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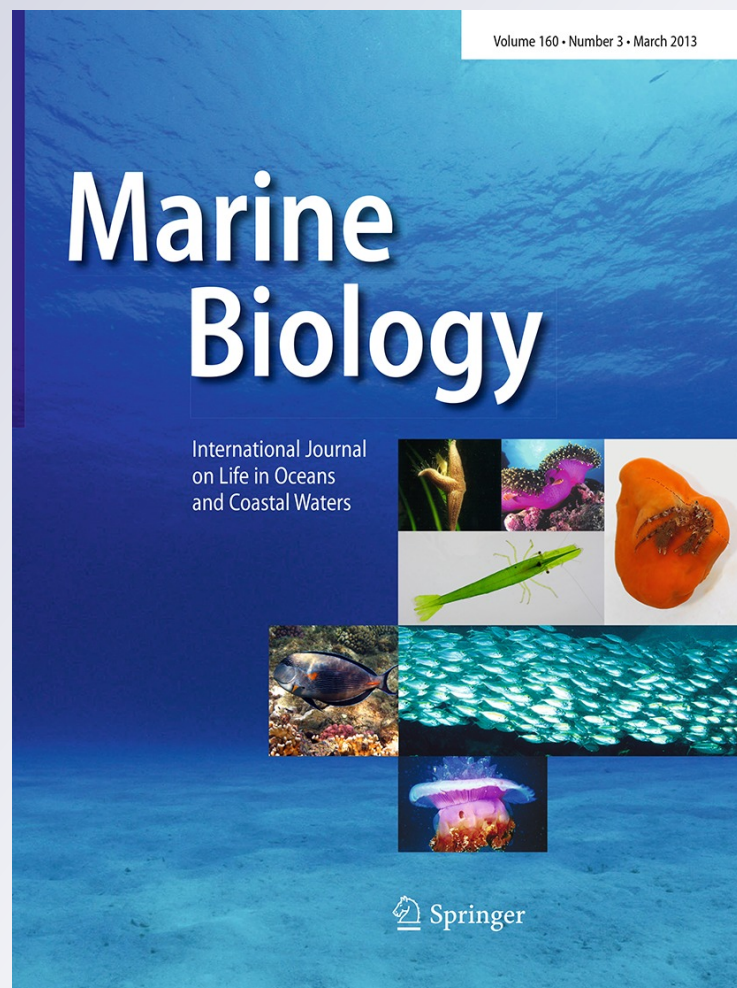
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Macrofaunal responses to structural complexity are mediated by environmental variability and surrounding habitats

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Abstract Investigating the context that surrounds each habitat is crucial to understand local responses of assemblages of species to habitats. Here, I tested whether responses of benthic macroinvertebrates to the structural complexity of experimental habitats were mediated by the characteristics of their surrounding habitats (i.e. rockpools or emergent-rock surfaces). Each type of surrounding habitat provided particular biotic (e.g. algal growth) and abiotic (e.g. temperature, water movement) conditions that were expected to affect benthic assemblages. The results show that (1) composition of entire assemblages was affected by the matrix and type of habitat; (2) effects of the matrix on the number of species varied depending on the different types of habitats; (3) abundant species showed specific responses to type of habitat, independently of the matrix; and (4) relationships between numbers of species and two major environmental variables (i.e. micro-algal biomass and sediment) varied depending on the type of habitats and the surrounding matrix. Generally, these findings demonstrate that understanding the consequences of the spatial structure of these habitats is essential to advance our knowledge on patterns of abundance and

distributions of functionally important species and ultimately the structure of intertidal assemblages.

Introduction

Ecologists have long been interested in species' associations with their habitats with the aim of understanding spatial variability in abundances of species (e.g. MacArthur and MacArthur 1961; MacArthur 1964; Pianka 1966). Habitats with different physical structure generally offer different resources (i.e. food, shelter) that are, in turn, exploited by different species (e.g. Downes et al. 2000). Local variation in the physical structure of habitats does not, however, completely explain the distribution and abundance of species at coarser scales, because the colonization of habitats is often greatly influenced by processes operating at regional scales (e.g. MacArthur and Wilson 1967). Generally, the realization that habitats may have different degrees of isolation depending on the nature of the surrounding matrix has prompted a whole body of work investigating the role of the matrix in which habitats are embedded (i.e. landscape context, Mazerolle and Villard 1999) and how it mediates the level of connectivity with neighbouring habitats (i.e. "connectivity is the degree to which the landscape facilitates or impedes movement among resource patches"; Taylor et al. 1993). The extent to which connectivity is altered depends on scale and the organisms' perception of changes in spatial patterns (e.g. Kotliar and Wiens 1990; Wiens 2002), the spatial configuration of patches (e.g. Roberts and Poore 2006), the surrounding matrix (e.g. Crowe 1996; Ricketts 2001; Debinski 2006; Tanner 2006) and dispersal among patches (e.g. Ewers and Didham 2006).

Most organisms are more likely to interact with organisms in neighbouring habitats than with more distant ones (Tilman

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1994). Such interactions with surrounding habitats are particularly important for sessile organisms (e.g. corals, Karlson and Cornell 2002; terrestrial plants, Pacala and Silander 1990; macroalgae, Goodsell and Connell 2008; bryozoans, terHorst and Dudgeon 2009). The magnitude of interactions with surrounding habitats across habitat boundaries is also dependent on the quality of these surrounding habitats (Fagan et al. 1999; Ries and Sisk 2004). Dispersal and resource use are strongly influenced by the spatial structure of neighbouring habitats, which determines the structure and dynamics of natural assemblages (Tilman 1994; Loreau and Mouquet 1999; Ricketts 2001). Empirical studies on patterns of diversity and distribution of species in naturally isolated patches of habitat have shown that the nature of the surrounding matrix determines the effective level of isolation of natural patches of habitat (Ricketts 2001). Furthermore, the extent to which the surrounding landscape, that is, the matrix (Ricketts 2001; Murphy and Lovett-Doust 2004), may function as a barrier to movement of animals between patches of habitats may depend on the extent and type of habitat it contains (e.g. Goodsell and Connell 2008; Johnson et al. 1992). Investigating the matrix that surrounds each habitat is therefore crucial to understand local responses of assemblages of species to habitats.

Historically, most studies of the roles of matrix have been done in terrestrial systems, although there is growing evidence that matrix habitats are also a fundamental component of connectivity (i.e. dispersal) within marine systems (e.g. Tanner 2006; Goodsell and Connell 2008; Hovel and Fonseca 2005). In marine systems, connectivity between patches of habitat is generally thought to be great due to many marine species having planktonic larval stages (Scheltema 1974). Consequently, most research on the effects of the type of the surrounding matrix has been focused on differences in connectivity and colonization of patches. For example, the matrix and structure of seagrass patches are important determinants of spatial patterns and variability of fish assemblages (Gullstrom et al. 2008) and marine crustaceans (Skilleter et al. 2005). Nevertheless, experimental manipulations to test hypotheses about the effects of spatial arrangement and composition of habitats remain scarce (but see Tanner 2006; Goodsell and Connell 2008; Hovel and Lipcius 2001; Macreadie et al. 2009). It is difficult to separate the effects of the matrix from those of changes in the habitats themselves (Macreadie et al. 2009, 2010). For example, finding differences among assemblages in seagrass patches near and far from mangroves could not be solely attributed to the effects of the matrix (i.e. mangroves). The seagrass patches—the focal habitat—could also be altered by their proximity to mangroves, which ultimately could explain the differences in assemblages. It is, therefore, essential to separate these effects to understand better how the matrix affects species' responses to different types of habitats.

Here, I investigated the responses of benthic assemblages to structural complexity under different surrounding habitats. In particular, I tested the hypothesis that assemblages should vary according to the matrix in which patches of habitats are embedded (Hypothesis 1). Alternatively, not all types of habitats may be affected in the same way by their matrix. This model would be supported if there were an interaction between effects of type of habitat and context (Hypothesis 2). I tested these predictions by deploying two types of experimental habitats in two different matrices: rockpools and emergent-rock surfaces (i.e. open rock). These two different matrices have consequences for assemblages colonizing experimental habitats because it affects biotic (e.g. algal growth) and abiotic (e.g. temperature, water movement) factors: rockpools are completely submerged during the tidal cycle and are often covered by loosely compacted turfs (Akioka et al. 1999; Hull 1999; Worthington and Fairweather 1989), whilst emergent-rock surfaces are exposed to air during low tides and thus subject to desiccation. For example, the structure of biogenic habitats is affected by their position in the shore (e.g. length and packedness of coralline turfs; Akioka et al. 1999), which, in turn, might determine how organisms use these habitats (Worthington and Fairweather 1989). Such variability in the nature of the surrounding habitats is determinant for benthic assemblages colonizing biogenic habitats since it affects colonization or movement of organisms in focal patches of habitat (e.g. Cole 2009).

Methods

Experimental design

This study was done on intertidal rock platforms at the Cape Banks Special Scientific Research Area, Botany Bay (NSW, Australia) from November 2009 to February 2010. I surveyed areas 100s of metres apart with similar orientation and exposure to waves on gently sloping low-shore rock platforms or large boulders, 0.3–0.6 m above mean low water. In these areas, I selected rockpool and emergent-rock locations that had patches of *Corallina officinalis* L. Rockpools were of similar size and depth; small (area <1 m²) and/or deep rockpools (depth >0.5 m) were not included since these characteristics can have major effects on the assemblages of macroalgae (Martins et al. 2007; Underwood and Skilleter 1996). Emergent-rock surfaces were selected in areas that were completely emerged during low tides. In total, there were 10 separate locations: 5 rockpools and 5 emergent-rock areas. Thus, the factor *Location* was necessarily nested in the type of matrix. It should be noted that it would not be feasible to find enough individual rockpools of appropriate dimensions to accommodate each

experimental habitat (see details below) separately. To control for possible confounding effects of shading and wave action, all locations were approximately horizontally oriented and subject to moderate wave action. Care was taken to ensure that rockpool and emergent-rock locations were large enough to accommodate all experimental units whilst keeping distances between experimental units similar to those outside rockpools (i.e. >50 cm apart).

Experimental habitats were independently attached and interspersed amongst algal turfs in rockpool or emergent-rock, using stainless steel screws and rubber washers. Experimental habitats are uniform and have same general history (e.g. they are the same age), which reduces the variability among experimental units (Underwood and Chapman 2006). This is a central aspect of this study as it removes the confounding effect of variability in natural coralline turfs between rockpools and on emergent-rock, which would have confounded the experiment because of structure of these turfs determines assemblages that colonize these habitats (Kelaher et al. 2001). Thus, using experimental habitats, the variability between assemblages in rockpools or on emergent-rock should be attributable to environmental variables or resources associated with these surrounding habitats, rather than any differences in structure of the focal patches of habitat.

Experimental habitats

Two types of artificial turf (Grassman Pty Ltd., NSW, Australia) were selected (types *A* and *C* in Matias et al. 2010) to construct the experimental habitats. These turfs were chosen because of their differences in length ($A < C$) and also in density of fronds ($A > C$), although they provide comparable amounts of surface of fronds to be colonized [i.e. 26.5 (*A*) and 25.9 (*C*) cm²]. These characteristics maximized the structural differences needed to test hypotheses about different types of habitats (Matias et al. 2010, 2011). The variation between types of habitat falls within the dimensions of naturally occurring coralline turfs on rocky reefs (Akioka et al. 1999). Benthic assemblages in experimental habitats would therefore be affected by the combined effect of density and length of fronds. A previous study using these artificial habitats determined that these two types of habitats are colonized by significantly different numbers of species ($C > A$). Hereafter, for clarity, I refer to the types of fronds as *short* (i.e. *A*) or *long* (i.e. *C*).

Experimental habitats were made of squares of artificial turf (10 × 10 cm²) that were attached to a base of wire mesh using cable ties. Previous work has shown that experimental habitats of this size are appropriate to test hypotheses about different types of habitats (Matias et al. 2007, 2010). Numerous invertebrates rapidly colonize artificial turfs after just 14 days of deployment (Olabarria 2002; Kelaher 2005).

Fifty days after deployment, there are significant differences between assemblages colonizing habitats with different structural diversity (Matias et al. 2007). After 4 months, diversity and abundance of invertebrates in artificial turfs are not different from those in natural turfs (i.e. *Corallina* sp.; Kelaher 2003a), which suggests that they are consistent with the natural assemblages. From this, I considered 4 months as appropriate for testing hypotheses about the effects of matrix and structure of habitats.

After 4 months, I carefully placed a plastic bag over the experimental habitat before removing the screws. This procedure ensured that all epiphytes and fauna associated with each sample were completely recovered. I cut two sub-samples (2 × 2 cm²) from the middle of each artificial turf and placed them in separate labelled plastic bags for chlorophyll extraction (see next section); all samples were immediately frozen at −80 °C. I washed the remainder of each artificial turf in a 500-µm sieve, and all invertebrates were sorted and counted under a binocular microscope at 16× magnification. All molluscs were identified to the finest possible taxonomic resolution, either species or morphospecies, that is, as surrogate for taxonomic species when taxonomic classification is immediately available (e.g. Underwood and Chapman 2006).

Estimating micro-algal biomass and sediment

I quantified micro-algal biomass and accumulated sediment on experimental habitats to investigate how the variability in environmental variables is related to the variability among assemblages (Kelaher et al. 2001). These environmental variables are important because many of the marine gastropods colonizing these habitats feed on micro-algae, diatoms and detritus (Beesley et al. 1998). Also, it has been shown experimentally that sediment particles are structural components of coralline turfs and some species of gastropods show preference for turfs with greater amounts of sediment (Olabarria and Chapman 2001). To measure the variability of each of the environmental variables and how they related to the variability of assemblages, I estimated micro-algal biomass and the amount of sediment in each experimental habitat. Micro-algal biomass was estimated using the concentration of chlorophyll-*a* as a proxy (Thompson et al. 1999; Murphy et al. 2005).

Preliminary trials were done to determine commonly used inorganic solvents (acetone, methanol and dimethylformamide (DMF); Thompson et al. 1999; Murphy et al. 2005) would degrade the synthetic turfs and modify spectrophotometric readings. Results showed that extractions using DMF had no measurable differences in spectrophotometer readings when compared with blanks (i.e. with no artificial turfs) and were therefore appropriate for this study. Micro-algal biomass was estimated from chlorophyll-*a*

(mg l⁻¹) overnight extraction in dimethylformamide (DMF) from each of two subsamples that had been previously frozen. The concentration of chlorophyll-*a* in the solvent was calculated using the following equation (Porra et al. 1989; Murphy et al. 2005):

$$\text{chlorophyll-}a = 12(A_{664} - A_{750}) - 3.11(A_{647} - A_{750}) \quad (1)$$

where *A* is the absorbance at the indicated wavelength.

The amount of sediment in each experimental habitat was estimated by collecting sediment particles using a 63-mm sieve. Sediment samples were then dried in an oven for 48 h at 80 °C and weighted. The relationships between numbers of species and each of the two environmental variables were examined by correlations (*n* = 15 in each correlation).

Analyses of data

Predictions about whether or not assemblages colonizing habitats with different structure were different depending on their surrounding habitats were tested using PERMANOVA (Anderson 2001) on Bray–Curtis dissimilarities calculated on Log(*X* + 1) transformed abundances of species; Type was a fixed factor (2 levels: short vs long); Matrix was a fixed factor (2 levels: rockpool or emergent-rock). As explained in the previous section, the experimental habitats that were attached either in rockpool or on emergent-rock were in no way paired, so they were independent from each other. From this, Location was a random factor nested in Matrix. All multivariate analyses were done using PRIMER 6.0 and PERMANOVA+ (PRIMER-E Ltd, Plymouth).

Predictions about numbers of species in different types of habitats and matrices were tested using ANOVA with Type, Matrix and Location as in previous analyses. When appropriate, data were transformed following a Cochran's test for homogeneity of variances (Underwood 1997). Additional ANOVAs comparing the densities of the most abundant species were used to test whether these responded consistently to different types of habitats and matrices. Post hoc comparisons of means were made using Student–Newman–Keuls (SNK) tests. All univariate tests were done using WinGMAV 5.0 (EICC, The University of Sydney).

Results

Diversity and structure of assemblages

I collected 7,288 individuals belonging to 58 morphospecies (hereafter species), 44 of which were found in rockpools, whereas only 38 species were found in open rock.

The four most abundant species (>85 % individuals) were the bivalve *Lasaea australis* (Lamarck, 1818), the gastropods *Amphithalamus incidata* (Frauenfeld, 1867), *Austrocochlea porcata* (Adams, 1851) and *Eatoniella atropurpurea* (Frauenfeld, 1867). The remainder of species had relatively smaller abundances; 19 of these species were represented by a single one.

Entire assemblages varied depending on interaction between Type and Location (PERMANOVA: Type × Location (Matrix) interaction, Table 1a; Fig. 1). Differences between assemblages colonizing different types of turfs were consistent in rockpool or emergent-rock (Pair-wise comparisons, Table 1b). In contrast, dissimilarity between assemblages in rockpool or on emergent-rock was consistently greater in habitats with long turfs (Table 1c). Generally, dissimilarity between assemblages in habitats with short versus long turfs was consistent across different locations, but the magnitude of such differences varied (Table 1d).

The number of species varied with matrix, although these differences depended on the type of habitat (ANOVA: Type × Matrix interaction, Table 2a; Fig. 2). With regard to the comparisons between each Matrix within each level of the factor Type, there were significantly greater numbers of species in short turfs, whilst on emergent-rock, there were significantly greater numbers of

Table 1 (a) PERMANOVA and pair-wise comparisons of assemblages in different type of habitats (2 levels: long vs short); Matrix [2 levels: rockpool (RP) vs emergent-rock (ER)] using Bray–Curtis distances calculated on Log(*X* + 1) transformed abundances; Location is a random factor nested in Matrix. Pair-wise significance tests were done for significant comparisons (b, c and d). Multivariate patterns (nMDS) are in Fig. 1

(a) Source	DF	MS	Pseudo- <i>F</i>		
Type = <i>T</i>	1	12,297.0	6.7**		
Matrix = <i>M</i>	1	7,276.7	3.1**		
Location (<i>M</i>) = <i>L</i> (<i>M</i>)	8	2,353.5	2.1***		
<i>T</i> × <i>M</i>	1	7,351.1	4.0*		
<i>T</i> × <i>L</i> (<i>M</i>)	8	1,848.4	1.6**		
Residual	40	1,145.0			
Pair-wise comparisons					
Average Bray–Curtis dissimilarity between groups <i>T</i> × <i>M</i>					
(b) Short versus long		(c) RP versus ER			
RP	63**	Short	47		
ER	60*	Long	74**		
(d) Average Bray–Curtis dissimilarity between groups <i>T</i> × <i>L</i> (<i>M</i>)					
Location	1	2	3	4	5
RP	60	63	41	65	64
ER	67	62	48	62	72

Numbers in the bottom part of the table indicate average Bray–Curtis dissimilarity between levels of each significant comparison. Levels of significance: * *P* < 0.05, ** *P* < 0.01 and *** *P* < 0.001



Fig. 1 Multivariate nMDS ordination of Bray–Curtis distances between assemblages colonizing different type of habitats and matrix. Each symbol represents a centroid calculated for each combination of Type, Matrix and Location (using the averaged abundances of each species across replicates; $n = 3$). Different symbols and colours indicate different type of habitats and matrix: turfs with long fronds in rockpools (filled circle) and emergent-rock (filled square); turfs with short fronds inside rockpools (open circle) and emergent-rock (open square); data were $\text{Log}(X + 1)$ transformed

Table 2 (a) ANOVA of numbers of species in different types of habitats (2 levels: long vs short) and matrix [2 levels: rockpool (RP) vs emergent-rock (ER)]; Location was a random factor nested in Matrix. SNKs for the comparisons (b) Matrix (Type) and (c) Type (Matrix). Means, standard errors and SNK tests are also indicated in Fig. 2

(a) Source	DF	MS	F
Type = <i>T</i>	1	1.4 ^a	0.2
Matrix = <i>M</i>	1	50.4	5.9*
Location (<i>M</i>) = <i>L(M)</i>	8	8.5 ^a	1.2
<i>T</i> × <i>M</i>	1	98.8 ^a	13.5***
<i>T</i> × <i>L(M)</i>	8	9.8	
Residual	40	6.8	
Transform: none			
SNK			
(b) Matrix (Type)	Short	Long	
	RP = ER	RP < ER	
(c) Type (Matrix)	RP	ER	
	Short > long	Short < long	

Levels of significance: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$
^a Tested against pooled Residual + $T \times L(M)$

species in long turfs (SNK tests, Table 2b; Fig. 2). With regard to the comparisons between each Type within each level of the factor Matrix, the numbers of species in longer turfs were greater when these were on emergent-rock; in contrast, there were no differences in numbers of species in

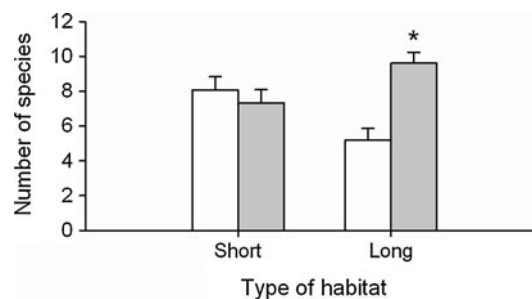


Fig. 2 Diversity of assemblages in different type of habitats and matrix. Mean (\pm SE, $n = 15$) numbers of species in different type of habitats and matrix; white bars indicate rockpools; shaded bars indicate emergent-rock surfaces

short turfs depending on the matrix (SNK tests, Table 2b). These results suggest that effects of type of habitats were, in fact, dependent on their surroundings, thus supporting hypothesis 2 (i.e. not all types of habitats were affected in the same way by their matrix).

The most abundant species generally responded to the type of habitat and not the matrix (Table 3; Fig. 3). There were larger densities of the bivalve *L. australis*, gastropods *E. atropurpurea* and *A. porcata* in habitats with shorter turfs (SNK at $P < 0.05$, Table 3). *A. incidatus* also occurred in greater numbers in habitats with shorter turfs, and in significantly greater densities in location 3 (Table 3).

Environmental variables

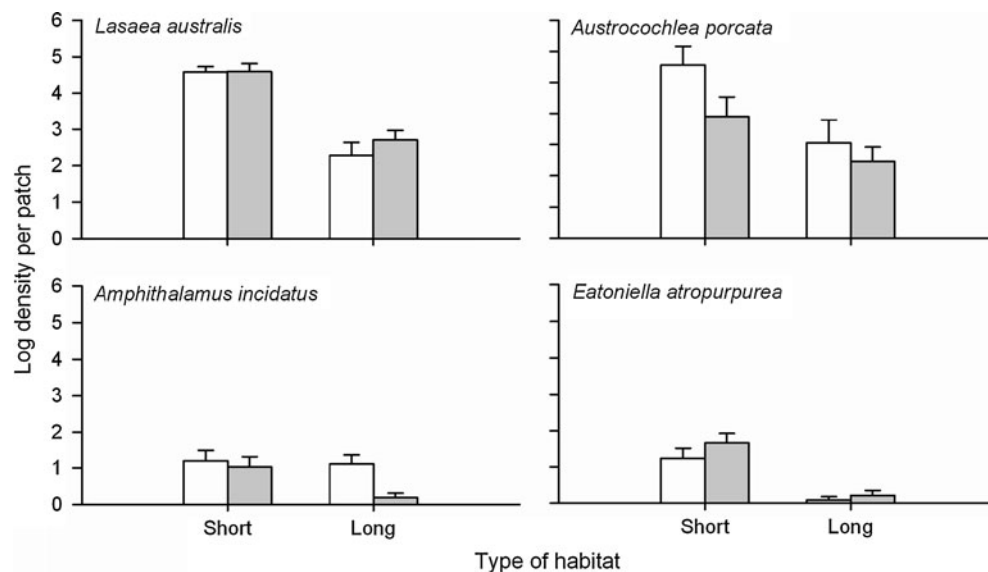
There was considerable variability in dry weight of sediment across different locations, although dry weight of sediment per patch was consistently greater in shorter turfs (Table 4). The dry weight of sediment per patch varied between 74 g (location 5) and 125 g (location 2). In contrast, the concentration of chlorophyll-*a* was not affected by type or matrix of habitats, even though there was a Type × Location (Matrix) interaction (Table 4). The concentration of chlorophyll-*a* per patch was relatively consistent across several locations (53–74 $\mu\text{g ml}^{-1}$), although, in location 4, there was a relatively high average value of 131 $\mu\text{g ml}^{-1}$. No significant differences or pattern was found in the rank order of means of concentration of chlorophyll-*a*.

The strength of the relationship between numbers of species and sediment varied depending on Type and Matrix (Fig. 4). On emergent-rock, the relationship between sediment and numbers of species was different depending on the type of turfs (short, $r = 0.19$, $F_{1,15} = 0.5$, $P > 0.4$; long, $r = 0.81$, $F_{1,15} = 27.2$, $P < 0.001$). In rockpools, there were no significant relationships between amounts of sediment and numbers of species in either type of turfs (short, $r = 0.003$, $F_{1,15} = 0.0$, $P > 0.9$; long, $r = 0.45$,

Table 3 ANOVA of most abundant species: bivalve *L. australis* (a), and gastropods *A. porcata* (b), *A. incidatus* (c), and *E. atropurpurea* (d) in different types of habitats (2 levels: long vs short) and matrix (2

levels: rockpool (RP) vs emergent-rock (ER)); and Location was a random factor nested in Matrix; means and standard errors are in Fig. 3

Source	DF	(a)		(b)		(c)		(d)	
		MS	F	MS	F	MS	F	MS	F
Type = <i>T</i>	1	67.8 ^a	69.5***	14.7	6.7*	4.3 ^a	5.2*	25.0	21.7**
Matrix = <i>M</i>	1	0.5	0.3	4.8	1.5	3.2	2.4	1.1	1.3
Location (<i>M</i>) = <i>L</i> (<i>M</i>)	8	1.6 ^a	1.7	3.2	3.1**	1.3 ^a	1.6	0.8	1.3
<i>T</i> × <i>M</i>	1	1.2	1.2	1.1	0.5	2.2 ^a	2.6	0.3	0.3
<i>T</i> × <i>L</i> (<i>M</i>)	8	1.3 ^a		2.2	2.1	0.5		1.2	1.8
Residual	40	0.9		1.0		0.8		0.6	
Transform		Ln(<i>X</i> + 1)		Ln(<i>X</i> + 1)		Ln(<i>X</i> + 1)		Ln(<i>X</i> + 1)	
SNK		Short > long		Short > long		Short > long		Short > long	

Levels of significance: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ ^a Tested against pooled Residual + $T \times L(M)$ **Fig. 3** Densities of most abundant species in different type of habitats and matrix. Mean (\pm SE, $n = 15$) densities of most abundant species *L. australis*, *A. porcata*, *A. incidatus* and *E. atropurpurea* in different types of habitats and matrix; 'white bars' indicate rockpools; shaded bars indicate emergent-rock surfaces

$F_{1,15} = 3.6$, $P > 0.08$). Most patches with shorter turfs had approximately 40 g of sediment, suggesting a maximal amount of sediment that turfs can retain. Similarly, the relationship between chlorophyll-*a* and numbers of species depended on the matrix and the type of turfs. In rockpools, there was no significant relationship in either type of turfs (short, $r = 0.38$, $F_{1,15} = 2.47$, $P > 0.1$; long, $r = 0.07$, $F_{1,15} = 0.06$, $P > 0.8$), whilst on emergent-rock, there was a significant relationship in long turfs ($r = -0.55$, $F_{1,15} = 6.16$, $P < 0.03$) but in short turfs ($r = -0.36$, $F_{1,15} = 2.04$, $P > 0.1$).

Discussion

This study demonstrated that (1) the composition of assemblages was affected by the matrix (i.e. rockpools or

emergent-rock) and type of habitat, but this varied in magnitude among random locations; (2) the effects of the matrix on the number of species varied between the different types of habitats; (3) abundant species showed specific responses to type of habitat, independently of the matrix; (4) relationships between numbers of species and two major environmental variables varied depending on the type of habitats and the matrix. Generally, findings demonstrate that responses to different types of habitats are dependent on the surrounding habitat, even though several common species did not show any particular response to different matrices. The challenge for investigating biotic responses to structure of natural habitats is therefore to determine whether the context in which these habitats occur modifies the physical structure (e.g. Driscoll and Donovan 2004), the resources (e.g. Van Elven et al. 2004), or the potential pool of species colonizing habitats (e.g. Lawton 1999).

Table 4 ANOVA of (a) weight of sediment and (b) concentration of chlorophyll-*a* in different type of habitats (2 levels: long vs short) and matrix [2 levels: rockpool (RP) vs emergent-rock (ER)]; Location was a random factor nested in Matrix

Source	DF	(a)		(b)	
		MS	F	MS	F
Type = <i>T</i>	1	0.5 ^a	9.2**	15,206.4	3.7
Matrix = <i>M</i>	1	0.4	1.3	427.6	0.1
Location (<i>M</i>) = <i>L</i> (<i>M</i>)	8	0.3 ^a	5.3***	7,442.4	13.2***
<i>T</i> × <i>M</i>	1	0.0 ^a	0.0	0.8	0.0
<i>T</i> × <i>L</i> (<i>M</i>)	8	0.1		4,124.3	7.3***
Residual	40	0.1		562.2	
Transform		Ln(<i>X</i> + 1)		None	
SNK		Short > long			

Levels of significance: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$
^a Tested against pooled Residual + $T \times L(M)$

The relationships between structure of habitat and patterns of diversity of benthic invertebrates have been previously studied using coralline turfs naturally occurring on rock platforms (e.g. Akioka et al. 1999; Kelaher et al. 2001) or in artificial turfs (Kelaher 2003a, b; Matias et al. 2010). There have, however, been fewer studies that have investigated coralline turfs in rock pools (but see Hull 1999; Bussell et al. 2007). Rockpools are extremely variable (e.g. in size, depth and shade) which possibly explains why there is great variability in composition of faunal assemblages colonizing algae in rockpools (Huggett and Griffiths 1986; Metaxas and Scheibling 1994; Hicks 1980; Hull 1999). The results of the current study showed, in contrast, that assemblages colonizing habitats in rockpools were considerably less variable than those on emergent-rock surfaces. This discrepancy might be because several natural species of macroalgae may change growth form as a result of physical characteristics of

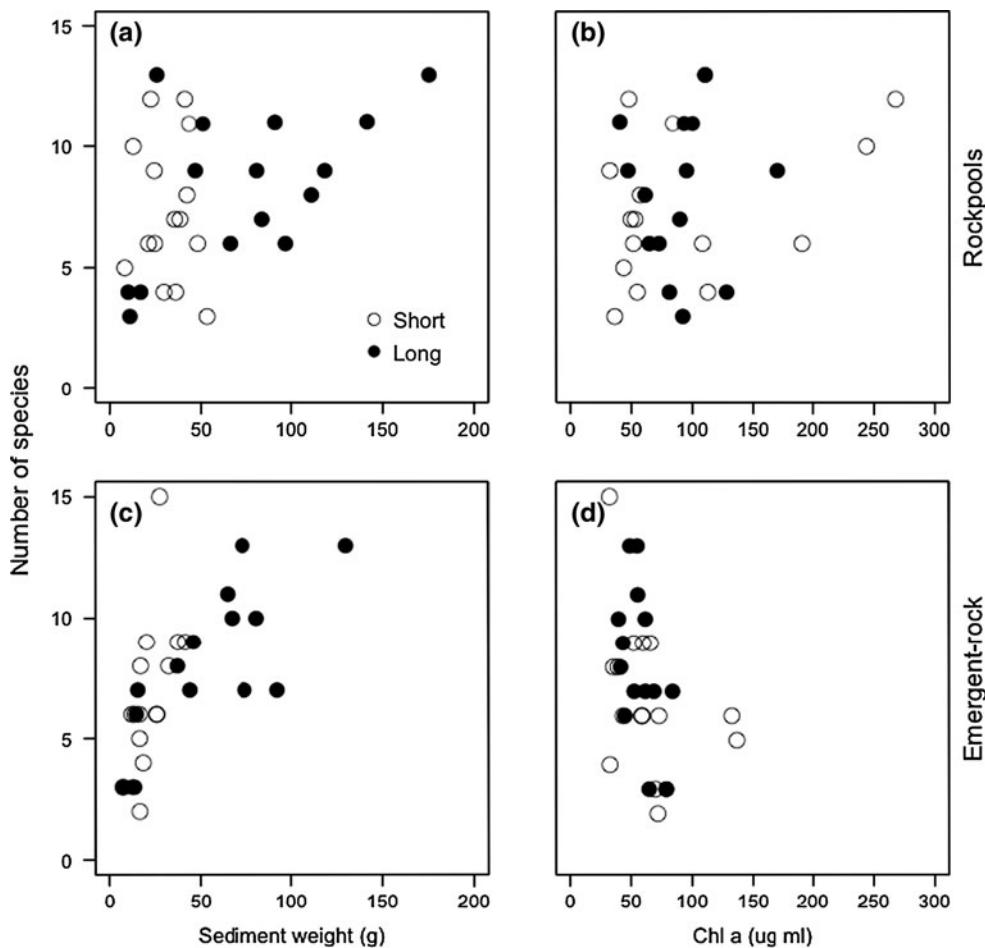


Fig. 4 Relationships between numbers of species and environmental variables (sediment or chlorophyll-*a*). Environmental variables were measured in different types of habitats (i.e. short vs long) under different matrix [i.e. rockpools, (a, b); emergent-rock, (c, d)].

Different symbols indicate the types of habitats (short, white circles; long, black circles). Coefficients of correlation and significance values in “Results” section

rockpools (e.g. coralline turfs have different morphologies in rockpools and non-rockpools surfaces; Akioka et al. 1999), which ultimately modifies the type of habitat provided for invertebrate species (Metaxas and Scheibling 1994). In the present study, however, experimental habitats had the same structure and period of colonization across different matrices, which removed potential differences in habitat structure and therefore any difference between the different matrices must be attributed to differences other than those in habitat structure.

An alternative explanation is that habitats under different contexts provide different resources so that the assemblages colonizing such habitats are also different (e.g. Andren 1994; Steffan-Dewenter et al. 2002; Collinge et al. 2003; Skilleter et al. 2005). The colonization of similar experimental habitats embedded in different matrices has been previously studied (e.g. sand vs seagrass, Tanner 2006), although the quantification of resources in different matrices remains scarce. In artificial seagrass beds, the diversity and biomass of macroalgal epiphytes—an important resource associated with faunal assemblages—differ depending on the context in which artificial patches are embedded (i.e. varying proximity to rocky reefs, Van Elven et al. 2004). The present results showed that two environmental variables shown to be important for many marine gastropods (i.e. micro-algal biomass and accumulated sediment; Beesley et al. 1998; Kelaher et al. 2001; Olabarria and Chapman 2001) were greatly influenced by the location on the shore, which was probably better explained by differences in wave-exposure to ocean swell between locations (Underwood 1984). This was expected since different wave-exposure is known to affect the accumulation of sediment (Prathep et al. 2003; e.g. Motta et al. 2003) and micro-algal growth (e.g. Thompson et al. 2005) in intertidal habitats. Furthermore, the variance of these environmental variables was only correlated with the numbers of species in particular combinations of habitat and matrix (i.e. long turfs on emergent-rock), which indicates that the importance of environmental variables may not be the same across all habitats in this system. Thus, these results are further evidence of the importance of determining the appropriate scales at which benthic assemblages respond to habitat structure and other environmental variables (e.g. food availability). Future studies could investigate these responses at finer spatial scales to further advance our understanding of the patterns of distribution of benthic assemblages in relation to environmental variability.

Another potential source of variability between assemblages in different habitats might be attributed to changes in biotic interaction (e.g. predation, Hughes and Grabowski 2006; inter-specific competition, Spooner and Vaughn 2006; Matias et al. 2012) depending on the matrix in which habitats were deployed. Generally, habitats with longer turfs had greater numbers of species. In rockpools,

however, there were no differences in numbers of species between types of habitats. Common species *L. australis* and *Amphithalamus incidatus* did not occur in similar numbers inside or outside of rockpools; other common species *A. porcata* and *E. atropurpurea* occurred in similar numbers in either matrix (Fig. 3). These observations might be explained by previous evidence that competition between species of gastropods might be dependent on the quality of the habitat (e.g. “habitat suitability”, Firth and Crowe 2010) possibly due to differential competitive ability of species depending on the habitat in which they are found (Keough et al. 1997). Furthermore, several species of gastropods show habitat-associated survival as a result of variability in structural components of the habitat (e.g. amount of sediment, Olabarria and Chapman 2001). Future research on these assemblages should investigate whether the structure of patches of habitat affects competitive interactions.

These results may have additional implications for our understanding of the distribution and abundance of species in intertidal rocky shores. Many common grazers in intertidal rocky shores (e.g. gastropods *A. porcata*, *Bembicium nanum*, *Nerita atramentosa*, and limpet *Patelloida* sp.) recruit in large numbers to coralline turfs—artificial or natural—and then disperse to the surrounding emergent-rock. Experiments in different regions (e.g. Australia, Chile and Ireland; Kelaher et al. 2004) showed that assemblages in coralline habitats may vary depending on the pool of species of each region, which is possibly explained by different matrices in which coralline habitats were embedded in those different regions. On many Australian shores, coralline turfs occur predominantly in low-shore areas; on rocky shores, in other parts of the world, coralline turfs occur almost exclusively in rockpools (e.g. UK, Bussell et al. 2007), with low-shore areas often dominated by other macroalgal beds (e.g. fucoids). Understanding the consequences of the spatial structure of these habitats complements our knowledge on patterns of abundance and distributions of functionally important species and ultimately the structure of intertidal assemblages.

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