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Availability of microhabitats explains a widespread pattern and informs theory on ecological engineering of boulder reefs

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ABSTRACT

The availability of suitable microhabitats has emerged as a key requirement for maximising species diversity gains from ecological engineering of coastal habitats. This includes intertidal boulder field habitat, which is threatened by increasing urbanisation. We examined faunal use of microhabitats offered by natural intertidal boulders on two continents, South Africa and Australia, and then used artificial boulders to test possible mechanisms driving the observed patterns. Gaps often occur between the undersides of boulders and the substratum on which they lie. Substrata underneath boulders are generally uneven, so gaps can occur anywhere along the boulder undersurface, but gaps are generally larger near the edges of naturally-occurring boulders. Boulder edges were found to provide a microhabitat that had greater densities of almost all macrofauna than closer to the centre of boulder undersides. To test the model that microhabitat use of boulder edges reflects their larger gap sizes (relative to boulder centres), artificial boulders were constructed with the underside surface either flat, or with a gap underneath mimicking the mean size of the gap normally found only under boulder edges (when their average shape is considered among numerous naturally-occurring boulders). Artificial boulders were deployed intertidally for seven weeks, and macrofaunal colonisation was compared (a) between flat boulders and those with gaps, and (b) between edges and centres. Five times more macrofauna colonised boulders with artificial gaps, while no effect of proximity to edges was found when the gap-width was controlled for. The size of gaps under boulders appears to be an important microhabitat feature that can explain a widespread distributional pattern in the diverse assemblages of boulder fields. Such gaps are clearly used by numerous species, including some that are rare or commercially important. Provision and augmentation of this microhabitat should be considered for any ecological engineering project that involves intertidal or subtidal boulders.

1. Introduction

Boulder reefs are key habitats that can be degraded or lost during coastal urbanisation, and that are artificially replaced in projects of ecological engineering or restoration (Chapman, 2012; Chapman, 2013; Kilfoyle et al., 2013; Støttrup et al., 2014). This habitat has featured in the recent push to understand how artificial substrata, including seawalls and breakwaters, compare ecologically to the natural substrata they often replace (Tan et al., 2015; Dong et al., 2016; Ferrario et al., 2016), and what can be done to maximise the habitat value of engineered structures (Browne and Chapman, 2014; Dafforn et al., 2015; Perkins et al., 2015; Evans et al., 2015). A consensus has developed (Aguilera et al., 2014; Firth et al., 2014; Coombes et al., 2015; Martins et al., 2016) that consideration of small-scale microhabitats is crucial, and this is particularly relevant to boulder fields, in which a wide range of species are habitat, or microhabitat, "specialists" (Chapman, 2012). There is still much ambiguity regarding which features of microhabitats constitute their specific requirements; for example, it is currently unknown why a range of boulder species appear to aggregate on certain boulders, while large proportions of other boulders are mostly unutilised (Chapman, 2002; Grayson and Chapman, 2004; Smoothey and Chapman, 2007; Liversage and Benkendorff, 2013). Our inability to identify which features attract such aggregations to boulders must reduce the efficiency of ecological engineering projects that aim to maximise species richness, and there is an increasing recognition that such projects would benefit from as extensive an understanding as possible of the system's general natural history (Hawkins et al., 2015), particularly if it were possible to mimic the desired properties in artificial boulders.

The provision of different quality of habitat by different sized intertidal boulders is one aspect of boulder habitat has been widely studied (Sousa, 1979; McGuinness, 1987). Small boulders are easily moved by wave action, while very large boulders are moved only during extreme

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events (e.g. Mastronuzzi and Sanso, 2000; Goto et al., 2007). Movement interrupts successional sequences of attached communities, resulting in a "patchwork" of successional stages across naturally-occurring boulder fields (Sousa, 1979). During recent attempts at ecological engineering of a boulder habitat (Firth et al., 2014), few effects of boulder size have been found when boulders have been stabilised. In situations where boulders are not stabilised, but overturned relatively frequently, the habitats provided by the undersides of boulders generally support more organisms than the upper sides (Maughan and Barnes, 2000; Le Hir and Hily, 2005), and are occupied for a variety of reasons. For some species, this is probably associated with protection from predators. For example, juvenile sea urchins often shelter in cryptic habitats under boulders as a response to predators (Sala and Zabala, 1996), while, as adults, they fulfill the same function as miniature boulders themselves, offering protection to small molluscs (Tarr et al., 1996; Chapman and Smoothey, 2014), which rapidly disappear on removal of the urchins (Day and Branch, 2002; Chapman and Smoothey, 2014). Other species, such as detritivores, may benefit from trapping of large particulate material immediately under boulders or enrichment by small particles of detritus in the sediments that often accumulate there (e.g. Lopez and Levinton, 1987; Riisgard and Banta, 1998). Growth rates of suspension feeders can be altered through very small scale manipulation of hydrodynamics (McQuaid and Mostert, 2010), and such species may be able to take advantage of accelerated water flow immediately around boulders as waves break (Denny et al., 2003; Benner et al., 2010). The types of species that are "specialists" of boulders (Chapman, 2012) include such detritivores, for example the South African holothurian, *Roweia stephensoni*. This species is virtually confined to, or at least shows very heavy dependence on the undersides of boulders (Foster, 1994; pers. obs).

The boulders themselves are also heterogenous environments, as there is evidence that the undersides of individual boulders provide numerous microhabitats. An early account of these microhabitats was provided by Choi and Ginsberg (1983), who described the presence of multiple "microzones" across the under-surfaces of individual boulders in Florida. The microzone close to boulder edges was dominated by crustose algae, whereas the microzone close to the centre of the underside was dominated by sessile polychaetes. More recent work has provided further evidence of under-boulder microhabitat diversity, and highlights the dissimilarity of microhabitats at areas close to the boulder edge vs areas close to the centre of the underside for mobile species. For example, Liversage et al. (2012) found that in South Africa and Australia, chitons were consistently positioned at 60–80% of the distance from the centre point to the edge, with variability occurring depending on the underlying substratum type.

Factors driving differences in species associations with certain under-boulder microhabitats may include: 1) the microhabitat's proximity to the boulder edge, and 2) the width of the gap between the boulder and the underlying substratum in the microhabitat. Proximity to the edge may be important for reasons such as light availability and growth of algae, which is greater on exposed surfaces (e.g. Pacheco et al., 2010), and so likely greater at boulder edges than near centres of undersides. Alternatively, the gap between the boulder and underlying substratum may be important simply because, particularly for larger species, space is required for their bodies to fit. Teasing apart effects of "edge-proximity" and the "under-boulder gap" by sampling naturally-occurring boulders is, however, difficult because these variables can be confounded. Microhabitats in close proximity to edges generally have greater gap widths relative to microhabitats near the center of boulder undersides. Although the gap width at any given position under a boulder will vary contextually (i.e. according to the boulder's shape, or how it rests relative to adjacent boulders or other reef features) it has been demonstrated empirically that the gap is greater close to the edge when the average of many boulders is considered (Liversage, 2012). Understanding the importance of such boulder variables may be key for engineering of this habitat (Chapman, 2012, 2013). In this study, inter-microhabitat patterns on naturally-occurring boulders were quantified from sites in South Africa and Australia. Then, in the former country, the causality behind the correlative pattern found was tested in a manipulative field experiment (sensu Underwood, 1990). Artificial boulders were constructed that allowed the underside gap-width to be manipulated and we measured variables from them related to abundances and diversity of colonising species. The hypothesis of importance was whether more macrofauna would colonise boulders with the greater gap-widths. 'Edge-proximity' may also separately be an important factor, so the hypothesis was tested that more macrofauna would occur close to the edge, even if the gap-width there is the same as at the centre of the underside. In addition, our experiment was designed to examine whether the "gap-width" and "edge-proximity" factors have separate or interactive effects.

2. Material and methods

Patterns on naturally-occurring boulders were quantified with an initial mensurative experiment. Mobile macrofauna were sampled at two random sites near Cape St Francis in South Africa (34°11′44.2″S, 24°52′11.5″E) and three near Sydney in eastern Australia (Cape Banks 33°59′52.4″S + 151°14′40.0″E, Long Bay 33°57′51.2″S + 151°15′09.8″E, Long Reef 33°44′17.5″S + 151°18′39.4″E). Twelve boulders were haphazardly selected and overturned in the South African sites, and twenty in the Australian sites. Photographs were taken of the underside surface, as well as the side view. To eliminate the effects of their size, only boulders of similar dimensions were sampled, with the mean underside surface area measured from the photographs being 213 cm^2.

Counts of mobile organisms (>3 mm) were taken from the photographs. Densities were measured by dividing counts by area, which was measured using the scaled photographs after being imported into the programme SketchUp v8. Measurements were taken from two areas: 1) centre-area, defined as the area within 0–33% of the distance from the centre point (centroid) of the underside to the circumference, or 2) edge-area, defined as the area within 66–100% of the distance from the underside centroid to the circumference. When viewed from two-

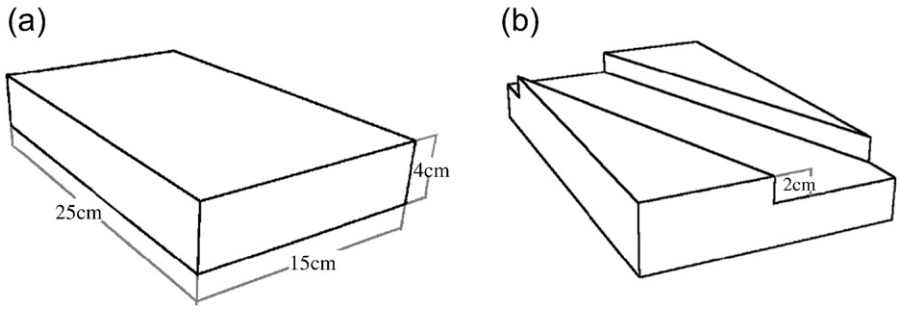

Fig. 1. Diagrams of artificial concrete boulders (a) with undersides that are flat, and (b) with gap added, that were deployed at two sites at Cape St Francis. The upper-side of the boulder as seen in the diagram was the side in contact with the substratum in the boulder fields.

Table 1
PERMANOVA comparing multivariate macrofaunal assemblages and ANOVA comparing univariate abundances, numbers of species, and Shannon-Weiner diversities of total numbers of mobile macrofauna on different positions under boulders (edges and centres) in two sites in South Africa and three sites in eastern Australia. When interaction terms were non-significant (>0.25) they were eliminated to provide a stronger test of the relevant null-hypothesis (Underwood, 1997). "–" denotes eliminated term. Heterogeneity of variances was tested with Cochran's Test in all univariate analyses. [1]Ln(x + 1) transformed data, *$P < 0.05$.

Source	South African sites									Australian sites							
	Assemblages		Total abundances		No. of species		Shannon-Weiner diversity			Assemblages		Total abundances[1]		No. of species		Shannon-Weiner diversity	
	df	MS	F	MS	F	MS	F	MS	F	df	MS	F	MS	F	MS	F	MS	F
Site (Si)	1	2951.9	1.47	38.90	4.38*	3.08	8.00*	20.18	4.81*	2	2627	1.72	0.53	1.05	1.52	1.12	0.15	0.95
Position on boulder (Po)	1	5675.5	2.83*	64.39	7.26*	3.08	8.00*	19.46	3.01	1	20,099	7.68*	20.05	23.05*	43.35	9.32	4.33	12.56
Si × Po	1	634.6	–	0.03	–	0.02	–	6.47	1.54	2	2619	1.72	0.87	1.71	4.65	3.44*	0.34	2.11
Residual	20	2007.9		8.87		0.39		4.20		54	1523		0.51		1.35		0.16	
				Cochran's Test $C = 0.39$, $P > 0.05$		Cochran's test $C = 0.37$, $P > 0.05$		Cochran's test $C = 0.57$, $P > 0.05$					Cochran's test $C = 0.26$, $P > 0.05$		Cochran's test $C = 0.32$, $P > 0.05$		Cochran's test $C = 0.36$, $P > 0.05$	

dimensional photographs, these distances are slightly different from those on actual boulders. To account for the curvature of boulders, slight adjustments of the locations of edge and centre areas were made on the photographs. The extent of these adjustments for each boulder was calculated using the additional photograph of the boulder's side view, which allowed curvature to be measured (Liversage, 2012). The centroid was estimated visually (Liversage et al., 2012). Half the boulders were sampled from the centre and half from the edge. The entire area within the defined 'centre-area' was measured, but for the 'edge-area', measurements were taken from eight quadrats that had a total area equal to the centre. This allowed comparisons from the centre and edge to be done from the same amount of area for each boulder.

It was predicted that assemblages of mobile species in the two microhabitats would be different and total abundances would be greater at edges than centres. Numbers of species and Shannon-Weiner diversity indices were also quantified to investigate patterns of species diversity occurring in each microhabitat. Separate analyses were done for South Africa and Australia, with multivariate assemblage data being analysed using PERMANOVA in PRIMER v6 (Plymouth Marine Laboratory, UK) with 9999 permutations and Bray-Curtis resemblances. Similarity Percentages (SIMPER) was used to determine the relative contribution of species to differences between microhabitats, and nMDS plots were used to visualise differences. WinGMAV5 (EICC, The University of Sydney) was used to analyse univariate data of total macrofaunal abundances, numbers of species, and Shannon-Weiner diversity indices. The assumption of homogeneity of variances was tested using Cochran's *C*-Test, and data were transformed if necessary to satisfy this assumption. All analyses were mixed-model and orthogonal, with "Position on boulder" (centre or edge) as a fixed factor and "Site" as a random one. When interaction terms of fixed and random factors had *P* values > 0.25 they were eliminated from analyses to increase the power of relevant tests of hypotheses (Underwood, 1997).

The manipulative experiment was done only in South Africa, at the same two sites used in the mensurative experiment. There were two treatments, involving one set of artificial boulders that were flat on their upper and under sides (Fig. 1a) and another set with a diagonal indentation of 2 cm on one side (Fig. 1b). The dimensions of this indentation were based on the average gap-width known from naturally occurring boulders (Liversage, 2012). The diagonal placement was chosen to allow for the largest possible gap area within the indentation. Twelve boulders of each type were deployed at each site. To ensure there were no artefacts associated with deploying artificial boulders in unsuitable places, each artificial boulder was deployed in a position where a similarly sized natural boulder had been moved out of the way. This ensured that the substratum underneath artificial boulders had the same amount of unevenness as naturally occurring boulders. The unevenness was mostly the result of coarse pebbles and cobbles that generally result in at least some space underneath most parts of a boulder's centre-area, though on average less than around the edge-area (Liversage, 2012). After the boulders had been left in the field for seven weeks, they were found again and photographs that included scale bars were taken of the assemblages on their undersides.

Densities of mobile species, as well as numbers of species, were measured from the horizontal area of the diagonal indentation on boulders with increased gap width, and within the same diagonal area on flat boulders. Individuals were counted if any part of their body was positioned within the defined sampling area. To control for effects of proximity to boulder edges separately to the presence of a gap, boulders were further divided into those that were sampled at their edges and those sampled at their centres, using the same definitions of these

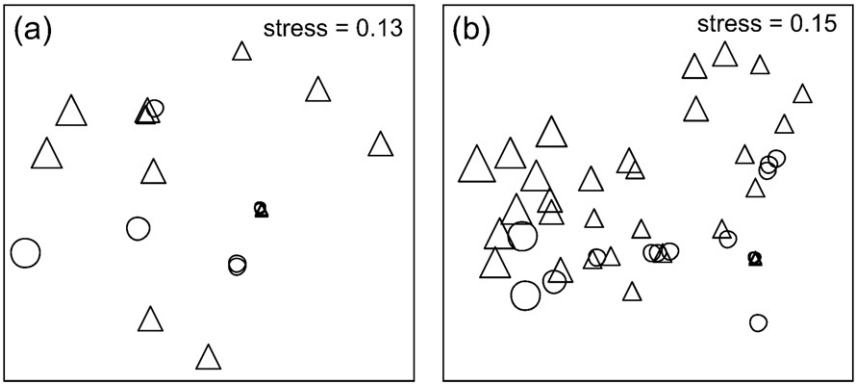

Fig. 2. nMDS plots of mobile macrofauna pooled from (a) two South African sites and (b) three eastern Australian sites. Assemblages were on the undersides of naturally-occurring boulders, sampled at either their edges (triangles) or centres (circles), $n = 6$ for South Africa, $n = 10$ for Australia. The size of symbols represents the total density of macrofauna in each sample, the smallest symbols had no macrofauna and the largest had up to $14 \cdot dm^{-2}$.

Table 2
Contributions to measures of dissimilarity, calculated in PRIMER v6, between undersides of boulders sampled at their edges or centres. Taxa shown are those that together contributed 95% to measures of dissimilarity between the treatments. The dissimilarity:standard deviation ratio indicates the reliability of the taxon when used to differentiate between groups, with a value >1 being considered a reliable indicator.
Clarke (1993).

		Mean density·dm^{-2}				
		Boulder edges		Boulder centres	Dissimilarity: standard-deviation ratio	% contribution to dissimilarity
South African taxa	*Roweia stephensoni* (sea cucumber)	**1.22**	>	nil	1.36	41.19
	Ischnochiton oniscus (chiton)	**0.79**	>	nil	0.86	27.78
	Chiton politus (chiton)	**0.45**	>	0.26	0.78	13.08
	Helcion pruinosus (limpet)	0.07	<	**0.52**	0.48	6.28
	Polynoidae (polychaete)	**0.23**	>	nil	0.47	4.96
Eastern Australian taxa	*Ischnochiton australis* (chiton)	**2.04**	>	0.72	1.08	36.39
	Ischnochiton fruticosus (chiton)	**0.69**	>	0.23	0.64	17.68
	Heliocidaris erythrogramma (urchin)	**0.89**	>	0.10	0.66	16.79
	Cryptoplax striata (chiton)	**0.58**	>	nil	0.46	11.13
	Ischnochiton versicolor (chiton)	**0.69**	>	nil	0.53	7.42
	Conus sp. (snail)	**0.10**	>	nil	0.19	1.66
	Parvulastra exigua (seastar)	nil	<	**0.17**	0.26	1.60
	Ischnochiton elongatus (chiton)	**0.05**	>	nil	0.18	1.57

areas as in the mensurative experiment, but occurring only within the diagonal area. Similarly to the mensurative experiment, each boulder was measured on either its edge or its centre to ensure independent measurements.

Data were analysed in PERMANOVA to test the hypotheses that assemblage structure would differ between boulders with vs without gaps, and between boulders sampled at edges vs centres. WinGMAV5 was also used to test the hypotheses that total abundances would be greater under 'gap' boulders, and under boulders sampled at their edges. A small proportion of replicates were lost during the deployment, resulting in some treatments having only four remaining replicates, so sample sizes for all treatments were randomly reduced to four to retain a balanced design (Underwood, 1997). Bray-Curtis resemblances were used for the multivariate analysis, with 9999 permutations and a dummy variable of one added due to sparsity of data values (Anderson et al., 2008). If *P* values of interaction terms were >0.25, they were eliminated from the analysis to provide a more powerful test of the relevant null hypothesis (Underwood, 1997).

3. Results

The initial mensurative experiment showed that mobile species assemblages differed consistently between boulders at edges vs centres (Table 1, Fig. 2a, b). Data of individual species patterns are shown in Table 2. All the most abundant species had greater mean densities at edges (Table 2). Two species that contributed to the differing assemblages had greater mean abundances near the centre of the underside, although these species had highly variable abundances generally, as indicated by low ratios of dissimilarity to standard deviation (Table 2). When all macrofauna were considered as a single taxon, they were significantly more abundant at edges (Table 1) where densities were 2.5–3.5 times greater (Fig. 3a, b). There were differences between sites

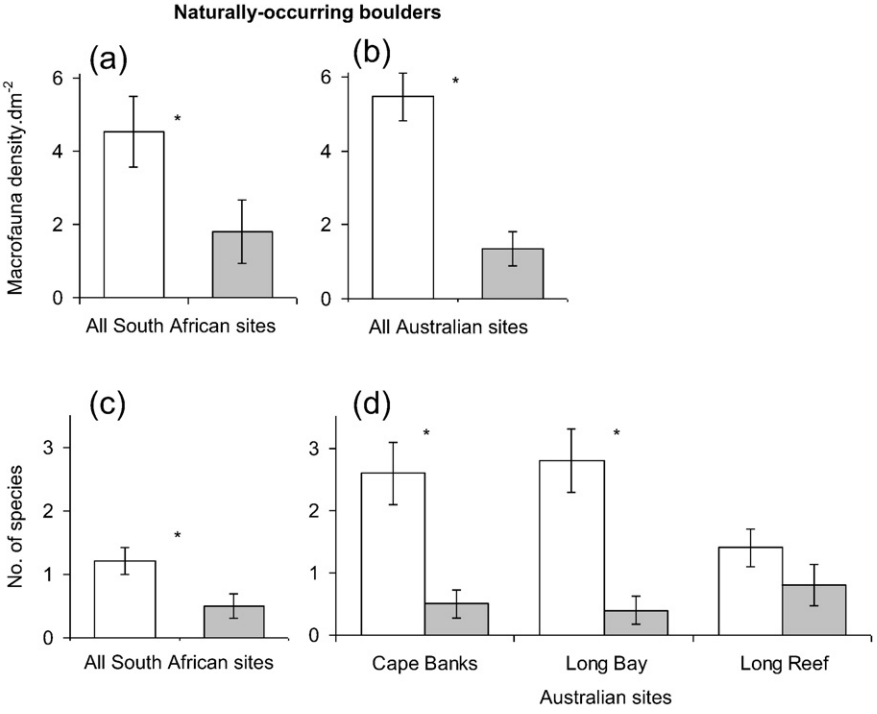

Fig. 3. Mean (±SE) (a) density of mobile macrofauna underneath boulders pooled from two sites in South Africa ($n = 6$) and (b) three sites in eastern Australia ($n = 10$), as well as numbers of species found in (c) both South African sites pooled and (d) the separate Australian sites. White bars represent boulders sampled at their edges, gray bars those sampled from their centres. *Denotes significant differences between treatments.

Table 3
PERMANOVA comparing multivariate macrofaunal assemblages and ANOVA comparing univariate abundances, number of species, and Shannon-Weiner diversities of all mobile macrofauna on artificial boulders with vs without gaps added to their undersides, and which were sampled on positions at either their edges or centres, from two sites in South Africa. All interaction terms that included the random factor 'Site' were non-significant (>0.25) so were eliminated to provide a stronger test of the relevant null-hypothesis (Underwood, 1997); $n = 4$. [1]Ln(x + 1) transformed data, [2]arcsine transformed data, *$P < 0.05$.

Source		Assemblages		Total abundances[1]		No. of species[2]		Shannon-Weiner diversity	
	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Site = Si	1	2390.2	1.63	0.73	1.06	10.99	0.76	0.037	0.32
Boulder type = Bo	1	2884.1	1.97	3.16	4.59*	39.67	2.73	0.315	2.70
Position on boulder = Po	1	852.6	0.58	0.05	0.07	1.65	0.11	0.001	0.01
Si × Bo	1	1609.2	–	0.23	–	1.65	–	0.037	–
Si × Po	1	1377.00	–	0.61	–	3.30	–	0.113	–
Bo × Po	1	944.3	0.64	0.04	0.05	0.55	0.04	0.001	0.01
Si × Bo × Po	1	1190.7	–	0.14	–	18.23	–	0.113	–
Residual	24	1465.5		0.69		14.55		0.117	
				Cochran's test $C = 0.31, P > 0.05$		Cochran's test $C = 0.43, P > 0.05$		Cochran's test $C = 0.61, P < 0.01$	

in South Africa, but effects of the "Site" factor were not interactive (Table 1). Similar patterns were found for numbers of species, which in South Africa were greater on boulder edges (Table 1, Fig. 3c). All the sites in Australia, except Long Reef, also had greater species numbers on edges (Table 1, Fig. 3d). Shannon-Weiner diversities did not appear to be affected by these factors except for some random spatial effects (Table 1).

The suite of species that colonised the artificial boulders after seven weeks in the South African sites were very similar to those present on naturally-occurring boulders. There was no evidence that the structure of assemblages on artificial boulders differed significantly either between those with vs without gaps, or those sampled at their edges vs centres (Table 3). When all macrofauna were considered together, their densities were greater within the gap compared to the same area on flat boulders (Fig. 4), but no difference was found on boulders sampled at edges compared to centres (Table 3). Numbers of species and Shannon-Weiner diversities were not affected by the factors in this experiment. Cochran's *C*-Test indicated no cases of significantly heterogeneous variances, except for Shannon-Weiner diversities (Table 3).

4. Discussion

Following the important early mensurative work of Sousa (1979), one of the first manipulations to the habitat underneath marine boulders was the work by McGuinness and Underwood (1986). Interest in this habitat has since grown and further manipulative experiments have been done in recent years (Liversage et al., 2012; Liversage et al., 2014), including studies on boulder reefs engineered to enhance species diversity gains (Chapman, 2012; Chapman, 2013; Kilfoyle et al., 2013; Støttrup et al., 2014) or the by-product of construction of structures such as seawalls (Green et al., 2012). We add to this body of work by identifying the importance of the microhabitat near edges of naturally-occurring boulders. This conclusion was derived using data from two continents, and is supported by additional results from locations further north of Cape St Francis within the South African Eastern Cape (KL, unpublished data) and from other types of boulder habitat in Australia (Liversage, 2016a). By manipulating this microhabitat at the South African sites, we showed that effects of under-boulder gaps (our proposed causative mechanism) were apparent but not clear-cut. Gaps influenced total macrofaunal abundances, but not the structure of whole assemblages nor species diversity variables. This indicates a causal link between gap-widths (which are generally greater under edges than centres of naturally-occurring boulders; Liversage, 2012) and overall macrofaunal abundance. The lack of an effect on assemblage structure and species diversity suggests, however, that not all aspects of these assemblages are influenced by gaps. Inferences from our results are limited by the sample sizes used, particularly in the case of rarer species. Many boulder species have extremely overdispersed distributions (Chapman, 2002; Grayson and Chapman, 2004; Liversage and Benkendorff, 2013). Inferences from our data would apply to common species, but for those with patchier distributions inferences may be more difficult.

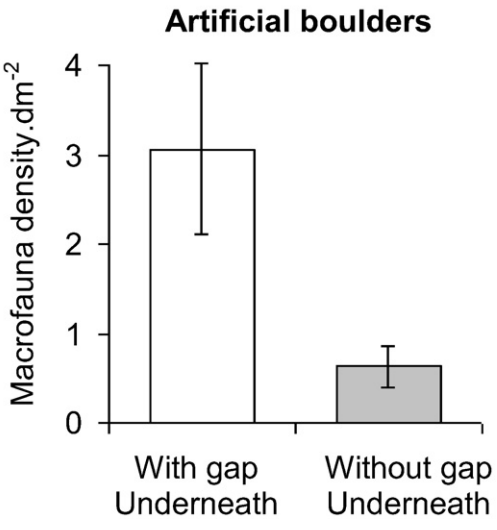

Fig. 4. Mean (±SE) density of mobile macrofauna that colonised artificial boulders with and without 2 cm gaps added to the boulder underside. Data shown are pooled from boulders sampled at either their edges or centres in two sites in South Africa; each bar represents means from 16 boulders.

Results concerning the proximity of a microhabitat to the boulder edge were clear, as there was no evidence that this factor affected biotic variables, either separately or interactively with effects of the gap. Overall, we conclude that, at least during early stages of colonisation, total numbers of macrofauna are greater at boulder edges probably because the microhabitat there features a wide gap, and not because of the position of the microhabitat within the under-boulder surface. The situation may be different in the later stages of colonisation. For example, intertidal boulders often have abundant encrusting algae on their edges (Choi and Ginsberg, 1983; Liversage, 2016b), which may influence mobile species, especially grazers, irrespective of the presence of a gap.

A number of aspects of a wide gap may be favourable to marine invertebrates under boulders. A simple explanation is that there is more space for their bodies. Especially for taxa with high profiled bodies, such as sea urchins and turbinid snails, areas associated with boulders where they are both protected from predators (e.g. Shepherd and Clarkson, 2001), and where there is space for their bodies, may be at a premium. The habitat-value of boulders providing such conditions was suggested in previous research of spaces underneath subtidal boulders (Alexander, 2013). Those with a large

empty volume underneath them, but not much area to enter that volume from outside (e.g. by predators), were positively associated with abundances of at least one taxon, the holothurians (Alexander, 2013). In contrast, Todd and Turner (1986) found evidence that sessile species not requiring much space were still associated with wider, compared to narrower, under-boulder gaps. They suggested that gap-width affects the water-flow regime which these species in turn respond to. This may especially be relevant to suspension feeders under boulders, such as the under-boulder holothurian we encountered, *Roweia stephensoni* (Foster, 1994).

The results from this study, together with those of previous studies on under-boulder microhabitats (Choi and Ginsberg, 1983; McGuinness and Underwood, 1986; Todd and Turner, 1986; Le Hir and Hily, 2005; Liversage et al., 2012; Alexander, 2013) show how a range of benthic species use under-boulder surfaces as discrete habitat patches, sheltered from predators and providing favourable environmental conditions as a result of occurring within a partially enclosed space or cavity. Some species appear to require such a cavity specifically under boulders (Kangas and Shepherd, 1984; Le Hir and Hily, 2005) as opposed to other types of reef cavities (e.g. Menge and Lubchenco, 1981; Richter et al., 2001; Gray and Hodgson, 2004). For example, the presence of "stabilised" sediment underneath boulders (Le Hir and Hily, 2005) appears to be favourable to some species (Foster, 1994; Liversage et al., 2012). Another factor is that, unlike cavities fixed in reefs, those underneath boulders can be moved and overturned. Partial movements of intertidal boulders have been measured as occurring approximately every month, and full overturning every 2–12 months depending on boulder size (McGuinness, 1987). Such habitat dynamism may favour these specialist species, possibly for reasons related to the "intermediate disturbance hypothesis" (Connell, 1978).

Habitat restoration is an important method of conserving and enhancing marine species diversity (Ellison, 2000; Van Katwijk et al., 2009; Beck et al., 2011). Engineered boulder reefs can create species diversity gains for fish (Støttrup et al., 2014) and rare invertebrates (Chapman, 2012). They are also used as a tool in certain fisheries such as abalone (McCormick et al., 1994; Roberts et al., 2007; Read et al., 2013), and our results concerning *Roweia stephensoni* suggest they could similarly be used as a tool in beche de mer fisheries, with both of these fisheries contributing to the economies of South Africa (e.g. Conand and Byrne, 1993; de Waal et al., 2012) and Australia (e.g. Mayfield et al., 2012; Eriksson and Byrne, 2015). Chapman (2012) proposed a number of considerations that need to be taken into account when undertaking engineering of boulder field habitat, including the time since the beginning of colonisation and, for some species, the size of boulder patches (Chapman, 2013). We have shown that smaller-scale microhabitat considerations are also important. If the goal of engineering a boulder field is to maximise macrofaunal abundances, then a design should be adopted similar to ours, which controls for the microhabitats being created. Overall, we recommended that future efforts to engineer the ecological attributes of marine boulder reefs take into account the importance of under-boulder microhabitats that provide suitable gap-widths to accommodate macrofauna.

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References

Aguilera, M.A., Broitman, B.R., Thiel, M., 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. Mar. Pollut. Bull. 87, 257–268.
Alexander, T.J., 2013. Cryptic invertebrates on subtidal rocky reefs vary with microhabitat structure and protection from fishing. Mar. Ecol. Prog. Ser. 481, 93–104.
Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth.
Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61, 107–116.
Benner, R., Browne, T., Brückner, H., Kelletat, D., Scheffers, A., 2010. Boulder transport by waves: progress in physical modelling. Z. Geomorphol. Supp. 54, 127–146.
Browne, M.A., Chapman, M.G., 2014. Mitigating against the loss of species by adding artificial intertidal pools to existing seawalls. Mar. Ecol. Prog. Ser. 497, 119–129.
Chapman, M.G., 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. Austral Ecol. 27, 211–228.
Chapman, M.G., 2012. Restoring intertidal boulder-fields as habitat for "specialist" and "generalist" animals. Restor. Ecol. 20, 277–285.
Chapman, M.G., 2013. Constructing replacement habitat for specialist and generalist molluscs: the effect of patch size. Mar. Ecol. Prog. Ser. 473, 201–214.
Chapman, M.G., Smoothey, A.F., 2014. Sea urchins provide habitat for rare chitons in intertidal boulder-fields. J. Exp. Mar. Biol. Ecol. 459, 31–37.
Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.
Choi, D.R., Ginsberg, R.N., 1983. Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida Reef Tract. Coral Reefs 2, 165–172.
Conand, C., Byrne, M., 1993. A review of recent developments in the world sea cucumber fisheries. Mar. Fish. Rev. 55, 1–13.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
Coombes, M.A., La Marca, E.C., Naylor, L.A., Thompson, R.C., 2015. Getting into the groove: opportunities to enhance the ecological value of hard coastal infrastructure using fine-scale surface textures. Ecol. Eng. 77, 314–323.
Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L., 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Front. Ecol. Environ. 13, 82–90.
Day, E., Branch, G.M., 2002. Effects of sea urchins (*Parechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). Ecol. Monogr. 72, 133–149.
De Waal, S.W.P., Balkhair, M., Al-Mashikhi, A., Khoom, S., 2012. Habitat preferences of juvenile abalone (*Haliotis mariae* Wood, 1828) along the Dhofar coast of Oman and implications for conservation. J. Agr. Mar. Sci. 17, 45–52.
Denny, M.W., Miller, L.P., Stokes, M.D., Hunt, L.J.H., Helmuth, B.S.T., 2003. Extreme water velocities: topographical amplification of wave-induced flow in the surf zone of rocky shores. Limnol. Oceanogr. 48, 1–8.
Dong, Y., Huang, X., Wang, W., Li, Y., Wang, J., 2016. The marine 'great wall' of China: local- and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. Divers. Distrib. DOI http://dx.doi.org/10.1111/ddi.12443.
Ellison, A.M., 2000. Mangrove restoration: Do we know enough? Restor. Ecol. 8, 219–229.
Eriksson, H., Byrne, M., 2015. The sea cucumber fishery in Australia's Great Barrier Reef Marine Park follows global patterns of serial exploitation. Fish Fish. 16, 329–341.
Evans, A.J., Firth, L.B., Hawkins, S.J., Morris, E.S., Goudge, H., Moore, P.J., 2015. Drill-cored rock pools: an effective method of ecological enhancement on artificial structures. Mar. Freshw. Res. 67, 123–130.
Ferrario, F., Iveša, L., Jaklin, A., Perkol-Finkel, S., Airoldi, L., 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. J. Appl. Ecol. 53, 16–24.
Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J., Hawkins, S.J., 2014. Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. Coast. Eng. 87, 122–135.
Foster, G.G., 1994. Aspects of the Biology and Ecology of Some Intertidal Holothurians (Echinodermata) Along the Eastern Cape Coast of South Africa. (PhD thesis). Rhodes University, South Africa.
Goto, K., Chavanich, S.A., Imamura, F., Kunthasap, P., Matsui, T., Minoura, K., Sugawara, D., Yanagisawa, H., 2007. Distribution, origin and transport process of boulders deposited by the 2004 Indian Ocean tsunami at Pakarang Cape, Thailand. Sediment. Geol. 202, 821–837.
Gray, D.R., Hodgson, A.N., 2004. The importance of a crevice environment to the limpet *Helcion pectunculus* (Patellidae). J. Molluscan Stud. 70, 67–72.
Grayson, J.E., Chapman, M.G., 2004. Patterns of distribution and abundance of chitons of the genus *Ischnochiton* in intertidal boulder fields. Austral. Ecol. 29, 363–373.
Green, D.S., Chapman, M.G., Blockley, D.J., 2012. Ecological consequences of the type of rock used in the construction of artificial boulder-fields. Ecol. Eng. 46, 1–10.
Hawkins, S.J., Mieszkowska, N., Firth, L.B., Bohn, K., Burrows, M.T., MacLean, M.A., Thompson, R.C., Chan, B.K.K., Little, C., Williams, G.A., 2015. Looking backwards to look forwards: the role of natural history in temperate reef ecology. Mar. Freshw. Res. 67, 1–13.
Kangas, M., Shepherd, S.A., 1984. Distribution and feeding of chitons in a boulder habitat at West Island, South Australia. J. Malacological Soc. Aust. 6, 101–111.
Kilfoyle, A.K., Freeman, J., Jordan, L.K., Quinn, T.P., Spieler, R.E., 2013. Fish assemblages on a mitigation boulder reef and neighboring hardbottom. Ocean Coast. Manag. 75, 53–62.

Le Hir, M., Hily, C., 2005. Macrofaunal diversity and habitat structure in intertidal boulder fields. Biodivers. Conserv. 14, 233–250.
Liversage, K., 2012. Ecology of Cryptic Habitats Under Intertidal Boulders. (PhD thesis). The University of Sydney, Australia.
Liversage, K., 2016a. Observations of relic intertidal assemblages in an inland marine-spring of Eyre Peninsula, South Australia. T. Roy. Soc. South Aust. 140, 46–56.
Liversage, K., 2016b. The influence of boulder shape on the spatial distribution of crustose coralline algae (Corallinales, Rhodophyta). Mar. Ecol. 37, 459–464.
Liversage, K., Benkendorff, K., 2013. A preliminary investigation of diversity, abundance, and distributional patterns of chitons in intertidal boulder fields of differing rock type in South Australia. Molluscan Res. 33, 24–33.
Liversage, K., Cole, V.J., McQuaid, C.D., Coleman, R.A., 2012. Intercontinental tests of the effects of habitat patch type on the distribution of chitons within and among patches in intertidal boulder field landscapes. Mar. Biol. 159, 2777–2786.
Liversage, K., Janetzki, N., Benkendorff, K., 2014. Associations of benthic fauna with different rock types, and evidence of changing effects during succession. Mar. Ecol. Prog. Ser. 505, 131–143.
Lopez, G.R., Levinton, J.S., 1987. Ecology of deposit-feeding animals in marine sediments. Q. Rev. Biol. 62, 235–260.
Martins, G.M., Jenkins, S.R., Neto, A.I., Hawkins, S.J., Thompson, R.C., 2016. Long-term modifications of coastal defences enhances diversity. Environ. Conserv. 43, 109–116.
Mastronuzzi, G., Sanso, P., 2000. Boulders transport by catastrophic waves along the Ionian coast of Apulia (southern Italy). Mar. Geol. 170, 93–103.
Maughan, B.C., Barnes, D.K., 2000. Epilithic boulder communities of Lough Hyne, Ireland: the influences of water movement and sediment. J. Mar. Biol. Assoc. U. K. 80, 767–776.
Mayfield, S., Mundy, C., Gorfine, H., Hart, A.M., Worthington, D., 2012. Fifty years of sustained production from the Australian abalone fisheries. Rev. Fish. Sci. 20, 220–250.
McCormick, T.B., Herbinson, K., Mill, T.S., Altick, J., 1994. A review of abalone seeding, possible significance and a new seeding device. Bull. Mar. Sci. 55, 680–693.
McGuinness, K.A., 1987. Disturbance and organisms on boulders I. Patterns in the environment and the community. Oecologia 71, 409–419.
McGuinness, K.A., Underwood, A.J., 1986. Habitat structure and the nature of communities on intertidal boulders. J. Exp. Mar. Biol. Ecol. 104, 97–123.
McQuaid, C.D., Mostert, B.P., 2010. The effects of within-shore water movement on growth of the intertidal mussel *Perna perna*: an experimental field test of bottom-up control at centimetre scales. J. Exp. Mar. Biol. Ecol. 384, 119–123.
Menge, B.A., Lubchenco, J., 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol. Monogr. 51, 429–450.
Pacheco, A.S., Laudien, J., Thiel, M., Heilmayer, O., Oliva, M., 2010. Hard-bottom succession of subtidal epibenthic communities colonizing hidden and exposed surfaces off northern Chile. Sci. Mar. 74, 147–154.
Perkins, M.J., Ng, T.P.T., Dudgeon, D., Bonebrake, T.C., Leung, K.M.Y., 2015. Conserving intertidal habitats: what is the potential of ecological engineering to mitigate impacts of coastal structures? Estuar. Coast. Shelf Sci. 167, 504–515.
Read, K.D., Lessard, J., Boulding, E.G., 2013. Improving outplanting designs for northern abalone (*Haliotis kamtschatkana*): the addition of complex substrate increases survival. J. Shellfish Res. 32, 171–180.
Richter, C., Wunsch, M., Rasheed, M., Kotter, I., Badran, M.I., 2001. Endoscopic explorations of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413, 726–730.
Riisgard, H.U., Banta, G.T., 1998. Irrigation and deposit feeding by the lugworm *Arenicola marina*, characteristics and secondary effects on the environment. A review of current knowledge. Vie Milieu 48, 243–257.
Roberts, R.D., Keys, E.F., Prendeville, G., Pilditch, C.A., 2007. Viability of abalone (*Haliotis iris*) stock enhancement by release of hatchery-reared seed in Marlborough. New Zealand. J. Shellfish Res. 26, 697–703.
Sala, E., Zabala, M., 1996. Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. Mar. Ecol. Prog. Ser. 140, 71–81.
Shepherd, S.A., Clarkson, P.S., 2001. Diet, feeding behaviour, activity and predation of the temperate blue-throated wrasse, *Notolabrus tetricus*. Mar. Freshwater Res. 52, 311–322.
Smoothey, A.F., Chapman, M.G., 2007. Small-scale variability in the dispersion of the sea urchin *Heliocidaris erythrogramma* among boulders. Mar. Ecol. Prog. Ser. 340, 89–99.
Sousa, W.P., 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60, 1225–1239.
Støttrup, J.G., Stenberg, C., Dahl, K., Kristensen, L.D., Richardson, K., 2014. Restoration of a temperate reef: effects on the fish community. Open J. Ecol. 4, 1045–1059.
Tan, E.L.Y., Mayer-Pinto, M., Johnston, E.L., Dafforn, K.A., 2015. Differences in intertidal microbial assemblages on urban structures and natural rocky reef. Front. Microbiol. http://dx.doi.org/10.3389/fmicb.2015.01276.
Tarr, R.J.Q., Williams, P.V.G., MacKenzie, A.J., 1996. Abalone, sea urchins and rock lobster: a possible ecological shift that may affect traditional fisheries. Afr. J. Mar. Sci. 17, 319–323.
Todd, C.D., Turner, S.J., 1986. Ecology of intertidal and sublittoral cryptic epifaunal assemblages I. Experimental rationale and the analysis of larval settlement. J. Exp. Mar. Biol. Ecol. 99, 199–231.
Underwood, A.J., 1990. Experiments in ecology and management: their logics, functions and interpretations. Aust. J. Ecol. 15, 365–389.
Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.
Van Katwijk, M.M., Bos, A.R., De Jonge, V.N., Hanssen, L.S.A.M., Hermus, D.C.R., De Jong, D.J., 2009. Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar. Pollut. Bull. 58, 179–188.