and Garrity 1983; Fairweather 1988). Thus, it is likely that the presence of crevices in sandstone seawalls may have different effects on survival and behaviour of grazers. For example, species such as *M. rugosa* and *S. pelliserpentis* were frequently seen during low tide in crevices in sandstone seawalls (pers. obs.). Therefore, because of the general lack of crevices in concrete seawalls, numbers of these species

could significantly differ between habitats if this microhabitat was sampled. Extensive presence of crevices may also alter patterns of movement of limpets and snails (Levings and Garrity 1983; Underwood and Chapman 1989) and limit the potential extent of their feeding excursions. Bulleri *et al.* (2004) showed that, on sandstone seawalls, *C. tramoserica* seemed to be unable to move across contiguous sandstone blocks being apparently restricted to the boundaries of the same block. In contrast, concrete seawalls make a more or less continuous surface that would not offer limitations for movement. Here, *C. tramoserica* was more frequent on concrete seawalls at high midshore levels although numbers were small in the two studied habitats.
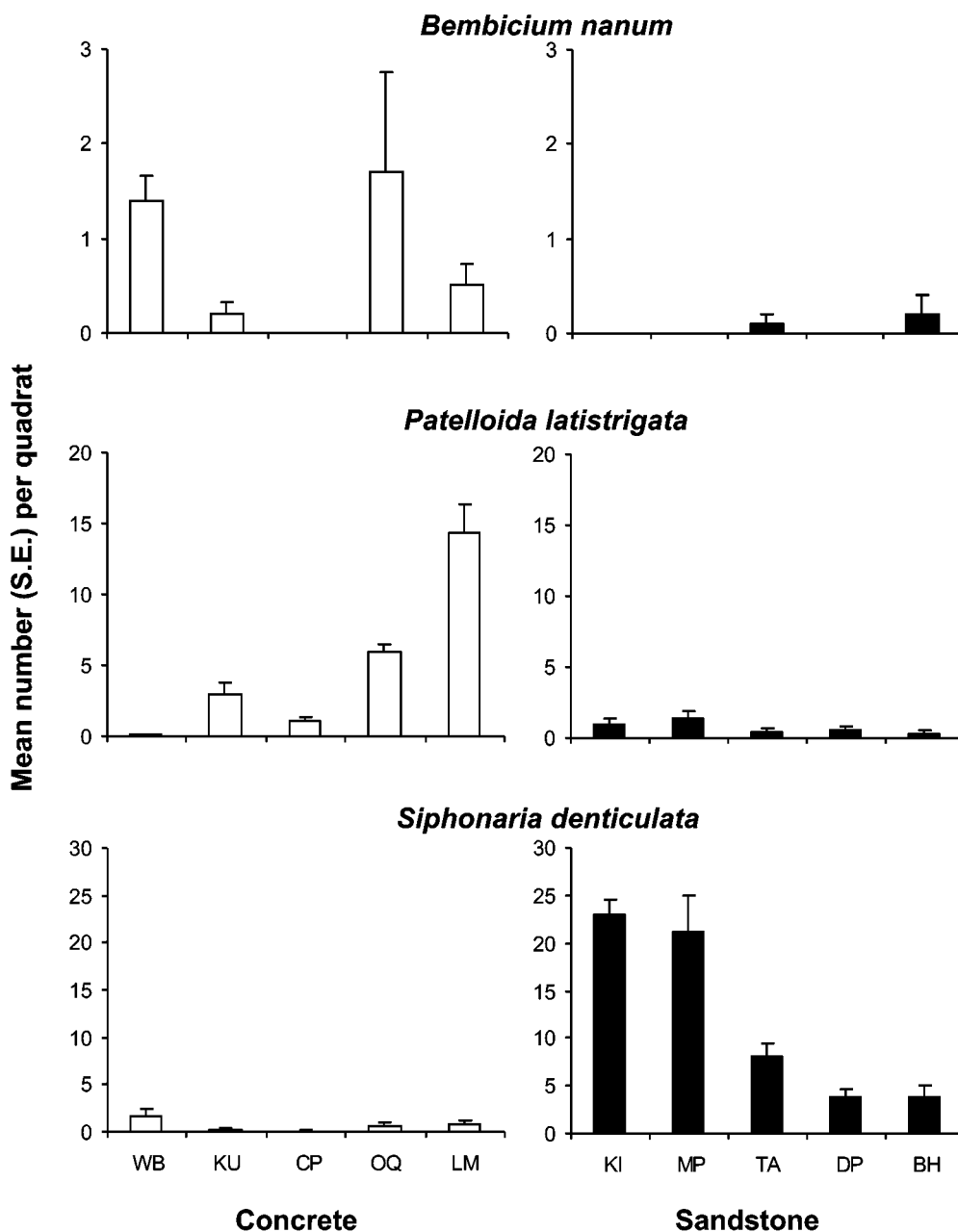


**FIGURE 3.** Mean number per quadrat (+ S.E.) of *Bembicium nanum*, *Patelloida latistrigata* and *Siphonaria denticulata* on concrete and sandstone seawalls at high midshore levels (n = 10 for each location). Code for locations as in Figure 1.
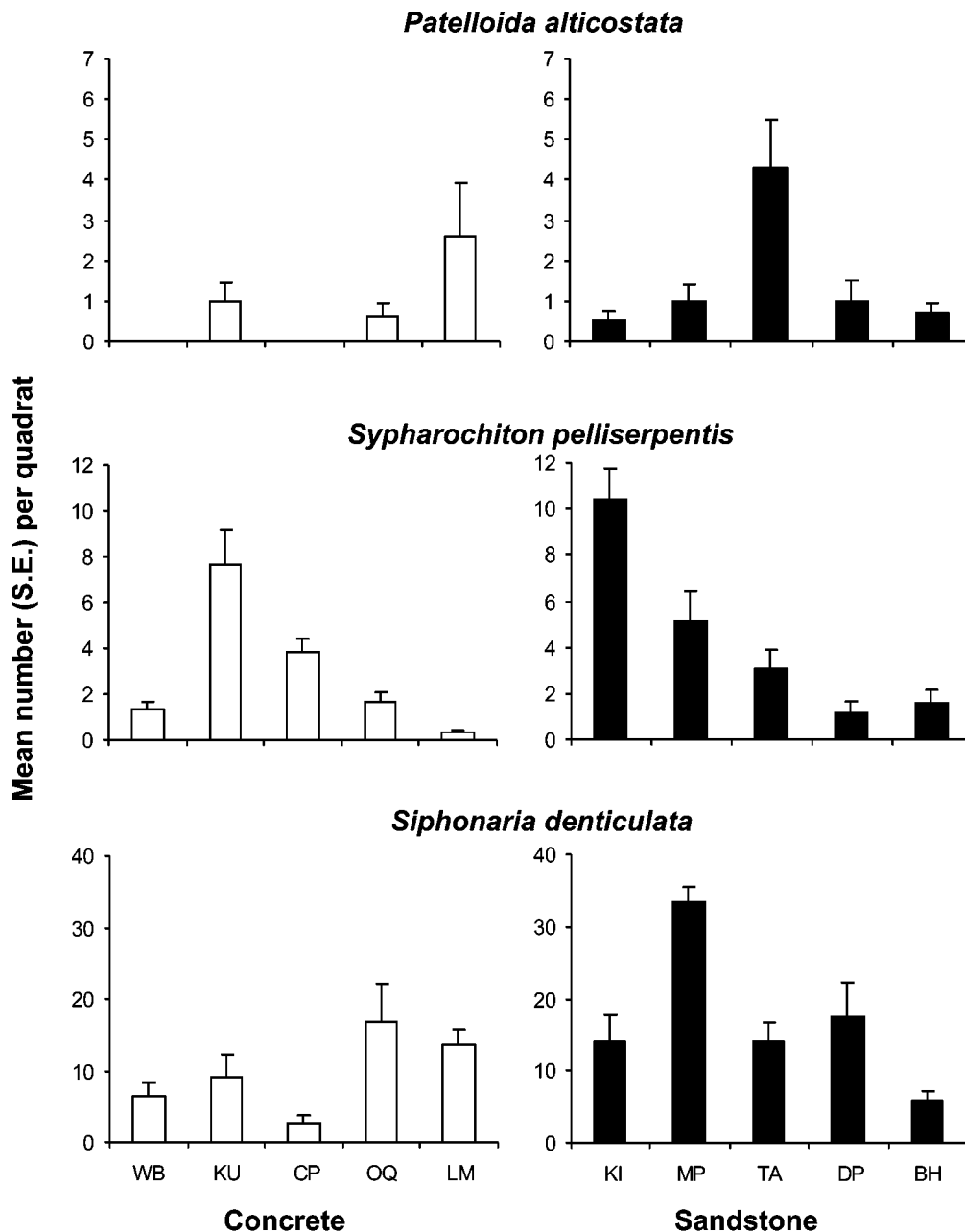
**FIGURE 4.** Mean number per quadrat (+ S.E.) of *Patelloida alticostata*, *Sypharochiton pelliserpentis* and *Siphonaria denticulata* on concrete and sandstone seawalls at low midshore levels (n = 10 for each location). Code for locations as in Figure 1.

Assemblages of sessile organisms differed only at high midshore levels, mainly due to the greater cover of oysters on concrete seawalls. Biological components of the substratum such as oysters, mussels, tubeworms and barnacles may affect differently the abundance and distribution of grazing molluscs by competing for space (Underwood *et al.* 1983) and altering complexity of surfaces (Jernakoff 1985). Recruitment and survival of juvenile grazers can be enhanced within aggregations of sessile organisms (Saier 2000; Sebastian *et al.* 2002), while dense covers can make a barrier for adults and large-sized species, which are generally unable to move, forage and/or home (Branch 1976; Creese 1982; Steffani and Branch 2003). However, analysis of correlation did not show consistent relationships among sessile and grazer taxa. Only *P. mimula* showed a significant correlation with percentage cover of oyster at high midshore levels ($p < 0.01$). This may explain

the greater frequency of this limpet on concrete seawalls, in which oysters were, in general, more abundant. In fact, on rocky shores and other natural habitats, this limpet is frequently found in association with oysters (Minchinton and Ross 1999).

Assemblages of grazers differed at high midshore levels although dissimilarities were mostly due to the greater numbers of *P. latistrigata* on concrete seawalls and those of *S. denticulata* on sandstone seawalls. These opposite patterns may be the result of differences in ecological processes between the two habitats at these tidal levels. On rocky shores in NSW, *P. latistrigata* can be found among the barnacle, *T. rosea*, which provides this limpet with shelter against desiccation, wave action and competition from the larger limpet *C. tramoserica* (Creese 1982). In addition, the predatory whelk, *Morula marginalba* Blainville, 1832, may greatly reduce numbers of both *P. latistrigata* and *T. rosea* on

rocky shores (Creese 1982; Moran 1985a). Here, *P. latistrigata* was more frequent and abundant on concrete seawalls at high midshore levels, although barnacles were sparsely found on this habitat (unpublished data). Predation by *M. marginalba* on sandstone seawalls could be more important for survival of *P. latistrigata* than, for example, availability of shelter by barnacles or outcome of competitive interactions. Thus, aggregations of *M. marginalba* in crevices similar to those observed on rocky shores (Moran 1985b) may translate in larger numbers of this whelk on sandstone seawalls and therefore *P. latistrigata* would be potentially subjected to a greater intensity of predation than on concrete seawalls.

In contrast to *P. latistrigata*, numbers of *S. denticulata* at high midshore levels were consistently lower on concrete than on sandstone seawalls. Although on sandstone seawalls *M. marginalba* may prey upon *S. denticulata* (pers. obs.), differences in numbers and occurrence of this limpet between habitats could greatly depend on variations in recruitment and food supply. Thus, concrete seawalls may lack some microhabitats required for successful recruitment or shelter and hence the small numbers. Alternatively, larger numbers on sandstone seawalls may be the result of enhanced recruitment into crevices and later migration of limpets to the surface of blocks. Furthermore, potential differences in availability of microalgal food between the two habitats may affect survival and growth of *S. denticulata* and alter the intensity of competitive interactions among grazers, with negative effects for this siphonarian on concrete seawalls (Underwood and Jernakoff 1981; Creese and Underwood 1982; Underwood 1984; Ortega 1985). Although there is some information on recruitment and succession of algae on artificial substrata (Neushul *et al.* 1976; Sousa 1979; Bailey-Brock 1989), there is, however, a lack of knowledge on microalgal dynamics on seawalls. Therefore, it is not yet known whether there are differences in microalgal dynamics among the substrata considered here and to what extent these differences could translate to different patterns of distribution and abundance of grazers between these two habitats. Nevertheless, it is difficult to explain how the processes mentioned above may affect two species of limpets of similar sizes and way of life in such a different way. Manipulative experiments will be required to test specific models that may explain the patterns found here.

In conclusion, concrete and sandstone seawalls provide a different habitat higher on the shore for grazing molluscs, even though the two habitats house a similar set of species. These results point out the necessity of a better understanding of the influence of the nature of materials used to build seawalls on the establishment, development and maintenance of intertidal assemblages (Bulleri *et al.* 2005). This information will be essential to manage the growing urban development in coastal areas in order to preserve biodiversity (Bulleri and Chapman 2004; Chapman, in press).

## References

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.

Anderson, M.J. & Underwood, A.J. (1994) Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *Journal of Experimental Marine Biology and Ecology* 184, 217–236.

Bailey-Brock, J.H. (1989) Fouling community development on an artificial reef in Hawaiian waters. *Bulletin of Marine Science* 44, 580–591.

Boyle, P.R. (1970) Aspects of the ecology of a littoral chiton, *Sypharochiton pelliserpentis* (Mollusca: Polyplacophora). *New Zealand Journal of Marine & Freshwater Research* 4, 364–384.

Branch, G.M. (1976) Interspecific competition experienced by South African *Patella* species. *Journal of Animal Ecology* 45, 507–529.

Branch, G.M. (1981) The biology of limpets: Physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology: an Annual Review* 19, 235–379.

Bulleri, F. (2005a) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. *Marine Ecology Progress Series* 287, 53–65.

Bulleri, F. (2005b) Experimental evaluation of early patterns of colonisation of space on rocky shores and seawalls. *Marine Environmental Research* 60, 355–374.

Bulleri, F. & Chapman, M.G. (2004) Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. *Marine Biology* 145, 381–391.

Bulleri, F., Chapman, M.G. & Underwood, A.J. (2004) Patterns of movement of the limpet *Cellana tramoserica* on rocky shores and retaining seawalls. *Marine Ecology Progress Series* 281, 121–129.

Bulleri, F., Chapman, M.G. & Underwood, A.J. (2005) Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. *Austral Ecology* 30, 655–667.

Carroll, C., Noss, R.F., Paquet, P.C. & Schumaker, N.H. (2004) Extinction debt of protected areas in developing landscapes. *Conservation Biology* 18, 1110–1120.

Chapman, M.G. (2003) Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. *Marine Ecology Progress Series* 264, 21–29.

Chapman, M.G. Intertidal seawalls as habitats for molluscs. *Journal of Molluscan Studies* (in press).

Chapman, M.G. & Bulleri, F. (2003) Intertidal seawalls – new features of landscape in intertidal environments. *Landscape and Urban Planning* 62, 159–172.

Clarke, K.R. (1993) Non-parametric multivariate analyses of

changes in community structure. *Australian Journal of Ecology* 18, 117–143.

Creese, R.G. (1981) Patterns of growth, longevity and recruitment of intertidal limpets in New South Wales. *Journal of Experimental Marine Biology and Ecology* 51, 145–171.

Creese, R.G. (1982) Distribution and abundance of the acmaeid limpet, *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia* 52, 85–96.

Creese, R.G. & Underwood, A.J. (1982) Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53, 337–346.

Delany, J., Myers, A.A. & McGrath, D. (1998) Recruitment, immigration and population structure of two coexisting limpet species in mid-shore tidepools, on the West Coast of Ireland. *Journal of Experimental Marine Biology and Ecology* 221, 221–230.

Fairweather, P.G. (1988) Predation creates haloes of bare space among prey on rocky shores in New South Wales. *Australian Journal of Ecology* 13, 401–409.

Glasby, T.M. & Connell, S.D. (1999) Urban structures as marine habitats. *Ambio* 28, 595–598.

Gray, D.R. & Hodgson, A.N. (2004) The importance of a crevice environment to the limpet *Helcion pectunculus* (Patellidae). *Journal of Molluscan Studies* 70, 67–72.

Harper, K.D. & Williams, G.A. (2001) Variation in abundance and distribution of the chiton *Acanthopleura japonica* and associated molluscs on a seasonal, tropical, rocky shore. *Journal of Zoology* 253, 293–300.

Hawkins, S.J. & Hartnoll, R.G. (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: an Annual Review* 21, 195–282.

Jernakoff, P. (1985) An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazings on the algal diversity and cover in an intertidal barnacle zone. *Journal of Experimental Marine Biology and Ecology* 88, 287–302.

Levings, S.C. & Garrity, S.D. (1983) Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* 67, 261–278.

McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.

McGuinness, K.A. (1989) Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama. *Marine Ecology Progress Series* 52, 21–28.

Menge, B.A. (1978) Predation intensity in a rocky intertidal community. *Oecologia* 34, 1–16.

Minchinton, T.E. & Ross, P.M. (1999) Oysters as habitat for limpets in a temperate forest. *Australian Journal of Ecology* 24, 157–170.

Moran, M.J. (1985a) Effects of prey density, prey size and predator size on rates of feeding by an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several species of prey. *Journal of Experimental Marine Biology and Ecology* 90, 97–105.

Moran, M.J. (1985b) The timing and significance of sheltering and foraging behaviour of the predatory intertidal gastropod *Morula marginalba* Blainville (Muricidae). *Journal of Experimental Marine Biology and Ecology* 93, 103–114.

Moreira, J., Chapman, M.G. & Underwood, A.J. Can seawalls sustain viable populations of limpets? *Marine Ecology Progress Series* (in press).

Neushul, M., Foster, M.S., Coon, D.A., Woessner, J.W. & Harger, B.W.W. (1976) An *in situ* study of recruitment, growth and survival of subtidal marine algae: techniques and preliminary results. *Journal of Phycology* 12, 397–408.

Ortega, S. (1985) Competitive interactions among tropical intertidal limpets. *Journal of Experimental Marine Biology and Ecology* 90, 11–25.

Petraitis, P.S. (1987) Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. *Journal of Experimental Marine Biology and Ecology* 109, 117–136.

Raimondi, P.T. (1988) Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *Journal of Experimental Marine Biology and Ecology* 123, 253–268.

Saier, B. (2000) Age-dependent zonation of the periwinkle *Littorina littorea* (L.) in the Wadden Sea. *Helgoland Marine Research* 54, 224–229.

Sebastian, C.R., Steffani, C.N. & Branch, G.M. (2002) Homing and movement patterns of a South African limpet *Scutellastra argenvillei* in an area invaded by an alien mussel *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 243, 111–122.

Sousa, W.P. (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49, 227–254.

Steffani, C.N. & Branch, G.M. (2003) Spatial comparisons of populations of an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis* along a gradient of wave energy. *South African Journal of Marine Science* 25, 195–212.

Underwood, A.J. (1976) Analysis of patterns of dispersion of intertidal prosobranch gastropods in relation to macroalgae and rock-pools. *Oecologia* 25, 145–154.

Underwood, A.J. (1978) An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33, 185–202.

Underwood, A.J. (1980) The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia* 46, 201–213.

Underwood, A.J. (1984) Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* 64, 211–222.

Underwood, A.J. (1997) *Experiments in ecology. Their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, U.K.

Underwood, A.J. (2004) Landing on one's foot: small-scale topographic features of habitat and the dispersion of juvenile gastropods. *Marine Ecology Progress Series* 268, 173–182.

Underwood, A.J. & Chapman, M.G. (1989) Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology* 134, 175–196.

Underwood, A.J. & Chapman, M.G. (1992) Experiments on topographic influences on density and dispersion of *Littorina unifasciata* in New South Wales. *In*: Grahame, J., Mill, P.J. & Reid, D.G. (Eds.), *Proceedings of the Third International Symposium on Littorinid Biology*. The Malacological Society of London, London, pp. 181–195.

Underwood, A.J. & Jernakoff, P. (1981) Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal community. *Oecologia* 48, 221–233.

Underwood, A.J., Denley, E.J. & Moran, M.J. (1983) Experimental analysis of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56, 202–219.

Williams, G.A. & Morritt, D. (1995) Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Marine Ecology Progress Series* 124, 89–103.