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The role of recruitment in structuring patterns of small-scale spatial variability in intertidal and subtidal algal turfs

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Abstract

Recruitment is often important in structuring patterns of distribution and abundance of algal assemblages. Intertidal and subtidal turfing algal assemblages consistently vary on small spatial scales (tens of centimetres), and this variability may be due to patterns of recruitment varying on similar spatial scales. The validity of this model was evaluated by testing the hypothesis that the numbers and types of taxa recruiting to turfs would vary at small spatial scales within intertidal and within subtidal habitats. Abundances of algal recruits were estimated on sandstone plates that were placed at a number of spatial scales within intertidal and within subtidal habitats (centimetres to tens of metres). Significant differences in entire assemblages were found only between habitats. This was explained by abundances of individual taxa, which generally varied between intertidal and subtidal habitats or between sites within habitats. Only small proportions of the overall spatial variation (dissimilarity) could be explained at the scale of replicate recruitment plates that were centimetres apart. Results indicate that while recruitment may contribute to differences between intertidal and subtidal habitats, it cannot explain the small-scale spatial variability in established turfing algal assemblages within these habitats. There was some evidence to suggest that recruitment may contribute to variability in established turfing algal assemblages but only over longer time scales than examined here.

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1. Introduction

Recruitment has long been recognised as an important ecological process that has the potential to structure patterns of distribution and abundances of many organisms (Underwood and Denley, 1984; Connell, 1985; Gaines and Roughgarden, 1985; Menge, 1991). It is particularly important in determining the structure of marine algal assemblages and can often explain the limited distribution exhibited by many species (Gunnill, 1980; Reed et al., 1988; Vadas et al., 1990; Viejo et al., 1999).

Assemblages of algae can show great variation in patterns of distribution, abundance and diversity on small spatial scales (e.g. Underwood and Chapman, 1998; Benedetti-Cecchi, 2000, tens of centimetres; Coleman, 2002a). This variation may be due to small-scale differences in the types and numbers of species recruiting on similar spatial scales. Prerecruitment processes that have been shown to influence the distribution and abundance of algae include the dispersal and availability of propagules (Deysher and Norton, 1982; Hoffmann and Ugarte, 1985; Andrew and Veijo, 1998) and environmental conditions that affect their deposition (Santelices, 1990). For example, algae cannot settle and grow in areas where their propagules do not reach even if prevailing environmental conditions would allow them to (Underwood and Denley, 1984). In contrast, even if propagules are in abundance, algae are unlikely to settle, grow and persist if environmental conditions are not favourable. For example, Brawley and Johnson (1991) found survival of *Pelvetia fastigiata* embryos to be dependent on conditions prevailing in the microhabitats in which they were placed.

Alternatively, the same numbers and types of species may initially recruit over small spatial scales, but differences in post-recruitment processes acting at similar spatial scales may subsequently lead to differences in assemblages on these scales (Santelices and Ojeda, 1984; Kendrick, 1994). Post-recruitment processes are important determinants of patterns of distribution and abundance of many species of algae. They include processes such as grazing (Underwood and Jernakoff, 1981; Jernakoff, 1983), competition (Fletcher, 1975; Breitburg, 1984; Benedetti-Cecchi and Cinelli, 1992) and a variety of physical disturbances (Hruby and Norton, 1979; Norton, 1983; Kennelly, 1987a,b; Kendrick, 1991).

The greatest proportion of variation in assemblages of intertidal and subtidal turfing algae around Sydney, Australia, can be explained at the scale of replicate quadrats, tens of centimetres apart (Coleman, 2002a). One explanation for this variability is that it is a result of differences in patterns of recruitment of algae on similar spatial scales. If this is so, then one would expect there to be (a) differences in entire assemblages of recruits and (b) differences in the types and numbers of species that comprise these assemblages, at small spatial scales (tens of centimetres or less) within intertidal and subtidal habitats. Small-scale variability in patterns of algal recruitment is evidence to suggest that pre-recruitment processes (the combined effects of which are reflected in patterns of recruitment) are important in structuring assemblages of turfing algae.

2. Materials and methods

This experiment was done from October 2000 to January 2001 on the intertidal sandstone shores and subtidal reefs of Cape Banks Scientific Marine Research Area,

Botany Bay (see Coleman, 2002a for map showing location of Cape Banks). Sandstone recruitment plates ($6 \times 6 \text{ cm}^2$) were attached to bars of wood with stainless steel bolts in areas of low intertidal and shallow subtidal turfing algae. This was done in two randomly chosen intertidal and two randomly chosen subtidal sites (approximately 60 m apart). Intertidal and subtidal sites were not horizontally separated, i.e. they were randomly positioned horizontally. For example, one intertidal site was on a point while one subtidal site was in a bay. At each site, pairs of bars were placed in two randomly chosen patches of



Fig. 1. nMDS plots showing relationships between assemblages of algae that recruited to intertidal (shaded) and subtidal (clear) recruitment plates. Diamonds and squares represent randomly chosen sites within habitats. Plots for raw (i) and presence/absence (ii) data at 1- (a), 2- (b) and 3-month (c) sampling times are shown. Points on the plots are patch centroids. n=2 patches per site and 4 replicate plates per patch.

turf approximately 1 m apart to test hypotheses about differences at the scale of tens of centimetres. Four replicate plates from each scale (patch, site and habitat) were collected for sampling (without replacement) at each of three times (1, 2 and 3 months after being placed in the field). These times were chosen because 1 month was the minimum amount of time that plates had to be left out in the field for recruits to be identified to any reasonable taxonomic resolution (Coleman, unpublished data), and 3 months was considered to be the longest that plates could be left in the field before the effects of post-recruitment processes became too great. Recruitment was defined as the time at which individuals were observed to enter a defined population, i.e. when they are first sampled (Keough and Downes, 1982).

At each of the times of sampling, plates were put in seawater and returned immediately to the laboratory where they were refrigerated at 3 °C until examination. The number of individual recruits (for coralline algae) or the percentage cover of individual species in five randomly chosen fields of view (FOV; approximately 1.33 cm²) were counted and identified to the lowest taxonomic level possible using a dissecting microscope. This was done for ephiphytes, canopy and primary cover, but data were pooled so total percentage covers can be greater than 100%. A 0.5-cm boundary around the edge and



Fig. 2. Mean (S.E.) Bray–Curtis dissimilarity values among assemblages that recruited onto plates for (a) raw and (b) presence/absence data for each of the spatial scales under investigation; replicate plates (R), patches (P), sites (S) and habitats (H) and for each of three times of sampling; 1 month (clear bars), 2 months (grey bars) and 3 months (black bars). n=4 replicate plates per patch. There is no S.E. bar on "habitat" because only comparison was possible (intertidal versus subtidal).

centre of plates was not sampled to avoid possible edge effects of the sides of plates and the presence of a screw in the centre, respectively.

3. Statistical analyses

Data were represented graphically using nonmetric multidimensional scaling plots (nMDS) to illustrate relationships among assemblages of recruits at different spatial scales.



Fig. 3. Number of taxa and abundances of some of the individual taxa of recruits on plates that were in intertidal (sites 1 and 2) and subtidal (sites 3 and 4) habitats for 1 (clear bars), 2 (grey bars) and 3 (clear bars) months. n=4 replicate plates per patch, 2 patches per site and 2 sites per habitat.

(a) 1 month		Number taxa		Ectocarpales ^a		Ceramiales ^a		Colpomenia sp.		Rhodymenia	
Source	<i>d.f.</i>	MS	F	MS	F	MS	F	MS	F	MS	F
Habitat = Ha	1	28.13	13.24	88.11	0.78	0.02	0.44	86.46	0.77	6.66	2.63
Site = Si (Ha)	2	2.13	4.76 ^{b,*}	112.54	420.20***	0.05	18.00*	111.75	2.50	2.53	2.11
Patch = Pa (Si (Ha))	4	0.50	1.12	0.27	0.03	0.00	0.10	44.66	2.13	1.20	13.54***
Residual	24	0.44		9.07		0.03		20.99		0.09	
		Coralline algae		Cyanophyceae		Petalonia sp.ª		Rhodophyte filaments		Ulvales	
Source	<i>d.f.</i>	MS	F	MS	F	MS	F	MS	F	MS	F
На	1	3.45	8.36 ^{b,*}	12,752.05*	59.52*	3.38	6.76	3.82	135.29**	26,912.00	3.87
Si (Ha)	2	0.39	0.96	214.25	214.25***	0.50	0.31	0.03	0.16	6962.00	9.39*
Pa (Si (Ha))	4	0.42	0.87	1.00	0.01	1.62	2.76	0.17	1.43	741.13	5.53**
Residual	24	0.49		96.01		0.59		0.12		133.98	
(b) 2 months		Number taxa		Ectocarpales ^a		Bryopsis sp.		Colpomenia sp.		Rhodymenia ^a	
Source	<i>d.f.</i>	MS	F	MS	F	MS	F	MS	F	MS	F
На	1	6.13	49.00*	35.28	0.78	3.78	0.19	496.13	172.27**	0.05	9.00
Si (Ha)	2	0.13	0.14	45.17	22.99**	20.41	8.95*	2.88	7.16*	0.01	0.50
Pa (Si (Ha))	4	0.88	0.81	1.97	0.08	2.28	0.14	0.40	0.03	0.01	0.92
Residual	24	1.08		24.46		16.22		13.98		0.01	
		Coralline algae ^a		Cyanophyceae		Petalonia sp.		Rhodophyte filaments ^a		Ulvales	
Source	<i>d.f.</i>	MS	F	MS	F	MS	F	MS	F	MS	F
На	1	22.78	13.21 ^{b,*}	37,812.50	402.78***	55.13	10.03 ^{b,*}	1.81	1.11	34,907.43	140.24**
Si (Ha)	2	1.54	0.89	4.50	0.06	5.78	1.05	1.62	648.00***	248.91	7.24*
Pa (Si (Ha))	4	1.82	3.52*	76.50	0.65	5.35	0.99	0.00	0.01	34.36	0.07
Residual	24	0.52		117.83		5.40		0.26		484.96	

Table 1 Analyses of variance of the number and abundances of taxa that recruited to plates after 1, 2 and 3 months

(c) 3 months		Number tax	a	Ectocarpa	les	Bryopsis sp	a	Champia	sp.	<i>Ralfsia</i> sp) .
Source	<i>d.f.</i>	MS	F	MS	F	MS	F	MS	F	MS	F
На	1	0.03	0.06	28.50	1.49	5984.18	3.68	1282.71	17.76 ^{b,**}	29.65	6.52
Si (Ha)	2	0.53	5.67	19.14	612.52***	1624.68	4.29	89.11	1.23	4.55	0.43
Pa (Si (Ha))	4	0.09	0.06	0.03	0.00	378.51	1.56	63.78	0.32	10.63	1.13
Residual	24	1.68		18.86		241.8		200.38		9.40	
		Colpomenia sp.ª		Coralline algae		Cyanophyceae		Petalonia sp. ^a		Rhodophyte filaments	
Source	<i>d.f.</i>	MS	F	MS	F	MS	F	MS	F	MS	F
На	1	187.70	257.65***	53.30	245.03***	13,325.28	68.28*	784.08	43.56*	0.01	0.00
Si (Ha)	2	0.02	0.00	0.04	0.07	195.16	5.79	18.00	0.09	0.00	0.00
Pa (Si (Ha))	4	59.30	1.07	0.64	0.68	33.73	0.23	204.49	2.34	0.55	1.14
Residual	24	55.26		0.95		145.58		87.57		0.49	
		Ulvales ^a									
Source	<i>d.f.</i>	MS	F								
На	1	19,007.6	12.19								
Si (Ha)	2	1559.75	4.91 ^{b,*}								
Pa (Si (Ha))	4	403.15	1.27								
Residual	24	303.69									

Factors were habitat (intertidal and subtidal, fixed), sites (two random, nested within habitats) and patches (two, random, nested within sites and habitats). n=4 replicate plates per patch.

^a Variances were heterogeneous and P < 0.01 was used.

^b Term was tested over pooled data.

**P*<0.05.

**P < 0.01.

****P*<0.001.

The significance of these relationships were tested using analysis of similarities (ANO-SIM) (Clarke, 1993), which was performed using data for each replicate recruitment plate. All multivariate analyses were done on raw data (i.e. untransformed) to obtain estimates of variation that reflected the abundances, distributions and species composition of assemblages, and on presence/absence data to get estimates of variation that were related to the species present and their distribution, that is, the number of quadrats they occupied.

The proportion of variability explained at each of the spatial scales (among replicate plates, between patches, between sites and between habitats) was determined by using Bray–Curtis measures of dissimilarity from each of the appropriate spatial scales. For example, for between habitat variation, Bray–Curtis dissimilarity (BCD) measures were calculated between the intertidal and the subtidal centroid. For between site variation, BCD measures were calculated between the two intertidal sites and then the two subtidal sites (n=2 BCD measures). Similarly, for between patch variability, BCD measures were calculated between centroids from each patch within a site (n=4 measures), and for among replicate variability, BCD measures were calculated between pairs of individual replicates from each patch (n=8 measures). At each scale (except habitat where there was only one possible BCD value), the replicate BCD measures were averaged for comparison and graphical representation. This was done for each time separately.

In addition, abundances of individual taxa within assemblages were analysed using analysis of variance (ANOVA). Cochran's test was done prior to ANOVA to test for homogeneity of variances. Where variances were heterogeneous, data were not transformed (as no transformation seemed appropriate for this type of data), but a conservative P < 0.01 was used.

4. Results

At all times of sampling, there were significant differences in assemblages of recruits to intertidal and subtidal habitats (raw data: R=0.935, 1, 1 for 1, 2 and 3 months, respectively, presence/absence data: 0.976, 0.624, 0.579; P<0.01; Fig. 1). Although ANOSIM showed that there were differences among sites at all three times (raw data: R=0.768, 0.653, 0.702, presence/absence data: 0.688, 0.414, 0.374; P<0.01; Fig. 1), pairwise comparisons, however, showed that there was rarely any differences between the two replicate sites within each habitat. A similar pattern was found for patches within sites within habitats. ANOSIM indicated differences among assemblages at all three times (raw data: R=0.690, 0.512, 0.590, presence/absence data: R=0.574, 0.349, 0.263; P<0.01; Fig. 1) but pairwise comparisons between patches within sites within habitats were almost all nonsignificant.

For raw data, only a small proportion of the between habitat variability was explained at the scale of replicate recruitment plates at all three times of sampling (Fig. 2a). Dissimilarities ranged between 28% and 52% for replicate recruitment plates, 23% and 40% between patches within sites and 25% and 45% between sites within habitats (Fig. 2a). The average dissimilarity between intertidal and subtidal habitats was 94.6%. For presence/absence data, a relatively greater proportion of the between habitat variation could be explained at the scale of replicate plates. After just 1 month, 25% of the overall

dissimilarity (H) was explained at the scale of replicates (*R*) (Fig. 2b). This increased to 54% after 2 months and 73% after 3 months indicating that variation at the scale centimetres becomes increasingly more important with time (Fig. 2b). Measures of dissimilarity between intertidal and subtidal habitats averaged 52%. This was substantially lower than for raw data suggesting that abundances of taxa of recruits in assemblages are a major contributor to variability between intertidal and subtidal habitats.

The number of taxa varied between intertidal sites after 1 month was greater in intertidal than in subtidal habitats after 2 months and not different at any scale after 3 months (Fig. 3, Table 1). Patterns of recruitment of individual taxa to intertidal and subtidal habitats were complicated with different patterns emerging at different times. Some species showed differences between intertidal and subtidal habitats at some times (*Champia* sp., *Colpomenia* sp., *Petalonia* sp., Rhodophyte filaments and Ulvales; Fig. 3, Table 1) or all times (coralline algae and Cyanophyceae; Fig. 3). Abundances of other taxa were variable at the scales of sites within habitats at some (*Bryposis* sp., Ceramiales, *Colpomenia* sp., Rhodophyte filaments and Cyanophyceae) or all (Ulvales and Ectocarpales) times (Table 1). Only three taxa (*Porphyra* sp., coralline algae and Ulvales) showed differences in abundances at the scale of patches within one intertidal site (Table 1), and this only occurred at one time. Almost all taxa showed no spatial variability in abundances at least one time of sampling.

5. Discussion

Patterns of variability in assemblages of algal recruits did not reflect the great spatial variability exhibited by established turfing algal assemblages. There were differences in the number and abundances of taxa of algal recruits between intertidal and subtidal habitats and sometimes between sites within habitats. This was reflected in patterns of spatial variability with only a small proportion of the overall variability being explained at the smallest scale of the experiment replicate recruitment plates separated by centimetres. Thus, the hypothesis that recruitment can explain the great small-scale spatial variability in turfing algal assemblages was rejected. Although spatial variability exhibited by established turfing algal assemblages, it cannot fully explain it.

The lack of variability in algal recruitment at small spatial scales may be due to a number of factors. First, it may be due to uniform dispersal of propagules at the spatial scales examined here. The prevailing currents at Cape Banks may be such that propagules are distributed evenly along the shore. Indeed, the water within Cape Banks often appears to form an eddy that is isolated from the tidal flows of Botany Bay (personal observation). Alternatively, these patterns may be a function of the time of year that the experiment was done (October to December; austral spring). Not all species of algae recruit at this time, and it is possible that those that do have wide ranges of dispersal (e.g. *Enteromorpha*; Amsler and Searles, 1980) resulting in uniform patterns of recruitment at the spatial scales were examined here. If this were so, then repeating the experiment at other times of the year would reveal additional species whose patterns of recruitment vary on small spatial scales. This has implications for the timing of disturbances that create free space and the

composition of resulting assemblages (Foster, 1975; Sousa, 1979; Kennelly, 1987a; Reed, 1990, Benedetti-Cecchi and Cinelli, 1994; Airoldi, 2000). Patches that are formed at other times of the year may show greater variability on small spatial scales and appear to be more important in contributing to the small-scale spatial variability in established turfs. Indeed, the fact that variability in the species composition of recruits increased over time is evidence to suggest that this may be the case.

There was some variation in the abundances of certain taxa of algal recruits between intertidal and subtidal habitats and occasionally between sites within these habitats. Recruitment may, therefore, contribute to differences in assemblages of turfing algae at these, but not at smaller, spatial scales. Variation in patterns of recruitment of algal taxa between habitats and among sites may be a result of spatial variation in the availability, dispersal and settlement of algal propagules (Deysher and Norton, 1982; Andrew and Veijo, 1998). For example, some species do not disperse over long distances, hence, will only recruit close to where adult plants are found (Sundene, 1962; Anderson and North, 1966; Koehl et al., 1988; Kendrick and Walker, 1995). Indeed, abundances of many species of algae in established turfs vary at the scale of sites (tens of metres; Coleman, 2002a,b), and recruitment of these species may be restricted to the same spatial scales. Similarly, the distribution of certain taxa in turfs was found to be limited to intertidal or subtidal habitats (e.g. Martensia fragilis is found almost exclusively in intertidal habitats and Amphiroa anceps in subtidal habitats; Coleman, 2002b). Thus, between habitat, differences in patterns of recruitment may be a result of the dispersal of propagules being limited to one or the other habitat.

Alternatively, different places can differ with respect to various physical and biological processes occurring within them. Consequently, even if propagules do recruit uniformly, variation in these processes may lead to variation in recruitment success or survival. For example, differences in abundances of taxa of algal recruits between intertidal and subtidal habitats and among sites within these habitats may be a result of differences in the number and abundances of micrograzers on recruitment plates. After 3 months, there were differences in faunal assemblages on plates in terms of species composition, distributions and abundances at the scales of habitats and sites within habitats (Coleman, 2002b). Thus, spatial variation in grazing may result in differential mortality of algal recruits on similar spatial scales. For example, the presence of specific types and abundances of grazers in some places may lead to the mortality of certain species of algae in these places (Robles and Cubit, 1981; Brawley and Adey, 1981). Alternatively, some types of invertebrate grazers can increase or enhance the dispersal and possibly germination of certain species of algae (Buschmann and Santelices, 1987; Buschmann and Bravo, 1990), hence, these animals may, in fact, increase the types or abundances of algal recruits in places where they occur. Other factors that are variable and could potentially influence survival of recruits between intertidal and subtidal habitats include desiccation at low tide (Brawley and Johnson, 1993) and light (Graham, 1996).

One interesting result was that the amount of variability in the composition of assemblages of recruits (presence/absence data) increased from 1 to 3 months (Fig. 2b), suggesting that either the effects of post-recruitment processes on initial assemblages of recruits become increasingly more important with time, or that the longer plates are left in the field, the more chance there is that new and rare taxa will recruit. Further analyses on

the total and average numbers of taxa were done to evaluate these models. It was expected that if the first model was correct, then at each spatial scale, the total number of species would not change, but the average number would. In contrast, the second model would be supported if both the total and the average number of species increased over time. It was generally found that the total and the average number of species were similar after 1 and 2 months but increased at 3 months (Fig. 4, Table 2). Thus, the second model is supported. That is, there are more species arriving in replicates over time (from 2 to 3 months) and these species are different. Recruitment may, therefore, significantly contribute to the small-scale spatial variability in established turfs, but only due to its additive effects over large time scales.

One methodological issue that requires consideration is the method of attaching recruitment plates to the substratum. In this experiment, recruitment plates were not flush with the substratum. Rather, they were slightly raised above it. While this intentionally eliminated the effects of horizontal growth from the surrounding turf and grazing by macrogastropods and limpets (because they could not gain access to them), there are some potential artefacts associated with this procedure. First, recruitment plates in intertidal habitats may have been



Fig. 4. Total (a) and average (b) number of taxa of recruits for each spatial scale at 1 (clear bars), 2 (grey bars) and 3 (black bars) months. See Table 2 legend for factors and sample sizes for each scale. "O" refers to the overall (i.e. between habitat) variability.

Table 2

Analyses of variance of the total and average numbers of species of recruits at relevant spatial scales

(a) Replicates (total number spec	ies only)				
Source	<i>d.f.</i>	MS	F		
Time	2	9.70	10.58*		
Habitat	1	20.17	23.61*		
Site (habitat)	2	0.85	1.78		
Patch (site (habitat))	4	0.48	0.47		
Time \times habitat	2	7.51	8.19*		
Time \times site (habitat)	4	0.92	1.60		
Time \times patch (site (habitat))	8	0.57	0.56		
Residual	72	1.02			
(b) Patches	Total nu	mber species	Average number species		
Source	<i>d.f.</i>	MS	F	MS	F
Time	2	20.79	24.95**	2.32	9.56*
Habitat	1	8.17	24.50*	4.82	22.83*
Site (habitat)	2	0.33	0.57	0.21	1.72
Time \times habitat	2	5.54	6.65	1.88	7.75*
Time \times site (habitat)	4	0.83	1.43	0.24	1.98
Residual	12	0.58		0.12	
(c) Sites	Total nu	mber species ^a	Average number species		
Source	<i>d.f.</i>	MS	F	MS	F
Time	2	14.58	175.00***	1.17	10.06*
Habitat	1	4.08	49.00***	2.40	20.72**
Time \times habitat	2	1.58	19.00**	0.94	8.11*
Residual	6	0.08		0.12	
(d) Habitats	Total nu	mber species	Average number species		
Source	<i>d.f.</i>	MS	F	MS	F
Time	2	6.17	2.85	0.64	0.73
Residual	3	2.17		0.88	

Analyses for replicates (a) refers to the total number of taxa in each replicate. The average number of taxa could not be calculated at this scale as n=1 per replicate. Patches (b) refers to the total number of taxa per patch (n=2 totals per site) and the average number of taxa per patch (n=2 averages per site). Similarly, sites (c) refers to the total and average number of taxa per site (since n=2 site per habitat, n=2 totals/averages per habitat). Habitats (d) refers to the total number of taxa per habitat (n=2 per time) and the average number per habitat (n=2 per time).

^a Variances were heterogeneous and P < 0.01 was used.

*P < 0.05.

***P* < 0.01.

****P* < 0.001.

more prone to desiccation at low tide than naturally produced patches of substratum that are flush with the surrounding turf. This may have lead to mortality of certain species of algal recruits on plates resulting in domination by a few more "tolerant" species. Any effect of plates being raised above the substratum, however, were consistent at all levels of this experiment. It remains to be tested whether results would be consistent if variability in recruitment was measured in similarly small patches created in existing turfing algal assemblages. Unfortunately this is difficult to do due to the small size of recruits and the necessity of returning substrata to the laboratory for sampling.

In conclusion, recruitment may contribute to but cannot fully explain the small-scale spatial variability in assemblages of intertidal and subtidal turfing algae. There is evidence to suggest that post-recruitment processes such as grazing, competition or physical disturbances act on patterns produced by recruitment to further increase or add to small-scale spatial variability in established turfing algal assemblages.

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