Journal of the Marine Biological Association of the United Kingdom, 2010, 90(1), 169–192. © Marine Biological Association of the United Kingdom, 2010
doi:10.1017/S0025315409991123

Effects of topography on the environment

A.C. JACKSON[1]

Centre for Research on Ecological Impacts of Coastal Cities, Marine Laboratories A11, School of Biological Sciences, The University of Sydney, NSW 2006, Australia, [1]Present address: Environmental Research Institute, North Highland College, UHI Millennium Institute, Castle Street, Thurso, Caithness, KW14 7JD, UK

Greater understanding of patterns of distributions of organisms and their causal mechanisms are required if the consequences of climatic change are to be fully realized. Associations between topographic features of the environment and distributions of organisms are frequently assumed to be a consequence of provision or modification of local conditions by those features. Such assumptions are rarely supported empirically and there is increasing evidence that topographic features do not always influence variables in the way we might anticipate. Thus, data about how features of habitat influence environmental conditions, including availability of food, are likely to be useful for understanding how and why organisms are found where they are. Such data are few and rigorous descriptions about what defines particular features of habitat are seldom provided or are simplistic. For hard substrata in aquatic environments, crevices are often prominent features with which many species associate. Crevices have frequently been assumed, but not demonstrated, to ameliorate conditions by increasing humidity, moderating (usually reducing) temperatures and by decreasing forces from wave-impacts and water-flow. This study provided clear definitions and tests of various hypotheses about how crevices altered the local environment. The main predictions were that crevices would be cooler, more humid, more sheltered from water-movement and support more micro-algae than areas away from crevices. Manipulative experiments using artificial habitats and measurements on natural rocky shores were carried out on multiple shores over two years to understand how crevices affected local conditions. Crevices were indeed cooler, more humid, supported more micro-algae and more sheltered from water-flow than open areas nearby, but conditions did not always vary in ways that were expected. Effects were often complex, with factors such as season, height on the shore and tidal conditions interacting to influence how crevices affect environmental conditions. Without this detailed information, assumptions about the reasons animals associate with features of habitat cannot be tested.

Keywords: crevice, intertidal, rocky shore, environmental variables, distribution, shelter, climate change

Submitted 26 May 2009; accepted 6 August 2009; first published online 19 January 2010

INTRODUCTION

Distributions of organisms are often patchy and their abundances can vary in unpredictable ways (Paine & Levin, 1981). The physical conditions to which organisms are exposed also vary in predictable (e.g. seasons, daylight and tides) and unpredictable (e.g. daily or hourly variations in temperature, wind and humidity) ways at a variety of scales. Small-scale differences in abundance and diversity are caused by behavioural responses to small-scale physical conditions (e.g. topography and habitat; Raffaelli & Hughes, 1978; Underwood & Chapman, 1989) and/or biotic interactions with other individuals or species (competition and predation; Branch, 1984; Underwood & Chapman, 1996).

Intertidal rocky shores can be stressful places (McMahon, 1990). During low tide, emersion can cause desiccating conditions and temperatures are very much more variable, reaching greater extremes. Repeated hard frosts during sequences of low tides can kill many intertidal organisms (Crisp, 1964) and high temperatures can increase desiccation, heat-stress and mortality (Hofmann & Somero, 1995; Williams & Morritt, 1995). Impacts from breaking waves and water-flow from tides, winds and waves cause lift or shear-stresses that can dislodge organisms from the substratum (Gaylord *et al.*, 1994; Gaylord, 2000; Denny & Gaylord, 2002). Breaking waves can also generate forces that break or cause physical damage to organisms (Denny *et al.*, 1985).

Rocky shores are frequently complex topographically at different spatial scales (Kohn & Leviten, 1976; Underwood & Chapman, 1989; Beck, 1998) and environmental variables (e.g. temperature, light, humidity, rates of water-flow and forces from impacts by waves) vary in response to topographic structures (Helmuth & Hofmann, 2001; Denny *et al.*, 2003; O'Donnell, 2008). Small animals including mobile gastropods, sessile barnacles and bivalve molluscs are often numerous (Stephenson & Stephenson, 1972) and can respond physiologically (e.g. Garrity, 1984) or behaviourally (e.g. Fairweather, 1988) to small-scale variation in conditions. As a consequence they often demonstrate large variation in distributions and densities through time and space (Paine, 1980; Underwood, 2000; Underwood & Chapman, 2000) and have frequently been observed to associate with particular features of their habitat. These features are typically assumed to provide or to modify some resource appropriate for that activity (e.g. food, mates, shelter from inclement environmental conditions or refuge from predation, Raffaelli & Hughes, 1978; Werner *et al.*, 1983; Duffy & Hay, 1991). These assumptions are frequently argued as reasons for the

Corresponding author:
A.C. Jackson
Email: angus.jackson@thurso.uhi.ac.uk

prevalent use of such microhabitats by intertidal organisms (Raffaelli & Hughes, 1978; Moran, 1985; Fairweather, 1988).

Some effects of topography are undeniable, e.g. amounts of light are smaller in shaded areas (Takada, 1999). Recent, innovative studies have considered the effects of topography on wave forces (O'Donnell, 2008; O'Donnell & Denny, 2008) and temperature (Helmuth & Hofmann, 2001; Harley, 2008). Effects on other variables by other features are less certain and there is increasing indication that topographic features do not always influence variables in the way we might anticipate or intuitively believe (e.g. Underwood & Chapman, 1989). Studies on airflow (Cleugh, 2002), wave-impacts; (Denny *et al.*, 2003; Helmuth & Denny, 2003) and temperatures (Fitzhenry *et al.*, 2004) show that environmental variability is not always easily predicted on the basis of local topography.

If variables are not varying as expected in relation to topographic features, then animals associating with those features may be responding to conditions or variables other than those described. Assumptions regarding the amelioration of environmental variables by topographic features may be unreliable. If such assumptions and predictions from these assumptions are to be valid or useful, it is important that changes of variables in response to topography are directly quantified.

For hard substrata in aquatic environments, crevices are often prominent features with which various species associate (Emson & Faller-Fritsch, 1976; Raffaelli & Hughes, 1978; Fairweather, 1988; Gray & Hodgson, 2004; Bergey, 2005). Crevices have frequently been assumed to ameliorate conditions by increasing humidity, moderating (usually reducing) temperatures and by decreasing forces from wave-impacts and water-flow. A few studies have measured conditions in crevices. For example, Marchetti & Geller (1987) measured desiccation and temperature in the turban snail *Tegula funebralis* (Adams) and showed that crevices had no effect on temperature but a significant reduction in water-loss in relation to open areas. Desiccation stress in chitons is less inside than outside crevices (Harper & Williams, 2001) and a species of air-breathing fish uses supralittoral crevices as nests where relative humidity is greater inside than outside (Shimizu *et al.*, 2006). Crevices can also provide a refuge where the risk of abrasion is reduced (e.g. Bergey, 2005) and reduce risks of mortality by providing a refuge that predators cannot access (Hughes & Elner, 1979; Catesby & McKillup, 1998). They can also provide resources other than a suitable environment. Growth of micro-algae is often limited by excessive temperatures and light (Underwood, 1984; Ruban & Horton, 1995) and in sedimentary systems, bright conditions favour assemblages dominated by diatoms (Whitcraft & Levin, 2007). Conditions in crevices may therefore favour the growth of microalgae which are food for many intertidal grazers but with fewer diatoms than in nearby assemblages outside of crevices.

Conditions that generate biological patterns may be complex (e.g. Harley, 2008; Miller *et al.*, 2009), yet, studies have tended to measure or assume how topographic features influence single environmental variables. In reality, multiple factors will vary and covary. Rigorous descriptions about what defines particular features of habitat are also seldom provided or are simplistic (Harper & Williams, 2001; Bergey, 2005). The present study provides clear definitions and tests of various hypotheses about how crevices alter multiple environmental variables (Table 1).

Conditions were measured in a variety of natural or artificial crevices. Standardized artificial crevices were used to establish how particular attributes of crevices influenced environmental variables. Conditions were also measured in natural crevices to establish whether similar patterns occurred in the field. Without this information, assumptions about the reasons animals associate with crevices or other features of habitat, cannot be tested. The results, discussed in relation to other studies, will improve our understanding of how crevices affect the environment at scales relevant to intertidal animals. Our ability to predict how and why animals disperse through their environment will be improved and more detailed models and hypotheses can now be proposed.

Table 1. Predictions and their explanatory models for environmental variables measured in crevices and open areas. See Materials and Methods for definitions of terms.

Variable	Model	Prediction
Temperature: (maxima, ranges, differences)	(1) Greater shading reduces temperatures in crevices	Crevices < open areas
	(2) Less exposure to air and/or greater likelihood of wave-splash will reduce temperatures more on the lower than on the upper shore	Lower < upper
	(3) Less exposure to air and/or greater likelihood of wave splash will reduce temperatures more on wave-exposed than on wave-sheltered shores	Exposed < sheltered
Humidity	Greater topographic complexity of crevices than of open areas reduces air-flow and increases retention of moisture, increasing humidity	Crevices > open areas
Water flow	(1) Greater topographic complexity of crevices than of open areas reduces water-flow	Crevices < open areas
	(2) Orientation of crevices affects channelling of water	Parallel ≠ perpendicular
	(3) Increasing exposure to waves will increase rates of water flow	Exposed > sheltered
Wave force	(1) Greater topographic complexity of crevices than of open areas reduces shear forces caused by breaking waves	Crevices < open areas
	(2) Orientation of crevices affects breaking waves	Parallel ≠ perpendicular
Micro-algae	(1) Smaller temperatures and less intense radiation in crevices than in open areas encourage growth of micro-algae	Crevices > open areas
	(2) More intense light in open areas than in crevices favours assemblages of micro-algae dominated by diatoms	Crevices < open areas

MATERIALS AND METHODS

Locations and habitats

Conditions in crevices were measured or manipulated at several rocky sandstone shores on the open coast around Sydney, New South Wales, Australia (Figure 1). On these shores, boulders, natural faults and the abrasive action of waves form numerous crevices of varying sizes, orientations and aspects. Crevices could not be defined by the presence of animals because (a) animals may respond to features that provide some resource (e.g. shelter), not all of which are crevices and (b) many crevices may not be occupied by animals at any time of sampling. Criteria for identifying crevices were first defined, therefore, at an intertidal location where species of gastropod were abundant, for which availability of shelter is important (e.g. *Nerita atramentosa* Reeve and *Morula marginalba* Blainville). Both these species frequently associate with topographic features such as crevices and rockpools (Underwood, 1975; Moran, 1985). One hundred topographic features that varied widely in size and shape yet appeared to be suitable candidates for being crevices were characterized in terms of length, width and depth. Consistent ranges of the absolute and relative magnitudes of these dimensions were used as criteria to define a crevice. Criteria were then tested (by seeing if other 'would-be' crevices also conformed) and refined at a second location. Transects across the shore were surveyed independently for crevices by two people and the results compared. The counts and dimensions of crevices were nearly identical indicating that the method was repeatable and identification of crevices could be standardized.

To be defined as a crevice, cracks in the rock had to have:

- A length:width ratio greater than 3:1, e.g. a crack with a width of 2 cm must have a length of at least 6 cm to be a crevice; length is the longest dimension of the crevice, width is the dimension perpendicular to length and across the opening of the crack.
- A width $\geq$1 cm and a depth $\geq$1 cm along its entire length (a size relevant for most intertidal snails); depth is the dimension perpendicular to length and going into the crack.
- A width:depth ratio less than 3:1, e.g. a crack with a depth of 30 cm cannot be wider than 90 cm to be a crevice.
- During low tide, no standing water $>$1 cm deep over more than half the length (otherwise the crack is a different feature of the shore, i.e. a rockpool).

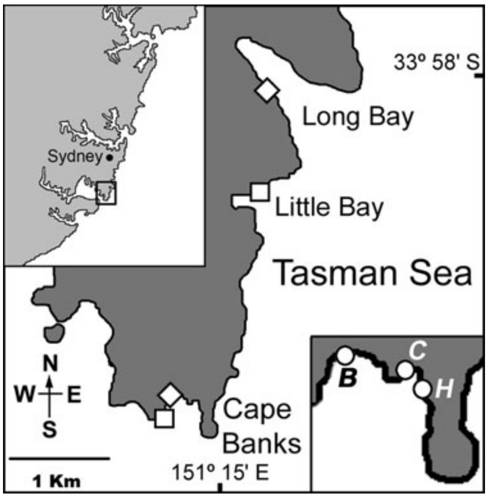

Fig. 1. Locations used for measurement of environmental variables in crevices or open areas on experimental slabs (circles; *H*, *Hormosira* flats; *C*, *Chamaesipho* flats; B, Beach) and on wave-exposed (squares) or wave-sheltered (diamonds) natural rocky shores.

Where a crevice was relatively large or very variable in size, several measures of length, width and depth were taken and the averages used.

Environmental variables

To account for all relevant variation, variables need to be measured over sufficient time and space (Denny *et al.*, 2004). Environmental variables (see below) were thus measured during low tide in crevices or open areas in: (1) artificial experimental units; and (2) natural rocky shores on multiple occasions on multiple shores during warm or cool months over one (or for some variables over two) years. Sampling effort was concentrated during the warmer months, when effects of crevices were expected to be greatest.

Artificial habitats

Artificial habitats were created by attaching six sandstone slabs (400 × 400 × 40 mm) to the rock platform using stainless steel fittings (Dynasets—Ramset, Australia) at each of three locations which appeared to differ in their exposure to waves (Figure 1). All slabs were within a few centimetres height on the shore to minimize differences in emersion. A 350 mm length of PVC pipe (50 mm diameter) cut in half lengthways was attached to each slab. The pipe was fitted so that one long edge was flush with the surface of the slab and the other was raised from the surface by 20 mm, thus forming a hemi-tubular recess (Figure 2). This shelter had a length:width ratio $>$3:1, a depth and width each $>$1 cm and a width:depth ratio $<$3:1, i.e. it was a crevice. Of the six slabs, three were oriented with the crevice parallel to the shoreline, opening away from the direction of the incoming waves; three were oriented with the crevice perpendicular to the shore (Figure 2). Crevices perpendicular to the shoreline opened to the north (Hormosira flats) or the west (Chamaesipho flats and Beach) and those parallel to the shoreline opened to the east (Hormosira flats) or the north (Chamaesipho flats and Beach). In the southern hemisphere, north-facing aspects receive the most sunlight. The surface of the slabs away from the crevice also provided open areas in which conditions could be measured. Thus, at each of the two locations, environmental variables (temperature, relative humidity, water-flow, wave-force and micro-algal food) were measured in artificial crevices or open areas that were of the same size, shape and position on the shore and were in either of two orientations.

Natural habitats

Environmental variables (temperature, relative humidity and water-flow) in three natural crevices and in three open areas (defined as being $>$50 cm from a crevice and not in some

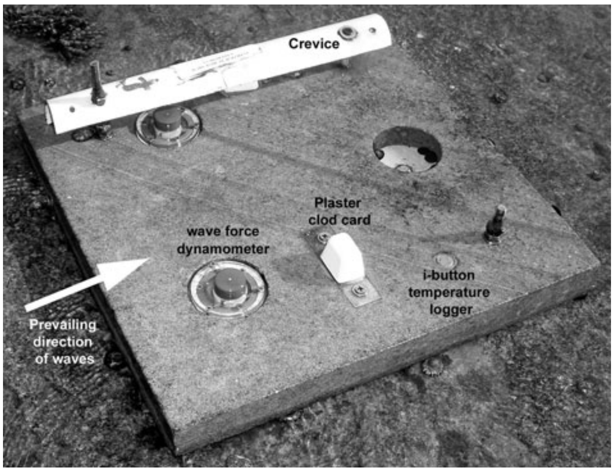

Fig. 2. An experimental slab showing a crevice perpendicular to the shoreline, dynamometers for measuring lateral shear forces, i-buttons for recording rock temperature and clod cards for measuring relative rates of water flow.

other feature of the shore e.g. rockpool or boulder), were measured at each of two heights on the shore (see below) at each of four locations on the Sydney coast that appeared to differ in their exposure to waves (two sheltered, two exposed; Figure 1). Exposed shores faced the prevailing swell (south-east) whereas sheltered shores faced north-east or were protected by an offshore rocky reef. The vertical range of the shore inhabited by *N. atramentosa* (an abundant grazing gastropod) was divided into five equal bands. Conditions representing the upper or the lower shore were measured in crevices in the second and fourth bands (counting from the top of the shore). Mean elevations above the zero tide level of these bands were measured in relation to benchmarks of known elevation, using a surveyor's level. Thus, the two habitats differed in their size, shape, orientation and position on the shore. To ensure representative sampling, three crevices and open areas were used to measure environmental variables and were haphazardly selected from those available in each of these bands. Different crevices and open areas were used every second sampling occasion.

Temperature

Temperatures at the rock surface were measured in crevices or open areas using small data-loggers (I-buttons; Maxim, California). Small recesses were drilled into the rock (22 mm diameter, 15 mm deep) and i-buttons were affixed with silicone sealant. I-buttons recorded temperature every 10 minutes and were deployed for 2 weeks at a time. Three metrics were calculated, using similar reasoning and methods to Fitzhenry *et al.* (2004). For each full day that I-buttons were deployed, the 'daily maximum' was calculated for each i-button as an 'acute' measure of thermal stress. These daily maxima constituted the 98th percentile of temperatures for that day and corresponded with the highest temperature that occurred for at least 30 minutes during that day. Thermal stress is dependent on the recent thermal history of an organism (Buckley *et al.*, 2001; Halpin *et al.*, 2002) and may be greater when organisms experience temperatures much hotter than those to which they are acclimated. Days with large ranges of temperature could also induce greater thermal stress than days with small temperature ranges. Thus, daily temperature ranges (the difference between the 98th and 2nd percentiles) were calculated and used as replicates to compare the various treatments. The relative value of different habitats may change as the amount of stress changes (Menge & Branch, 2001), so the maximum concurrent difference between crevices and open areas was also calculated as a measure of the relative value of being in different habitats (NB: this differs from the maximum difference of Fitzhenry *et al.*, 2004). Measures of more 'chronic' stress (e.g. average daily maximum—Fitzhenry *et al.*, 2004) are not possible without continuous records of temperature which were not logistically possible in this study.

Temperatures were measured in crevices or open areas on:

(a) experimental slabs on three randomly-chosen occasions during each of the winter of 2006 (May–August; mean maximum air temperature 17–20°C) and the following summer (November 2006–March 2007; mean maximum air temperature 24–26°C). On each occasion, temperatures were compared among locations, orientation of slabs, habitats and replicate slabs. Each sampling occasion contained data from spring and from neap tides so, using sampling occasions as replicates, mean or maximal concurrent differences in temperature between artificial crevices and open areas were compared among sampling periods, locations, day or night, and spring or neap tides. Day- and night-times were treated separately. Daytime was defined as from sunrise +1 hour to sunset−1 hour and night-time as from sunset +1 hour to sunrise−1 hour. Mean or maximal concurrent differences in temperature between habitats for spring tides were collected from the day of full or new moon plus two days either side and likewise, for neap tides, from the 5 days around quarter-moon;

(b) natural rocky shores on five occasions during summertime (November–March in 2006–2007 or 2007–2008) and on two occasions during winter conditions (May–August 2007). On each occasion, temperatures in crevices or open areas were compared among locations with different exposures to waves, heights on the shore, habitats and three replicate sites. Mean or maximal concurrent differences in temperature between crevices and open areas were compared among exposures, locations, upper or lower shore and spring or neap tides. Sampling periods (i.e. summer or winter) were analysed separately because they differed in the number of sampling occasions (replicates).

Relative humidity

Relative humidities were measured using electronic probes (humidity stick; Testo, Lenzkirch). The sensors were placed either within the crevice or in open areas nearby. For the artificial habitats, the mean values of two probes in each crevice/open area were used as replicates. Relative humidity was measured on four occasions between November 2006 and February 2007 on experimental slabs and on three occasions between January and March 2007 on natural rocky shores.

Water-flow and wave-forces

Water-flow and forces applied by moving water (e.g. from breaking waves) are inextricably entwined. For instance, rates of water flow may (or may not) be greater in wave-exposed than in wave-sheltered areas and large waves are not required to create strong currents. They are, however, quite different variables, one measuring overall water movement, the other measuring forces (e.g. shear and lift) applied by water movement. Water-flow affects gas transport, supply of food and nutrients and suspension/deposition/erosion of sediment whereas forces exerted by breaking waves have greater influence on opportunities to forage and risk of damage or dislodgement (Denny, 1993; Raffaelli & Hawkins, 1996). It is, therefore, useful to have information about each.

Integrated measures of water flow were obtained from the loss in mass by dissolution from blocks of plaster (Thompson & Glenn, 1994). For sandstone slabs, plaster blocks were stuck to strips of Perspex and attached with screws in crevices or open areas. Due to limited space, one plaster block was used per habitat on each slab. Rates of water flow were measured on ten occasions, five each in the winter of 2006 or the summer of 2006–2007. For natural habitats, rates of water flow were measured on four occasions in the summer of 2006–2007 and three times in the winter of 2007. Plaster blocks were attached with silicone sealant to small squares of thin Perspex which were then glued to the shore with epoxy resin. Blocks were not attached directly to the shore because of problems with adhesion. Two plaster blocks were used to provide a mean measure for each crevice/open area.

Lateral shear forces exerted by breaking waves and water current at the surface of the substratum were measured inside artificial crevices or in open areas of sandstone slabs using small dynamometers (Denny, 1983). Briefly, when a dynamometer is hit by a wave, an elliptical scratch is made on a smoked-glass slide; 'The direction of the scratch being parallel to the applied force and the maximum excursion of the scratch from the centre-point being proportional to the magnitude of the force' (Denny, 1983). Dynamometers were calibrated using weights which correspond to known forces (F; <0.5N, <0.75N, <1.0N, and <1.5N). Calibration formed concentric rings on the smoked-glass, which were marked into four quadrants. Forces were quantified by measuring the percentage cover of scratches in each calibration ring in each quadrant. $\sum \log_e(\% \times F)$ was calculated for each quadrant and summed for the four quadrants to give an integrated measure of force applied to the dynamometer in all horizontal directions. Shear forces were measured on seven occasions during winter (May to August, 2006–2007) and on six occasions during summer (October to March, 2006–2007).

Availability and types of micro-algae

Amounts of chlorophyll-*a* (chl-*a*) on experimental slabs were estimated using an index of abundance derived from field-based colour infrared (CIR) images. Full details of the method are described in Murphy *et al.* (2006), but briefly consist of capturing images at near infra-red (NIR; 758–833 nm), and red (645–689 nm) wavelengths. Algal cells scatter NIR light but chl-*a* absorbs red light. A ratio of NIR and red wavelengths therefore quantifies the amount of absorption by chl-*a* and is an accurate index of the amounts of chl-*a* present on the rock surface (Murphy *et al.*, 2006). Calibration of images to account for differences in illumination and to standardize to per cent reflectance allowed amounts of chl-*a* to be compared among habitats, slabs or locations. CIR images were collected on two occasions. During summer 2006–2007, six regions of interest (ROI) were randomly sampled from under crevices and six from unshaded areas away from the crevices from the surface of each of four experimental slabs (two parallel to and two perpendicular to the shoreline) at each of three locations (a total of 144 ROI). During winter 2007, six ROI were sampled from crevices or away from crevices from each of eight experimental slabs at each of two locations (a total of 192 ROI).

Types and relative amounts of different pigments in assemblages of micro-algae were estimated using field spectrometry (Murphy *et al.*, 2005b). Spectra were measured on two occasions: winter 2006 (three spectra from under crevices or away from crevices on each of four slabs parallel to or perpendicular to the shoreline at two locations, i.e. 96 spectra); and summer 2006–2007 (four spectra from under crevices or away from crevices on each of four slabs parallel to or perpendicular to the shoreline at three locations, i.e. 192 spectra). Many absorptions by pigments are weak or are overlapping and gross variations in the brightness of the substratum make it difficult to compare spectra acquired from different targets. To compensate for these effects and to enhance subtle absorptions by pigments, all spectra were placed on the same plane of reference using spectral derivate analysis. Fourth-derivative spectra were calculated from pseudo absorbance (Log 1/Reflectance) spectra using combined differentiation and smoothing (Savitzky & Golay, 1964), with a 30 nm smoothing window. Each absorption feature in the spectrum is shown as a peak above the zero baseline of the derivative, the height of which is indicative of the relative amount of absorption made by the pigment causing that absorption. Relative amounts of absorption by pigments are thus calculated as the maximal derivative reflectance of each peak. The identities of the pigments causing each absorption were inferred by comparing the wavelength position of maximal absorbance to published wavelengths of absorption by pigments *in vivo*. Pigment values were all multiplied by 10,000 to facilitate analysis. Absorptions by 5 different pigments were selected to separate different groups of micro-algae, specifically; carotenoids (493 nm), phycoerythrocyanin (574 nm), chlorophyll-*c* (chl-*c* 636 nm), chlorophyll-*b* (chl-*b* ~ 651 nm) and chl-*a* (684 nm). Sensible comparisons among amounts of pigments need to account for differences in total amounts of algae among samples. This was done by normalizing the amounts of pigments in each sample, relative to the amount of chl-*a* (which is a reliable estimator of the amount of algae; Murphy *et al.*, 2005a) in that sample. Relative amounts of pigments from samples were first analysed as multivariate data (nMDS plots and dissimilarities of samples within or between treatments). The percentage contributions of different pigments to differences among samples were examined (SIMPER; Clarke & Warwick, 2001). Pigments that made consistently large contributions to dissimilarities were then analysed individually as univariate data.

RESULTS

The main trends and patterns in the variables measured are summarized in Tables 2 & 3.

Elevations of upper or lower shore

The actual elevations of the areas of upper or lower shores above zero tide-level differed from location to location and

Table 2. Summaries of main trends in differences in temperature and humidity between crevices (Cr) and open (Op) areas during different seasons in (a) artificial experimental habitats oriented parallel (Par) or perpendicular (Perp) to the shoreline and (b) during spring (Sp) or neap (Np) tides on upper (U) or lower (L) levels on natural rocky shores. This is a summary of many analyses, so significance of patterns is not implied. In general, results are, however, significant, either in terms of the magnitude of differences or as frequency of occurrence. Refer to Figures 3–8 and Appendices 1.1, 1.2, 2.1, 2.2, 3.1 & 3.2 for details of analyses. X, comparison not relevant.

	Maximal temperature		**Temperature range**		**Mean temperature difference (open–crevice)**		**Maximal temperature difference (open–crevice)**		**Humidity**
(a) Artificial habitats									
Season	Winter < summer		Winter < summer		Winter < summer		Winter < summer		summer
Habitat	Cr < Op	Cr < Op	Cr < Op	Cr < Op	X	X	X	X	Cr < Op
Orientation	Par = Perp	Par = Perp	Par = Perp	Par = Perp	Par = Perp	Par = Perp	Par = Perp	Par = Perp	Par = Perp
Type of tide	X	X	X	X	Sp < Np	Sp > Np	Sp = Np	Sp > Np	X
(b) Natural habitats									
Season	Winter < summer		Winter < summer		Winter < summer		Winter < summer		summer
Habitat	Cr < Op	Cr < Op	Cr < Op	Cr < Op	X	X	X	X	Cr < Op
Type of tide	X	X	X	X	Sp = Np	Sp > Np	Sp = Np	Sp > Np	X
Height (exposed)	U > L	Variable	U = L	Variable	U > L	U > L	U > L	U > L	U < L
Height (sheltered)	U = L	Variable	U > L	Variable	U > L	U > L	U > L	U > L	U < L

the difference between upper or lower shores ranged between 0 and 156 cm (Table 4).

Temperature

ARTIFICIAL CREVICES

Open areas were hotter and had greater ranges of temperature than crevices on every sampling occasion (Figure 3; analyses in Appendix 1.1). Maximal lowtide temperatures did not differ between slabs of different orientation and slabs with perpendicular crevices differed between locations on only one occasion. Mean and maximal concurrent differences in daytime, lowtide temperatures between crevices and open areas were significantly greater in summer than in winter (although seasons were not replicated) and the effect of spring or neap tide was larger during warm than during cool months although this was not significant (Figure 4; Appendix 1.2). Crevices were also always slightly warmer at night (Figure 4).

Table 3. Summaries of main trends in differences in water flow and wave forces between crevices (Cr) and open (Op) areas during different seasons in (a) artificial experimental habitats oriented parallel (Par) or perpendicular (Perp) to the shoreline and (b) on upper (U) or lower (L) levels on natural rocky shores. Patterns were defined by either significant differences in analyses (ANOVA) or by significantly greater tendencies than expected, for differences to be in a particular direction (binomial test). Refer to Figures 9 & 10 and Appendices 4.1 & 4.2 for details of analyses.

	Water-flow (δ g)		**Index of wave-force**	
(a) Artificial habitats				
Season	Cool = Warm		Cool = Warm	
Habitat	Cr < Op	Cr < Op	Cr < Op	Cr < Op
Crevice orientation	Par > Perp	Par > Perp	Par > Perp	Par > Perp
Waves	Exp < Shelt	Exp < Shelt	Exp > Shelt	Exp > Shelt
(b) Natural habitats				
Habitat (upper shore)	Cr < Op	Cr < Op	X	X
Habitat (lower shore)	Cr < Op	Cr < Op	X	X

NATURAL CREVICES

In summer, maximal temperatures in crevices were always cooler and temperature ranges smaller and almost always significantly cooler or smaller than open areas (Figure 5). The size of this effect varied and was often dependent on height on the shore; maximal temperatures or temperature ranges on the lower shore were cooler or smaller than on the upper shore (e.g. January 2007, height × habitat interaction $F_{1,576} = 15.4$, $P < 0.001$; Appendix 2.1). During winter, maximal temperatures and temperature ranges were generally less, but not always significantly less in crevices than those in open areas. Maximal temperatures and temperature ranges in habitats or at heights on the shore often interacted with locations but there were no consistent patterns associated with particular shores. When pooled across habitats and locations, differences in temperature between the upper and the lower shore were greater for wave-exposed than for wave-sheltered conditions (e.g. May 2007 exposure × height interaction $F_{1,38} = 5.6$, $P < 0.05$; Appendix 2.1).

Maximal concurrent differences in temperature between habitats were always greater during spring than during neap tides in summer (Figure 6b) but not in winter (Figure 6d; tide $F_{1,70} = 13.7$, $P < 0.001$ and $F_{1,22} = 0.3$, $P = 0.59$ for summer and winter, respectively; Appendix 2.2) and when averaged

Table 4. Mean elevations (m; N = 4 measurements) of upper or lower natural rocky shores at four locations on the Sydney coast (see Figure 1).

Exposure to waves	**Location**	**Position**	**Mean elevation**
Exposed	Cape Banks	Upper	2.11
		Lower	1.76
Exposed	Little Bay	Upper	2.6
		Lower	1.04
Sheltered	Cape Banks	Upper	1.14
		Lower	1.14
Sheltered	Long Bay	Upper	1.34
		Lower	1.30

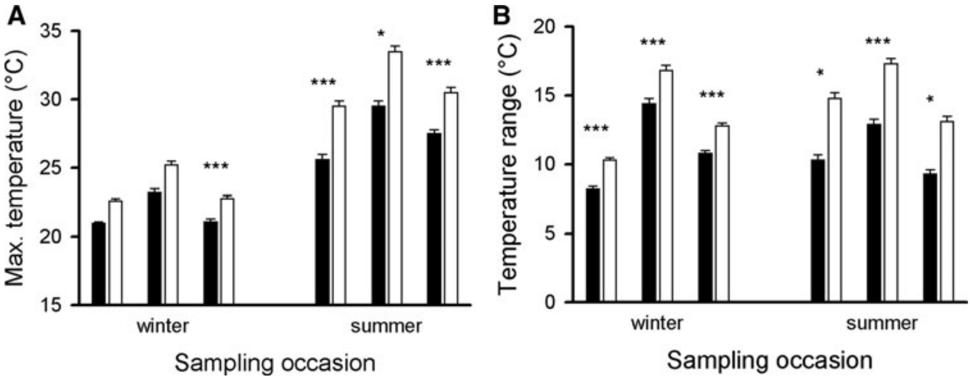

Fig. 3. (A) Mean (+SE, N = 12 experimental slabs) maximal; (B) range of temperatures in crevices (black bars) or open areas (white bars) on experimental slabs, for three sampling occasions in each of a summer or a winter. Data were pooled across locations, orientations and replicate slabs. Asterisks indicate significant differences between crevices and open areas from *post hoc* pairwise comparisons (Student–Newman–Keuls tests): *, $P < 0.05$; ***, $P < 0.001$. See Appendix 1.1.

across type of tide, were also significantly greater on the upper shore than on the lower shore in warm and in cool months (Figure 6, height, $F_{1,70} = 11.7$, $P = 0.001$ and $F_{1,22} = 7.0$, $P = 0.02$ for summer and winter, respectively; Appendix 2.2).

Relative humidity

Humidity varied in a straightforward fashion and was, as predicted, greater in crevices than in open areas for each of sandstone slabs and natural rocky shores. On four occasions during warm months, relative humidity was always significantly greater (by 4 to 16%) in artificial crevices than in open areas nearby (Figure 7, e.g. January 2007 habitat $F_{1,8} = 45.2$, $P < 0.01$; Appendix 3.1) and there was no effect of location or orientation of crevice. Relative humidity on natural rocky shores was mainly influenced by habitat and height on shore. On each of three occasions, relative humidity was greater (and nearly always significantly greater) in crevices than in open areas for all combinations of exposure to waves, height on shore and location (Figure 8A; e.g. March 2007 habitat $F_{1,66} = 169.7$, $P < 0.001$; Appendix 3.2). Relative humidity tended to be significantly greater on the lower than on the upper shore (Figure 8B) but there was a single exception for crevices on sheltered shores on one sampling occasion where there was no difference.

Water flow

On experimental slabs, loss of mass was less from clod cards in crevices than from those in open areas (Figure 9). These differences were significant on four out of five occasions in each of winter and summer (e.g. habitat $F_{1,19} = 11.3$, $P < 0.01$; Appendix 4.1). There was no significant interaction between habitat and orientation of the slab. Yet, on every occasion, for clod cards in crevices, loss of mass was greater from slabs with perpendicular crevices than from slabs where crevices were parallel to the shoreline. This pattern did not occur in open areas on slabs whose crevices were perpendicular or parallel (perpendicular > parallel on 11 of 20 occasions). If habitats on slabs of different orientation are equally likely to have greater water-flow, this result is extremely unlikely ($\chi^2 = 11.6$, df = 1, $P < 0.001$). Loss of mass from the more wave-exposed location was always less than from the wave-sheltered location.

Clod cards from different heights on natural rocky shores were analysed separately because they were submersed for different durations, thus affecting dissolution of the plaster.

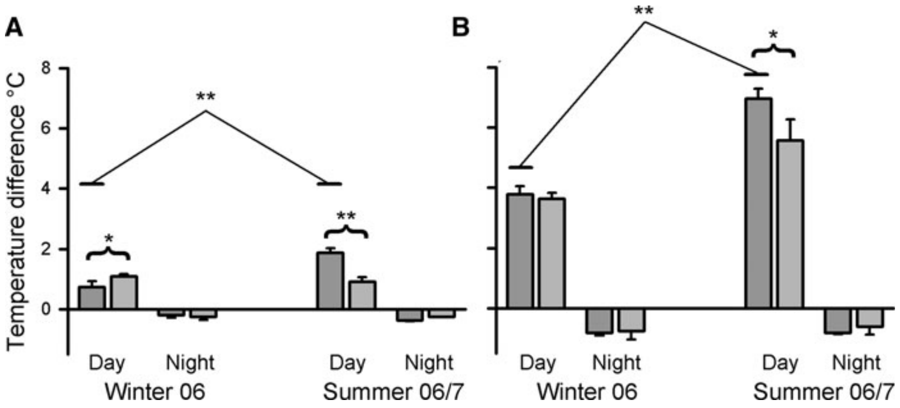

Fig. 4. (A) Mean (+ or − SE; N = 6); (B) maximal (+ or − SE; N = 6) differences in temperature between crevices and open areas of experimental slabs for spring (dark grey bars) or neap (light grey bars) tides at different times of day and for summer or winter. Data were pooled across two locations. Significant differences from *post hoc* pairwise comparisons (Student–Newman–Keuls tests) are marked by asterisks: *, $P < 0.05$; **, $P < 0.01$. See Appendix 1.2.

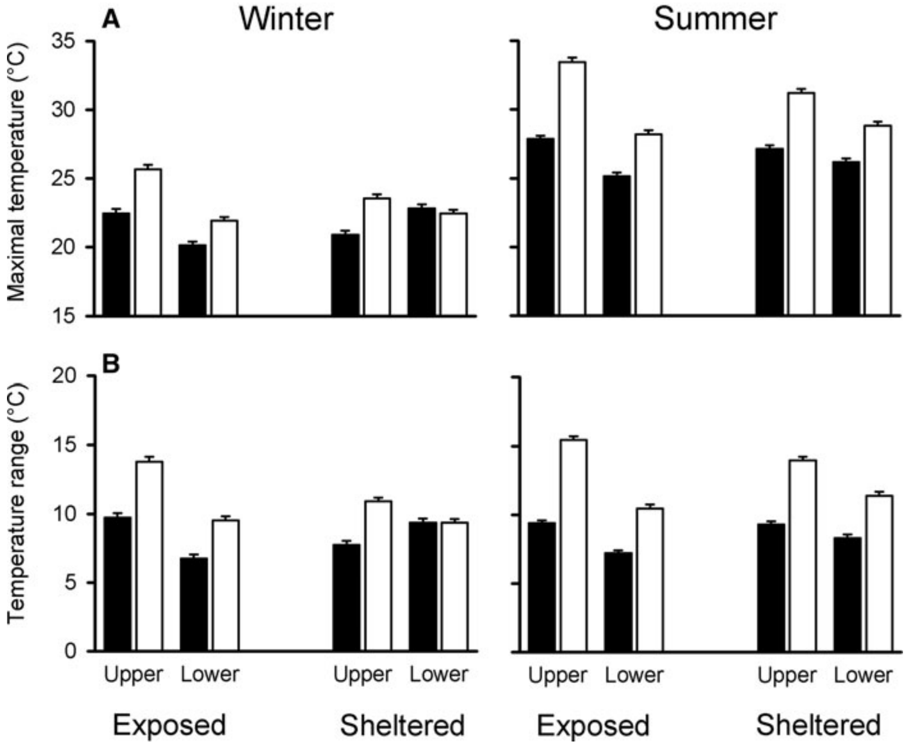

Fig. 5. (A) Mean (+SE, N = 396 summer or 156 winter) maximal temperatures on natural rocky shores; (B) mean range of temperatures (+SE, N = 396 summer or 156 winter) for crevices (black bars) or open areas (white bars) on upper or lower areas of exposed or sheltered shores during summer or winter. Data were pooled across five (summer) or two (winter) sampling occasions, four locations and three sites. Significant differences are not shown because the values in the figure are combined from multiple analyses (see Appendix 2.1). Analyses were carried out separately to avoid complex 6-factor analysis and because the number of days sampled on each occasion differed.

Loss of mass from clod cards for each height, exposure or location was generally greater in open areas than in crevices (Figure 10, e.g. winter 3rd occasion habitat × location $F_{2,18} = 6.9$, $P < 0.01$ and $F_{2,18} = 6.9$, $P < 0.01$ for upper or lower shore, respectively; Appendix 4.2). On some occasions, clod cards in crevices lost more mass than those in open areas, but these mean differences were never significant (e.g. upper exposed shores, Figure 10A). Individual clod cards in crevices did, however, often lose more mass than those in open areas (data not shown).

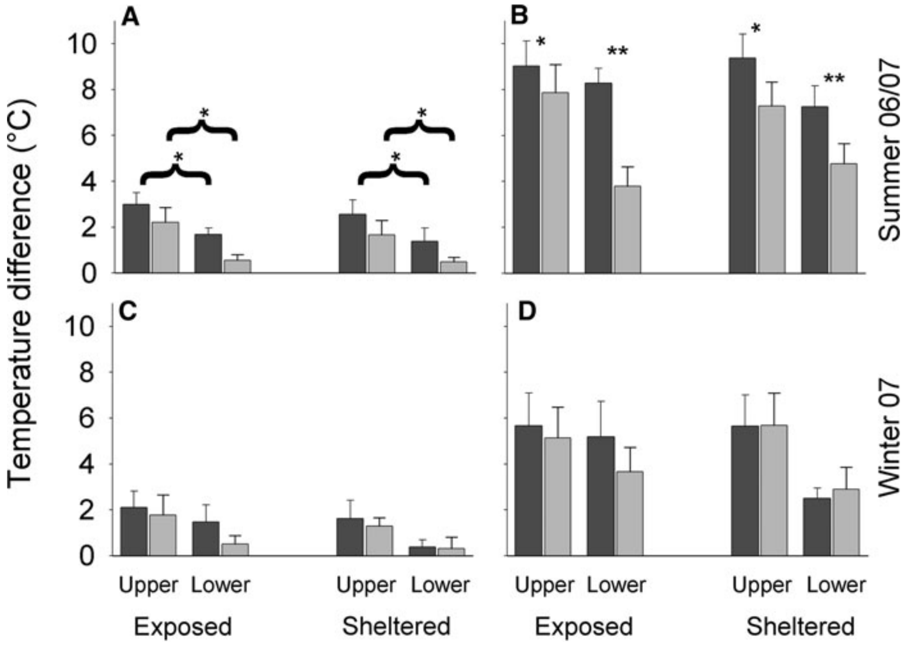

Fig. 6. (A & C) Mean (+SE; N = 10 or 4 respectively, pooled across locations); (B or D) maximal (+ or − SE N = 10 or 4 respectively, pooled across locations) concurrent differences in temperature between crevices and open areas for spring (dark grey bars) or neap (light grey bars) tides and for summer or winter on upper or lower areas of natural rocky shores. *, $P < 0.05$; **, $P < 0.01$. See Appendix 2.2.

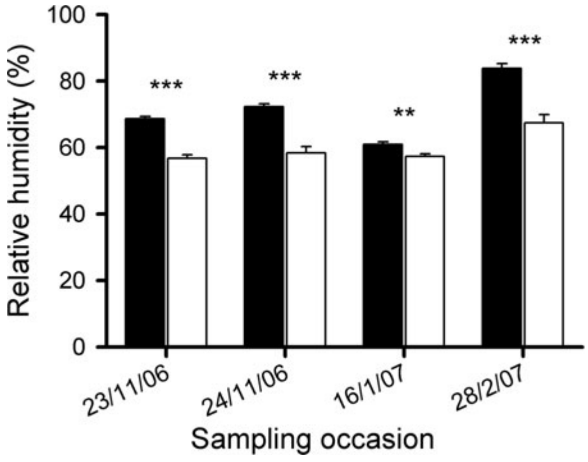

Fig. 7. Mean (+SE; N = 12 experimental slabs) relative humidities in crevices (black bars) or open areas (white bars). Data are pooled across locations and orientations. **, $P < 0.01$; ***, $P < 0.001$. See Appendix 3.1.

Wave forces

There were differences between habitats in shear forces at the surface of the substratum and these were very variable, but were seldom significant (Appendix 5). There was a trend for wave-forces to be greater on experimental slabs with crevices facing away from oncoming waves than on slabs with crevices oriented perpendicular to waves; 11 out of 13 sampling occasions showed this pattern. If wave forces are equally likely to be greater

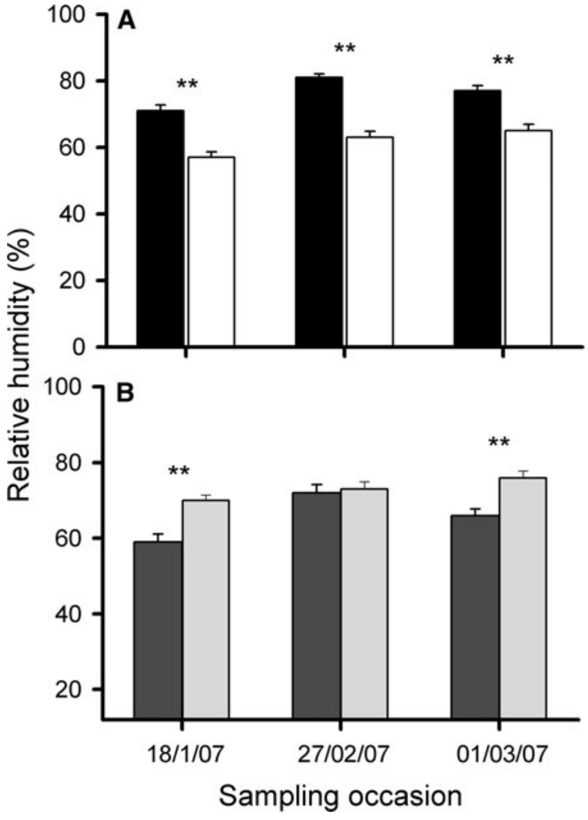

Fig. 8. Mean (+SE; N = 40) relative humidities (A) in crevices (black bars) or open areas (white bars) on natural rocky shores. Data pooled across heights on shore and locations; (B) on the upper (dark grey bars) or lower shore (light grey bars). Data have been pooled across habitats and locations. **, $P < 0.01$. See Appendix 3.2.

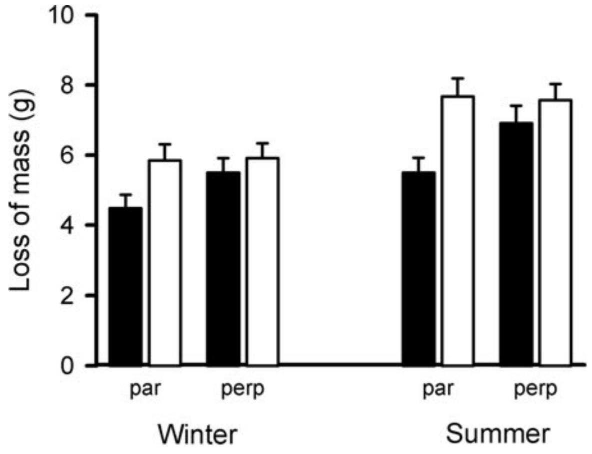

Fig. 9. Mean (+SE; N = 30) loss of mass (g) by dissolution from plaster clod cards in crevices (black bars) or open areas (white bars) on experimental slabs, where crevices were either perpendicular or parallel to the shoreline during winter or summer. Data were pooled across five occasions at two locations. Significant differences are not shown because the values in the figure are combined from multiple analyses. Analyses were carried out separately because: (i) repeated measurements were done on the same slabs and were not independent; and (ii) of differences in duration of submersion among occasions. See Appendix 4.1.

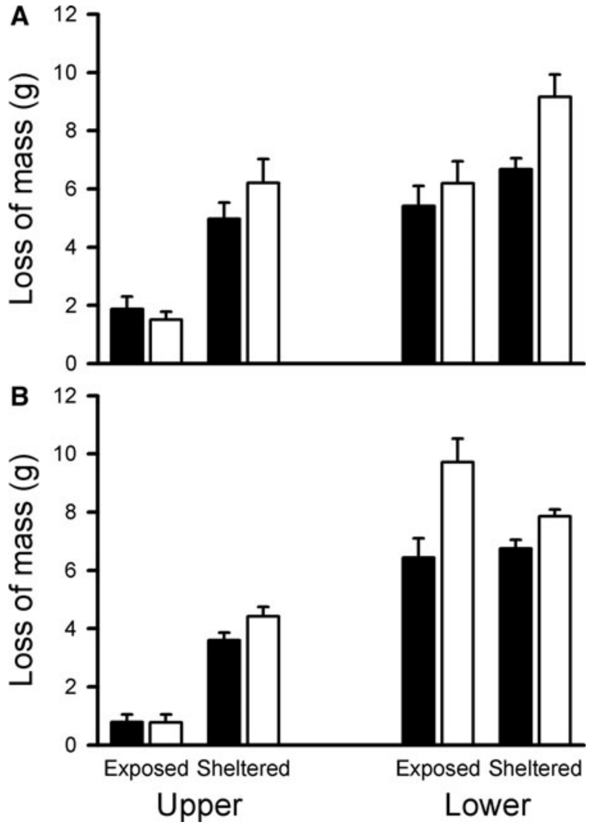

Fig. 10. Mean (+SE; N = 18 winter or 24 summer) loss of mass (g) from plaster clod cards deployed in crevices (black bars) or open areas (white bars) on different occasions during (A) winter or (B) summer on the upper or lower areas of wave-exposed or wave-sheltered shores. Data are pooled across sampling occasions and locations. Significant differences are not shown because the values in the figure are combined from multiple analyses. Analyses were carried out separately because of differences in duration of submersion among heights and occasions. See Appendix 4.2.

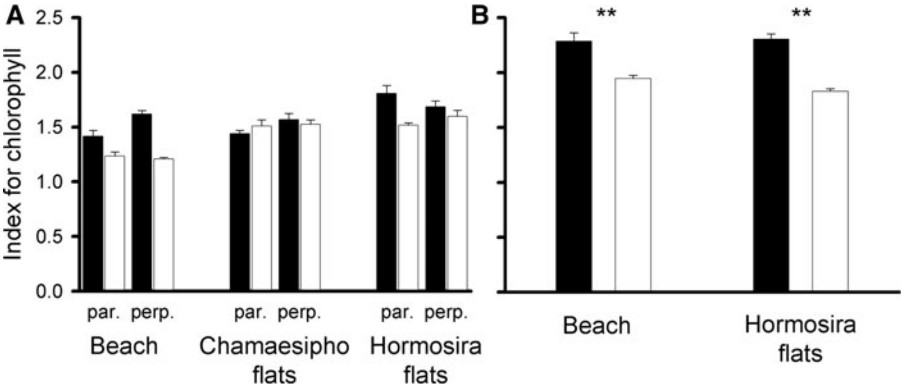

Fig. 11. Index for amounts of micro-algal chlorophyll-*a* in crevices (black bars) or open areas (white bars) on experimental slabs. (A) Mean (+SE, N = 12 regions of interest (ROI) from three locations at Cape Banks (see Figure 1) during summer 2006–2007. Data from the two replicate slabs for each treatment have been pooled. Crevices were parallel (Par.) or perpendicular (Perp.) to the shoreline; (B) mean (+SE, N = 48 ROIs) from two locations during winter 2007. Orientation was disregarded and data from replicate slabs were pooled. *, $P < 0.05$; **, $P < 0.01$. See Appendix 6.

in either orientation of crevice, this result is unlikely (binomial test $P < 0.05$). Although seldom significantly different, on ten out of eleven occasions, wave-forces were greater at the location that appeared to have greater exposure to waves. This is significantly more frequent than expected if shores of either exposure are equally likely to have the larger wave-forces (binomial test: $P < 0.01$; on two occasions bad weather prevented collection of data from one of the two locations).

Availability of food

The index for amounts of micro-algal chl-*a* was often greater in crevices than in open areas (Appendix 6). During summer, these differences were significant for each orientation of slab at Beach (Student–Newman–Keuls (SNK) tests between habitats for the interaction of habitat × slab (location × orientation), $P < 0.05$; Figure 11A). During winter, amounts of chl-*a* were greater in crevices than in open areas for 15 of 16 slabs measured, of which 13 differences were significant (SNK tests between habitats for the interaction of habitat × slabs (location), $P < 0.001$; Figure 11B).

nMDS plots show that compositions of pigments (and thus assemblages of micro-algae) differed between crevices and open areas during summer, but not during winter, although these seasons were not replicated (Figure 12). During summer, dissimilarities in pigments between habitats were calculated for each of the 24 slabs. Dissimilarities between crevices and open areas (0.0388 ± 0.004) were of the order of 8 times greater than dissimilarities within these habitats (crevices; 0.0058 ± 0.001, open; 0.0046 ± 0.002—SIMPER, Clarke & Warwick 2001). Differing amounts of phycoerythrocyanin (found only in cyanobacteria) and chl-*b* (found only in green algae), contributed most to differences between habitats. At each location, phycoerythrocyanin was more abundant in crevices than in open areas (Appendix 7; Figure 13A). Amounts of chl-*b* were also significantly greater in crevices than in open areas at Chamaesipho flats and at Hormosira flats, but not at Beach (Appendix 7; Figure 13B). Orientation of crevice had no effect on these pigments.

DISCUSSION

Measurements of environmental variables in carefully standardized artificial habitats (crevices or open areas) and in

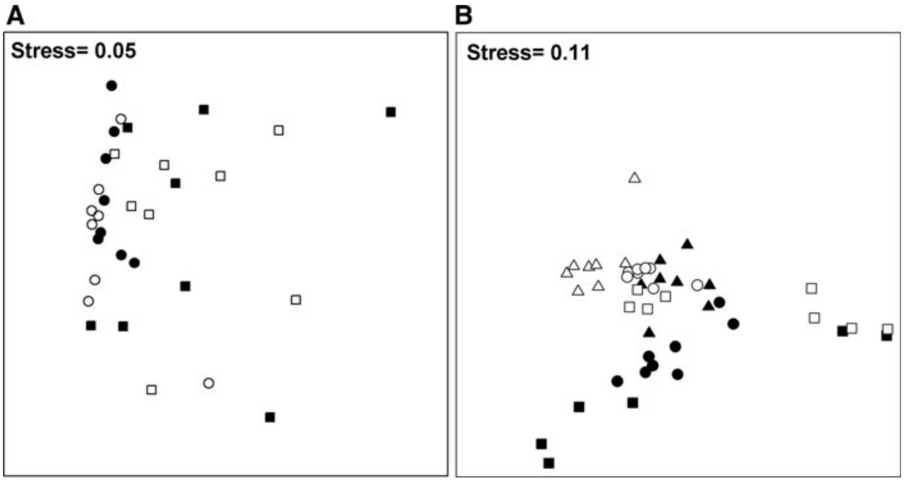

Fig. 12. Non-metric multidimensional scaling plots showing separation in multivariate space of relative amounts of four pigments from samples of micro-algae from crevices (black symbols) or open areas (white symbols) from (A) two locations during winter 2006 and (B) three locations during summer 2006–2007 at Cape Banks (Beach, triangles; Chamaesipho flats, circles; Hormosira flats, squares).

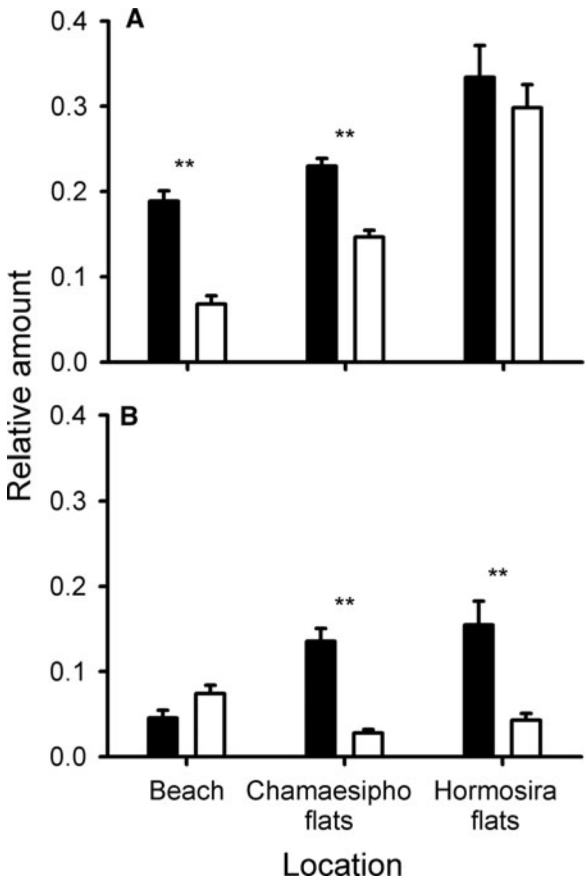

Fig. 13. Mean (+SE, N = 36 spectra) relative amounts of pigments from spectrometric sampling at Cape Banks during summer 2006–2007 contributing to differences in composition of biofilm. (A) Amounts of phycoerythrocyanin; (B) amounts of chlorophyll-*b*. Data were pooled across orientations and replicate slabs. **, $P < 0.01$. See Appendix 7.

similar habitats on structurally variable natural rocky shores demonstrated three key points.

(1) Environmental conditions in crevices differ strongly from those in open areas nearby.
(2) Several, but not all, of the variables measured in crevices and open areas differed as one would intuitively expect.
(3) The relative influence of crevices on these variables can depend on numerous factors including exposure to waves, height and orientation on the shore, ambient (seasonal) conditions and stage of the lunar cycle (spring or neap tides).

On rocky shores there is often massive spatial and temporal variability in distributions of organisms. Responses in physiology, morphology or behaviour, to differences in environmental conditions such as temperature, humidity and movement of water (that are believed to be important) are often assumed to be associated with or cause these distributions. Behavioural responses such as aggregation or use of different habitats cannot, however, always be predicted from differences in such variables. For example, Stafford & Davies (2004) found no difference in the likelihood of aggregation by snails in crevices when the shore was hotter and more desiccating than when cooler and less desiccating. Likewise, during within-population comparisons of a species of littorinid snail, the use of shelter (crevices) by males or non-gravid females was not affected by ambient air temperature (Pardo & Johnson, 2004). Denny *et al.* (2006), using long term heat budgets and knowledge of lethal temperatures for *Lottia gigantea* predicted that lethal temperatures within their vertical range on the shore, occurred on very few orientations or elevations of substrata and on only three occasions over five years (but see Miller *et al.*, 2009). Lethal upper temperatures were not, therefore, the sole determinant of the upper limit of distribution. Such examples merely serve to emphasize the need for greater understanding of how the environment varies in relation to habitats. Clearly the environment does not always differ with habitat in ways that we expect or animals are not always responding to the variables we assume are important.

During low tide, temperatures of organisms may not be the same as those of the surrounding air or the rock on which they sit and are influenced by characteristics of the organism and of the environment (Helmuth, 1998; Helmuth & Hofmann, 2001). Denny *et al.* (2006) show that even air temperatures can, however, be used as accurate predictors of body temperature. As predicted, maximum daily temperatures and temperature ranges (measures of acute thermal stress) of rocky substrata in crevices were significantly smaller than in open areas for natural or artificial habitats (Figure 3). The warmer temperatures in artificial crevices than in open areas at night (Figure 4) are unlikely to be of importance in warmer environments, but may be of consequence where low temperatures become a limiting factor, e.g. where frosts occur (Crisp, 1964; Strasser *et al.*, 2001). Although no data are presented from natural intertidal crevices in colder conditions, it seems reasonable to assume that similar patterns would occur. Indeed, Crisp (1964) suggests that crevices can ameliorate severe cold. Thus, in some conditions, crevices may provide a warm thermal refuge during low tides.

As predicted for natural rocky shores, maximal temperatures (averaged across habitats; Figure 5) and the maximal concurrent differences between the two habitats (averaged across types of tide; Figure 6) on the lower shore were less than those on the upper shore. Whether this was caused by differences in aerial exposure (i.e. differences in the time over which the rock could heat up) or because the lower shores were more likely to receive wave-splash (e.g. directly via cooler water temperatures or indirectly via greater evaporative cooling of moisture from wave-splash) is not clear.

During summer, the significantly greater maximal concurrent differences in temperature between crevices and open areas (on artificial or natural substrata) during spring than during neap tides (Figures 4 & 6) was probably caused by either or both of two mechanisms. Durations of exposure (and consequently, opportunities for warming) are greater during spring than during neap tides and, in Sydney, low tide during spring tides occur around 14.00 (or 15.00 during daylight savings time), which is often the hottest time of day. This contrasts with neap tides which occur at around 08.00 or 20.00. The absence of such differences between spring and neap tides during cool months may be a reflection on generally lower temperatures. On cool cloudy days from May–August, even with midday spring low tides, the maximum recorded daily temperatures could occur when habitats were submerged and could not differ in temperature (i.e. the water temperature was greater than the maximal air temperature). Harley (2008) also demonstrated interactions between shore level and the timing of the tides on temperature of the substratum.

The greater differences in temperature between heights on exposed than on sheltered shores (Figure 5A, B) were probably a function of the relative elevations of the areas sampled. Areas constituting upper or lower shore were determined by the distribution of organisms. At more wave-exposed locations, the upper shores were at greater elevations than those at sheltered locations whereas lower shores were at more similar heights. Habitats at greater elevations will have longer periods of exposure and will thus, be more likely to reach greater temperatures than those lower down the shore. Another explanation is that greater wave splash during low tide at wave-exposed shores would cool the lower shore more than on wave-sheltered shores but there was no evidence for this (Figure 5A, B). Because of the poor correlation of predicted or measured wave-forces (see below), Denny *et al.* (2006) conclude that direct measurements of wave-splash are the only way to predict the effects of wave-splash on the temperatures of intertidal animals (or habitats).

In the standardized conditions on sandstone slabs there was very little variation among replicates, but on natural rocky shores there was often large variation among replicate crevices or open areas. This is not surprising given the far greater variation in dimensions and aspect of natural habitats and reflects the demonstration of large small-scale spatial variability in temperature by Helmuth *et al.* (2002). In the present study, temperatures in different habitats interacted in complex ways among ambient conditions, exposures to waves, height on the shore and stage of the tidal cycle. Denny & Paine (1998) and Helmuth (1999) describe different, but similarly complex interactions for temperatures between ambient conditions and stage of the tidal cycle where interactions differed from place to place, emphasizing the complex spatial and temporal nature of environmental variables.

Overall mean temperatures or mean concurrent differences in temperature were not calculated because when submerged during high tide, habitats cannot differ in temperature and effects of habitat would be underestimated. In summer when the water is often cooler than the air, being submerged would decrease the mean temperature, whereas in winter, the reverse would be true. Overall mean temperatures could be calculated for when habitats were emersed but the number of measurements and hence accuracy of estimation would differ between locations and heights on the shore.

Animals in a variety of environments use crevices that are damp, instead of drier, open areas (e.g. land crabs; Diesel & Horst, 1995; intertidal fish; Shimizu *et al.*, 2006; bats; Siivonen & Wermundsen, 2008). In agreement with predictions and with data from other studies (Marchetti & Geller, 1987; Harper & Williams, 2001; Shimizu *et al.*, 2006), intertidal crevices in this study always had greater relative humidity than open areas. Greater relative humidity, perhaps as a consequence of greater retention of surface moisture or less air-flow may be a reliable and unambiguous influence of topographically more complex habitats such as crevices, across a wide range of conditions.

Moving water, altering risk of dislodgement, can affect behaviour and movement of mobile benthic animals in addition to influencing survival and risk of damage to plants and animals. Despite their known importance, there are still relatively few data for water flows or forces applied by breaking waves on rocky shores, particularly in relation to specific features of habitat (Gaylord, 2000). Various methods have been used to predict exposure to waves and wave forces including biological indices (Ballantine, 1961) or indices based on topography and prevailing winds (e.g. Burrows *et al.*, 2008) or measured directly by various devices (e.g. Jones & Demetropoulos, 1968; Denny, 1983; Gaylord, 1999; Boller & Carrington, 2006). Gaylord (2000) demonstrated that predictions of forces from the theory of fluid dynamics are often inaccurate and the velocity of water in breaking waves can differ greatly over very small spatial scales (e.g. cm, Helmuth & Denny, 2003; Denny *et al.*, 2004). The speeds and forces applied by water almost certainly differ according to where they are measured in relation to different topographies. For example, orientation of crevices may influence the flow of water through them; crevices parallel to the primary direction of water-flow may 'channel' water (and increase rates of flow or shear forces) in comparison to crevices that face away from the direction of water-flow or to open areas. Very few data have been collected from different habitats, but some preliminary data suggest that for some orientations, water velocities may be greater in crevices than in adjacent 'unsheltered' areas (O'Donnell & Denny, 2008). To understand the effects of different habitats on hydrodynamics and the responses by animals, it is essential that measurements are made in relation to the different habitats in which they occur.

In this study, interpretations of water flow were difficult because differences in loss of mass from exposed or sheltered shores are likely to have been caused by differences in duration of submersion in addition to differences in exposure to waves. This was particularly the case for exposed locations, where the upper shores were at greater elevations and in calm conditions, were submersed for much less time than those on sheltered shores. In general, water flow was reduced in crevices in relation to open areas but was also dependent on crevice orientation. Artificial crevices parallel to shoreline and facing away from the sea had slower flow-rates than crevices perpendicular to the shoreline but it was not immediately clear how and why the orientation of a crevice affected rates of water-flow in open areas nearby. Water flows in some natural crevices were sometimes greater than in open areas which, again, may be a consequence of greater 'channelling' of water through a restricted space. These results were occasional, not significant and may be confounded by slight differences in elevation, with clod-cards in crevices unavoidably being slightly lower (~5 cm) than open areas. Wave-forces were very unpredictable and not dependent on habitat or orientation of crevices, but did tend to be greater at the nominally more wave-exposed location. Such variability in relation to habitats supports observations from elsewhere about the importance of small-scale effects of topography on wave forces (Helmuth & Denny, 2003; Denny *et al.*, 2004; O'Donnell & Denny, 2008).

All primary productivity via photosynthesis is driven by the availability of light but may be hampered by too little (e.g. filamentous algae, Harley, 2002) or too much (e.g. micro-algae, Ruban & Horton, 1995). As anticipated, values of an index strongly correlated with amounts of micro-algal chl-*a*, were often significantly greater (and never smaller) in crevices than in open areas on artificial habitats. This may of course only be partially correct, because at some point, e.g. in very deep narrow crevices, availability of light may become a limiting factor and amounts of micro-algae may decrease. An alternative explanation for the greater amounts of algae in crevices is that crevices are used as shelter and not for feeding (i.e. algae are only less in open areas because it is consumed there). This is unlikely because densities of animals on the slabs were small when CIR imaging was done and thus the intensity of grazing anywhere on the slabs would have been minimal. Because crevices were artificial and differed from natural crevices in size, shape, material, etc., animals may respond differently to them despite the effects on environmental conditions being similar in the two types of habitat. Thus observed differences in amounts of chl-*a* may be a reflection of environmental conditions or behaviour by animals in these artificial habitats.

Habitats not only differed in amounts of micro-algae, but also varied in photosynthetic pigments (and thus, the types of micro-algae present). Although seasons were not replicated, there appeared to be less difference in composition of pigments during winter than during summer (Figure 12). During summer, in contrast with predictions, amounts of diatoms (chl-*c*) did not differ between crevices or open areas and were relatively small in nearly every sample. Crevices did have, however, relatively more phyco-erythrocyanin (cyanobacteria) and chl-*b* (green algae) than did open areas. Reasons for these differences are unclear, but are presumably linked in some way to the differing environmental conditions between these habitats.

What is apparent from this study is that small-scale features of habitats, such as crevices, can have major influences on a range of environmental conditions. Nevertheless, features of habitat do not always alter environmental conditions in the way we might expect and variables often interact to change the way in which environmental conditions vary. For example, rock temperatures vary between crevices and open areas, but relative temperatures are affected differently by season, by spring or neap tides and by height on the shore. Improved understanding of variability in the environment, as provided here, will improve our ability to use such differences as explanatory mechanisms for observed patterns of distribution or behaviour of intertidal organisms.

ACKNOWLEDGEMENTS

A.C.J. was supported by funds from the Australian Research Council through the Centre for Research on Ecological Impacts of Coastal Cities. Many thanks to Tony Underwood for helpful discussion throughout the study, to Basil Panayotakas who contributed greatly to the design and construction of the artificial habitats, to Richard Murphy who helped measure micro-algal pigments and to all the staff at EICC for help with fieldwork and analysis of data.

REFERENCES

Ballantine W.J. (1961) A biologically defined exposure scale for the comparative description of rocky shores. *Field Studies* 1, 1–19.

Beck M.W. (1998) Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. *Marine Ecology Progress Series* 169, 165–178.

Bergey E.A. (2005) How protective are refuges? Quantifying algal protection in rock crevices. *Freshwater Biology* 50, 1163–1177.

Boller M.L. and Carrington E. (2006) *In situ* measurements of hydrodynamic forces imposed on *Chondrus crispus* Stackhouse. *Journal of Experimental Marine Biology and Ecology* 337, 159–170.

Branch G.M. (1984) Competition between marine organisms—ecological and evolutionary implications. *Oceanography and Marine Biology* 22, 429–593.

Buckley B.A., Owen M.E. and Hofmann G.E. (2001) Adjusting the thermostat: the threshold induction temperature for the heatshock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. *Journal of Experimental Biology* 204, 3571–3579.

Burrows M.T., Harvey R. and Robb L. (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology Progress Series* 353, 1–12.

Catesby S.M. and McKillup S.C. (1998) The importance of crevices to the intertidal snail *Littoraria articulata* (Philippi) in a tropical mangrove forest. *Hydrobiologia* 367, 131–138.

Clarke K.R. and Warwick R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation.* Plymouth, UK: PRIMER-E, 172 pp.

Cleugh H.A. (2002) Field measurements of windbreak effects on airflow, turbulent exchanges and microclimates. *Australian Journal of Experimental Agriculture* 42, 665–677.

Crisp D.J. (1964) The effects of the severe winter of 1962–63 on marine life in Britain. *Journal of Animal Ecology* 33, 165–210.

Denny M. and Gaylord B. (2002) The mechanics of wave-swept algae. *Journal of Experimental Biology* 205, 1355–1362.

Denny M.W. (1983) A simple device for recording the maximum force exerted on intertidal organisms. *Limnology and Oceanography* 28, 1269–1274.

Denny M.W. (1993) *Air and water: the biology and physics of life's media.* Princeton, NJ: Princeton University Press.

Denny M.W., Daniel T.L. and Koehl M.A.R. (1985) Mechanical limits to size in wave swept organisms. *Ecological Monographs* 55, 69–102.

Denny M.W., Helmuth B., Leonard G.H., Harley C.D.G., Hunt L.J.H. and Nelson E.K. (2004) Quantifying scale in ecology: lessons from a wave-swept shore. *Ecological Monographs* 74, 513–532.

Denny M.W., Miller L.P. and Harley C.D.G. (2006) Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. *Journal of Experimental Biology* 209, 2420–2431.

Denny M.W., Miller L.P., Stokes M.D., Hunt L.J.H. and Helmuth B.S.T. (2003) Extreme water velocities: topographical amplification of wave-induced flow in the surf zone of rocky shores. *Limnology and Oceanography* 48, 1–8.

Denny M.W. and Paine R.T. (1998) Celestial mechanics, sea-level changes, and intertidal ecology. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 194, 108–115.

Diesel R. and Horst D. (1995) Breeding in a snail shell—ecology and biology of the Jamaican montane crab *Sesarma jarvisi* (Decapoda, Grapsidae). *Journal of Crustacean Biology* 15, 179–195.

Duffy J.E. and Hay M.E. (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72, 1286–1298.

Emson R.H. and Faller-Fritsch R.J. (1976) An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. *Journal of Experimental Marine Biology and Ecology* 23, 285–297.

Fairweather P.G. (1988) Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology* 100, 63–68.

Fitzhenry T., Halpin P.M. and Helmuth B. (2004) Testing the effects of wave exposure, site, and behaviour on intertidal mussel body temperatures: applications and limits of temperature logger design. *Marine Biology* 145, 339–349.

Garrity S.D. (1984) Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65, 559–574.

Gaylord B. (1999) Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. *Journal of Experimental Marine Biology and Ecology* 239, 85–124.

Gaylord B. (2000) Biological implications of surf-zone flow complexity. *Limnology and Oceanography* 45, 174–188.

Gaylord B., Blanchette C.A. and Denny M.W. (1994) Mechanical consequences of size in wave-swept algae. *Ecological Monographs* 64, 287–313.

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

Halpin P.M., Sorte C.J., Hofmann G.E. and Menge B.A. (2002) Patterns of variation in levels of Hsp70 in natural rocky shore populations from microscales to mesoscales. *Integrative and Comparative Biology* 42, 815–824.

Harley C.D.G. (2002) Light availability indirectly limits herbivore growth and abundance in a high rocky intertidal community during the winter. *Limnology and Oceanography* 47, 1217–1222.

Harley C.D.G. (2008) Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Marine Ecology Progress Series* 371, 37–46.

Harper K.D. and 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.

Helmuth B.S.T. (1998) Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecological Monographs* 68, 51–74.

Helmuth B.S.T. (1999) Thermal biology of rocky intertidal mussels: quantifying body temperatures using climatological data. *Ecology* 80, 15–34.

Helmuth B.S.T. and Denny M.W. (2003) Predicting wave exposure in the rocky intertidal zone: do bigger waves always lead to larger forces. *Limnology and Oceanography* 48, 1338–1345.

Helmuth B.S.T., Harley C.D.G., Halpin P.M., O'Donnell M., Hofmann G.E. and Blanchette C.A. (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298, 1015–1017.

Helmuth B.S.T. and Hofmann G.E. (2001) Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 201, 374–384.

Hofmann G.E. and Somero G.N. (1995) Evidence for protein damage at environmental temperatures—seasonal changes in levels of ubiquitin conjugates and Hsp70 in the intertidal mussel *Mytilus trossulus*. *Journal of Experimental Biology* 198, 1509–1518.

Hughes R.N. and Elner R.W. (1979) Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. *Journal of Animal Ecology* 48, 65–78.

Jones W.E. and Demetropoulos A. (1968) Exposure to wave action; measurements of an important ecological parameter on rocky shores of Anglesey. *Journal of Experimental Marine Biology and Ecology* 2, 46–63.

Kohn A.J. and Leviten P.J. (1976) Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* 25, 199–210.

Marchetti K.E. and Geller J.B. (1987) The effects of aggregation and microhabitat on desiccation and body-temperature of the black turban snail, *Tegula funebralis* (A. Adams, 1855). *Veliger* 30, 127–133.

McMahon R.F. (1990) Thermal tolerance, evaporative water-loss, air-water oxygen-consumption and zonation of intertidal prosobranchs—a new synthesis. *Hydrobiologia* 193, 241–260.

Menge B.A. and Branch G.M. (2001) Rocky intertidal communities. In Bertness M.D., Gaines S.D. and Hay M.E. (eds) *Marine community ecology*. Sunderland, MA: Sinauer Associates, pp. 221–251.

Miller L.P., Harley C.D.G. and Denny M.W. (2009) The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. *Functional Ecology* 23, 756–767.

Moran M.J. (1985) 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.

Murphy R.J., Tolhurst T.J., Chapman M.G. and Underwood A.J. (2005a) Estimation of surface chlorophyll-*a* on an emersed mudflat using field spectrometry: accuracy of ratios and derivative-based approaches. *International Journal of Remote Sensing* 26, 1835–1859.

Murphy R.J., Underwood A.J. and Pinkerton M.H. (2006) Quantitative imaging to measure photosynthetic biomass on an intertidal rock-platform. *Marine Ecology Progress Series* 312, 45–55.

Murphy R.J., Underwood A.J., Pinkerton M.H. and Range P. (2005b) Field spectrometry: new methods to investigate epilithic micro-algae on rocky shores. *Journal of Experimental Marine Biology and Ecology* 325, 111–124.

O'Donnell M.J. (2008) Reduction of wave forces within bare patches in mussel beds. *Marine Ecology Progress Series* 362, 157–167.

O'Donnell M.J. and Denny M.W. (2008) Hydrodynamic forces and surface topography: centimeter-scale spatial variation in wave forces. *Limnology and Oceanography* 53, 579–588.

Paine R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49, 667–685.

Paine R.T. and Levin S.A. (1981) Intertidal landscapes—disturbance and the dynamics of pattern. *Ecological Monographs* 51, 145–178.

Pardo L.M. and Johnson L.E. (2004) Activity and shelter use of an intertidal snail: effects of sex, reproductive condition and tidal cycle. *Journal of Experimental Marine Biology and Ecology* 301, 175–191.

Raffaelli D. and Hawkins S.J. (1996) *Intertidal ecology*. London: Chapman & Hall.

Raffaelli D.G. and Hughes R.N. (1978) Effects of crevice size and availability on populations of *Littorina rudis* and *Littorina neritoides*. *Journal of Animal Ecology* 47, 71–83.

Ruban A.V. and Horton P. (1995) Regulation of nonphotochemical quenching of chlorophyll fluorescence in plants. *Australian Journal of Plant Physiology* 22, 221–230.

Savitzky A. and Golay M.J.E. (1964) Smoothing and differentiation of data by simplified least squares procedures. *Analytical Chemistry* 36, 1627–1639.

Shimizu N., Sakai Y., Hashimoto H. and Gushima K. (2006) Terrestrial reproduction by the air-breathing fish *Andamia tetradactyla* (Pisces; Blenniidae) on supralittoral reefs. *Journal of Zoology* 269, 357–364.

Siivonen Y. and Wermundsen T. (2008) Characteristics of winter roosts of bat species in southern Finland. *Mammalia* 72, 50–56.

Stafford R. and Davies M.S. (2004) Temperature and desiccation do not affect aggregation behaviour in high shore littorinids in north-east England. *Journal of Negative Results* 1, 16–20.

Stephenson T.A. and Stephenson A. (1972) *Life between tidemarks on rocky shores.* San Francisco: W.H. Freeman and Company.

Strasser M., Reinwald T. and Reise K. (2001) Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria* in the Northern Wadden Sea. *Helgoland Marine Research* 55, 190–197.

Takada Y. (1999) Influence of shade and number of boulder layers on mobile organisms on a warm temperate boulder shore. *Marine Ecology Progress Series* 189, 171–179.

Thompson T.L. and Glenn E.P. (1994) Plaster standards to measure water motion. *Limnology and Oceanography* 39, 1768–1779.

Underwood A.J. (1975) Comparative studies on biology of *Nerita atramentosa* Reeve, *Bembicium nanum* (Lamarck) and *Cellana tramoserica* (Sowerby) (Gastropoda-Prosobranchia) in SE Australia. *Journal of Experimental Marine Biology and Ecology* 18, 153–172.

Underwood A.J. (1984) The vertical-distribution and seasonal abundance of intertidal microalgae on a rocky shore in New South Wales. *Journal of Experimental Marine Biology and Ecology* 78, 199–220.

Underwood A.J. (2000) Experimental ecology of rocky intertidal habitats: what are we learning? *Journal of Experimental Marine Biology and Ecology* 250, 51–76.

Underwood A.J. and 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. and Chapman M.G. (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107, 212–224.

Underwood A.J. and Chapman M.G. (2000) Variation in abundances of intertidal populations: consequences of extremities of environment. *Hydrobiologia* 426, 25–36.

Werner E.E., Gilliam J.F., Hall D.J. and Mittelbach G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64, 1540–1548.

Whitcraft C.R. and Levin L.A. (2007) Regulation of benthic algal and animal communities by salt marsh plants: Impact of shading. *Ecology* 88, 904–917.

and

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

Correspondence should be addressed to:
A.C. Jackson
Environmental Research Centre
North Highland College
UHI Millennium Institute
Castle Street, Thurso, Caithness, KW14 7JD, UK
email: angus.jackson@thurso.uhi.ac.uk

Appendix 1.1. Analyses of variance for (a) maximal and (b) range of temperatures in crevices or open areas on experimental sandstone slabs on three sampling occasions during each of winter or summer. Daily maxima (98th percentile of temperatures for that day) were measured as an 'acute' measure of thermal stress. Daily temperature ranges (the difference between the 98th and 2nd percentiles) were also measured because thermal stress is dependent on the recent thermal history of an organism. Daily values were used as replicates (N = 9–14 days) to compare among locations (Loc, random), orientation of crevice on slab (Orient, fixed; parallel or perpendicular to the shoreline), habitat (Hab, fixed, crevice versus open area), experimental slabs (Sl, random). Non-significant interactions #pooled (interactions containing random factors) or $^{\$}$ eliminated (interactions containing only fixed factors) if $P > 0.25$ or if its mean square underestimated the residual mean square.

(a) Maximal temperature Source of variation	**Winter**												**Summer**											
	May 2006				**August 2006**				**May 2007**				**December 2006**				**January 2007**				**March 2007**			
	df	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***
Loc	1	26.8	7.7	0.006	1	0.5	0.1	0.80	1	2.5	0.3	0.58	1	2.5	0.3	0.63	1	1.3	0.1	0.83	1	23.5	3.2	0.11
Orient	1	5.9	0.2	0.75	1	0.7	0.1	0.77	1	2.1	0.1	0.79	1	12.6	1.3	0.29	1	23.3	0.6	0.58	1	7.7	1.1	0.33
Hab	1	227.5	43.9	0.1	1	219.6	22.5	0.13	1	223.4	45.8	<0.001	1	1215.5	130.3	<0.001	1	1317.4	188.5	0.04	1	719.3	28.3	<0.001
Sl (Loc × Orient)	8	1.3$^{\#}$			8	8.8			8	7.7	1.5	0.16	8	10.5			8	11.1$^{\#}$			8	7.8		
Loc × Orient	1	34.9	10.1	0.002	1	2.7$^{\#}$			1	17.7	2.3	0.17	1	6.0$^{\#}$			1	37.5	1.3	0.25	1	3.0$^{\#}$		
Loc × Hab	1	5.2	3.8	0.08	1	9.8	1.4	0.24	1	2.3$^{\#}$			1	0.0$^{\#}$			1	7.0	2.6	0.14	1	4.4$^{\#}$		
Orient × Hab	1	0.0$^{\$}$			1	6.5$^{\$}$			1	0.2$^{\$}$			1	3.0$^{\$}$			1	9.2$^{\$}$			1	0.3$^{\$}$		
Hab × Sl (Loc × Orient)	8	1.53			8	3.8$^{\#}$			8	5.7			8	1.2			8	2.9			8	4.5$^{\#}$		
Loc × Orient × Hab	1	0.1$^{\#}$			1	15.1	2.2	0.14	1	1.0$^{\#}$			1	1.3$^{\#}$			1	1.1$^{\#}$			1	17.9$^{\#}$		
Residual	288	3.5			192	7.0			312	5.2			288	25.8			312	28.4			312	26.0		
1-pooled	9	1.4	0.4	0.94	200	6.9			9	5.2			9	1.2			9	2.7	0.1	0.99	320	25.5		
2-pooled	296	3.5				8.1	1.2	0.31	10	4.9	0.9	0.49	10	1.1	0.0	1.00	320	28.0			321	25.5		
3-pooled													9	10.0	0.4	0.94					322	25.4		
4-pooled																					9	7.3	0.3	0.98

(b) Temperature range Source of variation	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***
Loc	1	6.9	4.2	0.07	1	191.3	21.1	0.001	1	1.9	0.3	0.63	1	3.4	0.3	0.59	1	13.0	1.2	0.31	1	5.2	1.0	0.35
Orient	1	0.0	0.0	0.98	1	0.3	0.0	0.87	1	3.0	0.4	0.54	1	11.0	2.3	0.37	1	17.9	1.0	0.51	1	46.3	6.8	0.23
Hab	1	364.7	67.2	<0.001	1	321.0	53.5	<0.001	1	324.1	37.0	0.001	1	1554.8	459.3	0.03	1	1532.4	633.7	<0.001	1	1230.0	231.4	0.04
Sl (Loc × Orient)	8	1.6	0.3	0.96	8	9.7			8	7.8			8	10.6	0.3	0.95	8	11.3	0.3	0.96	8	5.3	0.3	0.97
Loc × Orient	1	21.0	12.8	0.007	1	3.8$^{\#}$			1	4.8$^{\#}$			1	4.8	0.5	0.52	1	18.6	1.7	0.24	1	6.8	1.3	0.29
Loc × Hab	1	0.9$^{\#}$			1	6.1$^{\#}$			1	0.4$^{\#}$			1	3.4	7.4	0.02	1	1.2$^{\#}$			1	5.3	1.6	0.24
Orient × Hab	1	0.4$^{\$}$			1	10.4	1.7	0.22	1	13.4	1.5	0.24	1	4.5	9.8	0.01	1	7.9$^{\$}$			1	0.1	0.0	0.97
Hab × Sl (Loc × Orient)	8	0.9			8	6.2			8	10.1			8	0.5			8	2.5			8	3.3	0.2	0.99
Loc × Orient × Hab	1	2.6$^{\#}$			1	4.3$^{\#}$			1	6.6$^{\#}$			1	0.1$^{\#}$			1	2.9$^{\#}$			1	27.3	8.3	0.02
Residual	288	5.6			192	17.9			312	7.1			288	31.8			312	35.4			312	17.4		
1-pooled	296	5.4			9	6.0			9	9.7			9	0.5	0.0	1.0	9	2.6						
2-pooled	297	5.4			10	6.0	0.3	0.97	10	8.8	1.2	0.27					10	2.4	0.1	1.0				
3-pooled					9	9.1	0.5	0.87	9	7.5	1.1	0.4												
4-pooled																								

Appendix 1.2. Analyses of variance for (a) mean and (b) maximal concurrent differences in temperature between crevices and open areas on experimental slabs. This provides a measure of the relative value of being in different habitats. Sampling occasions ($N = 3$) were used to compare among sampling period (Per, random, 2 levels), locations (Loc, random, 2 levels), time of day (Ti, fixed; day or night), type of tide (Td, fixed; spring or neap). nt, no test due to lack of appropriate denominator for F ratio. Non-significant interactions [#]pooled (interactions containing random factors) or [$]eliminated (interactions containing only fixed factors) if $P > 0.25$ or if its mean square underestimated the residual mean square.

Source of variation		**(a)**			**(b)**		
	df	**MS**	**F**	***P***	**MS**	**F**	***P***
Per	1	0.5	7.5	0.22	20.9	156.5	0.05
Loc	1	0.0	0.5	0.62	1.3	9.8	0.2
Ti	1	24.2	nt		394.4	nt	
Td	1	0.2	nt		1.2	1.5	0.44
Per × Loc	1	0.1	0.7	0.40	0.1	0.2	0.66
Per × Ti	1	0.9	625.0	0.009	18.6	27.9	<0.001
Per × Td	1	1.0	124.6	0.06	0.8	1.3	0.27
Loc × Ti	1	0.1	549.6	0.03	0.9	1.4	0.25
Loc × Td	1	0.1	8.2	0.21	0.0[$]		
Ti × Td	1	0.3	0.2	0.73	2.5	1.7	0.42
Per × Loc × Ti	1	0.0	0.0	0.96	0.1[#]		
Per × Loc × Td	1	0.0	0.1	0.76	0.6[#]		
Per × Ti × Td	1	1.6	48.8	<0.001	1.5	2.2	0.15
Loc × Ti × Td	1	0.0			0.1[$]		
Per × Loc × Ti × Td	1	0.0			0.0[#]		
Residual	32	0.1			0.7		
1-pooled	33	0.1			0.7		
2-pooled					0.7		
3-pooled					0.7		

Appendix 2.1. Analyses of variance of temperatures in crevices or in open areas on natural rocky shores for daily maxima in (a) winter and (c) summer and for daily ranges in (b) winter and (d) summer. See Materials and Methods or Appendix 1.1 for reasons for using these metrics. Daily values were used as replicates (N = 13 days) to compare among exposure to waves (Exp, fixed, sheltered versus exposed), locations (Loc, random, 2 levels nested in Exp), height on shore (Ht, fixed, low or high), habitat (Hab,– fixed, crevice versus open area), site (random, 3 levels nested in the interaction Exp × Loc × Ht × Hab), $^{\&}$data were transformed (ln (*x*)) where necessary, to reduce homogeneity of variance. Non-significant interactions $^{\#}$pooled (interactions containing random factors) or $^{\$}$eliminated (interactions containing only fixed factors) if $P > 0.25$ or if its mean square underestimated the Residual mean square. Figure 5 illustrates the general patterns, for each season, using mean values pooled across sampling occasions.

(a) Winter—maximal temperature **Source of variation**		**May 2007**			**August 2007**		
	df	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp.	1	34.3	0.3	0.64	73.2	0.6	0.53
Loc (Exp)	2	112.0	2.5	0.10	127.3	1.9	0.16
Ht.	1	115.0	2.5	0.12	480.0	7.2	0.01
Hab.	1	274.3	1.1	0.41	853.8	12.8	0.001
Si (Exp × Loc × Ht × Hab)	32	44.8			66.2		
Exp × Ht	1	252.7	5.6	0.02	728.2	10.9	0.002
Exp × Hab	1	6.0	0.0	0.89	203.9	3.1	0.09
Ht × Loc (Exp)	2	56.3$^{\#}$			66.0$^{\#}$		
Hab × Loc (Exp)	2	257.0	5.7	0.008	140.5$^{\#}$		
Ht × Hab	1	262.0	3.2	0.21	128.1	1.9	0.17
Exp × Ht × Hab	1	0.9	0.0	0.93	83.7	1.3	0.27
Hab × Ht × Loc (Exp)	2	80.9	1.8	0.18	4.8$^{\#}$		
Res	576	4.9			14.1		
1-pooled	34	45.5	9.3	0.00	62.6		
2-pooled	36				62.7		
3-pooled	38				66.8	4.7	0.00

(b) Summer—maximal temperature **Source of variation**		**November 2006**			**January 2007**			**Februar 2007**			**December 2007**			**February 2008**		
	df	**MS$^{\&}$**	**F**	***P***	**MS**	**F**	***P***	**MS$^{\&}$**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp.	1	0.57	5.50	0.14	264.8	0.4	0.58	137.3	0.5	0.55	254.7	2.2	0.27	16.3	0.1	0.84
Loc (Exp)	2	0.10	2.34	0.11	616.5	35.4	<0.001	270.9	12.9	<0.001	114.9	4.4	0.02	316.6	5.6	0.009
Ht.	1	0.74	16.72	<0.001	2162.6	9.9	0.09	1313.2	7.1	0.12	1754.0	81.8	0.01	1063.7	10.7	0.08
Hab.	1	1.63	36.94	<0.001	3825.4	11.9	0.07	1975.5	5.4	0.15	2846.7	18.8	0.05	2329.7	5.4	0.15
Si (Exp × Loc × Ht × Hab)	32	0.05			18.5			20.7			25.8			57.0	2.8	<0.001
Exp × Ht	1	0.16	3.60	0.07	628.1	2.9	0.23	289.2	1.6	0.34	96.3	4.5	0.17	132.1	1.3	0.37
Exp × Hab	1	0.19	4.21	0.04	23.7	0.1	0.81	76.7	0.2	0.69	22.8	0.2	0.74	0.8	0.0	0.97
Ht × Loc (Exp)	2	0.00$^{\#}$			217.5	12.5	<0.001	185.0	8.8	<0.001	21.3	0.8	0.45	99.0	1.7	0.19
Hab × Loc (Exp)	2	0.04$^{\#}$			322.3	18.5	<0.001	368.3	17.6	<0.001	151.7	5.8	0.007	432.1	7.6	0.002
Ht × Hab	1	0.01	0.15	0.74	267.3	15.4	<0.001	448.7	21.4	<0.001	267.4	10.3	0.003	93.5	0.9	0.44
Exp × Ht × Hab	1	0.02	0.20	0.70	24.4	1.4	0.24	116.8	5.6	0.02	73.0	2.8	0.10	12.1	0.1	0.76
Hab × Ht × Loc (Exp)	2	0.09	2.01	0.15	0.0$^{\#}$			25.3$^{\#}$			30.0$^{\#}$			101.2	1.8	0.19
Res	576	0.05			21.9			18.6			25.4			20.5		
1-pooled	34	0.05			17.4	0.8	0.79	21.0	1.1	0.28	26.1	1.0	0.43			
2-pooled	36	0.04	0.97	0.52												

Appendix 2.1. Continued

(c) Winter—temperature range Source of variation		May 2007			August 2007		
	df	MS	F	*P*	MS	F	*P*
Exp.	1	97.0	0.4	0.60	26.9	0.2	0.71
Loc (Exp)	2	257.1	5.1	0.01	143.1	1.9	0.17
Ht.	1	541.7	4.0	0.18	456.5	6.0	0.02
Hab.	1	713.0	2.3	0.27	1300.1	17.0	<0.001
Si (Exp × Loc × Ht × Hab)	32	50.2	12.9	<0.001	74.3		
Exp × Ht	1	480.2	3.6	0.20	565.6	7.4	0.01
Exp × Hab	1	35.4	0.1	0.77	284.7	3.7	0.06
Ht × Loc (Exp)	2	134.3	2.7	0.08	91.2$^{\#}$		
Hab × Loc (Exp)	2	312.8	6.2	0.005	165.9$^{\#}$		
Ht × Hab	1	189.2	2.2	0.28	197.3	2.6	0.12
Exp × Ht × Hab	1	16.5	0.2	0.70	59.5	0.8	0.38
Hab × Ht × Loc (Exp)	2	86.7	1.7	0.19	4.6$^{\#}$		
Res	576	3.9			13.2		
1-pooled	34				70.2		
2-pooled	36				71.3		
3-pooled	38				76.3	5.8	0.00

(d) Summer—temperature range Source of variation		November 2006			January 2007			February 2007			December 2007			February 2008		
	df	MS$^{\&}$	F	*P*	MS	F	*P*	MS$^{\&}$	F	*P*	MS	F	*P*	MS	F	*P*
Exp.	1	14.6	7.6	0.11	0.1	0.0	0.99	0.3	0.1	0.83	180.3	1.1	0.41	0.8	0.0	0.97
Loc (Exp.)	2	1.9	3.4	0.04	299.3	15.5	<0.001	4.5	9.6	<0.001	167.0	5.9	0.006	424.5	7.3	0.003
Ht.	1	12.8	22.8	<0.001	1121.4	7.9	0.11	28.5	17.2	0.05	1712.3	27.9	0.03	946.4	5.8	0.14
Hab.	1	19.2	34.1	<0.001	4060.1	11.3	0.08	28.7	3.0	0.23	3714.4	23.6	0.04	2934.8	6.2	0.13
Si (Exp × Loc × Ht × Hab)	32	0.6			20.2			0.5			28.0			58.2	3.5	<0.001
Exp × Ht	1	1.8	3.3	0.08	145.1	1.0	0.42	4.8	2.9	0.23	60.8	1.0	0.42	94.4	0.6	0.53
Exp × Hab	1	1.2	2.1	0.16	21.6	0.1	0.83	0.0	0.0	0.95	27.9	0.2	0.71	7.5	0.0	0.91
Ht × Loc (Exp)	2	0.1$^{\#}$			141.7	7.4	0.002	1.7	3.5	0.04	61.4	2.2	0.13	162.4	2.8	0.08
Hab × Loc (Exp)	2	0.2$^{\#}$			360.7	18.7	<0.001	9.5	20.3	<0.001	157.6	5.6	0.008	472.8	8.1	0.001
Ht × Hab	1	0.1	0.1	0.79	243.9	12.6	0.001	3.1	6.5	0.02	365.4	12.9	0.001	135.8	0.8	0.46
Exp × Ht × Hab	1	0.2	0.1	0.76	6.9	0.4	0.55	0.7	1.4	0.25	75.0	2.7	0.11	24.7	0.2	0.74
Hab × Ht × Loc (Exp)	2	1.3	2.3	0.12	4.7$^{\#}$			0.1$^{\#}$			31.9$^{\#}$			163.9	2.8	0.07
Res	576	0.4			24.6			0.2			18.0			16.4		
1-pooled	34				19.3	0.8	0.81	0.5	2.0	0.00	28.3	1.6	0.02			
2-pooled	36		1.3	0.1												

Appendix 2.2. Analysis of variance for mean or maximal concurrent differences in temperature between crevices and open areas on natural rocky shores during summer 2006–2007, 2007–2008 or winter 2007. This provides a measure of the relative value of being in different habitats. Sampling occasions (N = 5 summer or N = 2 winter) were used to compare among exposure to waves (Exp, fixed sheltered versus exposed), locations (Loc, random, 2 levels nested in Exp), height on shore (H^t, fixed, low or high), type of tide (Td, fixed; spring or neap. Non-significant interactions $^{\#}$ were pooled if $P > 0.25$ or if its mean square underestimated the residual mean square.

Concurrent difference Source of variation	**Summer**							**Winter**						
		Mean			**Max**				**Mean**			**Max**		
	df	**MS**	**F**	***P***	**MS**	**F**	***P***	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp	1	2.2	0.7	0.51	0.1	0.0	0.92	1	2.5	0.6	0.53	4.3	0.2	0.72
Loc (Exp)	2	3.3	1.4	0.25	8.6	0.9	0.41	2	4.6	3.5	0.05	24.5	5.5	0.01
Ht	1	35.5	15.2	<0.001	111.9	11.7	0.001	1	8.5	6.6	0.02	31.1	7.0	0.02
Td	1	17.0	2.5	0.26	130.9	13.7	<0.001	1	1.4	1.1	0.31	1.3	0.3	0.59
Exp × Ht	1	0.5	0.2	0.66	0.1	0.0	0.94	1	0.0	0.0	0.85	8.0	1.8	0.19
Exp × Td	1	0.0	0.0	0.96	1.5	0.2	0.69	1	0.4	0.3	0.58	3.1	0.7	0.41
Ht × Loc (Exp)	2	3.1$^{\#}$			5.9$^{\#}$			2	0.8$^{\#}$			9.2$^{\#}$		
Td × Loc (Exp)	2	6.9	3.0	0.06	10.9$^{\#}$			2	1.4$^{\#}$			0.3$^{\#}$		
Ht × Td	1	0.1	0.1	0.80	17.6	1.8	0.18	1	0.1	0.1	0.82	0.2	0.0	0.84
Exp × Ht × Td	1	0.2	0.1	0.79	10.8	1.1	0.29	1	0.4	0.3	0.59	0.9	0.2	0.66
Td × Ht × Loc (Exp)	2	0.4$^{\#}$			0.3$^{\#}$			2	0.3$^{\#}$			0.2$^{\#}$		
Res	64	2.4			9.9			16	1.5			4.9		
1-pooled	66	2.3			9.6			18	1.3			4.4		
2-pooled	68	2.3			9.7			20	1.3			4.0		
3-pooled	70				9.6			22	1.3			4.5		

Appendix 3.1. Analyses of variance for relative humidity in crevices or open areas on experimental sandstone slabs, recorded as an index of desiccation stress on four sampling occasions during summer 2006–2007. Experimental slabs were used as replicates (N = 3) to compare among locations (Loc, random), habitat (Hab, fixed; crevice versus open area) and orientation of crevice on slab (Orient, fixed; parallel or perpendicular to the shoreline). Non-significant interactions $^{\#}$ were pooled (interactions containing random factors) or \$ eliminated (interactions containing only fixed factors) if $P > 0.25$ or if its mean square underestimated the residual mean square.

Source of variation		**23 November 2006**			**24 November 2006**			**16 January 2007**			**28 February 2007**		
	df	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	105	28.5	<0.001	70	2.8	0.11	8	1.0	0.33	218	4.7	0.04
Hab	1	862	234.6	<0.001	1156	45.2	<0.001	80	10.1	0.005	1606	33.8	<0.001
Orient	1	10	0.7	0.56	0	0.0	0.96	3	0.4	0.56	18	0.4	0.54
Loc × Hab	1	7$^{\#}$			65$^{\#}$			3$^{\#}$			75$^{\#}$		
Loc × Orient	1	15	4.2	0.06	3$^{\#}$			1$^{\#}$			40$^{\#}$		
Hab × Orient	1	5$^{\$}$			11$^{\$}$			9$^{\$}$			23$^{\$}$		
Loc × Hab × Orient	1	1$^{\#}$			15$^{\#}$			15$^{\#}$			77$^{\#}$		
Residual	16	4			25			8			45		
1-pooled	17	3			25			9			46		
2-pooled	18				23			8			46		
3-pooled	19				26			8			47		

Appendix 3.2. Analyses of variance for relative humidity in crevices or open areas on natural rocky shores on three sampling occasions during summer 2006–2007, recorded as an index of desiccation stress. Replicate measurements (N = 5) were used to compare among exposure to waves (Exp, fixed, sheltered versus exposed), locations (Loc, random, 2 levels nested in Exp), height on shore (Ht, fixed, low or high), habitat (Hab, fixed, crevice versus open area), site (random, 3 levels nested in the interaction Exp × Loc × Ht × Hab). #non-significant interactions pooled ($P > 0.25$).

		18 January 2007			27 February 2007			1 March 2007		
	df	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp	1	0.0	0.0	0.99	525.3	1.4	0.35	234.6	0.2	0.67
Loc (Exp)	2	726.8	15.5	<0.001	366.8	7.7	0.001	976.6	16.8	<0.001
Ht	1	2236.6	3.8	0.19	17.1	0.1	0.85	2215.5	8.3	0.10
Hab	1	3767.5	64.1	<0.001	6606.6	8.6	0.10	2989.0	169.7	<0.001
Exp × Ht	1	19.0	0.0	0.87	103.5	0.3	0.64	40.6	0.2	0.73
Exp × Hab	1	86.1	1.5	0.18	374.1	0.5	0.56	23.1	1.3	0.53
Ht × Loc (Exp)	2	587.6	12.5	<0.001	353.8	7.4	0.001	266.4	4.6	0.01
Hab × Loc (Exp)	2	58.8	1.3	0.29	769.4	16.1	<0.001	17.6#		
Ht × Hab	1	49.6	0.2	0.67	52.8	1.1	0.30	70.3	0.6	0.51
Exp × Ht × Hab	1	90.3	0.4	0.58	19.0	0.4	0.53	35.1	0.3	0.63
Hab × Ht × Loc (Exp)	2	208.7	4.5	0.02	28.5#			113.9	2.0	0.14
Residual	64	46.9			48.5			58.1		
1-pooled	66				47.9			56.9		

Appendix 4.1. Analyses of water flow in crevices or open areas on experimental sandstone slabs on five sampling occasions during (a) winter 2006 and (b) summer 2006–2007. Water-flow is an important environmental variable, affecting gas transport, supply of food and nutrients and suspension/deposition/erosion of sediment. Integrated measures of water flow were obtained from the loss in mass by dissolution from blocks of plaster (clod cards). Clod cards from experimental slabs (N = 3) were used as replicates to compare water flow among locations (Loc, random), orientation of crevice on slab (Orient, fixed; parallel or perpendicular to the shoreline), habitat (Hab, fixed, crevice versus open area). #non-significant interactions pooled ($P > 0.25$).

(a) Winter 2006 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	0.4	0.5	0.48	12.2	59.9	<0.001	18.7	38.3	<0.001	11.5	28.6	<0.001	53.6	51.7	<0.001
Orient	1	1.7	2.1	0.16	2.1	10.2	0.005	2.7	5.6	0.03	1.1	2.8	0.11	0.6	0.6	0.44
Hab	1	8.8	11.3	0.003	0.9	4.5	0.04	9.2	18.9	<0.001	5.9	14.7	0.001	9.3	8.9	0.008
Loc × Orient	1	0.1#			0.1#			0.0#			0.2#			0.0#		
Loc × Hab	1	0.2#			0.0#			0.2#			0.0#			1.1#		
Orient × Hab	1	3.0	3.9	0.06	0.7	1.7	0.41	1.4	2.9	0.11	1.5	3.7	0.07	1.5	1.4	0.25
Loc × Orient × Hab	1	0.8#			0.4	2.0	0.17	0.0#			0.3#			0.0#		
Res	16	0.9			0.2			0.6			0.4			1.2		
1-pooled	17	0.9			0.2			0.5			0.4			1.1		
2-pooled	18	0.8			0.2			0.5			0.4			1.1		
3-pooled	19	0.8						0.5			0.4			1.0		

(b) Summer 2006–2007 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	6.5	9.0	0.007	18.0	43.3	<0.001	18.8	26.0	<0.001	16.3	13.0	0.002	24.2	7.9	0.01
Orient	1	3.5	4.9	0.04	1.6	3.8	0.07	2.1	2.9	0.11	5.4	4.3	0.05	1.1	0.4	0.55
Hab	1	17.9	24.7	<0.001	7.7	18.4	<0.001	7.3	10.2	0.005	9.3	7.4	0.01	21.0	6.8	0.02
Loc × Orient	1	0.4#			0.4#			0.2#			0.6#			1.5#		
Loc × Hab	1	0.2#			0.0#			0.4#			0.1#			3.3#		
Orient × Hab	1	4.3	6.0	0.02	1.2	2.8	0.11	2.6	1.0	0.50	4.6	3.6	0.07	5.9	1.9	0.18
Loc × Orient × Hab	1	0.0#			0.0#			2.6	3.6	0.07	0.1#			0.0#		
Res	16	0.8			0.5			0.8			1.4			3.4		
1-pooled	17	0.8			0.4			0.8			1.4			3.2		
2-pooled	18	0.7			0.4			0.7			1.3			3.2		
3-pooled	19	0.7			0.4						1.3			3.1		

Appendix 4.2. Analyses of loss of mass from plaster clod cards (index of water flow) on natural rocky shores on the upper or lower shore during (a) winter 2007 (three sampling occasions) and (b) summer 2006–2007 (four sampling occasions). See Materials and Methods or Appendix 4.1 for importance of water flow. Three replicate clod cards were used to compare water flow among exposure to waves (Exp, fixed, sheltered versus exposed), locations (Loc, random, 2 levels nested in Exp) and habitat (Hab, fixed, crevice versus open area). $^{\#}$non-significant interactions pooled ($P > 0.25$). Clod cards from different heights on the shore were analysed separately because they were submersed for different durations, thus affecting dissolution of the plaster.

(a) Winter **Height 2 (upper shore)** **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp	1	52.2	25.7	0.04	165.0	3.4	0.21	73.6	16.3	0.06
Loc (Exp)	2	2.0	27.8	<0.001	48.2	30.2	<0.001	4.5	10.6	0.001
Hab	1	0.8	11.6	0.003	1.5	0.3	0.67	1.1	0.4	0.60
Exp × Hab	1	1.1	15.6	0.001	13.0	2.2	0.28	1.6	0.6	0.53
Hab × Loc (Exp)	2	$0.0^{\#}$			5.9	3.7	0.05	2.9	6.9	0.007
Res	16	0.1			0.6			0.4		
1-pooled	18	0.1								

Height 4 (lower shore) **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp	1	7.0	0.1	0.78	34.7	2.3	0.27	48.7	5.2	0.15
Loc (Exp)	2	69.1	94.5	<0.001	15.4	5.6	0.01	9.5	20.3	<0.001
Hab	1	10.0	4.7	0.16	29.0	8.4	0.10	12.1	3.8	0.19
Exp × Hab	1	0.9	0.4	0.58	31.7	9.2	0.09	2.6	0.8	0.46
Hab × Loc (Exp)	2	2.1	2.9	0.08	3.4	1.3	0.31	3.2	6.9	0.007
Res	16	0.7			2.7			0.5		
1-pooled	18									

(b) Summer **Height 2 (upper shore)** **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp	1	39.3	4.8	0.16	74.4	32.4	0.03	84.3	23.6	0.04	101.2	5.3	0.15
Loc (Exp)	2	8.3	5.5	0.01	2.3	7.3	0.005	3.6	9.1	0.002	19.2	73.5	<0.001
Hab	1	1.0	0.3	0.62	3.3	10.4	0.005	2.2	5.6	0.03	2.5	9.4	0.007
Exp × Hab	1	3.2	1.1	0.41	2.9	9.1	0.007	1.1	2.9	0.11	1.9	7.3	0.01
Hab × Loc (Exp)	2	2.9	2.0	0.17	$0.0^{\#}$			$0.1^{\#}$			$0.1^{\#}$		
Res	16	1.5			0.4			0.4			0.3		
1-pooled	18				0.3			0.4			0.3		

Height 4 (lower shore) **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Exp	1	4.2	0.17	0.72	22.7	0.4	0.61	11.9	0.3	0.62	5.1	0.1	0.84
Loc (Exp)	2	24.7	26.3	<0.001	62.1	34.2	<0.001	35.4	23.6	<0.001	94.4	52.3	<0.001
Hab	1	15.6	16.7	0.007	35.6	19.6	0.003	28.4	19.0	<0.004	39.5	21.9	<0.001
Exp × Hab	1	1.8	2.0	0.18	14.2	7.8	0.01	7.5	5.0	0.04	8.9	4.9	0.04
Hab × Loc (Exp)	2	$0.7^{\#}$			$1.1^{\#}$			$1.2^{\#}$			$2.0^{\#}$		
Res	16	1.0			1.9			1.5			1.8		
1-pooled	18	0.9			1.8			1.5			1.8		

Appendix 5. Analyses of forces exerted by waves in crevices or open areas on experimental slabs during (a) winter 2006, four sampling occasions and (b) summer 2006–2007, four sampling occasions, (c) winter 2007 three sampling occasions and (d) summer 2007–2008, two sampling occasions. Scratched areas on smoked-glass slides in wave devices (see Materials and Methods) provided integrated estimates of wave-forces. Forces exerted by breaking waves can reduce opportunities to forage and cause damage or dislodgement. Wave devices on experimental slabs (N = 3) were used to compare among locations (Loc, random), orientation of crevice on slab (Orient, fixed; parallel or perpendicular to the shoreline) and habitat (Hab, fixed, crevice versus open area). Non-significant interactions $^{\#}$pooled (interactions containing random factors) or $^{\$}$eliminated (interactions containing only fixed factors) if $P > 0.25$ or if its mean square underestimated the residual mean square.

(a) Winter 2006 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc		–	–	–	–	–	–	1	8.9	0.3	0.62	191.1	2.8	0.11
Orient	1	44.7	1.1	0.32	308.5	4.8	0.06	1	38.3	1.1	0.31	420.2	0.8	0.53
Hab	1	0.4	0.0	0.92	3.5	0.1	0.82	1	131.2	3.8	0.07	107.0	1.6	0.23
Loc × Orient	1	214.8	5.4	0.05	167.1	2.6	0.15	1	7.2$^{\#}$			517.3	7.6	0.01
Loc × Hab								1	3.9$^{\#}$			2.9$^{\#}$		
Orient × Hab								1	1.6$^{\$}$			55.0$^{\$}$		
Loc × Orient × Hab								1	1.3$^{\#}$			17.6$^{\#}$		
Res	8	39.6			64.5			16	40.4			75.1		
1-pooled								17	38.1			71.7		
2-pooled								18	36.2			67.9		
3-pooled								19	34.7					

(b) Summer 2006–2007 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	14.9	0.3	0.60	45.3	0.5	0.47	673.5	12.2	0.003	59.7	0.5	0.49
Orient	1	56.9	1.1	0.31	167.3	2.0	0.17	536.8	17.0	0.15	85.4	0.7	0.41
Hab	1	22.2	0.4	0.52	3.3	0.0	0.84	2.7	0.0	0.94	1.0	0.0	0.93
Loc × Orient	1	2.3$^{\#}$			1.9$^{\#}$			31.6	0.6	0.46	131.4$^{\#}$		
Loc × Hab	1	1.0$^{\#}$			74.9$^{\#}$			355.4	6.4	0.02	92.3$^{\#}$		
Orient × Hab	1	1.4$^{\$}$			0.5$^{\$}$			57.3	0.2	0.76	30.1$^{\$}$		
Loc × Orient × Hab	1	1.2$^{\#}$			68.0$^{\#}$			375.9	6.8	0.02	32.5$^{\#}$		
Res	16	61.2			89.0			55.4			125.1		
1-pooled	17				87.7						119.6		
2-pooled	18				87.0						118.1		
3-pooled	19				82.8						118.8		

(c) Winter 2007 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	332.9	8.0	0.01	1071.2	5.6	0.03	33.2	0.5	0.49
Orient	1	1.5	0.0	0.85	79.6	0.1	0.78	256.6	1.7	0.41
Hab	1	42.8	1.0	0.32	651.0	3.4	0.08	474.5	7.1	0.02
Loc × Orient	1	0.1$^{\#}$			607.0	3.2	0.09	148.1	2.2	0.15
Loc × Hab	1	25.4$^{\#}$			125.9$^{\#}$			35.9$^{\#}$		
Orient × Hab	1	16.7$^{\$}$			0.2$^{\$}$			99.9	1.5	0.24
Loc × Orient × Hab	1	5.6$^{\#}$			81.5$^{\#}$			6.6$^{\#}$		
Res	16	47.4			202.6			72.1		
1-pooled	17	45.0			195.4			68.3		
2-pooled	18	43.9			191.6			66.5		
3-pooled	19	41.6								

(d) Summer 2007–2008 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	974.5	19.1	<0.001	7.6	1.2	0.28
Orient	1	0.0	0.0	0.99	4.4	29.1	0.12
Hab	1	65.0	1.3	0.27	42.7	8.5	0.21
Loc × Orient	1	289.1	5.7	0.03	0.2	0.0	0.88
Loc × Hab	1	51.2$^{\#}$			5.0	0.8	0.38
Orient × Hab	1	26.1$^{\$}$			3.9	0.1	0.85
Loc × Orient × Hab	1	25.2$^{\#}$			64.7	10.6	0.005
Res	16	52.7			6.1		
1-pooled	17	51.1					
2-pooled	18	51.1					

Appendix 6. Amounts of chlorophyll-*a* (as a measure of availability of micro-algal food) on experimental slabs were estimated using the ratio vegetation index (RVI) derived from digital colour infrared images. Analyses of variance for RVI (a) during summer 2006–2007. Regions of interest from the images ($N = 6$) were used to compare among locations (Loc, random, 3 levels), orientation of crevice on slab (Orient, fixed; parallel or perpendicular to the shoreline), slabs (random; 2 levels nested in Loc × Orient) and habitat (Hab, fixed, crevice versus open area); (b) for eight slabs at each of two locations during winter 2007. To simplify analysis and because previously it had no effect, orientation was not included in the second experiment.

(a) Summer **Source of variation**	**df**	**MS**	**F**	***P***	**(b) Winter** **Source of variation**	**df**	**MS**	**F**	***P***
Loc	2	0.96	2.9	>0.1	Loc	1	0.12	0.12	0.74
Orient	1	0.08	1.9	>0.3	Slab (Loc)	14	1.04	66.41	<0.001
Slab (Loc × Orient)	6	0.33	37.7	<0.001	Hab	1	7.98	36.31	0.10
Hab	1	0.89	3.0	>0.2	Loc × Hab	1	0.22	0.7	0.41
Loc × Orient	2	0.04	0.1	>0.8	Hab × Slab (Loc)	14	0.31	19.8	<0.001
Loc × Hab	2	0.30	6.3	<0.05	Residual	160	0.02		
Orient × Hab	1	0.02	0.1	>0.7					
Hab × Slab (Loc × Orient)	6	0.05	5.4	<0.001					
Loc × Orient × Hab	2	0.15	3.2	>0.1					
Residual	120	0.01							

Appendix 7. Different types of micro-algae contain different combinations of pigments. Thus, information about the composition of pigments in an assemblage of micro-algae provides information about the types of micro-algae in that assemblage. Types and relative amounts of different photosynthetic pigments in assemblages of micro-algae were estimated using derivative analysis of field spectrometry data. To account for differences in total amounts of algae among samples, amounts of pigments in each sample were normalised relative to the amount of chl-*a* in that sample. Analyses of variance of relative amounts of three pigments that made consistently large contributions to multivariate dissimilarities in pigments among samples (see Materials and Methods). During (a) winter 2006; ($N = 3$) and (b) summer 2006–7 ($N = 4$) spectra were used to compare amounts of pigments among locations (Loc, random, winter: 2 levels, summer: 3 levels), orientation of crevice on slab (Orient, fixed; parallel or perpendicular to the shoreline), slabs (random; 4 levels nested in Loc × Orient) and habitat (Hab, fixed, crevice versus open area). Pigment values were all multiplied by 10,000 to facilitate analysis. # non-significant interactions pooled ($P > 0.25$).

(a) Winter 2006 **Source of variation**		**Phycoerythrocyanin**			**Chl-*c***			**Chl-*b***		
	df	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	1	0.618	11.6	0.004	1.053	13.0	0.003	0.076	0.9	0.36
Orient	1	0.084	1.6	0.23	0.050	0.6	0.44	0.002	0.0	0.87
Hab	1	0.006	0.1	0.77	0.010	0.1	0.72	0.003	0.1	0.86
Slab (Loc × Orient)	12	0.057			0.087			0.092		
Loc × Orient	1	0.006$^{\#}$			0.011$^{\#}$			0.000$^{\#}$		
Loc × Hab	1	0.035$^{\#}$			0.016$^{\#}$			0.068	1.9	0.19
Orient × Hab	1	0.029	0.4	0.53	0.001	0.0	0.94	0.021	0.6	0.48
Hab × Slab (Loc × Orient)	12	0.078			0.082			0.038		
Loc × Orient × Hab	1	0.004$^{\#}$			0.050$^{\#}$			0.009$^{\#}$		
Res	64	0.022			0.044			0.038		
1-pooled	13	0.072			0.080			0.036	0.9	0.53
2-pooled	14	0.069	3.2	0.00	0.075		0.08	0.085	2.2	0.02
3-pooled	13	0.053	2.4	0.01	0.081		0.06			
(b) Summer 2006–2007 **Source of variation**	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***	**MS**	**F**	***P***
Loc	2	0.589	5.5	0.01	0.047	4.8	0.02	0.025	0.7	0.49
Orient	1	0.004	0.6	0.53	0.007	1.4	0.35	0.002	1.0	0.42
Hab	1	0.307	10.5	0.08	0.001	0.2	0.71	0.195	1.9	0.30
Slab (Loc × Orient)	18	0.108	51.4	<0.001	0.010	9.2	<0.001	0.034	16.1	<0.001
Loc × Orient	2	0.007	0.1	0.93	0.005	0.5	0.63	0.002	0.1	0.94
Loc × Hab	2	0.029	4.0	0.03	0.006	2.6	0.10	0.101	5.5	0.01
Orient × Hab	1	0.031	4.2	0.05	0.005	1.9	0.19	0.003	0.1	0.72
Hab × Slab (Loc × Orient)	18	0.007$^{\#}$			0.003$^{\#}$			0.020$^{\#}$		
Loc × Orient × Hab	2	0.007			0.002			0.002		
Res	144	0.002			0.001			0.002		
1-pooled	20	0.007	3.5	0.00	0.003	2.5	0.00	0.018	8.7	0.00