COLONIZATION OF GASTROPODS ON SUBTIDAL REEFS DEPENDS ON DENSITY IN ADJACENT HABITATS, NOT ON DISTURBANCE REGIME

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ABSTRACT

Habitats dominated by algal canopies are often altered by physical disturbances of varying severity, changing environmental conditions and biological processes. We used Artificial Seaweed Units (ASUs) to test whether severity of physical disturbances on algal canopies affects the post-disturbance colonization of gastropods on subtidal reefs. Specifically, we examined patterns of assemblage structure of gastropods to test the hypothesis that the extent and intensity of canopy removal affects the post-disturbance colonization of ASUs, testing the consistency of these effects among four regions encompassing a ~6° latitudinal gradient in southwestern Australia. Because adjacent habitats can act as a source of new colonists (either as drifting migrants or as a source of propagules) from the perimeter surrounding perturbed areas, we also predicted that patterns of colonization (types and total abundances of colonizers) were influenced by the available pool of individuals at the scale of reefs. Three reefs were selected within each region. On each reef, ASUs were placed in the centre of circular canopy clearings of different size (0, 3, 13 and 50 m^2) and intensity (50% *vs* 100%), and retrieved after 3 months. Resulting assemblages occupying the ASUs were quantitatively representative of the adjacent (undisturbed), algal-associated, assemblages at the scale of reef. Within reefs, recruited assemblages largely mimicked those associated with erect red algae. However, neither disturbance size nor intensity affected the colonization patterns across reefs and regions. These results suggest that algal-associated gastropods, regardless of the prevalent mode of dispersion, are resilient to physical disturbances to canopies across broad geographical regions as long as the pool of potential colonists is maintained. A high dispersal ability of gastropods likely ensures a quick colonization of recovering algal habitats.

INTRODUCTION

Habitats dominated by canopies of laminarian (kelps) and fucalean algae are conspicuous elements of temperate shores. At small spatial scales (metres), these habitats are often punctuated by physical disturbances (e.g. wave action, ice scour) that vary in severity (extent, intensity and frequency), and create gaps of varying sizes (Wernberg, 2006). Changes in the physical structure of subtidal canopies affect both environmental conditions (Wernberg, Kendrick & Toohey, 2005) and biological processes (Tilman & Kareiva, 1997). For example, a dense canopy attenuates hydrodynamic flows, affecting the supply of both larvae and passively dispersing animals (Boller & Carrington, 2006). Similarly, differences in predation pressure between disturbed and unaltered canopies can shape the responses of entire communities to habitat configuration (Roberts & Poore, 2005; Overholtzer-McLeod, 2006).

The post-disturbance colonization of gaps by algae and sessile animals on rocky coasts has been widely described, either in isolation (Dudgeon & Petraitis, 2001; Cervin, Aberg & Jenkins, 2005; Wernberg, 2006), or in combination with other physical and biological mechanisms such as grazing (Cervin *et al.*, 2004). In contrast, the colonization by assemblages of mobile invertebrates, particularly epifaunal organisms that rely on algae as an important habitat, remains largely unstudied. For example, the importance of the size of the area to be colonized, and therefore the distance from a potential source of colonists, in determining patterns of colonization is poorly understood (Underwood & Chapman, 2006). Algae differ vastly in size, shape and species composition across spatial and temporal scales (Leliaert *et al.*, 2000), making it difficult to test specific hypotheses regarding colonization patterns for these animal assemblages. This difficulty is exacerbated across broad geographical scales, where biogeographical transitions cause considerable changes in the species composition of algae (Leliaert *et al.*, 2000; Wernberg, Kendrick & Phillips, 2003b).

Identical artificial substrates (Artificial Seaweed Units, hereafter ASUs) provide a standardized habitat (identical size, shape and complexity) and have been used as experimental units within a hierarchy of spatial scales to test specific models of colonization patterns (e.g. Edgar, 1991; Olabarria, 2002; Underwood & Chapman, 2006; Cole, Chapman & Underwood, 2007; Rule & Smith, 2007). These artificial habitats have the potential to attract most elements of the mobile invertebrate fauna in their near vicinity (Edgar & Klumpp, 2003; Rule & Smith, 2005). Colonization of these new patches of habitat by epifaunal assemblages is determined by a complex set of processes acting at different spatial and temporal scales. Our understanding of the relative importance of different abiotic and biotic mechanisms on these patterns of colonization is, however, limited (Rule & Smith, 2007; Chapman & Underwood, 2008). In particular, it is important

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to disentangle the effects of processes operating at small scales (from centimetre to a few metres) from those influencing patterns of colonization at large scales (i.e. 10 s of kilometres). Generally, most variation in the structure of assemblages has been found at the smallest scales (from centimetre to a few metres) (Chapman & Underwood, 2008). As a result, the causal processes of small-scale variation (i.e. disturbances) are particularly worthy of examination (Chapman & Underwood, 2008). Incorporating such examination within hierarchical designs that include variability across geographical regions is key to determine the generality of these processes (Witman & Dayton, 2001).

In this study, we used ASUs to test whether severity of physical disturbances to algal canopies affects the post-disturbance colonization of gastropods on subtidal reefs. Specifically, we examined patterns of assemblage structure (taxonomic richness, hereafter referred to as 'richness', and abundances of colonizing individuals) of gastropods to test the hypothesis that the extent and intensity of canopy removal affects the post-disturbance colonization of gastropods into ASUs. We tested the consistency of these effects among four regions, separated by 100s of km, encompassing a ~6° latitudinal gradient (~750 km of coastline) in a tropical to temperate transition area in southwestern Australia. Adjacent habitats can act as a source of new colonists (either as drifting migrants or as a source of propagules) from the perimeter surrounding the impacted area, in both quantitative (numbers of colonists) and qualitative (identity of colonists) terms (Underwood & Keough, 2001; Cole *et al.*, 2007). Consequently, we also predicted that patterns of colonization (types and total abundances of colonisers), at the scale of reefs, would be influenced by the available pool of individuals.

MATERIALS AND METHODS

Study area

This study was conducted on wave-exposed rocky reefs, between 8 and 12 m depth, at four regions in southwestern Australia: Kalbarri, Jurien Bay, Marmion and Hamelin Bay (Fig. 1). A consistent gradient in sea surface temperature is observed all-year round with a lack of major oceanographic events (such as regional upwelling) altering these climatic patterns (Fig. 1; Pearce, 1991). Three reefs, all separated by at least 1 km, were randomly selected within each region. All reefs were predominantly covered by macroalgae, primarily the small, canopy-forming, kelp *Ecklonia radiata* (Wernberg *et al.*, 2003a) and frondose fucalean algae (mostly the genera *Sargassum* and *Scytothalia*). Patches of small (generally <25 cm) erect red algae were interspersed between the larger stands of canopy-forming algae (see Wernberg *et al.*, 2003b, for a detailed description of floristic assemblages). Although there is some variation in the species composition among the regions, the structure of these algal assemblages does not vary among the four regions; for example, kelp density and biomass are similar across regions (T. Wernberg *et al.*, unpubl.).

Colonization of experimental clearings by gastropods

Physical (pulse) disturbances were mimicked by manipulating the extent and intensity of canopy removal. At each reef, circular canopy clearings of three different sizes (3, 13 and 50 m^2; equivalent to ~2, 4 and 8 m diameter, respectively), and an uncleared control (0 m^2), were created by removing the vegetation manually (Fig. 2). Clearing intensity was simulated by removing either 50% or 100% of the canopy coverage. The extent and intensity of the clearings represented realistic scenarios for the study area, with the 50 m^2 clearings representing the extreme of wave-induced disturbances (T. Wernberg, unpubl.). All clearings were in areas dominated by the kelp *Ecklonia radiata* (>70% coverage). Two plots of each orthogonal combination of extent and intensity were established on each reef (16 experimental plots per reef, including four controls, Fig. 3). Consequently, the experimental units simulating disturbances of different severity were replicated within reefs ($n = 2$) and within regions ($n = 6$), for a total of $n = 24$ plots of each treatment. All plots were established on horizontal reef surfaces, during the austral summer–autumn (February to April 2006). The centre of each experimental plot was marked with a metal stake drilled into the reef using a pneumatic drill, and labelled for subsequent identification. Two ASUs (nylon pan scourers, ~115 cm^3 volume; Fig. 2) were fixed with cable ties to each stake, 5–10 cm above the bottom. All ASUs were collected after 3 months by sealing them into separate sealable plastic bags. This duration is adequate for the establishment of entire faunal assemblages (Kelaher, 2005; Rule & Smith, 2005; Underwood & Chapman, 2006; Chapman & Underwood, 2008), and minimizes the experimental period to avoid the effect of storms. ASUs were stored frozen (−20°C) until processed. Once in the laboratory, each ASU was washed thoroughly in fresh water, including the contents within the plastic bag, which were then passed through a 0.5 mm sieve. All gastropods retained were identified to the lowest feasible taxonomic level. To maintain a balanced design, one ASU from each plot was analysed. Losses of ASUs as a result of adverse storms are common (Underwood & Chapman, 2006; Rule & Smith, 2007), particularly in areas exposed to large (and consistent) swells.

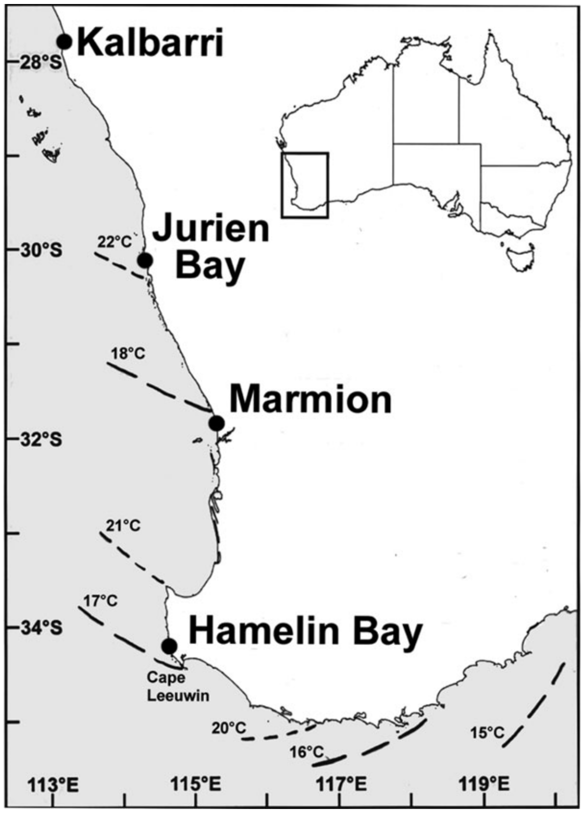

Figure 1. Map of southwestern Australia, showing the four regions of our study, and summer (short dash) and winter (long dash) surface isotherms (after Pearce, 1991).

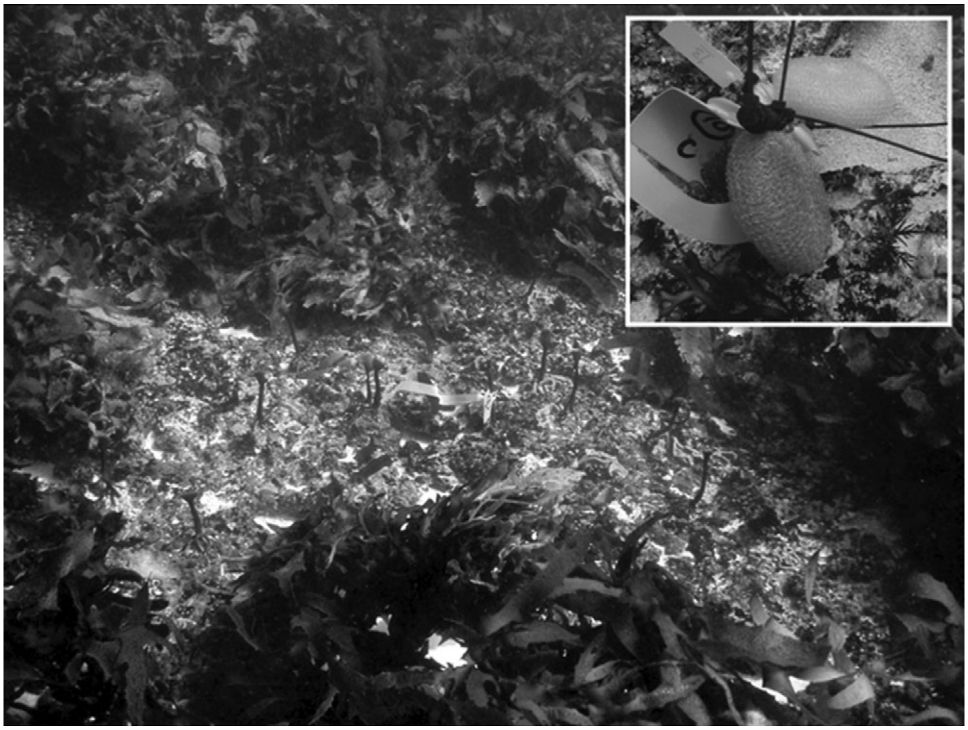

Figure 2. Example of experimental plot (complete canopy removal, 3 m^2). Inset: artificial Seaweed Units (ASUs) attached to a metal stake in the centre of an experimental clearing.

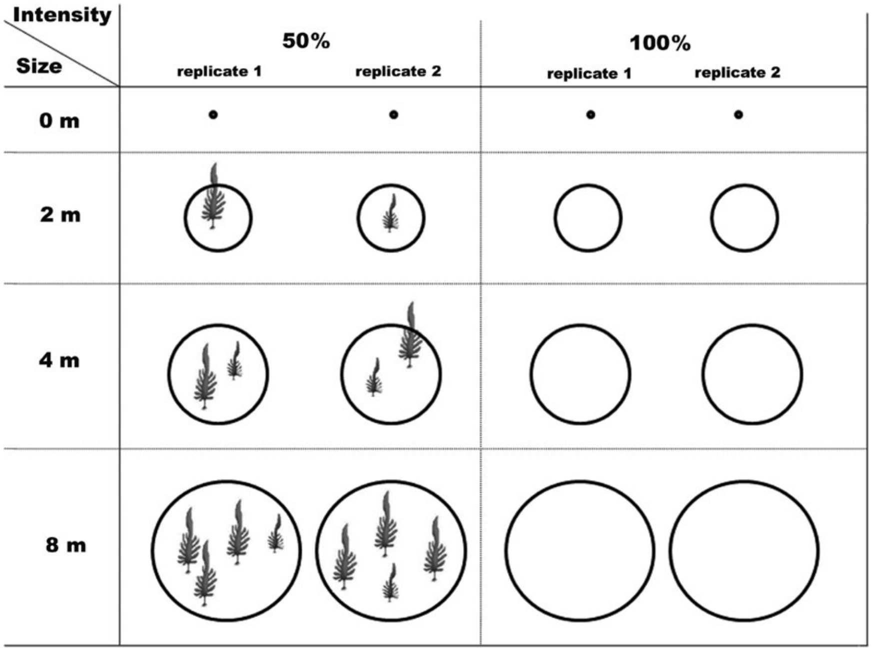

Figure 3. Diagram illustrating the experimental design to test whether size and intensity of canopy removal affects the post-disturbance colonization of gastropods into ASUs. Size refers to the diameter of the experimental canopy clearings. Experimental plots are not to scale; plots of size = 0 m represent uncleared controls. The 16 plots were replicated on each of the 12 reefs, so a total of 192 experimental plots were set up across the study area.

Sampling of gastropods in natural algal habitats

To determine the available pool of gastropods associated with natural (undisturbed) algal habitats, we collected all macroalgae within nine replicate 50 × 50 cm quadrats (0.25 m^2) on each reef. To account for the spatial heterogeneity in the configuration of the algal habitats, we sampled three quadrats from each of the three main types of habitat patches (the kelp *Ecklonia radiata*, fucalean algae and erect red algae). The level of replication was based on a previous study in the same study area (Tuya, Wernberg & Thomsen, 2008). Patches of different types of algae were, in all cases, interspersed and several metres apart. All algae were carefully hand-picked with the help of a knife and put in a calico bag. Laboratory procedures were the same as for ASUs. The total abundance of individuals per area of reef was the sum of the mean total abundances of individuals ($n = 3$) per habitat; total abundances were therefore expressed per 0.75 m^2. Because the three algal habitats were not proportionately distributed on each reef, we multiplied the mean total abundances of gastropods in each algal habitat by the proportion of reef covered by each habitat. This proportion was determined by measuring the distances each habitat covered along 10 randomly oriented 25 m transects on each reef.

Statistical analyses

Differences between factors were evaluated using multi- and univariate ANOVA. Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2005) was used to partition multivariate variation based on Bray-Curtis dissimilarities on abundance data, while univariate analyses were performed on two summary variables of the assemblage (total abundance of individuals and richness), and for the abundances of the five most common taxa. In all cases, data were analysed according to a mixed effects, four-factor model, incorporating the orthogonal combinations of the two factors that characterized the clearings: (1) 'Extent' (fixed factor with four levels); (2) 'Intensity' (fixed factor with two levels); and the two spatial scales used for the replication of these treatments, (3) 'Regions' (fixed factor with four levels, and orthogonal to the previous factors) and (4) 'Reefs' (random factor with three levels, nested within 'Regions'). All data were square-root transformed to stabilize variances and downweight the importance of highly abundant species, and alpha values fixed at the 0.01 level when heteroscedasticity remained (Cochran's *C*-test, $P < 0.05$).

Pearson product moment correlation was used to describe the relationship between the total number of individuals colonizing all the ASUs per reef (sum across all ASUs) and the available pool of individuals per reef. To take the identity of colonizers into account, we tested the relationship between the multivariate patterns (presence–absence) of the colonizers into the ASUs and those inhabiting the three algal habitats, using the RELATE routine (PRIMER 6.0). Rho values were calculated as Spearman rank correlations, and *P* values using 4,999 permutations. One-way ANOSIM tested differences in similarity of gastropod assemblages among ASUs and the three naturally occurring (undisturbed) algal habitats, followed by a test of differences in dispersion using the PERMDISP routine (PRIMER 6.0 package). Interpretations of pair-wise *R*-statistic values from the ANOSIM followed Clarke (1993), and non-metric multidimensional scaling (nMDS) ordination was used to visualize these similarities. In these tests, data were pooled across levels of disturbance regime, as a result of the lack of significant effects (see Results). Moreover, variability among replicates of each algal type on each reef, and from reef to reef within regions, was ignored by using their corresponding centroids.

RESULTS

A total of 433 specimens from 32 taxa were found in the 144 ASUs on the 12 reefs. Abundances of gastropods in the experimental plots ranged between 0 and 10 individuals ASU^{-1}. The patterns of post-disturbance colonization into the ASUs were independent of the imposed disturbance regimes; we did not observe any effects of the experimental factors (as main effects or as interaction terms, Table 1, $P > 0.05$ in all cases) neither for the multivariate assemblage, nor for the patterns of

Table 1. Results of multi and univariate ANOVA testing the effects of 'Extent' (fixed factor), and 'Intensity' (fixed) of disturbances, 'Regions' (fixed), and 'Reefs' (random and nested within 'Regions') on the entire gastropod assemblage structure (PERMANOVA), two descriptors of the gastropod assemblage (total abundance and richness, ANOVA) and on the abundances on the five most common taxa (ANOVA).

Source of variability (df)	Entire assemblage		Total abundance		Richness		*Bittium* spp.		Rissoidea		*Pyrene bidentata*		*Phasianella* spp.		*Thalothia* spp.	
	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Extent = Ext (3), Power = 0.8854	3307.07	0.89	0.45	0.51	0.40	0.46	0.31	1.51	0.08	0.18	0.02	0.17	0.01	0.59	0.00	0.50
Intensity = Int (1), Power = 0.7611	3645.68	0.90	1.22	0.96	1.34	2.09	0.00	0.00	0.00	0.01	0.00	0.00	0.17	1.90	0.02	2.58
Regions = Reg (3), Power = 0.7611	4145.86	0.69	6.05	2.81	3.42	2.42	0.27	0.44	0.88	2.01	0.28	3.50	0.31	1.83	0.01	0.56
Reefs (Reg) (8)	5986.05	1.95**	2.14	2.52*	1.37	2.92**	0.62	1.67	0.44	1.74	0.08	0.76	0.17	5.20**	0.02	1.61
Reg × Ext (9)	3532.79	0.95	0.87	0.98	0.86	1.62	0.20	0.45	0.46	2.00	0.14	0.88	0.03	0.83	0.01	1.65
Reg × Int (3)	2121.82	0.52	1.27	1.36	0.64	0.99	0.29	0.30	0.16	0.40	0.14	0.97	0.09	2.59	0.01	0.45
Reefs (Reg) × Ext (24)	3687.82	1.20	0.89	1.04	0.53	1.12	0.45	1.23	0.23	0.91	0.16	1.59	0.04	1.22	0.00	0.59
Reefs (Reg) × Int (8)	4016.48	1.30	0.93	1.09	0.64	1.37	0.94	2.54	0.41	1.63	0.14	1.38	0.03	1.10	0.02	1.72
Ext × Int (3)	4504.09	1.81	1.02	1.82	0.80	2.49	0.43	1.38	0.29	4.87	0.03	0.38	0.82	0.82	1.35	1.35
Reg × Ext × Int (9)	3131.65	1.26	0.56	0.97	0.32	0.98	0.31	1.40	0.06	0.28	0.10	0.41	0.00	0.24	0.55	0.55
Reefs (Reg) × Ext × Int (24)	2478.53	0.80	0.57	0.68	0.32	0.68	0.22	0.60	0.21	0.83	0.24	2.35	0.02	0.74	0.96	0.96
Residual (96)	3067.71		0.85		0.47		0.37		0.25		0.10		0.03		0.01	

Degrees of freedom (df) are in parentheses for each factor. Results of power analysis (Pass 6.0 statistical package) are indicated for each fixed factor (for $\alpha = 0.05$). Significant at $^{*}P < 0.05$, $^{**}P < 0.01$.

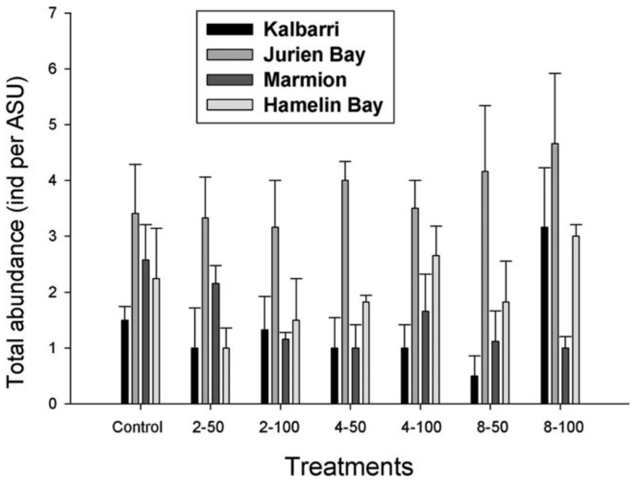

Figure 4. Mean total abundances of colonists per ASU associated with each experimental treatment (circular clearings of 2, 4 and 8 m of diameter in size, with a clearing intensity of 50% or 100% of the canopy) within each region. Error bars represent + SE of means ($n = 6$).

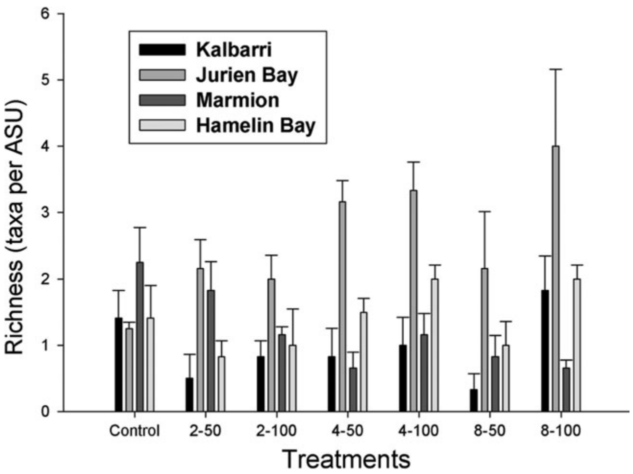

Figure 5. Mean richness of gastropods per ASU associated with each experimental treatment (circular clearings of 2, 4 and 8 m of diameter in size, with a clearing intensity of 50 or 100% of the canopy) within each region. Error bars represent + SE of means ($n = 6$).

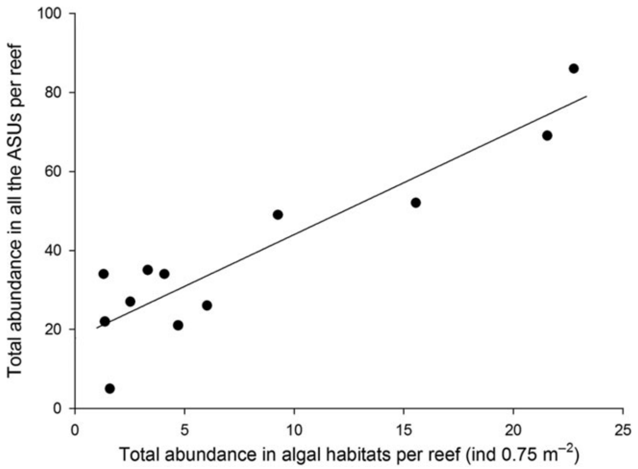

Figure 6. Relationship between the total abundances of gastropods that colonized all ASUs per reef and the total abundances of individual in adjacent, undisturbed, algal stands per reef ($n = 12$ reefs, $r = 0.88$).

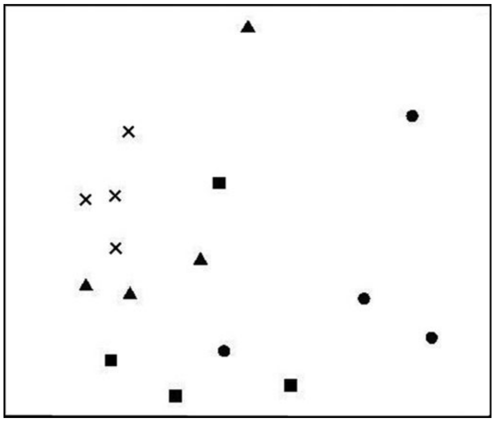

Figure 7. Two-dimensional non-metric multidimensional scaling plot (nMDS, stress = 0.15) showing location of centroids of prosobranch gastropod assemblages inhabiting natural (undisturbed) stands of the three algal habitats (●, *Ecklonia radiata* fronds; ■, Fucalean algal stands; ▲, Red algae), and the centroids of assemblages that colonized the ASUs (×).

total abundance and richness (Figs 4 and 5, Table 1). Five taxa (in decreasing order of overall abundance: *Bittium* spp., Rissoidea, *Pyrene bidentata*, *Phasianella* spp. and *Thalothia* spp.) accounted for more than the 50% of all the individuals observed. In the same way, the responses of these individual taxa to the experimental treatments lacked any consistent (and significant) patterns (Table 1; $P > 0.05$ in all cases). Significant differences in assemblage structure were only detected among reefs within regions (Table 1; $P < 0.05$). In all cases, the effects of disturbances on the colonization patterns of gastropods were irrespective of regions (Table 1; all interactions involving 'Regions' were not significant, $P > 0.05$).

Gastropods inhabiting algal assemblages were attracted to the ASUs. We detected a clear positive relationship (Pearson's $r = 0.88$) between the total number of individuals colonizing all the ASUs per reef and the density of total individuals inhabiting algal habitats on each reef (Fig. 6). Assemblages colonizing ASUs were very similar to those on naturally occurring erect red algae (their centroids clustered together in the nMDS, Fig. 7, and they were barely separable as indicated by the ANOSIM, R-statistic = 0.27). This result was reinforced by the detection of a significant correlation between the identities of gastropods colonizing the ASUs per reef and those found on the adjacent red algae (Rho = 0.25, $P = 0.05$). In contrast, the assemblages of ASUs differed from those of fucalean algae (ANOSIM, R-statistic = 0.45), and were highly distinct from those of kelps (their centroids were well separated from the centroids of the ASUs, R-statistic = 0.74). For the overall study, assemblages that recruited into the ASUs were considerably less dispersed (more similar), in terms of assemblage structure, than those naturally inhabiting the three algal habitats (Fig. 7; PERMDISP, $P < 0.001$ in all pairwise comparisons).

DISCUSSION

Severity of disturbance (extent and/or intensity) did not affect the colonization of gastropods into ASUs. Because the extent of disturbances did not affect colonization patterns, dispersal to the ASUs was not affected by the proximity to undisturbed areas we have tested for (0–8 m). A high dispersal ability of most caenogastropods typically provides maintenance of the faunal composition of disturbed habitats, and ensures a quick colonization of recovering algal habitats in both intertidal (Olabarria, 2002), and subtidal rocky reefs (Jorgensen & Christie, 2003; this study). As juveniles or adults, gastropods may disperse by crawling, or by drifting as a result of water motion (Martel & Diefenbach, 1993; Jorgensen & Christie, 2003). Moreover, some species have pelagic larvae to colonize new habitats efficiently (Waage- Nielsen, Christie & Rinde, 2003; Kelaher, 2005). This high capacity of dispersal by gastropods to colonize new habitats distant from adjacent natural habitats is similar to other faunal groups with apparently better mobility, such as effective swimming (e.g. amphipods; Gunnill, 1982), under similar scenarios of proximity to undisturbed habitats. Our study does not provide evidence to separate the colonization of ASUs by larvae dispersing through the water column, and by direct immigration (rafting, crawling, etc) from adjacent habitats. However, regardless of the mode of colonization, our results suggest that recruitment into ASUs, at least numerically, is mostly a reef-dependent process. Patterns of colonization were not influenced by the large-scale geographical (latitudinal) variability associated with regions. Therefore, broad-scale mechanisms associated with a progressive change in latitude, including both climate-related (e.g. a change in sea temperature) and non-climate related (e.g. purely biogeographical affinities), play no role in shaping such patterns across the study area. This result is consistent with studies that have identified most variability in colonization of ASUs by gastropods at the smallest scales (Chapman & Underwood, 2008).

Over short time scales (hours to a few days), colonization of gastropods into new habitats increases with the proximity to the source of colonizers (Edgar & Klumpp, 2003; Roberts & Poore, 2005). Our observations, however, indicate that over longer time scales (several months), the colonization of ASUs is not affected by proximity to undisturbed areas (within a reef). This suggests that the relationship between the patterns of colonization of faunal assemblages and the proximity to adjacent habitats inhabited by colonizers is likely to depend on the time scales available for colonization (Underwood & Chapman, 2006).

Marine ecologists have primarily studied changes in plant and animal assemblages following only the most severe type of disturbance simulations, for example, complete removal (100%) of habitat. However, disturbance events that cause full removal of habitat are infrequent compared to those which cause less severe (or partial) damage. In forests of the kelp *Ecklonia radiata* in Australasia, partial damage to the plants is common, though experiments that compare the response of assemblages to different regimes of disturbance have been uncommon (but see Kennelly, 1987). Unexpectedly, the different intensities of disturbance implemented (100% *vs* 50% of removal) did not influence the colonization patterns. Again, we attribute the large capacity of dispersion by gastropods as the mechanism responsible for the lack of consistent differences between total and partial clearings on a large time scale.

ASUs have been repeatedly applied in coastal studies, particularly in the last decade (Edgar & Klumpp, 2003; Mirto & Danovaro, 2004; Cole *et al.*, 2007; Rule & Smith, 2007; Chapman & Underwood, 2008). However, there is no consensus on whether assemblages recruiting to ASUs represent natural communities (Rule & Smith, 2005). We consider ASUs a useful tool to test ecological models in subtidal systems, and our results document some of their beneficial properties. First, the low dispersion (high similarity) of assemblages recruiting into the ASUs for the overall study reflects their insensitivity, compared with 'natural' algal habitats, to variation across large spatial scales. Second, at the reef scale, our study suggests that ASUs mimic erect red algae well. Third, at the scale of reefs, abundances on the ASUs are quantitatively representative of adjacent undisturbed assemblages.

Conclusions

Gastropod colonization patterns did not depend on severity of disturbance across several regions encompassing a latitudinal gradient. The assemblages colonizing ASUs resembled those of natural erect red algae, and were numerically representative of abundances in adjacent habitats. These results suggest that algal-associated gastropods, regardless of the prevalent mode of dispersion, are resilient to physical disturbances on canopies across broad geographical zones as long as a pool of potential colonists is maintained.

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