FEATURE ARTICLE

Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore

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ABSTRACT: Habitat complexity is a fundamental driver of ecosystem structure and function. Rocky intertidal shores are the classic model system for investigating theoretical and mechanistic models of habitat complexity, because the structural topography is largely biologically independent and stable over time. In the present study, we investigate how static (topographic complexity and heterogeneity) and dynamic (temperature landscape) components of habitat structure influence the abundance and body-size distribution of invertebrates on a rocky shore. Using a novel approach that included high-resolution 3D fractal surface and temperature measurements, we show that topographic complexity, temperature landscape and habitat heterogeneity had largely independent effects on species abundance and body size. Invertebrate abundance was associated with temperature landscape in 7 of 11 species, while variation in body-size was mostly driven by fractal topography in 7 of 10 species. Overall, the body size–abundance relationship was not influenced by habitat structure, indicating that the effects of habitat structure on body size and abundance were largely independent. The results illustrate the value of combining measures of static and dynamic habitat structure to explain and predict biological patterns on rocky shores.

KEY WORDS: Habitat structure · Rocky intertidal · Invertebrates · Fractal topography · Body-size spectra

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INTRODUCTION

Habitat structure is a critical driver of ecosystem composition and function (Heck & Wetstone 1977, Menge et al. 1985, Tews et al. 2004), and hence is often used as a physical surrogate in biodiversity mapping

Dynamic and static habitat traits determine associations of invertebrates on a rocky shore: limpets *Cellana tramoserica* under a ledge.

Photo: J. Meager

and conservation planning (e.g. Banks & Skilleter 2007, McArthur et al. 2010, Schlacher et al. 2010). The basic tenet of this approach is that the measures of habitat structure used are accurate and biologically relevant. Yet, measuring habitat structure can be technically challenging and there is little consensus on the correct metrics to use (Taniguchi et al. 2003).

Habitat structure is generally thought to have 2 independent components that depend on the resolution of the measurements in relation to the size of the organisms under study: heterogeneity, the relative abundance of different structural features such as crevices and macrophytes within a habitat; and complexity, the physical architecture of a habitat (McCoy & Bell 1991). Effects of habitat structure on organism body size and abundance can be interrelated because the availability of microhabitat space within a habitat depends both on

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abundance and body size (Morse et al. 1985, Downes et al. 1998). Smaller organisms can be more numerous than larger organisms in complex structure, because they have more useable space and require fewer resources per individual (Morse et al. 1985, Shorrocks et al. 1991, Gunnarsson 1992). Hence, habitat structure may shape the overall relationship between abundance and body size of an assemblage (i.e. body-size spectra *sensu* Petchey & Belgrano 2010).

The suitability of a set of habitat features to an organism can also vary over time. This is particularly evident on intertidal shores, where sun, wave and tidal exposure create a highly dynamic environment with substantial fluctuations in conditions over time and pronounced gradients in microclimates (Helmuth 1999, Harley & Helmuth 2003). Mobile invertebrates such as gastropods can respond to environmental extremes by moving between microhabitats to ameliorate thermal and desiccation stress (Garrity 1984, Moran 1985, Williams & Morritt 1995, Jones & Boulding 1999), whereas the distribution of sessile species is driven by the longer-term processes of settlement, growth and mortality (Underwood & Fairweather 1989, Hills et al. 1998).

Body size and abundance are therefore likely to be driven by an interaction between different components of habitat structure and microclimate. Rocky intertidal shores are the ideal experimental system to investigate the role of static and dynamic components of habitat structure in determining abundance and body size. On the middle to upper sections of rocky shores, large macrophytes are absent and the surface topography of bare rocks is in itself independent of the biotic community. Structure here is also stable over long time periods and the fauna are directly associated with the surface.

The metric of habitat structure that has gained most support for rocky intertidal shores is the fractal dimension (e.g. Beck 1998, Kostylev & Erlandsson 2001, Johnson et al. 2003, Frost et al. 2005). Fractal geometry describes the self-similarity of objects across scales, and provides the basis of the fractal dimension (Mandelbrot 1967), which increases from 1 to 2 as habitats become more complex (Bradbury & Reichelt 1983, Sugihara & May 1990). On rocky shores, this has been limited to 2D cross-sectional profiles and hence depends on profile orientation where structure is anisotropic (i.e. varies with direction). In contrast, the fractal surface dimension ($2 < D < 3$) measures how completely a 3D surface fills a volume (Murdoch & Dodds 2007, Zawada & Brock 2009) and corresponds closely to the human perception of surface roughness (Dubuc et al. 1989). To our knowledge, fractal surface dimension has not yet been measured on rocky shores.

In the present study, we investigate how static and dynamic habitat structure determine the abundance and body size of invertebrates on a rocky shore. We use an information theoretic approach to compare 4 measures of habitat structure: 3D fractal surface dimension, rugosity, habitat heterogeneity and temperature landscape. The latter measure represents the temperature of invertebrate microhabitats relative to adjacent substrata. Our model species span 2 orders of magnitude in body size and include mobile invertebrates (9 species) and sessile epifauna (2 species). We first test 3 predictive hypotheses based on theoretical predictions: (1) habitat heterogeneity and surface topography (rugosity and fractal surface dimension) have independent effects on body size and abundance patterns (McCoy & Bell 1991), (2) dynamic habitat structure (temperature landscape) predicts the size and abundance of mobile invertebrates, while static habitat structure is a better predictor of the size and abundance of sessile invertebrates (Garrity 1984, Raffaelli & Hawkins 1996) and (3) fractal surface complexity is the best static measure of habitat structure for body size and abundance patterns (Beck 1998, Frost et al. 2005). Finally, we determine whether the overall body-size spectrum of invertebrates is associated with surface topography, heterogeneity or dynamic habitat structure.

MATERIALS AND METHODS

Study sites and field sampling design. Data were collected from 2 adjacent sites on Point Cartwright (26° 41' S, 153° 8' E) on the Sunshine Coast in Queensland Australia: 'Kawana' and 'Platforms' (Fig. 1) between March 9 and 18, 2010. The Platforms site has a northerly aspect, while the Kawana site has a southeasterly aspect and hence more exposure to the prevailing wind and waves from the southeast. The mid to upper tidal zones on both shores have gently sloping rocky platforms dominated by bare rocky surfaces (92% of substrate) interspersed by small patches of sand, tidepools and boulders. Patches of biological structure (encrusting algae and barnacle shells) covered less than 2% of the survey area. Sampling took place within a 3 h period after low tide and was stratified within shore zones, corresponding to sites that were emersed for approximately 4 to 8 h (mid-shore strata) and 8 to 12 h (high-shore strata) on spring tides (Fig. 1). Quadrats (1 m²) were the sampling unit and were positioned at random, but with the provision that if the quadrat area encompassed 50% or more of standing water or sand it was not sampled. Eleven quadrats were taken at each of the 4 site × tidal strata combinations, such that 44 quadrat samples were taken in total.

Fig. 1. Location of sampling quadrats (squares, not to scale) within each shore zone (mid and upper tidal strata) and site (Platforms and Kawana), on Point Cartwright, Sunshine Coast, Australia. MHWS: mean high water springs. Tidal strata were mapped using a differential GPS (aerial image: Google Earth)

Where possible, fauna were identified, measured and counted on site, otherwise a photo was taken and a voucher specimen was collected for subsequent identification in the laboratory. Extremely abundant species (i.e. >1000 ind. m^{-2}) were sub-sampled by counting animals within a $0.25 m^2$ quadrat haphazardly positioned within the larger quadrat frame and multiplying the counts by 4. Maximum shell diameter was measured (see Raffaelli & Hughes 1978) for a total of 3089 invertebrates using a ruler (to 0.5 mm) or Vernier calipers in the field, or an eyepiece reticule in a dissection microscope in the laboratory (animals <2 mm in diameter).

Temperature landscape. Rock surface temperature is strongly related to thermal and desiccation stress experienced by invertebrates (Vermeij 1971, Marshall et al. 2010), and thus the temperature of microhabitats relative to adjacent bare rock plays an important role in determining habitat associations (Garrity 1984, Jones & Boulding 1999, Harley & Helmuth 2003). We measured the temperature of the rock surface at 5 random points (each covering $\sim 0.1 cm^2$) within each quadrat using a non-contact infrared thermometer (Digitech dual-IR) to an accuracy of $<0.5^\circ C$. Five microhabitat temperatures were then measured on the substrate surface to within 2 mm distance from the shell or body surface of 5 randomly selected invertebrates within each quadrat (following Garrity 1984). Five measurements gave adequate precision ($SE/mean < 0.04$) in temperatures both within and outside microhabitats. Where animals were patchily distributed, measurements were made within

5 randomly selected discrete patches. Where fewer than 5 invertebrates were present, points were selected at random. The difference between these measures (mean rock temperatures – mean microhabitat temperature; $n = 5$ for each measurement) gave a zero-centred metric of microclimate, which we here term ‘temperature landscape’ (*td*). Positive values indicate that temperatures were warmer on surrounding substrata than within microhabitats, zero values indicated no difference and negative values denote higher temperatures within microhabitats.

Digital photogrammetry and analysis of topography.

Four overlapping photos were taken of each quadrat from a fixed height (1 m) but from different positions, with a calibrated digital camera (Panasonic Lumix DMC-FT1, 12 MP) with a pixel resolution of 0.3×0.3 mm. Digital Terrain Models (DTMs) were computed using the Adam 3DM photogrammetric software package (Version 2.3.3) at an accuracy of ± 1 mm. Landmarks on the quadrat frame were used to level image sets to the x - y plane and to set the scale. The program located points in 3D using a least-squares bundle block adjustment algorithm. The residuals in each model were inspected, and points removed and bundle adjustments re-calculated where necessary. Final DTMs were visually inspected by comparing them to the original images, quadrat frames were cropped and redundant points removed to reduce datasets to around $100\,000 \times x \ y \ z$ coordinates per frame. Coordinates were then interpolated to $3000 \times$

3000 cell grids using natural-neighbours Delaunay triangulation in Matlab (Version 7.8, MathWorks) and exported as grey-scaled surface plots (i.e. z = pixel colour) in uncompressed TIFF files at a resolution of 600 dpi.

The high-resolution grey-scale surface plots were used to analyse the 3D surface topography in each quadrat with Image J (US National Institute of Health, Bethesda, MD, USA; <http://rsb.info.nih.gov/ij/>). Fractal surface dimension (D) was calculated using the Map-FractalCount plugin (Version 1; author: P. C. Henden) for ImageJ (<http://rsb.info.nih.gov/ij/plugins/index.html>). Briefly, the program used a shifting differential box counting (SDBC) algorithm that maximised the fit of boxes to the images in the x , y and z directions. D was the slope of the log-log relationship between the number and size of the boxes, and ranged from minimum complexity at 2 to maximum complexity at 3. Rugosity (Rq) was calculated as the standard deviation of the residuals from the regression plane using the SurfCharJ plugin of Image J (Version 1c; author: G. Chinga, www.gcsca.net/IJ/SurfCharJ.html).

To numerically describe habitat heterogeneity we quantified the relative abundance of 15 different structural components (Table 1) using random point counting (Coral Point Count; Kohler & Gill 2006). Images were gridded (2 columns $\times$ 3 rows) and 20 random points were overlain in each grid cell. Habitat heterogeneity (H) was based on Simpson's reciprocal index, and ranged from 1, when only one structural component was present in a quadrat, to 17 when all 15 structural components had equal coverage.

Table 1. Percentage cover of each structural component at each site (Kawana and Platforms) and shore zone (mid and upper), summed over the $11 \times 1 \text{ m}^2$ quadrat samples for each combination of site and strata

Structural component	Kawana		Platforms	
	Mid	Upper	Mid	Upper
Algae ^a	0.2	0	1.6	0.5
Barnacle shells	4.9	0	0	0
Boulders	0	0	14.2	23.6
Course rubble	0	0	0.0	0
Crevice	3.7	1.9	5.0	3.6
Dislodged seagrass	0	0	0	0.9
Fissures (cracks)	2.2	3.5	1.6	3.5
Flat pavement	83.2	91.5	54.3	54.7
Large flat rocks	0.0	0	12.3	5.1
Pits	0.1	1.2	0.7	2.1
Sand	0.0	0.5	4.2	3.1
Shell grit	0.5	0.1	0.2	0.1
Small rocks	0	0	0	1.6
Water	1.8	1.2	4.2	1.2
Other debris	3.4	0	1.9	0

^aPredominantly *Enteromorpha* spp.

Data analysis. Physical structure and temperature landscape was first compared between sites (Platforms, Kawana) and tidal strata (mid, upper) using 2-way, fixed-factor ANOVA. Linear modelling and model selection based on information theoretic criteria were used to determine the relationship between the abundance and body size of the common species (i.e. ≥ 20 individuals), and measures of habitat structure. Rugosity (Rq), fractal surface dimension (D), habitat heterogeneity (H) and temperature landscape (td) were included as continuous explanatory variables. Site, tidal strata and site $\times$ tidal strata were included as categorical explanatory variables to test whether the regression lines of abundance and body size against habitat structure were homogeneous among shores and strata. This was because previous research (e.g. Harley & Helmuth 2003, Marshall et al. 2010) suggests that the thermal ameliorating effect of habitat structure may be more pronounced (1) at the Platforms site because it is less exposed to wind and wave splash and (2) in the upper tidal strata because it is exposed to solar heating for longer. Because multiple body-size measurements were available for each measure of habitat structure (i.e. within each quadrat), analyses of size patterns included quadrat number as a random effect and were fitted using linear-mixed models (lme4 library Version 0.999375-35 of the R package Version 2.11.1; R Development Core Team 2010). Site $\times$ strata categories were excluded where data were insufficient. Scatter plots were used to check for linearity, and residual plots were used to assess the fit of models. Size data were normalised by $\log_e$ transformation and abundance data by square-root transformation.

In the case of both body size and abundance analyses, the set of *a priori* candidate models for each species included models with separate slopes to test if habitat structure effects depended on site and strata. To facilitate identifying and making inferences from the most parsimonious model, the global model including all explanatory variables was then simplified using a nested procedure that removed least significant terms until reaching a model that included only the intercept (Faraway 2005). The final model was selected from the candidate models using Akaike weights (w_i) based on second-order bias corrected Akaike's information criterion (AIC_c) (full equations in Burnham & Anderson 2002). This information theoretic approach gives a measure of the weight of evidence, or probability that the final model is the best model in the set, given the data (Burnham & Anderson 2002), and is now recommended over stepwise procedures (Whittingham et al. 2006, Mundry & Nunn 2009).

Inferences on the relative importance of explanatory variables are much improved by being based on all of the candidate models rather than just the final model

(Burnham & Anderson 2002, O'Hara & Tittensor 2010). The relative importance of each habitat structure variable was therefore determined over the subset of candidate models in which that variable appeared, using mean w_i to account for bias in representation from the nested model simplification procedure. The relative importance of each habitat structure variable was further assessed by determining if each variable was (1) within the 95% confidence set of candidate models (Zuur et al. 2009) and (2) more than twice as likely as the other variables in the set based on evidence ratios (Burnham & Anderson 2002).

Standardised major axis (SMA) regression was used to determine the relationship between abundance and body size (lmodel2 library Version 1.6-3; R-2.11.1) using mean values for both variables per quadrat. All 15 invertebrate species found were included, and the relationship was linearised by log-log transformation. SMA slopes were compared between site and strata using log-likelihood ratio tests (G^2 , smatr library Version 2.1; R-2.11.1). Abundance–body size residuals were then regressed against the habitat structure variables to test for the influence of habitat structure on body-size spectra.

RESULTS

Surface topography and temperature landscape

Temperature landscape (td) varied from a strong shading effect of microhabitats (i.e. 13.1°C cooler in microhabitats) to the reverse, with slighter cooler temperatures on the adjacent surface ($td = -2.7^\circ\text{C}$). The maximum temperature of the rock surface was 50°C. Microhabitats were significantly cooler than the surrounding substrata at Platforms than at Kawana ($F_{1,40} = 25.3$, $p = 0.025$), but similar between tidal strata ($F_{1,40} = 2.9$, $p = 0.1$, site $\times$ strata: $F_{1,40} = 0.1$, $p = 0.75$) (Table 2). Habitat heterogeneity (H) ($\log_{10}$ transformed, $F_{1,40} = 4.1$, $p = 0.049$) and fractal surface dimension (D) ($F_{1,40} = 5.4$, $p = 0.025$) were also higher at Platforms than Kawana, but did not differ between

strata or site $\times$ strata categories ($p = 0.3$ to 0.9). Rugosity (Rq) did not vary between sites, strata or site $\times$ strata ($p = 0.18$ to 0.64). The different measures of habitat structure were not significantly correlated (Fig. 2, all $p > 0.1$), and in general, measured separate habitat attributes (Fig. 3).

Invertebrate abundance

Overall, td was the best predictor of invertebrate abundance, but there was no single habitat structure variable that explained abundance in all species (Table 3). Multi-model averaging indicated that td was a key predictor in 7 (of 11) species, H was important in 4 species, Rq in 4 species and D in 2 species (Table 3). Eight of the 11 species examined had 2 or more habitat structure variables in the 95% CI interval set of candidate models (Table 3). In 2 species, the upper-shore barnacle *Chthamalus antennatus* and the whelk *Morula marginalba*, there was a clear 'best' model amongst the set of candidate models (i.e. $w_i > 0.8$; Table 4) that explained significant variation in abundance (i.e. $R^2 > 0.3$ and $p < 0.05$). In both instances, H was associated with abundance, but this relationship varied between sites and strata for *C. antennatus* and between sites for *M. marginalba* (Table 4, Fig. 4).

Invertebrate body size

Overall, D was the most important predictor of invertebrate body size. Multi-model averaging included D in 7 (of 10) species, H in 2 species, and td and Rq in only 1 species each (Table 5). There was a clear 'best' model amongst the set of candidate models for 5 of the 10 species examined (Table 6). *Cellana tramoserica* was significantly smaller in heterogeneous habitats, and *Morula marginalba* was significantly smaller in heterogeneous habitats only at the Platforms site (Table 6, Fig. 4). *Nodilittorina pyramidalis* was significantly larger in quadrats with higher fractal dimension (i.e. more convoluted surface) at Platforms (Fig. 4).

Table 2. Measures (mean $\pm$ SE) of temperature and habitat structure within each site and strata

Site and stratum	Substrata temp. ($^\circ\text{C}$)	Microhabitat temp. ($^\circ\text{C}$)	Temp. landscape (td) ($^\circ\text{C}$)	Fractal (D)	Heterogeneity (H)	Rugosity (Rq)
Kawana						
Mid	29.23 $\pm$ 1.38	27.94 $\pm$ 1.25	1.30 $\pm$ 0.74	2.44 $\pm$ 0.02	1.35 $\pm$ 0.09	41.81 $\pm$ 3.10
Upper	30.05 $\pm$ 2.07	30.21 $\pm$ 2.05	-0.16 $\pm$ 0.46	2.49 $\pm$ 0.02	1.34 $\pm$ 0.15	38.48 $\pm$ 2.77
Platforms						
Mid	34.44 $\pm$ 2.04	28.63 $\pm$ 1.69	5.82 $\pm$ 0.78	2.52 $\pm$ 0.03	1.63 $\pm$ 0.18	38.75 $\pm$ 5.08
Upper	39.00 $\pm$ 1.94	35.00 $\pm$ 1.67	4.00 $\pm$ 1.50	2.52 $\pm$ 0.02	1.50 $\pm$ 0.11	44.73 $\pm$ 3.55

Fig. 2. Relationship between the different measures of static and dynamic habitat structure. r : product-moment correlation coefficient ($n = 44$); td : temperature landscape

Table 3. Multi-model relative importance (mean Akaike weight, $\bar{w}_i$) of each measure of habitat structure as a predictor of invertebrate abundance, averaged over 12 candidate models for each species. The higher taxonomic group of each species is given in parentheses (Ga: gastropod; Ba: barnacles; Ch: chiton). +: explanatory variables that were included in the 95% confidence interval set; **bold** font denotes variables that had a similar likelihood to the optimal explanatory variable (i.e. evidence ratio of ≤ 2)

Species	Fractal surface (D)	Rugosity (Rq)	Heterogeneity (H)	Temp. (td) landscape
<i>Nodilittorina acutispira</i> (Ga)	0.016+	0.074+	0.007	0.024+
<i>Chthamalus antennatus</i> (Ba)	<0.001+	0.012+	0.182+	<0.001
<i>Nodilittorina unifasciata</i> (Ga)	0.002	0.015+	0.039+	0.036+
<i>Nodilittorina pyramidalis</i> (Ga)	0.010	0.031+	0.063+	0.107+
<i>Planaxis sulcatus</i> (Ga)	<0.001	<0.001	<0.001	0.125+
<i>Bembicium nanum</i> (Ga)	0.110+	0.010	<0.001	<0.001
<i>Morula marginalba</i> (Ga)	<0.001	<0.001	0.111+	<0.001
<i>Tesseropora rosea</i> (Ba)	0.002	0.031+	0.012	0.028+
<i>Littoraria undulata</i> (Ga)	0.114+	0.028+	0.009	0.111+
<i>Cellana tramoserica</i> (Ga)	0.002	0.084+	0.008	0.044+
<i>Acanthopleura gaimardi</i> (Ch)	0.002	0.028+	0.010	0.022+

Mean body size in *Nodilittorina acutispira*, *Planaxis sulcatus* and *Littoraria undulata* was largely determined by variation between quadrats rather than any measure of habitat structure, i.e. 'best' models ($w_i > 0.8$) included only the random-effect intercept (Table 6).

Scaling of body-size spectra

Here, we tested the hypothesis that the abundance-body size relationship of the invertebrate assemblage scaled to surface topography or dynamic habitat structure. The negative relationship between total animal abundance and mean body size was significant (log-log transformed, $n = 43$,

Fig. 3. Gridded Digital Terrain Models (DTM) for (a) a 1 m² quadrat with flat pavement and small surface fissures (fractal surface dimension, $D = 2.54$; rugosity, $Rq = 23.61$; habitat heterogeneity, $H = 1.37$; temperature landscape, $td = -1.30$) and (b) a quadrat with a ledge and prominent surface fissures ($D = 2.47$, $Rq = 51.26$, $H = 1.30$, $td = 1.91$). The surface in (b) has a more pronounced departure from a level plane, and hence the higher Rq

Fig. 4. Examples of final models including only a single habitat structure predictor: (a) habitat heterogeneity (H) and abundance (logarithmic scale) of *Chthamalus antennatus*, (b) H and abundance (logarithmic scale) of *Morula marginalba*, (c) fractal surface dimension and mean-body size of *Nodillittorina pyramidalis*, and (d) H and mean-body size of *M. marginalba*. (a–d) Circles: Kawana; triangles: Platforms. (a,b) White symbols: mid intertidal; black symbols: upper intertidal

Table 4. Final models of invertebrate abundance (full species names given in Table 3) in relation to habitat rugosity (Rq), fractal surface (D), habitat heterogeneity (H) and temperature landscape (td). Models summarised here are those with the highest Akaike weight (w_i) within each set of candidate models. n: number of individuals; Par.: number of model parameters (may include the overall intercept, site, strata, site $\times$ strata); R^2 : coefficient of multiple determination. Separate slopes (β) are given when regression coefficients differed between sites (K: Kawana; P: platforms), tidal strata (u: upper; m: mid) or site $\times$ strata. -: neither Rq , D , H nor td were included in the final model. * $p \leq 0.1$, ** $0.01 < p \leq 0.05$, *** $p \leq 0.01$ ($H_0: \beta = 0$)

Species	n	w_i	Par.	R^2	Regression coefficients (β)
<i>N. acutispira</i>	48249	0.28	3	0.17	$\beta Rq = -1.079^{**}_{u, 0.026_m}$
<i>C. antennatus</i>	4706	0.84	5	0.47	$\beta H = -0.89_{K,u}, 2.028^{***}_{K,m}, 1.71^{***}_{P,u}, 22.0^{**}_{P,m}$
<i>N. unifasciata</i>	855	0.38	2	0.08	–
<i>N. pyramidalis</i>	312	0.19	5	0.33	$\beta H = -1.02, \beta td = -0.20^{**}$
<i>P. sulcatus</i>	281	0.99	2	0.09	$\beta td = 0.18$
<i>B. nanum</i>	215	0.50	3	0.26	$\beta D = -6.57^*$
<i>M. marginalba</i>	118	0.99	4	0.30	$\beta H = -0.15_p, 2.74^{**}_K$
<i>T. rosea</i>	112	0.20	2	0.03	–
<i>L. undulata</i>	47	0.24	6	0.35	$\beta D = 2.74^*, \beta td = 0.05$
<i>C. tramoserica</i>	40	0.32	3	0.16	$\beta Rq = 0.01$
<i>A. gaimardi</i>	20	0.36	1	0.03	–

Table 5. Multi-model relative importance (mean Akaike weight, $\bar{w}_i$) of each measure of habitat structure as a predictor of invertebrate body size (full species names given in Table 3). R: number of candidate models; +: explanatory variables that were included in the 95% confidence interval set; **bold** font denotes variables that had a similar likelihood to the optimal explanatory variable (i.e. evidence ratio of ≤ 2)

Species	R	Fractal (D)	Rugosity (Rq)	Heterogeneity (H)	Temp. landscape (td)
<i>N. acutispira</i>	12	<0.001	<0.001	<0.001	0.002
<i>C. antennatus</i>	12	<0.001	<0.001	0.020+	0.002
<i>N. unifasciata</i>	12	0.457+	0.001	0.010+	<0.001
<i>N. pyramidalis</i>	10	0.162+	<0.001	0.0169	0.010
<i>P. sulcatus</i>	8	<0.001	<0.001	<0.001	<0.001
<i>B. nanum</i>	10	0.100+	<0.001	0.002	0.113+
<i>M. marginalba</i>	10	0.287+	<0.001	0.014+	<0.001
<i>T. rosea</i>	3	0.611+	0.004	0.258+	0.029
<i>L. undulata</i>	5	0.014	0.015+	0.007	0.011
<i>C. tramoserica</i>	10	0.122+	<0.001	0.144+	0.002

$r^2 = 0.23$, $p = 0.001$, SMA intercept = 9.46, slope = -2.46 , Fig. 5), and did not significantly differ between sites ($G^2 = 0.48$, $p = 0.49$) or strata ($G^2 = 1.46$, $p = 0.23$). However, this relationship was not significantly affected by D ($r^2 = 0.014$, $\beta \pm SE = -2.59 \pm 3.38$, $p = 0.45$), H ($r^2 = 0.004$, $p = 0.69$), Rq ($r^2 = 0.009$, $p = 0.65$), or td ($r^2 = 0.028$, $p = 0.67$), nor did we find any combined (joint) effects of predictor variables (all $R^2 < 0.036$). Hence, there was no significant support for the hypothesis that body-size spectra scaled to surface topography or dynamic habitat structure.

DISCUSSION

Our results demonstrate the value of including both dynamic (temperature landscape) and static structural components of habitats in studies investigating relationships between habitat structure and biota. Fractal surface dimension, rugosity, temperature landscape and habitat heterogeneity measured independent components of habitat structure (Figs. 2 & 3), and their value as predictors depended on the ecological response variable: temperature landscape was important in determining abundance, whereas fractal dimension had a key influence on body size.

Static habitat structure

This is, to our knowledge, the first study to measure the fractal dimension of rocky shores in 3D. We hypothesised that fractal surface dimension would be the best static measure of habitat structure to predict invertebrate body size and abundance, based on earlier studies on rocky shores (Kostylev et al. 1997, Beck 1998, Frost et al. 2005) and in other habitats (e.g. Warfe et al. 2008). While it was a good predictor of body size, it generally performed poorly in predicting abundance patterns. This may be because, like 2D fractal measures, fractal surface dimension does not adequately describe features that represent only a small proportion of the sampled surface (Hills & Thomason 1996, Beck 2000). Topographic features such as small fissures and pits can, however, have an important influence on local invertebrate abundance (Raffaelli & Hughes 1978, Menge et al. 1985, Underwood 2004).

Fractal surface dimension was calculated over 3 magnitudes of scale (from 1 to 1000 mm) and thus included scales likely to be

relevant to the size range of all the invertebrates in our study (Gee & Warwick 1994). In theory, the fractal geometry of habitat surfaces also scales directly with the relationship between body size and useable space, because fractal landscapes have a larger surface area at smaller scales (Morse et al. 1985, Sugihara & May 1990, Shorrocks et al. 1991, Gunnarsson 1992). In contrast, rugosity was based on departure from a level surface at a single scale (1 mm), and was sensitive to courser habitat features such as smooth curved surfaces (Fig. 3). This is likely to be the reason that the fractal dimension was a better predictor of body size than rugosity.

Table 6. Final models of invertebrate body size (mean $\pm$ SD, full species names given in Table 3) in relation to habitat rugosity (Rq), fractal surface (D), habitat heterogeneity (H) and temperature landscape (td). Models summarised here had the highest Akaike weight (w_i) within each the set of candidate models. n: number of individuals; Par.: number of model parameters (may include the overall intercept, site, strata, site $\times$ strata, and random variation between quadrats). Separate slopes (β) are given when regression coefficients differed between sites (K: Kawana; P: Platforms), tidal strata (u: upper; m: mid) or site $\times$ strata. –: neither Rq , D , H nor td were included in the final model. * $p \leq 0.1$, ** $0.01 < p \leq 0.05$, *** $p \leq 0.01$ ($H_0: \beta = 0$). Final linear mixed effect models were fitted using restricted maximum likelihood

Species	n	Body size (mm)	Par.	w_i	Regression coefficients (β)
<i>N. acutispira</i>	1003	1.7 ± 0.4	2	0.84	–
<i>C. antennatus</i>	517	3.8 ± 2.5	4	0.61	–
<i>N. unifasciata</i>	638	4.6 ± 1.9	4	0.92	$\beta D = 0.66_K, 1.50_P$
<i>N. pyramidalis</i>	294	3.6 ± 2.1	4	0.77	$\beta D = 2.42_K, 1.68_P^{***}$
<i>P. sulcatus</i>	59	13.6 ± 3.4	2	0.99	–
<i>B. nanum</i>	214	17.9 ± 4.6	3	0.75	–
<i>M. marginalba</i>	120	10.1 ± 7.3	4	0.87	$\beta H = 0.16_K, -0.52_P^*$
<i>T. rosea</i>	127	1.5 ± 1.7	3	0.61	$\beta D = -5.35$
<i>L. undulata</i>	47	4.1 ± 2.2	2	0.91	–
<i>C. tramoserica</i>	38	27.5 ± 12.8	4	0.51	$\beta D = -1.52, \beta H = -1.36^{***}$

Habitat heterogeneity was the best static habitat structure predictor of abundance patterns, and was associated with body size and abundance of the upper-shore barnacle *Chthamalus antennatus*. The index we used for habitat heterogeneity (Simpson's index) gives a measure of the variation in the distribution of habitat components, weighted towards the most common

structural components (Magurran 2004). Hence, it could capture structural variation not accounted for by fractal surface dimension or rugosity.

When estimating the fractal dimension (D) of natural surfaces, such as rocky substrata, investigators should consider that a number of methods may be used and they may produce different results (Zhou & Lam 2005, Zawada & Brock 2009). It is therefore difficult to compare estimates of D where different measurement and calculation techniques have been used; this should be the subject of future studies.

Dynamic habitat structure

In general, invertebrate abundance was associated with temperature landscape (Table 3), while static habitat attributes were better predictors of

body size (Table 5). A parsimonious explanation for this disparity is that the body size and abundance patterns in our study reflect processes occurring over different time scales, and hence are linked to different habitat features. Abundance of mobile species on rocky shores may simply reflect microhabitat preferences in response to short-term changes in dynamic habitat structure (i.e. temperature and microclimate landscape; Jones & Boulding 1999). In contrast, the link between static habitat structure (surface topography) and body size may be associated with the suitability of habitats for growth and survival over much longer time scales (Williams & Morritt 1995, Jones & Boulding 1999). However, temperature landscape was ranked second amongst the habitat structure variables in the modelling for abundance patterns of the barnacle *Tesseropora rosea*, suggesting that movement between habitats was not the only explanation for the observed decoupling of habitat effects on size and abundance patterns. The data therefore do not support the prediction that dynamic habitat structure would have little importance in explaining the size and abundance patterns of sessile invertebrates, and suggests that larval settlement patterns may also be affected by dynamic habitat structure.

Johnson et al. (2003) suggested that regional climatic differences may determine the value of surface complexity to rocky intertidal invertebrates. For example, a topographic feature providing suitable microclimate on a temperate shore may not provide sufficient refuge from thermal stress or desiccation on a tropical shore. Thus the subtropical location of our study site may

Fig. 5. Relationship between invertebrate abundance and body size fitted by standardised major axis regression (dotted lines, 95% confidence intervals). Both variables are averaged for each quadrat

explain why temperature landscape was such an important driver of invertebrate abundance in our study. Yet numerous field studies across geographic regions, including temperate areas and the tropics, have shown that intertidal invertebrates respond behaviourally to temperature gradients (e.g. Garrity 1984, Moran 1985, Williams & Morritt 1995, Helmuth 1999, Jones & Boulding 1999). On a finer scale, the relationships between temperature landscape and invertebrate abundance were also similar between sites in our study, despite the warmer substrata and stronger modulation of temperature extremes by microhabitats at the more sheltered 'Platforms' site (Table 2). Additional sites would be required to separate the effects of wave and wind exposure from other spatial processes. Nevertheless, our results indicate that temperature landscape is likely to be a valuable metric to be used in future studies of habitat structure on rocky shores, regardless of climatic zone.

Scaling of body-size spectra

Habitat structure did not influence body-size spectra in our study. One reason for this may be that primary space was not limiting, an explanation supported by the shallow slope of the body size–abundance relationship (Hughes & Griffiths 1988) and that bare rock accounted for 92% coverage of the overall quadrat surfaces in our study (Table 1). Negative animal abundance–size relationships such as those observed in our study are often observed in studies where body sizes span several orders of magnitude (Blackburn & Gaston 1997), and have been attributed to varying energetic requirements of animals of different sizes, coupled with size-specific patterns of habitat use (reviewed by Gaston & Blackburn 2000). In benthic systems, body-size spectra may also be an emergent property of complex synergistic and antagonistic interactions between species (Geller 1991, Navarrete & Menge 1997, Bruno 2003, Kostylev et al. 2005). Determining whether or not such processes were significant in the present situation would require specific manipulative field studies.

Conceptual models of habitat structure

As predicted, habitat heterogeneity and structural complexity (rugosity and fractal surface dimension) had very different effects on invertebrate abundance and body size. Hence, our study provided empirical support for the complexity and heterogeneity axes in the often-cited 3-axes graphical model of McCoy & Bell (1991). In the context of this conceptual framework, we included an additional dimension in our

study—dynamic habitat structure—and show that the predictive power of abundance models in our study was stronger when this aspect of habitat structure was taken into account. Temperature landscape is truly dynamic, and varies considerably over seasons and shorter time scales, whereas the topographic surface of rocky shores is relatively invariant over the life span of organisms living on rocky shores. Incorporating microclimate into conceptual frameworks of habitat complexity may be valuable, because it is more likely to match the biological role of habitat structure.

CONCLUSIONS

Habitat structure is an important driver of abundance and body size of invertebrates on rocky shores (Chapman 1994, Underwood & Chapman 1989, Johnson et al. 2003), and biological responses to variations in habitat features differ between taxa (Beck 2000, Tews et al. 2004, Firth & Crowe 2010). Here we show the effects of habitat structure differ even within species, and that the effects of habitat complexity on body size and abundance may be decoupled. Hence, no single metric of habitat structure was the best predictor of the observed biological patterns. Instead, it was the combination of temperature landscape and topographic complexity that best described the abundance and body size of invertebrates on rocky shores.

Acknowledgements. We thank M. Kalvatn for help in the field, D. Zawada and A. Greenhill for technical advice, and G. M. Martins and 3 anonymous reviewers for helpful comments on the manuscript. This work was partly funded by the Australian Federal Government (Environment Australia) administered in the field through South-East Queensland Catchments (SEQC) and the Sunshine Coast Regional Council (SCRC). We especially thank S. Chapman (SEQC) and M. Smith and J. O'Connor (SCRC) for championing the project.

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Editorial responsibility: Lisandro Benedetti-Cecchi, Pisa, Italy

*Submitted: November 16, 2010; Accepted: March 8, 2011
Proofs received from author(s): April 21, 2011*