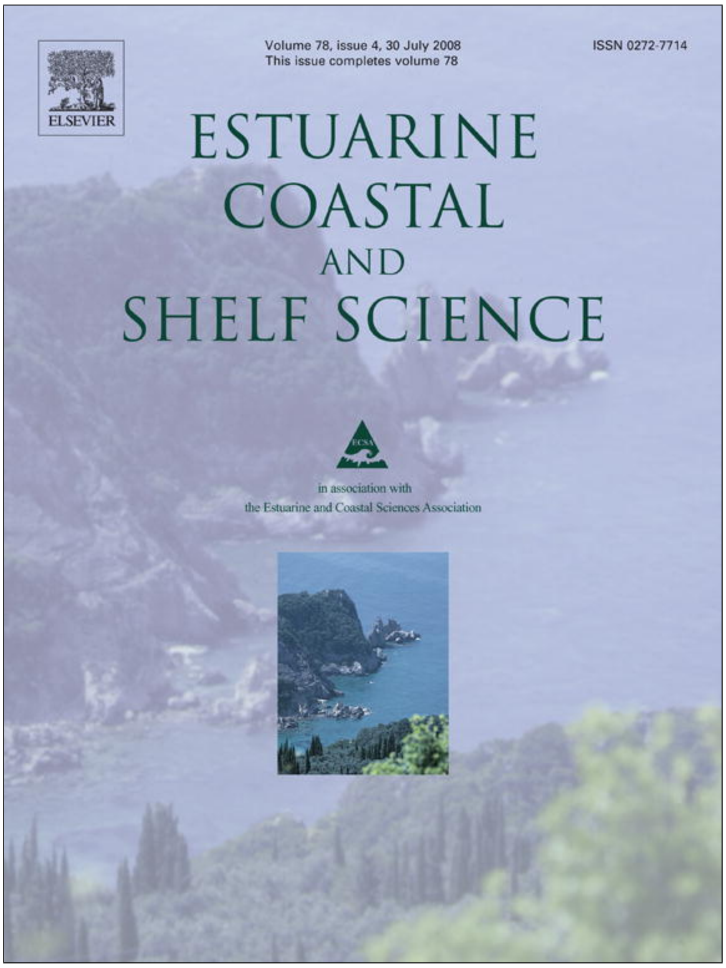
Volume 78, issue 4, 30 July 2008
This issue completes volume 78
ISSN 0272-7714
ELSEVIER
ESTUARINE
COASTAL
AND
SHELF SCIENCE
ECSA
in association with
the Estuarine and Coastal Sciences Association

Estuarine, Coastal and Shelf Science 78 (2008) 774–782

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats

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ARTICLE INFO

Article history:
Received 20 December 2007
Accepted 26 February 2008
Available online 6 March 2008

Keywords:
spatial patterns
reefs
algal habitats
gastropods
wave exposure
Western Australia

ABSTRACT

Reef landscapes dominated by canopy-forming species are often irregular mosaics of habitats, with important influences on associated fauna. This study tested if differences in the ecological patterns of mobile fauna inhabiting interspersed (morphologically distinct) algal habitats were altered by the spatial arrangement of reefs of varying proximity to the shoreline. Specifically, prosobranch gastropods were used as models to test that: (1) there were differences in the ecological patterns (species composition and abundances) between three algal habitats (the kelp *Ecklonia radiata*, fucalean macroalgae, and erect red algae); (2) the magnitude of these differences depended on the position of reef lines ('in-shore' vs. 'off-shore'); and (3) these effects were regionally consistent across a ~4° latitudinal gradient (~600 km of coastline) in Western Australia. The ecological patterns of algal-associated gastropods responded strongly to the presence of algal habitats with different physical structure at small spatial scales. Importantly, differences in assemblage structure (e.g. differences in total abundances) between habitats across the latitudinal gradient were especially accentuated on the in-shore reefs compared with the off-shore reefs, where a general amelioration of differences between habitats was observed, probably associated with a more widespread effect of stronger wave forces across habitats. Overall, red algae supported higher total abundances and species richness (per algal weight) compared to the other algal habitats, particularly on in-shore reefs. Patterns for individual species were considerably location-dependent, reflecting the natural variability of species across geographical gradients. In contrast, patterns at the assemblage-level were consistent, providing evidence for the existence of general rules underlying the assemblage-level organization of mobile invertebrates on subtidal reefs across this geographical gradient.

1. Introduction

Animals respond to variability in environmental conditions with fluctuations at spatial scales ranging from patchiness (meters) to variation along biogeographic gradients (100s–1000s of km). Linkages across multiple spatial scales, within and between bioregions, are increasingly being considered in the search for general patterns, merging biogeography and community ecology through the resurgence of macroecology (Brown, 1995). However, while most animal phyla are marine, the majority of described patterns come from terrestrial systems, partly as a result of the logistical challenges of fieldwork in marine environments (Clarke et al., 2007). Moreover, the majority of marine (benthic) ecological studies have focused on the effect of one biological (or physical) factor in isolation across a set of limited spatial scales, typically within restricted geographical zones. Studies focusing on the interactive effects of different factors on the ecological patterns of assemblages across bioregions have received comparably less attention; an experimental short-coming that limits the elaboration of general models (Duggins et al., 2001).

Landscapes dominated by canopy-forming foundation species (e.g. bushes, trees, corals, kelps, and seagrasses) are conspicuous elements of many natural systems (Bruno et al., 2003). These landscapes are often irregular mosaics of distinct habitats, providing a complex set of interspersed physical and biological environments, that affect the development and maintenance of faunal assemblages in both terrestrial (Wright, 2002; Keddy, 2005) and marine ecosystems (Dayton et al., 1992; Bertness et al., 1999; Hemminga and Duarte, 2000). For example, different algal hosts can present different assemblages of mobile invertebrates (Edgar, 1983; Taylor and Cole, 1994; Olabarria, 2002; Arroyo et al., 2004; Begin et al., 2004).

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doi:10.1016/j.ecss.2008.02.017

Hydrodynamic forces such as waves are the predominant cause of mechanical stress in coastal areas where they affect the morphology, physiology, distribution and interactions of organisms (Dayton et al., 1992; Siddon and Witman, 2003), such as in the case of algal-associated invertebrates (e.g. Engkvist et al., 2004; Jonsson et al., 2006). A range of features modifies the wave-induced mechanical stress exerted on coastal organisms. The configuration of the coast (e.g. the orientation of the shoreline, depth profile, and the arrangement of structural elements such as reefs, headlands, and islands) plays a key role on spatial scales from 100s kilometres to 100s meters (Wernberg, 2005), because it determines the attenuation of waves by physical mechanisms (friction, refraction, reflection, etc.). On smaller spatial scales, hydrodynamic forces are modified by biotic factors such as the physiognomy and biomechanical properties (e.g. size, structural strength, flexibility, and architecture) of the habitat forming algae (Bertness et al., 1999; Wernberg, 2005; Irving and Connell, 2006). For example, wave-induced forces are lower on small relative to large plants, and on plants with many relatively thin branches relative to those with a planar morphology (Denny, 1999; Boller and Carrington, 2006). Consequently, large algae with a leaf-like thallus (such as many laminarians), and the animals that live on them, are likely to be more vulnerable to the drag caused by waves than, for example, small algae with interstitial spaces between the branching structures.

This study is about algae–animal relationships over large landscapes. The aim was to test whether differences in the ecological patterns of mobile fauna inhabiting interspersed, but structurally distinct, algal habitats were altered by the spatial arrangement of reefs of varying proximity to the shoreline (in-shore vs. off-shore reefs). Prosobranch gastropods were used as models because they have a well defined taxonomy in Australasia, and because they can be easily collected relative to other mobile fauna. Moreover, patterns of abundance are fairly representative of a broader animal assemblage (Chapman and Underwood, 2008). The study hypothesized that: (1) assemblages differed between the common kelp *Ecklonia radiata*, fucalean macroalgae, and erect red algae; (2) the magnitude of these differences depended on the reef line position (in-shore vs. off-shore); and (3) these effects were consistent across large-scale regions (a $\sim$4° latitudinal gradient within a temperate bioregion in Western Australia).

2. Material and methods

2.1. Study area and sampling design

The study was carried out on shallow rocky reefs at three locations along a 4° latitudinal gradient ($\sim$600 km) in Western Australia (Fig. 1, Jurien Bay, Marmion Lagoon and Hamelin Bay). A characteristic feature of the coastline in south-western Australia is a series of aeolianite limestone reefs (and some emergent islands) parallel to the coast, at distances ranging from $<$1 to 10 km off-shore. Off-shore reefs ($\sim$4–10 km from the shoreline) are exposed to the prevailing SW and W oceanic swells. In-shore reefs ($\sim$0–2 km) are protected from these swells (Hegge et al., 1996; Phillips et al., 1997); as waves travel in-shore, they are attenuated by bottom friction, refraction, reflection, and breaking along the complex matrix of reefs and islands. As a result, the in-shore wave heights are generally 40–60% less than corresponding off-shore wave heights (Lemm et al., 1999). Three in-shore and three off-shore reefs, all separated by at least 1 km, were sampled within each location. All reefs were predominantly covered by macroalgae, primarily the small canopy-forming kelp *Ecklonia radiata*, coarsely branched fucalean algae (mainly the genera *Sargassum* with some *Scytothalia*), and erect red algae (e.g. the genera *Amphiroa*, *Callophycus*, *Plocamium*, *Pterocladia*, and *Rhodymenia*) (see Kendrick et al., 1999 for a detailed description of floral assemblages). These three habitats are characterised by clear differences in physiognomy: the kelp and fucalean algae are relatively large ($>$30 cm high), whereas kelp thalli have a planar morphology, fucoids have a bushy thallus structure with many relatively thin branches. Erect red algae are generally small ($<$30 cm), many have a thallus with branching structures, but a few have leaf-like structures. In all samples, the biomass of leaf-like red algae remained $<$5%.

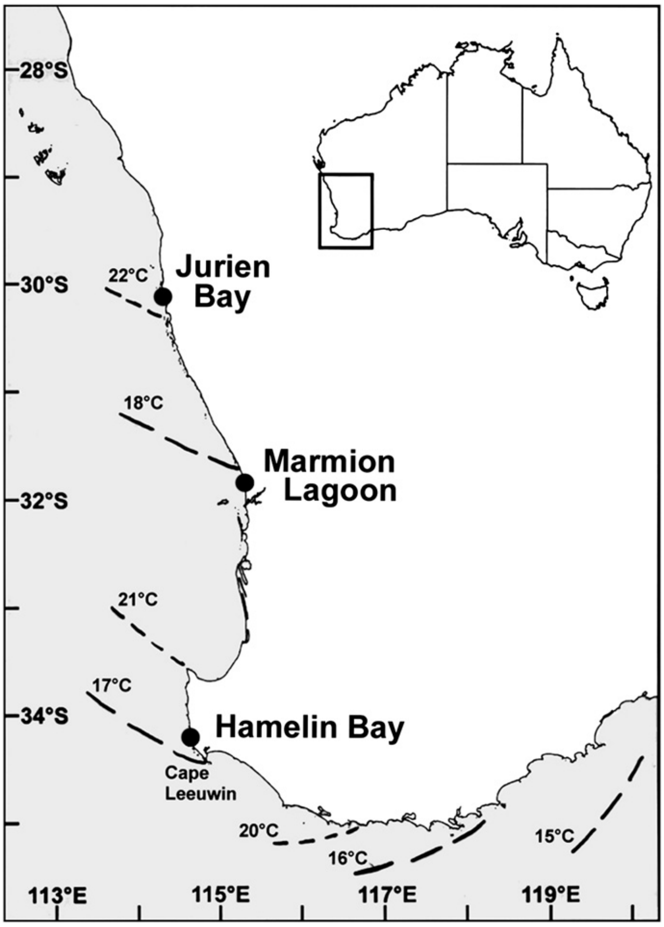

Fig. 1. Map of south-western Australia, showing the three locations of the study, and summer (short dash) and winter (long dash) surface isotherms (after Pearce, 1991).

2.2. Sampling and sorting

On each reef, a SCUBA diver collected all macroalgae within three replicate 50 × 50 cm quadrats (0.25 m^2) of each algal habitat. Each quadrat was positioned in an independent patch haphazardly selected several meters apart from other patches, avoiding edges, and thus encompassing only one type of algal habitat. The size of algal patches ranged between 15 and 30 m^2 for *Ecklonia*, and 2 and 6 m^2 for both fucalean and red algae. All algae were carefully hand picked with the help of a knife and put in a calico bag. Holdfasts were excluded to avoid confounding the comparison of canopies (Jorgensen and Christie, 2003; Arroyo et al., 2004; Christie et al., 2007). All samples were collected in February–April 2007. Samples were frozen ($-20\,^{\circ}$C) until processed in the laboratory. In the laboratory, samples were washed vigorously in fresh water, and passed through a 2 mm sieve. The wet weight of the algae was measured after shaking off excess water. All gastropods retained on the sieve were identified to the lowest feasible taxonomic level (for convenience, all taxonomic units will be referred to as species), and their densities and richness expressed as numbers per 100 g of algal wet weight. All taxonomy followed Wilson (1993).

2.3. Data analysis

Differences between categories (and combinations) of predictive factors were evaluated using multi- and univariate ANOVA. Permutational Analysis of Variance (PERMANOVA, Anderson, 2005) was used to partition both multivariate and univariate variabilities, because this approach allows multivariate testing for interactions, and uses permutations to calculate P-values. The latter was preferable because the data were from unknown distributions, over-dispersed, and contained many zeros. The test statistic (pseudo-F) is a multivariate analogue of the univariate Fisher's F ratio, and in the univariate context the two are identical when using Euclidean distance as the dissimilarity measure (Anderson, 2005). Data were analysed according to a mixed effects, four-factor ANOVA model, incorporating the factors: (1) 'Reef line' (fixed factor with two levels: in-shore vs. off-shore); (2) 'Algal Habitat' (fixed factor with three levels: *Ecklonia*, fucalean algae, erect red algae, and orthogonal to 'Reef line'); (3) 'Locations' (random factor with three levels, and orthogonal to the previous factors); and (4) 'Reefs' (random factor with three levels, nested within the interaction between 'Locations' and 'Reef line'). Data were square root transformed to downweight the most abundant taxa, and multivariate and univariate analyses were based on Bray–Curtis dissimilarities and Euclidean distances, respectively. P-values were calculated from 4999 unrestricted permutations of the raw data. When appropriate, pair-wise *a posteriori* comparisons were executed using 999 permutations. To visualize multivariate patterns, non-metric multidimensional scaling (nMDS) ordination was carried out on the square root transformed data. Only centroids for each algal habitat at both levels of proximity to the shoreline and each location were plotted. Differences in variability (dispersion) in assemblage structure between algal habitats, either in isolation or on each reef line, were tested through pair-wise comparisons with the PERMDISP routine (Anderson, 2004). Univariate analyses were done for two summary variables of the gastropod assemblage (total abundance of individuals and taxonomic richness, hereafter 'species richness'), and for the abundances of those individual taxa that contributed to ~90% of the total abundance for the overall study (see Section 3). All analyses were performed using the PRIMER 6.0 statistical package.

3. Results

3.1. Assemblage-level patterns

Large variations in gastropod assemblage structure were associated with the different sources of variability (Table 1). Nevertheless, several general trends were observed. First, differences in gastropod assemblage structure between algal habitats changed from in-shore to off-shore reefs, as highlighted by the PERMANOVA exerted on the multivariate data set ('RL × AH', $P < 0.05$, Table 1). These interactive effects were consistent across the latitudinal gradient ('Loc × RL × AH', $P > 0.05$, Table 1). Second, gastropods associated with kelps were distinct from those associated with red algae, and showed more variability in assemblage structure (mean multivariate dispersion = 55.54); their centroids were dispersed in the nMDS irrespective of the position on either in-shore or off-shore reefs (Fig. 2). Third, the heterogeneity (dispersion) of assemblages associated with fucalean algae (mean multivariate dispersion = 51.08) depended on the position in-reefs: on in-shore reefs, the assemblage centroids grouped with the red algae, whereas on off-shore reefs they were similar to the centroids of kelp fronds (Fig. 2). Thus, assemblages inhabiting fucalean algae on in-shore reefs were significantly less dispersed compared to off-shore reefs, and to assemblages found on kelp fronds on both in-shore and off-shore reefs ($P < 0.01$ for all these pair-wise comparisons, PERMDISP routine). Fourth, gastropods on erect red algae were quite similar in terms of assemblage structure (mean multivariate dispersion = 44.91); the majority of centroids associated with this algal group clustered together in the two-dimensional ordination space (Fig. 2). Particularly, those from the in-shore reefs showed little variability (mean multivariate dispersion = 35.55, Fig. 2), with a lower multivariate dispersion relative to all three algal groups on the off-shore reefs ($P < 0.01$ for all pair-wise comparisons, PERMDISP routine).

Red algae supported higher abundances and species richness of gastropods (per weight) compared to the other two algal habitats on both in-shore and off-shore reefs (Fig. 3, 'AH' as main effect, $P < 0.001$, Table 1). Differences in total abundances of gastropods (per weight) between the algal habitats changed from in-shore to off-shore reefs ('RL × AH', $P < 0.05$, Table 1). This interaction was the result of a disparity in the magnitude of differences between the three algal habitats from in-shore to off-shore reefs, rather than a change in the direction of the pattern. Specifically, differences in total abundances were reduced from in-shore to off-shore reefs. Patterns of species richness between algal habitats were, however, consistent from in-shore to off-shore reefs ('RL × AH', $P > 0.05$, Table 1), indicating a similarity in the magnitude of the effects from in-shore to off-shore reefs. Importantly, all of these patterns existed irrespective of locations ('Loc × RL', $P > 0.05$; 'Loc × AH', $P > 0.05$; 'Loc × RL × AH', $P > 0.05$; Table 1), suggesting a broad generality of these patterns across the latitudinal gradient.

Table 1

Results of multivariate and univariate ANOVA testing the effects of 'Reef line' (fixed factor), 'Algal Habitats' (fixed factor orthogonal to 'Reef line'), 'Locations' (random factor orthogonal to the previous factors), and 'Reefs' (random factor nested within 'Locations' and 'Reef line') on the structure of gastropod assemblages, total abundance of individuals, and species richness. Significant at $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns: not significant

Source of variability	df	Assemblage structure		Total abundance		Species richness	
		MS	Pseudo-F	MS	F	MS	F
Transformation and Cochran's test		Square root, N/A		Square root, $C = 0.15$ ns		Square root, $C = 0.06$ ns	
Reef line (RL)	1	21,425.92	2.85^{**}	23,572.84	12.08^{**}	0.428	16.92^{*}
Algal Habitats (AH)	2	21,112.21	2.80^{**}	56,393.09	12.51^{***}	0.348	18.69^{*}
Locations (Loc)	2	29,767.54	6.62^{**}	3224.03	1.55 ns	0.037	1.57 ns
Reefs (Loc × RL)	12	4489.98	1.78^{***}	2527.61	2.32^{***}	0.023	3.82^{**}
RL × AH	2	6177.00	1.93^{**}	10,854.44	5.57^{***}	0.029	2.20 ns
Loc × RL	2	7503.10	1.67 ns	1949.83	0.77 ns	0.025	1.06 ns
Loc × AH	4	7521.84	1.95^{*}	4504.94	2.05 ns	0.017	1.35 ns
Reefs (Loc × RL) × AH	24	3847.74	1.53^{***}	2197.43	2.02^{***}	0.013	2.21^{***}
Loc × RL × AH	4	3193.33	0.82 ns	1947.73	0.88 ns	0.013	0.97 ns
Residual	108	2508.70		1085.05		0.062	

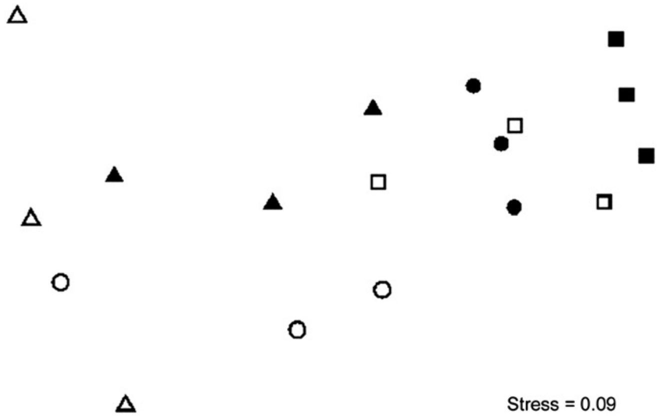

Fig. 2. Two-dimensional non-metric multidimensional scaling plot showing algal habitat centroids of prosobranch gastropod assemblages on in-shore (filled symbols) and off-shore reefs (unfilled symbols). Red algae (■), fucalean algal stands (●), and *Ecklonia radiata* fronds (▲).

3.2. Species-level patterns

A total of 47 prosobranch gastropod taxa were found at the three locations. Figs. 4–6 show which taxa dominated the assemblages associated with each algal habitat on both in-shore and off-shore reefs, at each location. For two of the three most abundant taxa for the overall study (*Phasianella* spp. and Hydrobidae), mean abundances (per algal weight) were higher on red algae relative to the other two algal groups, and on in-shore relative to off-shore reefs, irrespective of locations (Figs. 4–6, Table 2). However, differences between algal habitats and position on reefs (in-shore vs. off-shore) varied between locations for most taxa ('Loc × AH' and 'Loc × RL', $P < 0.05$, Table 2), potentially preventing the detection of main effects for the fixed factors (Table 2). In fact, the patterns of most taxa were, in general, considerably more location-dependent ('Loc × AH' and 'Loc', $P < 0.01$, in most cases, Table 2) compared to the patterns detected at the assemblage-level. This probably reflects species-specific geographical patterns in either the differences between the three algal habitats ('Loc × AH', Table 2), or in the general pattern of distribution of each taxon along the latitudinal gradient ('Loc' as a main effect, Table 2).

4. Discussion

It is generally acknowledged that changes in the physical structure of the habitat affect community organization (Beck, 2000). At small spatial scales, the existence of patches of (morphologically) different vegetated habitats has profound implications in the ecological patterns of mobile invertebrates that rely on these stands as habitats (Taylor and Cole, 1994; Begin et al., 2004; Wernberg et al., 2004; Schmidt and Scheibling, 2006). This work supports this model, specifically by showing that the habitats provided by different algal stands on subtidal reefs significantly affect the ecological patterns of associated gastropods. Importantly, these results add new insights into the potential role of reef-position (and hence the coastline configuration) in modifying these patterns between interspersed habitats, with possible implications for the organization of temperate hard-substrate animal assemblages. Variability in assemblage structure for each habitat was differently affected by reef line position, with a substantial alteration in the magnitude of the patterns (e.g. total abundances) between habitats from in-shore to off-shore reefs.

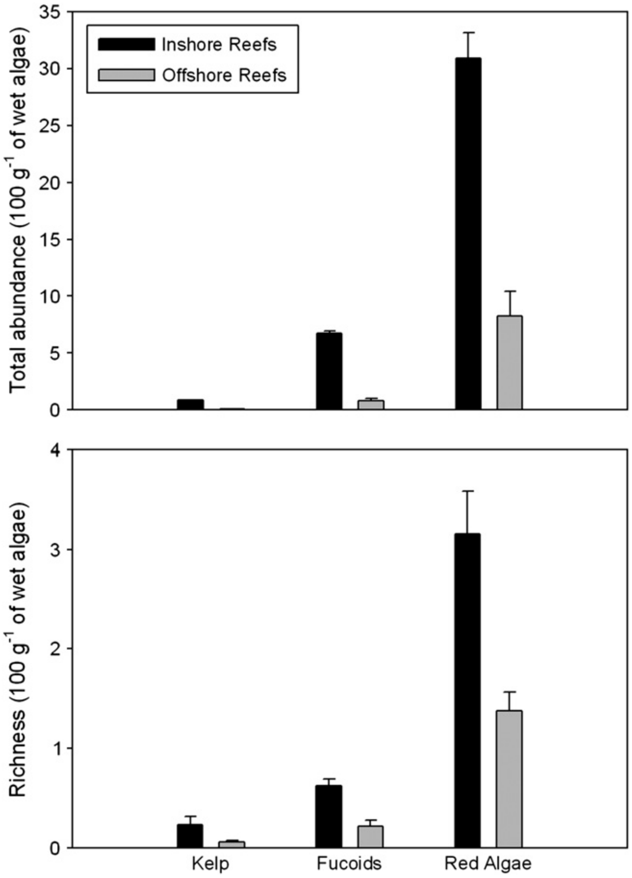

Fig. 3. Mean total abundance and species richness of prosobranch gastropods associated with each algal habitat on in-shore and off-shore reefs. Error bars are +SE of means ($n = 27$).

The habitat provided by each algal type is differentially affected by wave action. Algal morphology, especially size, strongly influence wave-induced drag forces, such that lower forces are imposed on small relative to large algae (Denny, 1999). Further, the ability to reconfigure into a more compact shape (i.e. reducing distances between neighbouring branches and/or thalli) has a drag-minimizing effect, reducing the forces experienced by algae (Johnson, 2001; Wernberg, 2005; Boller and Carrington, 2006). As a result of the larger, wider, and flattened fronds that have a greater surface exposed to water flow, large algae such as *Ecklonia radiata* and the animals that live on them, may be more affected by water motion than, for example, small erect red algae and their fauna. This potential amelioration in the intensity of flows among algal habitats can result in differences in the levels of stress experienced by gastropods. In this sense, the low densities of gastropods on the fronds of *E. radiata*, and in the fucalean algae on the off-shore (wave-exposed) reefs, could be attributed to wave-induced sweeping and frond whiplash of these algae, reducing gastropod abundances directly, or indirectly by regulating food items (e.g. epiphytes, Kiirikki, 1996). In contrast to *E. radiata*, the highly branched, fine, and densely packed structure of red algae, and to some extent fucalean algae, may compact more easily, ameliorating the intensity of flow-induced forces in their vicinity, and thus providing gastropods with a better opportunity for shelter and attachment to withstand movements induced by waves.

Differences in the ecological patterns of gastropods were especially accentuated on the in-shore reefs. On the off-shore reefs, however, differences in assemblage structure were less evident; the

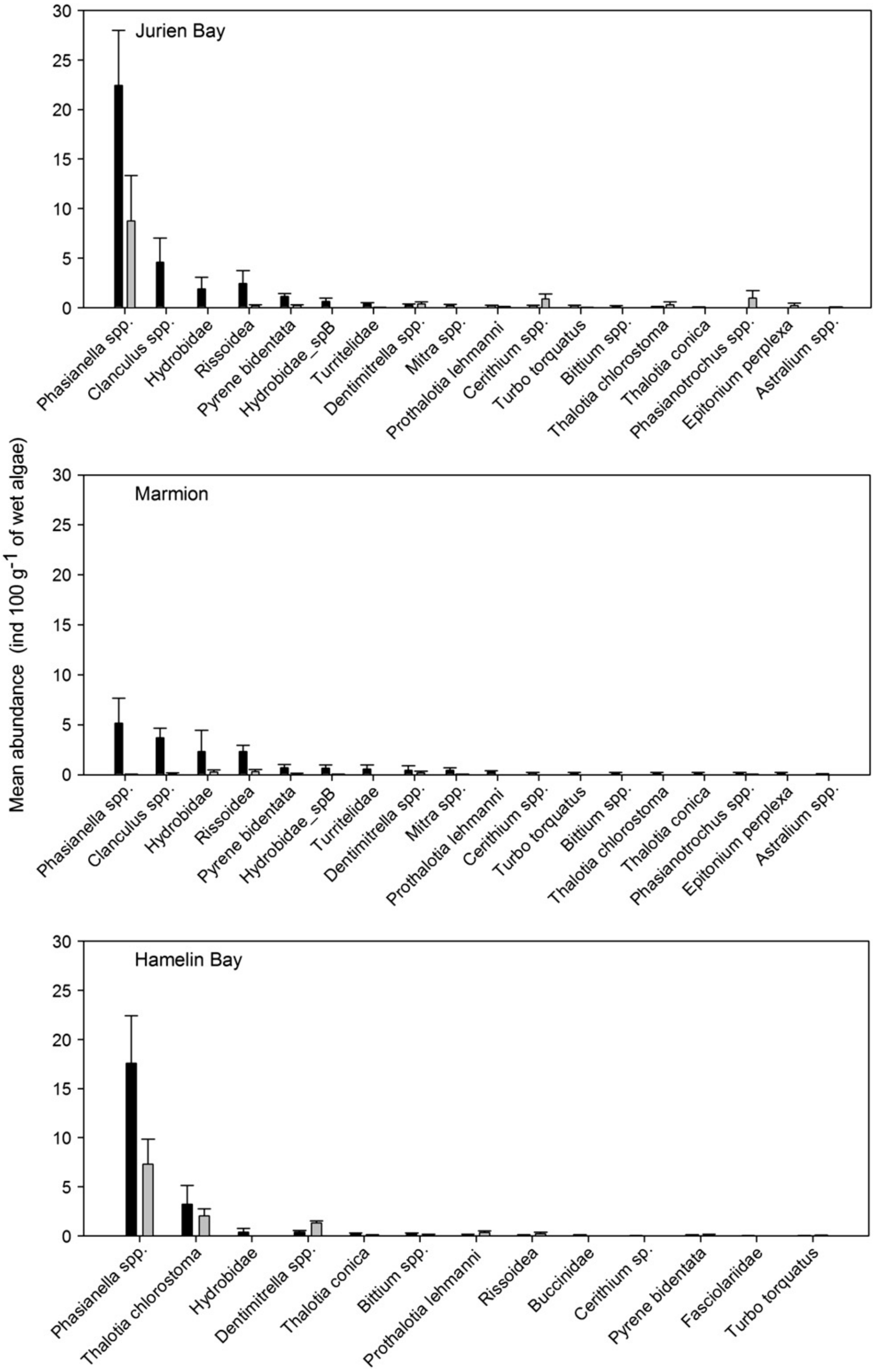

Fig. 4. Rank abundances of gastropods associated with erect red algae on in-shore (grey bars) and off-shore (white bars) reefs at each of the three locations. Taxa with a contribution <0.1% of total abundances were omitted. Error bars are +SE of means ($n = 9$).

effects of stronger wave forces (Lemm et al., 1999) are probably more widespread across habitats, resulting in an amelioration of differences between algal habitats in the ecological patterns (e.g. differences in total abundances). Despite this study demonstrating a dramatic difference in the abundance of organisms between in-shore and off-shore reefs, we cannot unambiguously distinguish between direct wave action, and other environmental factors that might co-vary with increasing distance from shore, such as nutrient levels, sedimentation, turbidity, abrasion, or fish predation pressure. However, it is most likely that the mechanical stress associated to wave action *per se* plays a large role in determining the patterns of prosobranch gastropods inhabiting algal fronds on shallow rocky reefs. Despite differences, at the landscape level, in algal assemblages on protected and exposed reefs in the study area (Phillips et al., 1997), there are no significant changes in species composition (Kendrick et al., 1999) to confound the observed

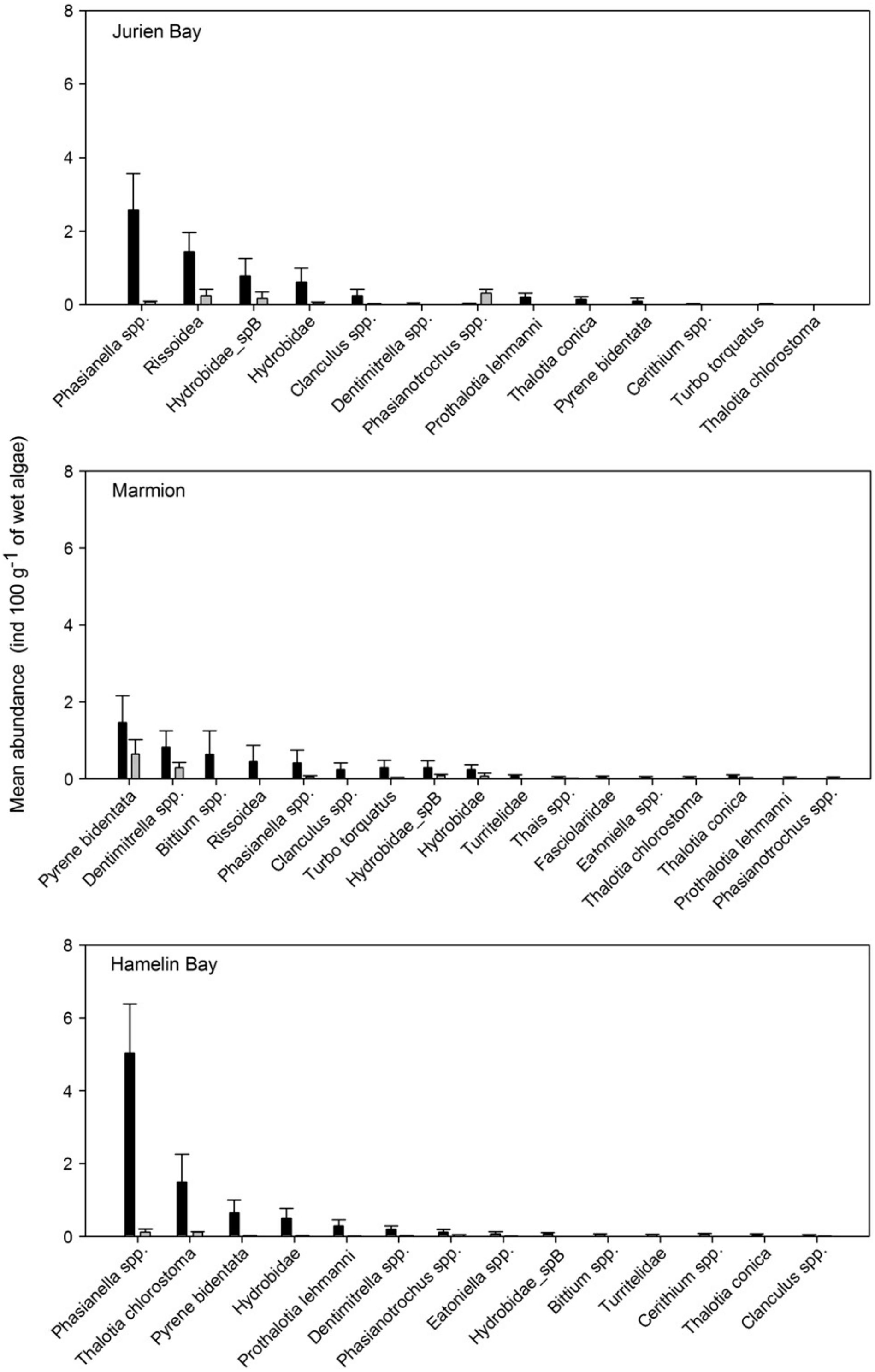

Fig. 5. Rank abundances of gastropods associated with fucalean algae on in-shore (grey bars) and off-shore (white bars) reefs at each of the three locations. Taxa with a contribution <0.1% of total abundances were omitted. Error bars are +SE of means ($n = 9$).

patterns. Moreover, these patterns were consistent between locations encompassing a 4° latitudinal gradient (~600 km coastline), suggesting the generality of these findings as a valid model for temperate, subtidal, forests in Western Australia.

Patterns in species composition and abundances (per algal weight) at small scales may be explained by three broad groups of processes: differential recruitment, mortality, and migration. Larvae and juvenile individuals could recruit in greater numbers to one habitat than to others or, if recruitment occurs evenly throughout the available habitats, differential mortality rates could lead to lower abundances; in this case, stands dominated by brown algae, especially *Ecklonia radiata*. Abundances of gastropods could be highest on red and fucalean algae because these algae provide a greater surface area per wet weight for food items (algal epiphytes, bacteria, etc.) (Bell et al., 1993), or because they provide a better refuge from predation, as complex branched habitats may

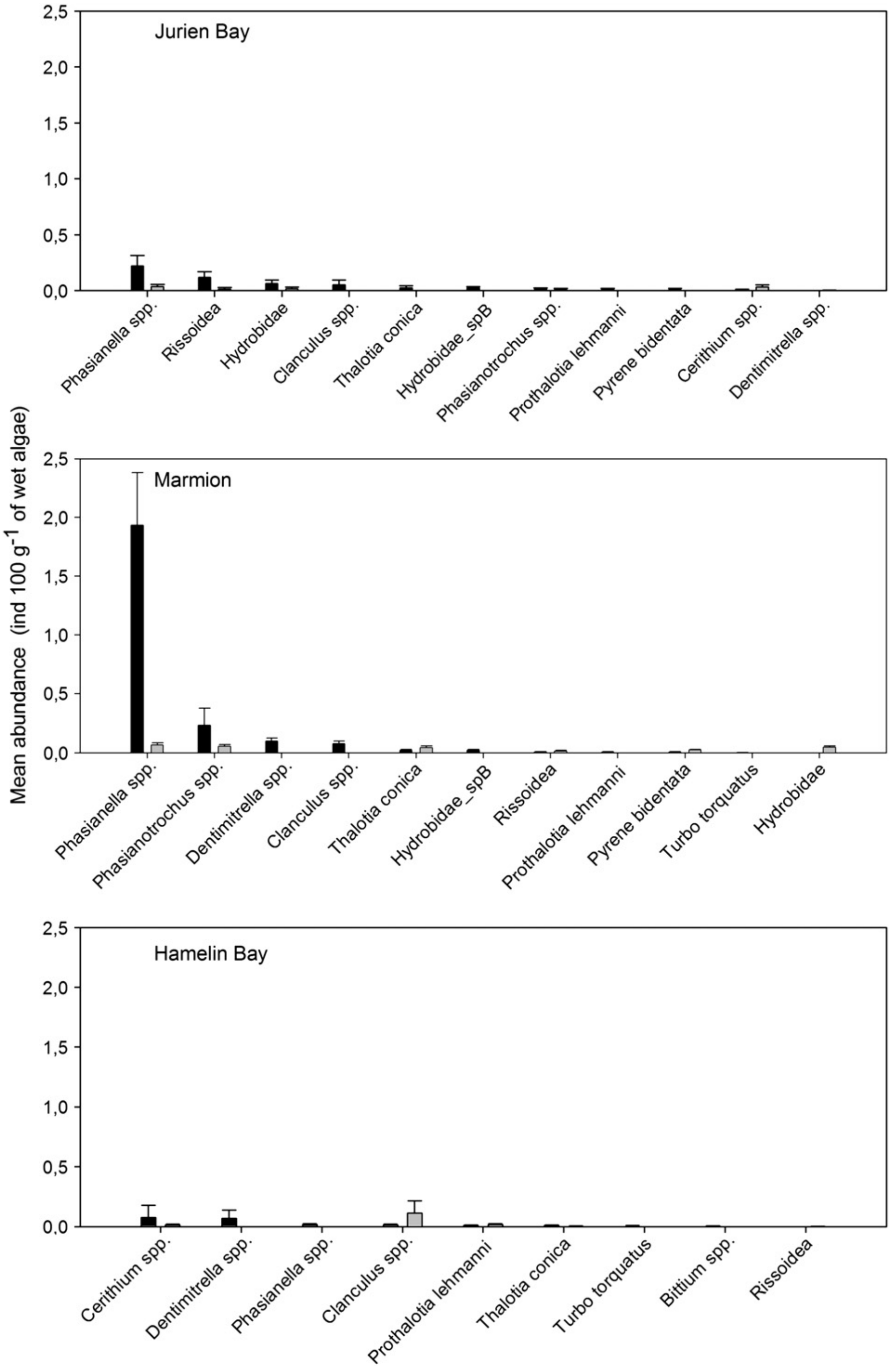

Fig. 6. Rank abundances of gastropods associated with the kelp, *Ecklonia radiata*, on in-shore (grey bars) and off-shore (white bars) reefs at each of the three locations. Taxa with a contribution <0.1% of total abundances were omitted. Error bars represent SE of means ($n = 9$).

give better protection from visual predators compared to more simple leaf-shaped morphologies (Edgar, 1983; Jacobi and Langevin, 1996). Moreover, brown algae can have important chemical defences against herbivores compared with red algae (Toth and Pavia, 2007); such inducible chemical defences are particular relevant in *E. radiata* (Luder and Clayton, 2004). Alternatively, if recruitment is similar between habitats, adults and juveniles could actively migrate between different algal patches, remaining in favoured habitats (Crowe and Underwood, 1998). The study, however, does not provide information to distinguish the relative importance of these causal processes.

Patterns for the overall gastropod assemblages were similar between locations, whereas patterns for individual species were more location-dependent. Potentially, this reflects the natural variability of species across large geographical gradients. However, it should be noted that the 'natural' variability associated with individual species did not obscure the general patterns identified by this work and these results, therefore, provide evidence for the existence of general rules underlying the assemblage-level organization of mobile invertebrates on subtidal reefs. These results reinforce the macroecological view that strong ecological patterns emerge from the 'noise' when numbers and scales are large.

Table 2

Results of ANOVA testing the effects of 'Reef line' (fixed factor), 'Algal Habitats' (fixed factor orthogonal to 'Reef line'), 'Locations' (random factor orthogonal to the previous factors), and 'Reefs' (random factor nested within 'Locations' and 'Reef line') on the abundances of those more abundant taxa. Significant at $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns: not significant

Source of variability	df	*Clanculus* spp.		*Dentimitrella* spp.		Hydrobidae		*Phasianella* spp.		*Phasianotrochus* spp.		*Pyrene bidentata*		Rissoidea		*Thalotia chlorostoma*	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Transformation and Cochran's test		Square root, $C = 0.38^{*}$		Square root, $C = 0.28^{*}$		Square root, $C = 0.36^{*}$		Square root, $C = 0.26^{*}$		Square root, $C = 0.81^{*}$		Square root, $C = 0.36^{*}$		Square root, $C = 0.19^{*}$		Square root, $C = 0.45^{*}$	
Reef line (RL)	1	24.32	4.11 ns	77,154.42	38.38 ns	93.28	101.78*	188,212.85	65.85*	16,976.85	0.544 ns	419,965.20	86.29*	108,190.90	21.03 ns	80.61	1.17 ns
Algal Habitats (AH)	2	32.51	3.13 ns	251,503.96	39.30 ns	47.37	14.67**	311,089.74	54.19*	17,082.71	45.89*	329,664.12	44.16 ns	62,943.80	24.43 ns	167.86	1.50 ns
Locations (Loc)	2	15.70	3.58*	68,775.71	18.36 ns	1.12	0.31 ns	381,625.84	104.00**	87,391.76	65.88**	79,683.00	68.20**	257,411.44	141.19***	185.22	17.57**
Reefs (Loc × RL)	12	4.37	2.31**	37,441.67	28.02**	3.56	1.21 ns	36,691.45	22.30**	13,263.68	11.63 ns	11,682.67	0.771 ns	18,230.80	10.78 ns	10.54	3.76**
RL × AH	2	9.54	2.90 ns	27,687.32	20.13 ns	42.99	13.68**	36,264.89	23.70 ns	21,802.00	0.602 ns	64,594.58	35.79 ns	5982.19	0.249 ns	40.22	1.16 ns
Loc × RL	2	5.90	1.34 ns	20,098.15	0.536 ns	0.91	0.25 ns	28,579.67	0.778 ns	31,178.22	23.50 ns	48,668.54	41.65*	51,436.80	28.21 ns	68.68	6.51**
Loc × AH	4	10.36	4.31**	63,992.21	30.40*	3.22	0.46 ns	57,398.33	24.13*	37,713.93	26.29*	74,637.32	44.56**	25,763.97	12.62 ns	111.84	19.14**
Reefs (Loc × RL) × AH	24	2.40	1.27 ns	21,047.83	15.75*	6.89	2.35**	23,779.27	14.45*	14,342.75	12.58 ns	16,747.76	11.05 ns	20,403.74	12.07 ns	5.84	2.08**
Loc × RL × AH	4	3.29	1.36 ns	13,749.14	0.653 ns	3.14	0.45 ns	15,296.99	0.643 ns	36,166.15	25.21 ns	18,043.66	10.77 ns	23,959.10	11.74 ns	34.60	5.92**
Residual	108	1.88		13,359.43		2.92		1645.62		1139.85		15,144.02		16,897.47		2.79	

Acknowledgements

This research was funded by an Australian Research Council Discovery grant (DP0555929) to T.W., while F.T. was supported by a postdoctoral research fellowship within the framework 'Plan de Formación y Perfeccionamiento' of the Spanish Ministry of Education and Sciences, and M.S.T. was supported by an international postdoctoral fellowship from The Danish Research Academy. We thank M. Vanderklift, L. MacArthur and three anonymous reviewers for providing positive comments on previous drafts, and K. Cook for helping with the sorting of samples. The work detailed in this paper complies with the laws of Australia.

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