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Community development on subtidal temperate reefs: the influences of wave energy and the stochastic recruitment of a dominant kelp

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Abstract Patterns of community development on subtidal rocky reefs in Marmion Lagoon, southwest Australia, were investigated with a settlement panel experiment. We tested the hypothesis that community development would differ between outer and inner reefs lines, because exposure to swell and wave energy was significantly greater on outer reefs. Following a 14-month deployment, we recorded pronounced variability between panels and sites, but did not detect any effect of wave exposure on the structure of panel assemblages. Subsequent data exploration suggested the importance of the presence of kelp recruits (*Ecklonia radiata*) in structuring the overall assemblage. Panel assemblages with kelp recruits were significantly different in structure to those without, principally because of greater space coverage of encrusting coralline algae and less coverage of red turfing algae, spirorbids, and bryozoans. Mature *E. radiata* act as ecosystem engineers in subtidal rocky reefs in southwest Australia. Our results suggested the importance of young, recruiting kelps in determining patterns of early community development on newly available hard substrata.

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Introduction

Temperate subtidal reef systems are structured by a range of physical and biological forces that act across varying spatial and temporal scales (Dayton 1985; Schiel and Foster 1986; Connell 2007). Key physical drivers include temperature (McGowan et al. 1998), oceanography (Dayton et al. 1999), and physical disturbance (Ebeling et al. 1985), while trophic interactions (Andrew and Jones 1990; Shears and Babcock 2002), competition (Dayton 1985; Bell and Barnes 2003), and facilitation (Arkema et al. 2009) are important biological determinants of ecological pattern, particularly at small to medium spatial scales. These factors may interact in complex and unpredictable ways, sometimes leading to widespread changes in community structure and loss of biodiversity and resources (see Wernberg et al. 2011 for recent review). Sound understanding of ecological pattern and process on temperate reefs, in conjunction with effective long-term monitoring, is vital for detecting and adapting to environmental change.

The coastline of southwest Australia represents a global hotspot of biodiversity and endemism for marine macroalgae (Phillips 2001; Kerswell 2006) and also supports rich and abundant assemblages of sessile invertebrates (Hatcher 1989) and reef fish (Hutchins 2001; Fox and Beckley 2005). Kelp-dominated subtidal reef systems are widespread in this region and play important roles in nutrient cycling, modification of water and sediment movement, and the provision of food and habitat for a range of ecologically or economically important species (Kirkman 1984; Kendrick et al. 1999; Wernberg et al. 2005, 2006). Over the past 15 years or so, enhanced research efforts have dramatically improved our knowledge of these kelp forest systems. Regarding ecological pattern, subtidal macroalgal assemblages in southwest Australia are characterized by high species richness and turnover (Kendrick et al. 1999; Smale et al. 2011), pronounced small-scale variability (Phillips et al. 1997; Smale et al. 2010), and predictable large-scale shifts in assemblage structure that correspond to a regional oceanic temperature gradient (Wernberg et al. 2003; Smale et al. 2010, 2011). Key processes that drive these patterns include the modification of the physical environment by the dominant kelp *Ecklonia radiata* (Toohey et al. 2004; Wernberg et al. 2005), pronounced habitat heterogeneity (Toohey et al. 2004, 2007), and wave-driven patchiness in macroalgal canopy cover (England et al. 2008; Wernberg and Goldberg 2008). At larger spatial scales, the poleward-flowing Leeuwin Current, which effects the connectivity of populations and communities as well as water temperature and nutrient availability, has strongly influenced the evolution and ecology of coastal southwestern Australia (Phillips 2001; Kendrick et al. 2009).

Despite an ever-growing body of research, some fundamental knowledge gaps remain. For example, it is evident that spatiotemporal variability in removal of macroalgal canopies by wave disturbance generates “open” space for colonization and leads to a mosaic of patches at different successional stages, which in turn promotes and maintains overall assemblage richness (Toohey et al. 2007; Wernberg and Goldberg 2008). However, patterns of recruitment and early community development onto newly available substrata are poorly known in this system compared with elsewhere, especially for sessile invertebrates. To date, the vast majority of data on settlement and recruitment stems from individual canopy formers, such as *Ecklonia radiata* (Wernberg 2009; Wernberg et al. 2010) and *Sargassum* spp. (Kendrick 1994; Kendrick and Walker 1994); there are almost no published studies on the recruitment and development of whole assemblages on subtidal reefs in southwest Australia (but see Toohey et al. 2007). As benthic community structure and local biodiversity patterns are strongly influenced by “bottom-up” processes (Dayton et al. 1992), documenting patterns of spatial variability in recruitment will enhance our understanding of the system as a whole.

Furthermore, the southwest Australian coastline is subject to intense wave action, due to persistent swell generated by the mid-latitude cyclones tracking across the Indian Ocean, coupled with a coastal geomorphology that offers relatively little protection from predominant southwesterly swells (Lemm et al. 1999). However, wave action is attenuated along many sections of coast by submerged reefs and small islands, which substantially reduce wave action at some nearshore habitats. These wave energy gradients have ecological implications, as exposure is a known determinant of kelp morphology and overall macroalgal assemblage structure, both in southwest Australia (Phillips et al. 1997; Wernberg and Thomsen 2005) and elsewhere (Dayton 1985; Hurd 2000). Ecological responses to wave exposure in this region have, however, been variable and location specific (Wernberg and Thomsen 2005), and further information on the influence of exposure on a range of taxa and life stages is required.

Here, we report on a settlement panel experiment conducted on subtidal reefs that aimed to examine the effect of wave exposure on patterns of community development of sessile flora and fauna. The study had the secondary objective of obtaining much-needed baseline information on the structure of juvenile assemblages in a biodiversity hotspot.

Methods

Study site

The study was conducted at Marmion Lagoon (31°48′18′′S, 115°42′11′′E), situated 20 km north of Perth, Western Australia (Fig. 1). This coastline is characterized by a series of 3 parallel submerged limestone reefs, which influence patterns of wave energy and water circulation within the lagoon. With regard to wave climate, heavy oceanic swells pummel the coastline throughout the year (Searle and Semeniuk 1985), which strongly influences seabed ecology and geomorphology. In addition, locally generated wind waves, predominantly from the southwest, persist during the summer months. Both types of waves are dampened, diffracted, and refracted as they approach the coast by the limestone reefs. This dissipation of energy as waves encounter each successive reef line produces a gradient of physical disturbance ranging from highly exposed sites (offshore reefs) to sites of low exposure (inshore reefs). During 2009, mean wave height (swell and sea combined) off Rottnest Island, ~40 km southwest of Marmion Lagoon, was 2.2 ± 1.0 m and ranged from 8.9 to 0.5 m, indicating the high-energy nature of the study location (based on >15,000 observations recorded by an offshore wave buoy maintained by Department of Transport, Western Australia).

Experimental design and panel deployment

Three sites were selected from both an outer and an inner reef line, to represent “high-” and “low-” wave energy habitats. Within each reef line, sites were between 1.5 and 5 km apart and were initially selected at random from a larger pool of potential sites. All sites were predominately medium to high relief limestone reef (vertical structures of 2–4 m). A priori examination of three different indicators of wave exposure showed that wave energy was significantly greater at sites on the outer reef line compared with the inner reef line (Fig. 2; significance determined with *t* test using 4 *df* and untransformed data). At each site, twelve 600-mm stakes of galvanized iron rebar were fixed vertically into reef by scuba

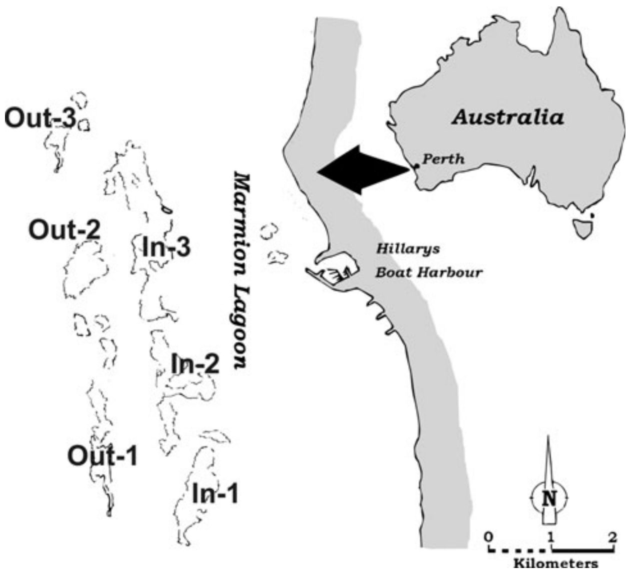

Fig. 1 Map of study area indicating the location of the 3 sites along each reef line in Marmion Lagoon, Perth, Western Australia. Approximate reef structure is also shown

divers using an underwater drill and heavy-duty mallet. Stakes were at least 2 m apart and, were possible, deployed along the reef line (i.e., north to south) perpendicular to the predominant swell direction. A 200 × 200 mm roughened PVC panel was then fixed to each stake, ~150 mm from the reef surface, with cable ties and clamps. Panels were roughened with an industrial sandblaster; the duration and areal coverage of sandblasting were standardized. Care was taken to ensure that each stake protruded perpendicularly from the substratum, so that each panel was mounted vertically and all panels were comparable in orientation. Panels were mounted vertically for ease of deployment and to ensure that panel orientation remained consistent. All large macroalgae within a 1 m radius of each stake was removed, to exclude the possibility of "thallus scour" disturbing the panel assemblages. Panels were deployed, as much as possible, on reef flats (rather than in the lee of ledges or on elevated ridges) to ensure that water movement around panels was comparable between sites and reef lines. The mean depth of panels at each site ranged from 6.6 ± 0.2 (SD) to 9.2 ± 0.3 m and did not differ between reef lines (*t* test: $df = 4$, $t = 1.92$, $P = 0.13$). Panels were deployed in March 2009 and collected in June 2010 by scuba divers, before being returned to the laboratory, in seawater, for analysis. During the 14-month deployment, panels were inspected and maintained (i.e., to replace cable ties and clamps) at tri-monthly intervals.

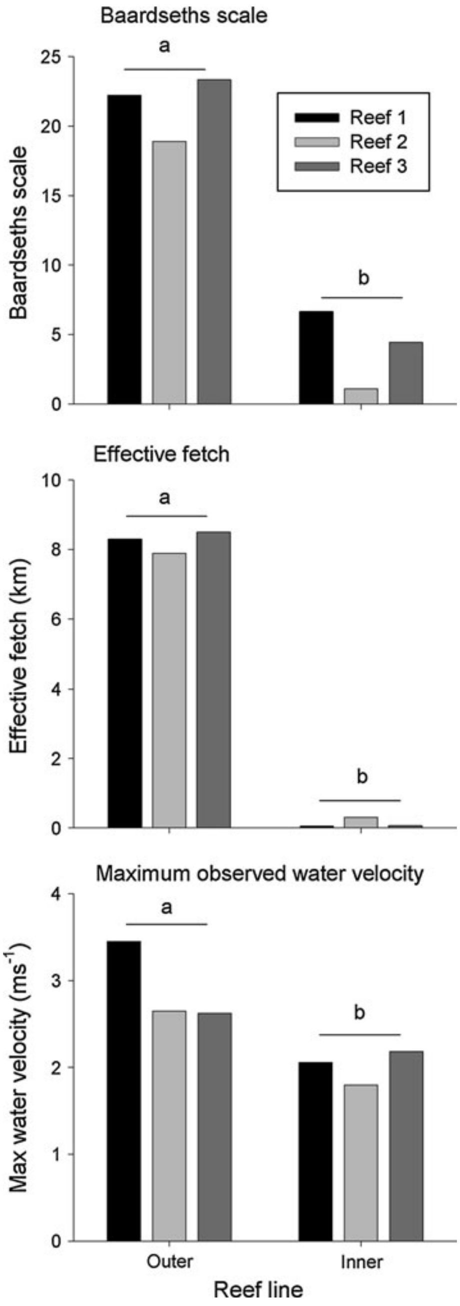

Fig. 2 Indicators of wave climate/exposure for each of the three study sites within the outer and inner reef lines. Baardseths scale and effective fetch are cartographic wave exposure indices (see Ruuskanen et al. 1999; Wernberg and Vanderklift 2010 for details on calculation and modifications). Maximum water velocities were measured at each site using spring scales (as described by Bell and Denny 1994). Spring scales (between 3 and 5 per site) were deployed for 4 weeks during the summer of 2001/02 and 4 weeks during the winter of 2002. All wave indices were greater on the outer reef line compared with the inner line (determined using *t* tests, with 4 *df*, on untransformed data), as indicated on plots with *lower-case letters*

Analysis

A high-resolution digital image of each panel was taken (using an Olympus Mju Tough 8010 14MP camera) immediately on return to the laboratory. Macro images of flora and fauna were also collected, and voucher specimens of all discernable taxa were taken and preserved accordingly. For analysis, images of panels were initially cropped 20 mm inside each edge (to account for "edge effects", see Todd and Turner 1986 and references therein); an analytical area of 160 × 160 mm was therefore obtained for each panel. A grid consisting of 100 squares was then digitally projected onto each image, and the dominant organism within each grid recorded to provide an estimate of percent cover. All macroalgae and macrofauna (>10 mm) were identified to the lowest taxonomic level possible (generally species for macroalgae and family or genus for fauna). Where microalgae or small, indiscernible macroalgae dominated a grid, a coarse taxonomic grouping was assigned (e.g., pink coralline encrusting, red turfing, green filamentous). In this manner, 32 distinct faunal groups (comprising principally of ascidians and bryozoans), 19 specific macroalgal groups, and 6 "coarse" taxonomic categories were used to quantify assemblage structure on the panels.

As some panels were lost during the experiment (at time of retrieval, the number of panels per site ranged from 8 to 12), 8 panels were randomly selected from each site for analysis to maintain a balanced design. Differences in multivariate assemblage structure between reef lines and sites were assessed with PERMANOVA, with sites (random, 3 levels), nested within "reef line" (fixed, 2 levels). Permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data; the transformation was used to down-weight the influence of abundant "coarse" taxonomic categories (e.g., red turfing) and large-space occupiers such as kelps. Tests used 999 permutations under a reduced model, and significance was accepted at $P < 0.05$. A PERMDISP test was also performed to test for differences in multivariate dispersion between reef lines. MDS plots based on the Bray-Curtis similarity matrix were generated to visualize multivariate partitioning between reef lines and sites. Differences in univariate metrics—such as total cover of macroalgae and invertebrates, and cover of individual dominant taxa—were also tested with PERMANOVA, using the model described above (but with matrices based on Euclidean distances of untransformed data, which is analogous to traditional ANOVA). All tests were conducted with PRIMER 6 (Clarke and Warwick 2001), using the PERMANOVA add-on (Anderson et al. 2007).

Results

Marine epiflora and fauna covered at least 92% of the surface area of every settlement panel after 14 months of immersion. The coarse taxonomic groups "red turfing algae" and "pink coralline encrusting algae" were dominant space occupiers, although individual discernible species such as the macroalgae *Amphiroa anceps* and *Ecklonia radiata* and the bryozoan *Triphyllozoon monoliferum* were also common on panels. The abundance of mobile invertebrate grazers observed on panels was very low; no more than five herbivorous gastropod molluscs were observed at any one site (on a total of 8–12 panels). MDS ordination suggested that assemblages on the outer reef line were not distinct from those on the inner reef and that variability between and within sites was high (Fig. 3). PERMANOVA detected no difference in assemblage structure between reef lines, but did detect significant variability between sites nested within reef lines (Table 1). PERMDISP showed that multivariate dispersion did not vary between reef lines ($F_{1,46} = 0.061$, $P = 0.83$). Similarly, the total cover of both macroalgae and invertebrates did not vary between reef lines but did differ significantly between sites (Table 1; Fig. 4).

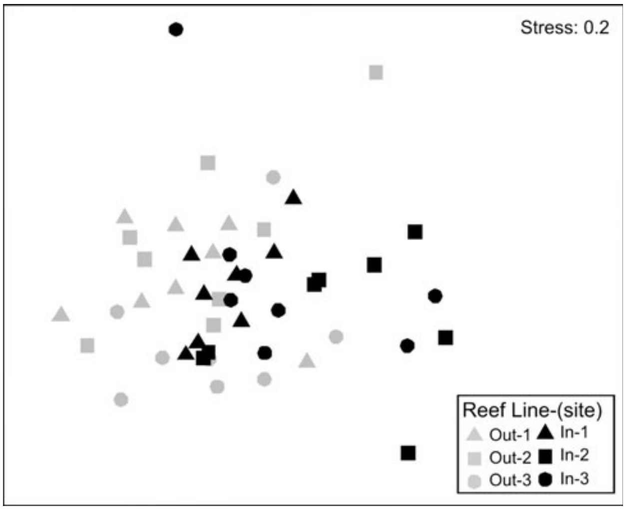

Fig. 3 MDS ordinations of panel assemblages based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data. Centroids represent a single-panel assemblage, with 8 panels per site and 3 sites nested within each reef line. *Centroid colors* represent reef lines while *centroid symbols* denote sites

Patterns for the 3 dominant floral and fauna space occupiers were also examined. For macroalgae, the percent cover of the kelp *Ecklonia radiata* and the red understory alga *Amphiroa anceps* did not differ between reef lines but did vary significantly between sites (Table 1; Fig. 4). For example, mean percent cover of *E. radiata* on the inner reef line ranged from 0 to 16.5 ± 6.5 between sites. The cover of *Ulva* spp. did not differ between reef lines or sites (Table 1; Fig. 4). A similar pattern was observed with fauna, in that the cover of the bryozoan *Triphyllozoon monoliferum*, the spirorbid polychaete *Filograna implexa,* and the colonial ascidian *Leptoclinides* sp. did not differ between reef lines, although *T. moniliferum* did differ between sites (Table 1; Fig. 4). The cover of all floral and faunal species varied considerably between panels within sites, as indicated by consistently large error bars (Fig. 4).

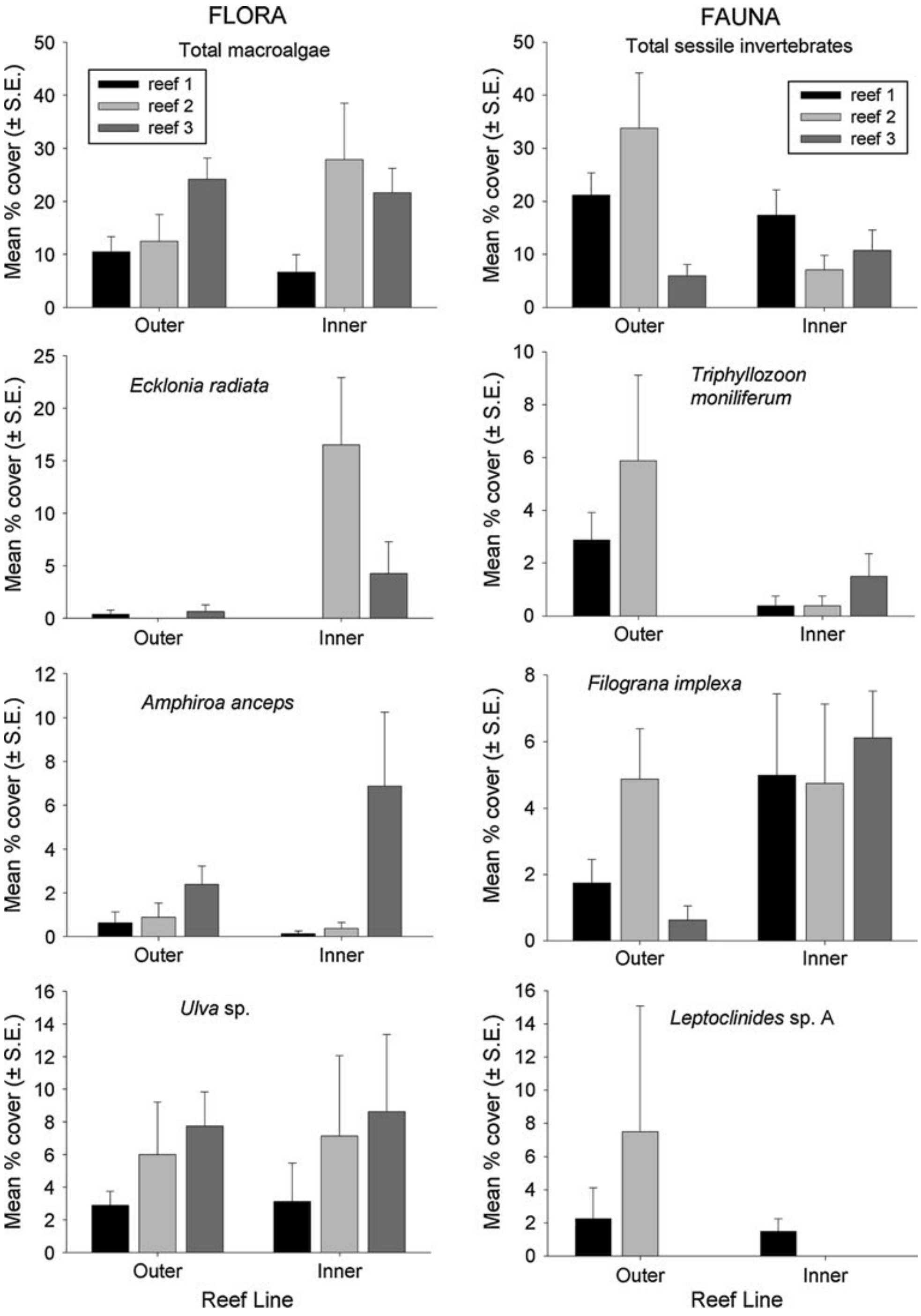

Fig. 4 Mean percent cover ($n = 8$) of all macroalgae and all sessile invertebrates on settlement panels at each of the three reefs nested within the two reef lines. Also shown are the three most dominant floral and faunal species. *Error bars* represent standard error (SE)

During the data-exploration process, it became evident that the presence/absence of the kelp *Ecklonia radiata* on settlement panels, which had attained a total length >40 cm, corresponded to a general shift in assemblage structure. A cluster analysis (based on 999 permutations, conducted with PRIMER) and resultant dendrogram indicated that samples were grouped, to large extent, by the presence/absence of *E. radiata* (Fig. 5). A SIMPROF test, which conducts a permutation test of the null hypothesis that sets of samples do not differ from each other in multivariate structure, detected significant ($P < 0.05$) dissimilarity between all but one of the samples that included *E. radiata* and all but one that did not (Fig. 5).

To investigate this further, samples were divided into two groups, a posteriori, to generate a factor based on the presence or absence of *Ecklonia radiata* (which was removed from the dataset for subsequent analyses). A Bray-Curtis similarity matrix, generated from square-root-transformed data, was used to construct an MDS ordination to visualize multivariate partitioning between levels

Table 1 Results of multivariate and univariate PERMANOVA analysis to test for differences between reef lines and sites (nested within reef line)

Response variable	Reef line		Site (Reef line)	
	$F_{1,4}$	P	$F_{4,42}$	P
MV assemblage structure	1.69	0.313	2.31	0.001*
Total macroalgal cover	0.15	0.911	2.73	0.038*
Ecklonia radiata	1.79	0.421	3.22	0.016*
Amphiroa anceps	0.26	1.000	3.67	0.001*
Ulva sp.	0.12	0.713	0.64	0.635
Total invertebrate cover	0.62	0.499	3.24	0.006*
T. moniliferum	1.11	0.397	3.50	0.021*
Filograna implexa	1.58	0.313	1.67	0.187
Leptoclinides sp. A	0.30	1.00	1.29	0.271

Permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data for multivariate (MV) assemblage structure. For univariate analysis, matrices were based on Euclidean distance and generated from untransformed data. Significant P values (at <0.05) are indicated with an asterisk

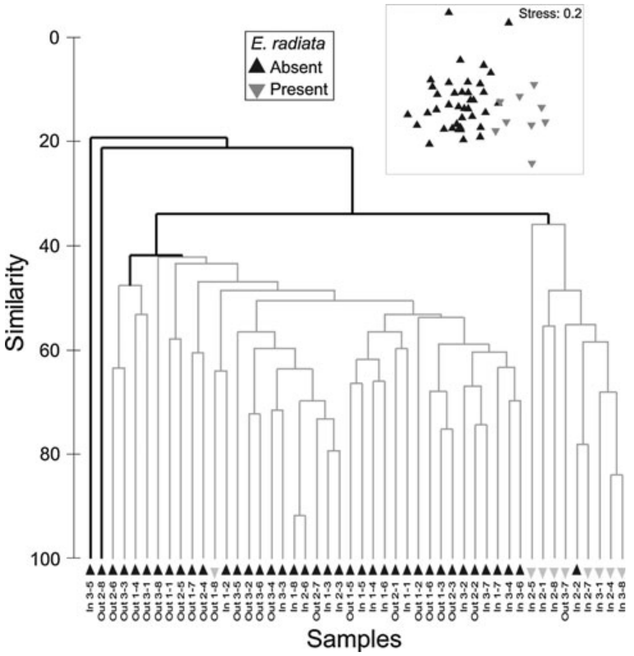

Fig. 5 Dendrogram depicting hierarchical clustering of panel samples based on multivariate assemblage structure. Samples are coded with *triangles* to indicate the presence (*light gray*) or absence (*black*) of *Ecklonia radiata*. A SIMPROF test was conducted to determine significant dissimilarity between sample clusters (at $P < 0.05$), as shown by *bold lines* in the dendrogram. *Inset* MDS shows multivariate partitioning between samples with and without *E. radiata*, based on a posteriori grouping of samples into levels of a factor derived from the presence/absence of kelp recruits (MDS based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data)

Table 2 Percentage contributions of individual taxonomic groups to observed differences between panels that did not include *Ecklonia radiata* recruits (‘*E. radiata*: Abs.’) and those that did (‘*E. radiata*: Pres.’), as determined by SIMPER

Taxon	*E. radiata*: Abs. Av. P.C.	*E. radiata*: Pres. Av. P.C.	Contr. (%)	Cum. (%)
Red turfing algae	6.14	1.75	17.93	17.93
Brown/red encrusting algae	2.32	4.87	13.09	31.02
Pink coralline encrusting algae	3.21	4.51	8.23	39.25
Ulva sp.	1.78	1.32	7.87	47.09
Filograna implexa	1.46	1.15	6.14	53.23
Amphiroa anceps	0.77	0.61	3.96	57.19
Triphyllozoon moniliferum	0.83	0.19	3.12	60.31

Overall dissimilarity between levels of the “presence/absence of *Ecklonia radiata*” factor (which was assigned a posteriori) was 68%. The mean percent cover (“Av. P.C.”, square-root transformed data) of each key taxon is shown for both levels of the factor. “Contr. (%)” refers to the contribution of each taxon to the overall dissimilarity between factor levels, while “Cum. (%)” is a running total of the contribution to observed dissimilarity

of the ‘*Ecklonia* presence/absence’ factor. The ordination indicated clear separation between the groups of samples (Fig. 5), while a one-way ANOSIM test showed that groups were moderately but significantly different ($R = 0.45$, $P = 0.001$, based on 999 permutations). Finally, a SIMPER analysis was conducted to determine which taxa were driving the overall difference between samples with and without *E. radiata* (Table 2). The percent cover of the coarse taxonomic grouping “red turfing algae”, was a principal driver of dissimilarity, being more abundant on panels without *E. radiata*. Conversely, the areal coverage of encrusting coralline algae was greater on panels with kelp recruits. Regarding individual species, *Ulva* sp., *Amphiroa anceps, Filograna implexa,* and *Triphyllozoon moniliferum* were major contributors to the dissimilarity between ‘*Ecklonia’* groups; all of which had greater coverage on panels without *E. radiata* (Table 2). Figure 6 shows representative images of panel assemblages with and without *E. radiata*, which clearly illustrates general differences in the two assemblage types.

Discussion

Exposure to swell did not affect the structure of recruiting assemblages or the space coverage of dominant flora and fauna. There are 3 logical interpretations of this observation: (1) the gradient of wave exposure we examined in Marmion Lagoon was not pronounced enough to influence

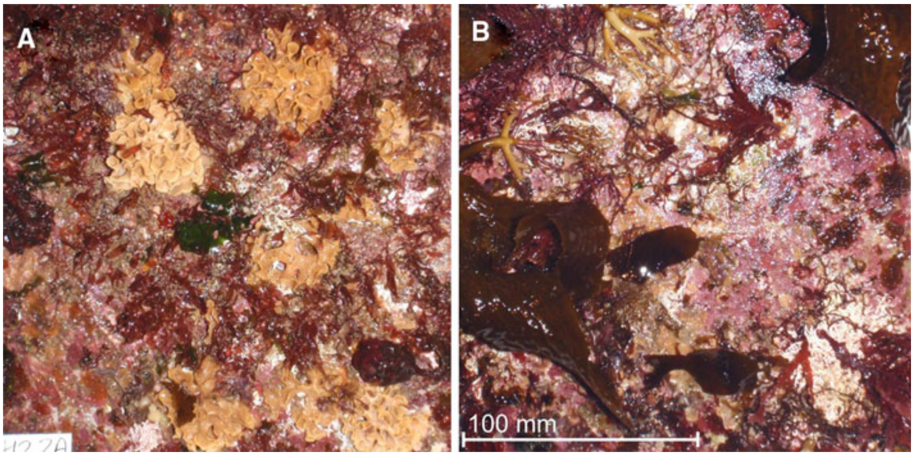

Fig. 6 Representative examples of panel assemblages without *Ecklonia radiata* recruits (**a**) and with *E. radiata* recruits (**b**)

early community development; (2) exposure to swell is important but was masked by other key factors that drive variability at the spatial scale of the study; or (3) wave energy does influence community development but the experimental design, which was a nested design with considerably greater power to detect differences at lower factor levels (i.e., 4 and 42 degrees of freedom for “site” and 1 and 4 degrees of freedom for “reef line”), limited our ability to detect ecological change along the wave exposure gradient. Clearly, exposure to swell is an important factor driving the ecology of subtidal environments, and differences in the structure of mature benthic assemblages between reef lines have been recorded in Marmion Lagoon previously (Hatcher 1989; Phillips et al. 1997). The study by Phillips et al. (1997) examined the same reef lines as the present study and recorded shifts in the structure of mature macroalgal assemblages along the exposure gradient, at the functional group level. This could suggest that wave exposure, at this spatial scale, has a relatively greater influence on well-established, mature assemblages than on early successional stages.

With regard to *Ecklonia radiata*, a significant effect of wave exposure on break forces of individual kelps along this wave exposure gradient has been reported previously (Thomsen et al. 2004). Conversely, studies on the morphology and demography of *Ecklonia radiata*, which sampled the same sites as the present study, did not detect significant variability between reef lines (Wernberg and Thomsen 2005; Wernberg 2009). It is likely that exposure to wave energy at this spatial scale (which perhaps represents a limited environmental gradient despite differences in exposure indices), affects this habitat forming species in subtle and non-consistent ways.

Crucially, the fact that recruiting panel assemblages did not differ between exposure levels does not suggest that mature benthic assemblages are unaffected by exposure to swell in Marmion Lagoon. Indeed, hydrodynamic forces may be more influential in structuring mature communities—large adults are often more susceptible to physical disturbance (Thomsen et al. 2004)—and less influential in driving patterns of recruitment and early community development. It is evident that at these spatial scales, the disturbance gradient is neither pronounced nor well defined, so that a gradient analysis approach (rather than categorical analysis) that incorporated “extremes” of the environmental gradient would be more appropriate (Somerfield et al. 2002; Lindegarth and Gamfeldt 2005). Even so, our results suggested that patterns of community development did not differ between outer and inner reef lines, which are characterized by significantly different wave climates.

We recorded significant variability between sites, suggesting that other processes acting at this spatial-scale influence settlement and recruitment onto hard substrata. Hatcher (1989) conducted surveys of established benthic assemblages in Marmion Lagoon at multiple spatial scales and also observed considerable variability between sites positioned 1–5 km apart within reef lines. This variability was attributed to alongshore currents that could influence the supply of recruits and suspended food to individual study sites. Similarly, in a study of recruitment into experimentally disturbed patches of macroalgae conducted in South Australia, Wernberg and Connell (2008) detected significant variability in community development between sites within exposure levels. Differences between sites a few kilometers apart were attributed to the availability of propagules, as recruiting assemblages were very similar in structure to nearby mature assemblages.

Here, variability between sites was perhaps driven by differences in physical reef structure and topography, which would influence both the flow of water around the panels and the surrounding assemblage composition (and therefore the potential supply of propagules/larvae from nearby adult populations). While great care was taken to deploy panels at comparable sites in terms of reef complexity and topography, these habitats are inherently heterogeneous in physical structure, which influences local hydrodynamic forces, post-disturbance community development, and alpha diversity (Toohey 2007). As such, differences between sites may have been caused by variability in the complexity, topography, and arrangement of rocky reef structures.

Consumption of recruiting flora and fauna by mobile invertebrates, which is known to be a key process in many kelp systems around the world (see Steneck et al. 2002 for review), was unlikely to be an important factor here. The abundances of gastropod molluscs and sea urchins are generally low (albeit with some localized dense aggregations) in southwest Australia compared with many other temperate systems (Vanderklift and Kendrick 2004; Wernberg et al. 2008), and the numbers of herbivores observed on panels were very low. Furthermore, recent evidence suggests that urchins preferentially (or even exclusively) feed on drift algae on these exposed reefs (Vanderklift et al. 2009). Herbivorous fish assemblages, however, can be both abundant and diverse in this region (Hyndes et al. 1999), and between-site variability in fish populations could potentially influence community development (Vanderklift et al. 2009); further work on the relative importance of trophic interactions in this system is clearly warranted.

The key finding of our study was the significant influence of *Ecklonia radiata* settlement and recruitment on patterns of early community development. *E. radiata* is an assemblage dominant within Marmion Lagoon; the mean density of adults at these study sites ranges from ~4 to 12 m^{-2} (Wernberg 2009). It is well known that mature canopies of *E. radiata* affect community structure and alpha diversity through modification of the physical environment, by reducing light and sediment cover (Toohey et al. 2004; Connell 2005; Wernberg et al. 2005). We have shown that recruitment of juvenile kelps, which does not vary between reef lines but does vary considerably at small to medium spatial scales and is highly stochastic (Wernberg 2009), influences community dynamics considerably. The mechanism for this was most likely a combination of reduced light levels (Connell 2003; Toohey et al. 2004), which inhibited the settlement and/or growth of a range of understory macroalgal species, and increased thallus scour across the panel surface, which physically abraded the substratum and thus restricted the establishment of both flora and fauna (Fowler-Walker and Connell 2007). Evidence of "kelp whiplash", such as abraded panel surfaces with little or no algal growth, was observed on a number of panels. This physical abrasion would have been particularly pronounced during the early winter of 2010, when kelp recruits were fairly large (total length >40 cm) and wave energy was great.

It should be noted that the presence of turfing algae can inhibit the settlement of *E. radiata* (Kennelly 1987). As such, variability in the establishment of turfing algae could have influenced kelp settlement and, consequentially, patterns of community development (rather than vice versa). However, while this is clearly important in wave-induced clearings in kelp canopies (Kennelly 1987), this was probably less important here as unoccupied space (or space occupied by filamentous algae) was abundant on most panels at the time of kelp settlement (Smale Personal Observation). It is, therefore, more likely external factors that caused spatial variability in recruitment patterns of kelp (rather than species of turfing algae), such as propagule density and local circulation patterns, were crucial in determining the trajectory of early community development on the panels.

In conclusion, exposure to swell, which differs between reef lines, did not influence assemblage structure on panels. This lack of ecological response suggests that the difference in water motion at this spatial scale is not sufficient to affect community establishment and development at Marmion Lagoon. We did, however, record significant differences in the structure of assemblages with and without *Ecklonia radiata* recruits. This ecosystem engineer (*sensu* Jones et al. 1994) has a strong influence on the structure of communities of various ages, across a range of spatial scales. This is important in determining colonization patterns on newly available hard substrata, such as storm-induced clearings in kelp canopies and man-made habitats associated with coastal development.

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