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## Effects of live coral, epilithic algal communities and substrate type on algal recruitment

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**Abstract** The recruitment of algae is a critical process during algal colonization and invasions, including coral-to-algal phase shifts. Although algae are widely assumed to colonize and kill corals, there is very little known about the recruitment dynamics of coral reef algae. This study tested the ability of two dominant macroalgae (Fucales including *Sargassum* spp. and *Lobophora variegata*) to settle and grow on healthy coral tissue. The study also explored the effects of interactions with prior occupants, and of abiotic substrate properties (texture, and ceramic and carbonate material). The results indicate that healthy corals were able to prevent attachment or survival of recruits of these macroalgae. This is a significant point, since it suggests that the replacement of corals by algae may often require prior stress or death in the coral tissue. Pre-conditioning of plates at different sites had some effects, but these were relatively minor, whereas there was considerable variation within sites. Some of this variation appeared to be related to the amount of turf algae or crustose coralline algae on the plates. Recruitment was generally, but not always, higher on plates with rougher texture. Overall, this preliminary

exploration indicates considerable potential for variability in outcomes of algal colonization, with implications for the dynamics of algal invasions. In particular, the results do not support suggestions that planktonic algal propagules can directly settle on and colonize healthy coral tissue.

**Keywords** Algal recruitment · Algal settlement · Coral-algal interactions · *Lobophora variegata* · *Sargassum*

### Introduction

The recruitment of benthic organisms is an important ecological stage that affects the abundance of adult populations and community structure, and is potentially a critical bottleneck for population dynamics. Populations of many invertebrates, fishes, and temperate algae are to a large extent regulated by their supply-side ecology (e.g. recruitment dynamics, Underwood and Fairweather 1989; Santelices 1990; Creed et al. 1996; Caley et al. 1996; Hughes et al. 2000; Wright and Steinberg 2001). However, there is very little information available on the supply-side processes of tropical algae (Ang 1985; Clifton 1997; Stiger and Payri 1999; Diaz-Pulido and McCook 2002; 2003).

The recruitment of algal populations is especially critical during coral reef degradation, which usually involves the replacement of hard corals by benthic algae (Hughes 1994; McCook 1999). During this replacement, algal recruitment is a key but under-recognized step in the invasion and colonization of adult algal populations. For example, there is a widespread perception that algae, such as *Sargassum* on the Great Barrier Reef (GBR), can and will colonize live corals, if conditions such as nutrients or herbivory are suitable (e.g. Bell and Elmetri 1995; see review in McCook et al. 2001). Previous studies of tropical algal recruitment and colonization have looked at the effects of herbivory on the development of epilithic algal communities (EACs)

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(Lewis 1986; Scott and Russ 1987; de Ruyter van Steveninck and Breeman 1987; Carpenter 1990; McCook 1997; Miller et al. 1999; Smith et al. 2001). However, very few experimental studies have explored the ability of algal propagules to settle and recruit onto healthy coral tissue, or the interactions with prior benthic occupants on tropical reefs (Diaz-Pulido and McCook 2002). There is considerable literature on temperate ecosystems suggesting that interactions between algal propagules and prior occupants are important to net recruitment, and hence to final community structure (Johnson and Mann 1986; Reed 1990; Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992; McCook and Chapman 1993; Van Tamelen and Stekoll 1997; Figueiredo et al. 1997; Worm and Chapman 1998).

The settlement and recruitment of algal propagules to benthic communities may require both suitable substrate and competition with prior occupants (Worm and Chapman 1998). Substrate texture, material, or chemical composition have been shown to affect the survival of germlings and productivity of algal communities (Norton and Fetter 1981; Santelices 1990; Amsler et al. 1992; Fletcher and Callow 1992; Carpenter and Williams 1993). On coral reefs, interactions between early stages of macroalgae and the major benthic groups, corals, crustose calcareous algae (CCA), and algal turfs, will be of critical importance during algal settlement and recruitment, especially after disturbance to corals (Diaz-Pulido and McCook 2002).

In this study we tested the ability of algal propagules to recruit onto healthy coral tissue, in comparison to recruitment on dead coral plates, and onto substrates pre-conditioned with different EACs at different sites. We also explored the relationship between abiotic properties of the substrate (i.e., surface texture and material) and algal recruitment and growth. Three specific hypotheses were tested:

- 1. Propagules of Fucales and *Lobophora variegata* cannot recruit onto healthy coral tissue, but can settle and recruit onto dead corals.
- 2. Recruitment of Fucales and *L. variegata* is influenced by the presence and type of EAC on the substrate.
- 3. Recruitment of Fucales and *L. variegata* is influenced by the surface texture and material of the substrate.

The study focused on two taxa of brown seaweeds, Fucales (predominantly *Sargassum* spp.) and *Lobophora variegata*. These algae are common and often abundant on coral reefs, both on the GBR and globally, and have been suggested to be involved in macroalgal blooms and reef degradation (de Ruyter van Steveninck and Breeman 1987; Hughes 1994; Diaz-Pulido and Diaz 1997; Lapointe 1997; McClanahan et al. 2001; Jompa and McCook 2002a). Throughout this paper, we use the term algal recruitment to refer to the combination of propagule settlement, attachment, and post-settlement

survival (or mortality) and growth (prior to our census; Santelices 1990).

## Methods

**General approach and study site** To investigate the effects of competitive interactions with coral tissue and other benthic organisms, we compared algal recruitment onto (1) healthy coral tissue and dead coral plates, (2) settlement plates pre-conditioned on different reefs, and clean settlement plates (as controls), and (3) settlement plates of different textures and materials (ceramic and carbonate), on the reef flat of an inshore coral reef on the GBR, Australia. We pre-conditioned plates at two different reefs to provide a range of pre-existing benthic occupants, of EACs in particular. In all, there were seven substrate treatments (full details of treatments are summarized in the horizontal axes of most figures).

The experimental site is on a very inshore island, Goold Island (18° 10' 85 S; 146° 10' 05 E), in the central section of the GBR (detailed description in McCook 2001). The island is 15 km from the mainland and is influenced by discharge from the Herbert River, particularly during the wet season (December to March). Turbid waters prevail most of the time (maximum 5–8 m horizontal visibility). The reef flat and slope are covered by luxuriant populations of Fucales seaweeds including *Sargassum* spp. (*S. siliquosum*, *S. baccharia*, *S. polycystum*, *S. fissifolium*, *S. oligocystum*, *S. swartzii*, and *Sargassum* sp.), *Turbinaria* spp., and *Hormophysa* spp., as well as other fleshy macroalgae, algal turfs, and corals (McCook 1999; personal observations). *Sargassum* wet biomass may reach more than 3,700 g/m<sup>2</sup> during the reproductive period in the austral summer months (December to April). *L. variegata* is often abundant as understory in *Sargassum* beds and covers about 10% and 40% of the benthos during summer and spring respectively (unpublished data).

The species of *Sargassum* in this area are highly seasonal, with peaks of biomass, maturation of reproductive structures, settlement, and recruitment during the warmer months of December through May (Price 1989; Martin-Smith 1993; personal observations). To ensure abundant propagules, we did the experiment during the peak of *Sargassum* recruitment, April–May (1999). Although the temporal patterns of *L. variegata* recruitment are not clear, the species clearly recruited during the experimental period.

Because of the limited dispersal shadows of *L. variegata* and *Sargassum* spp. propagules (de Ruyter van Steveninck and Breeman 1987; Kendrick and Walker 1995), we located the plates in a well-developed *Sargassum* bed with abundant understory thalli of *L. variegata*, within a relatively small area (ca. 9 m<sup>2</sup>) to minimize variations in propagule supply. All settlement plates were 11×11 cm side, with nine replicate plates per treatment randomly allocated to positions within the site. Settlement plates were bolted to the substratum using stainless steel screws and masonry plugs and located as close to the substrate as possible. The plates were left in the reef for a period of 1 month, then retrieved and examined in the laboratory using a stereomicroscope (at sufficient magnification to allow identification of undeveloped fucal propagules).

**Effects of live coral and of other benthic occupants on algal recruitment** To explore the ability of propagules of Fucales and *L. variegata* to recruit onto live coral tissue, we marked areas of live coral tissue (11×11 cm) on small colonies from a range of the most abundant species at the study site. Coral species used included massive *Porites australiensis* (three colonies), *Favites russelli* (two colonies), *Galaxea astreata*, *Cyphastrea chalcidicum*, *Goniastrea retiformis*, and *Astreopora listeri* (one colony each). Colonies were collected, maintained under water, and the surface of the coral tissue examined for algal recruits using a stereomicroscope; the colonies were then returned to the reef. Algal recruitment onto the live coral was compared to control settlement plates (11×11 cm)

made of dead massive *Porites* corals (*P. australiensis* or very similar species).

To explore the effects of competitive interactions with EACs, we compared algal recruitment on clean settlement plates (as controls) with that on settlement plates that had been pre-conditioned on two different reefs, to allow the development of pre-existing algal communities. Smooth terracotta ceramic settlement plates of 11×11 cm side were placed in reef areas with negligible populations of *Sargassum* spp. and *L. variegata*, 2 months immediately prior to the experiment. Pre-conditioning sites were chosen to provide a range of pre-existing occupants, especially EACs, and included the reef slope of an inshore island (Great Palm Island; 18° 40' 943 S; 146° 35' 397 E) at 6–8 m depth and the reef crest of a mid-shelf reef (Rib Reef; 18° 28' 422 S; 146° 52' 783 E) at 4–5 m depth. These pre-conditioned plates were then retrieved and checked for recruits of Fucales and *L. variegata* under a stereomicroscope (any such recruits were removed). The percentage cover of algal turfs, crustose calcareous algae (CCA), and bare substrate was estimated using a 100-point grid, and the height of the algal turf canopy measured. Plates were then deployed at the experimental site at Goold Island. Percentage cover of major benthic groups was also recorded at the end of the experiment (1 month later).

At the beginning of the experiment, pre-conditioned plates had developed EACs dominated by filamentous algal turfs, crustose coralline and other calcareous algae (CCA), and microbial films (Fig. 1). On plates pre-conditioned at Palm Island, the cover of algal turfs was higher than of CCA, both at the beginning and the end of the experiment. Plates pre-conditioned at Rib Reef initially had less cover of algal turfs than CCA, although the cover of these two groups was similar by the end of the experiment. The percentage cover of algal turfs was not significantly different between reefs ( $t = -0.94$ ,  $df = 16$ ,  $P = 0.36$ ), but the percentage cover of CCA was higher in the plates pre-conditioned at Rib Reef ( $t = 9.83$ ,

$df = 16$ ,  $P < 0.001$ , Fig. 1). Algal turfs generally had a canopy height of less than 5 mm and included species of brown algae (*Sphacelaria*, *Hincksia*), green algae (*Enteromorpha*, *Cladophora*, *Derbesia*), red algae (*Polysiphonia*, *Jania*, *Ceramium*), blue-green algae, and diatoms. The CCA assemblage generally consisted of species of non-geniculate coralline algae, but did include some small individuals of *Peyssonnelia*.

**Effects of substrate texture and material on algal recruitment: "abiotic" effects** Comparisons were made between ceramic settlement plates of two different textures, and between dead coral plates of two different textures. We did not compare coral and ceramic plates statistically. The coral plates had intrinsic texture or micro-porosity at a range of scales (difficult to quantify), so that any comparison of coral and ceramic materials is intrinsically confounded by differences in texture, and so should be interpreted cautiously. In particular, rough and smooth textures are not comparable between coral and ceramic plates.

Rough ceramic plates had surface pits of 0.5–2.0 mm size and 0.1–0.3 mm depth, while smooth ceramic plates had little significant rugosity greater than 0.005 mm. Rough coral plates were created by cutting grooves of 1.5–2.5 mm wide and 1.5–2.0 mm depth into similar plates to those used as controls for live coral ("smooth"). The surface of the coral plates was very porous, with micro cavities of 0.13–0.25 mm size and 0.1–> 3.8 mm depth.

**Variables and data analyses** The main response variable was density (number of recruits per plate), as a measure of recruitment, but we also measured length and width as measures of growth. Length (from holdfast to apex for Fucales or to distal margin for *L. variegata*) and width (longest dimension perpendicular to the length of the largest branch) were measured for five, randomly selected recruits per plate for each taxon (i.e., Fucales and *L. variegata*). Density and size measurements were made at the end of the experiment, using a stereomicroscope and a 10×10 cm grid as a guide. Size measurements were averaged between the five recruits to obtain a single value per plate.

Since the individuals of the dominant Fucales (*Sargassum* spp., *Turbinaria* spp., and *Hormophysa* spp.) are difficult to distinguish from each other during early stages (<2 mm), we refer to them collectively as Fucales. However, due to the high abundance of adult *Sargassum* spp. compared to other Fucales at our site, it is likely that most Fucales recruits on the plates were in fact *Sargassum* spp.

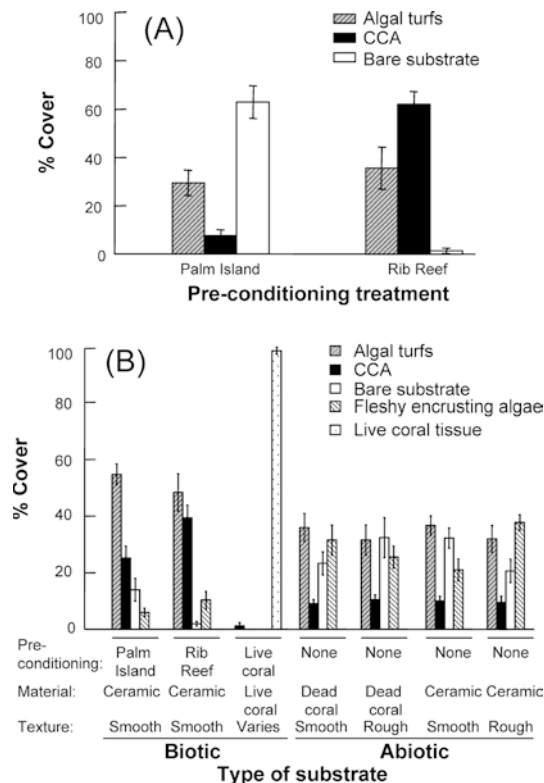
Data were analyzed separately for each effect (live coral, other occupants, and substrate texture and material), because the treatments were not factorial combinations. The comparison between live and dead coral did not require statistical comparison. The density and mean size of recruits of Fucales and *L. variegata* were compared between pre-conditioned and clean, ceramic control plates, using one-way ANOVAs and Bonferroni post-hoc comparisons. As well as simply comparing plates pre-conditioned on the two different sites, we also explored the potential effects of turfs and CCA using simple linear regressions. However, it is important to recognize that since both pre-conditioning treatments had algal turfs and CCA in varying amounts, it is difficult to separate the effects of these algal groups on recruitment. The effects of texture were analyzed within type of material using *t*-tests.

Both density and size data were transformed ( $\log_{10}$ ) for homogeneity of variance, based on Cochran's test for homoscedasticity, and were checked for normality of residuals (graphically). Minor transgressions of Cochran's test were accepted where these were unlikely to influence the conclusions.

## Results

### Algal recruitment onto healthy coral tissue

Healthy corals apparently excluded algal recruitment of Fucales and *L. variegata* in this study. No recruits were ever found on healthy coral tissue of any of the species.

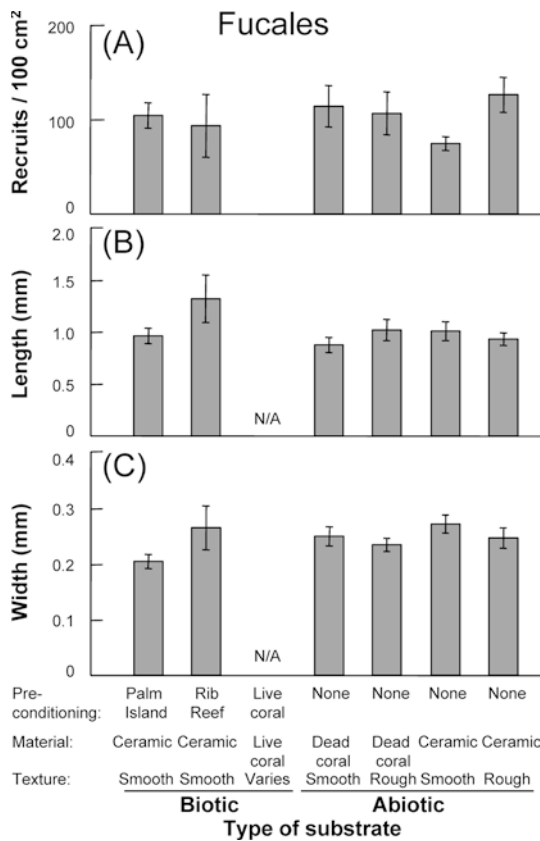


**Fig. 1A, B** Mean percentage cover of benthic organisms and bare substrate on settlement plates. **A** Cover in two pre-conditioning treatments (Palm Island and Rib Reef) at the beginning of the experiment. **B** Cover in all treatments at the end of the experiment. ( $\pm 1$  SE,  $N = 9$ ). CCA Crustose calcareous algae

In contrast, none of the other plates had no recruits, and dead coral settlement plates had about 100 and 10 recruits per plate, of *Fucales* and *L. variegata*, respectively (Fig. 2 and Fig. 3). We occasionally observed recruits of both taxa growing on small areas of dead coral tissue (<2 cm<sup>2</sup>) beside the healthy coral tissue.

Effects of pre-conditioning sites, algal turfs, and CCA

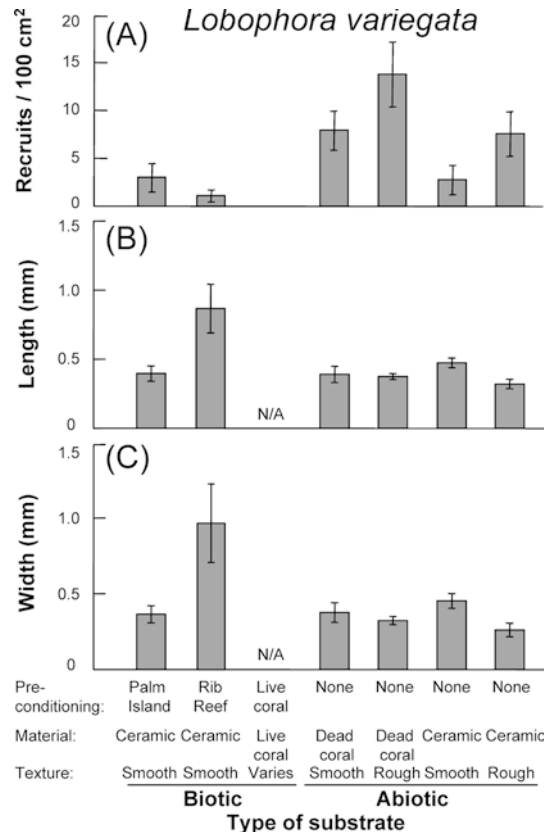
**Fucales** The recruitment of *Fucales* propagules was not significantly different between plates from the two pre-conditioned sites and control plates which had not been pre-conditioned (all smooth ceramic plates; Fig. 2, Table 1). Interestingly, recruits were distinctly longer and wider on plates pre-conditioned at Rib Reef (Fig. 2), although the difference was not statistically significant (Table 1).



**Fig. 2A–C** Means of density (A), length (B), and width (C) of recruits of *Fucales* (mainly *Sargassum* spp.) across pre-conditioning treatments, healthy live coral tissue, and coral and ceramic plates with different textures ( $\pm$  1 SE,  $n=9$ ). Comparison of live and dead coral shows that live coral tissue prevented the recruitment of algal propagules. Comparison of plates pre-conditioned at Palm Island and at Rib Reef and control (smooth ceramic) plates shows that pre-conditioning sites had minimal effects on recruitment. Comparison of smooth and rough ceramic plates shows that increased rugosity enhanced algal recruitment; comparison within the dead coral plates suggests that the differences in coral texture in this experiment had little effect on recruitment. *N/A* Not applicable

*Fucales* recruits were frequently observed growing both among algal turfs (between the filaments) and on CCA, as well as on bare substrate (with associated microbial films). Regression analyses indicated a significant, positive relationship between the cover of algal turfs and the density ( $r^2=0.244$ ,  $P=0.037$ ,  $n=18$ ), length ( $r^2=0.581$ ,  $P<0.001$ ,  $n=18$ ), and width ( $r^2=0.486$ ,  $P=0.001$ ,  $n=18$ ) of *Fucales* recruits on pre-conditioned plates. The height of the algal turf canopy was not significantly related to the density of *Fucales* recruits ( $P=0.114$ ) but was weakly, positively related to their length ( $r^2=0.263$ ,  $P<0.001$ ). CCA showed a significant negative relationship with the density ( $r^2=0.274$ ,  $P=0.026$ ,  $n=18$ ), and no clear relationship with the length ( $r^2=0.014$ ,  $P=0.637$ ,  $n=18$ ) or width ( $r^2=0.041$ ,  $P=0.422$ ,  $n=18$ ) of recruits on pre-conditioned plates.

**Lobophora variegata** The recruitment of *L. variegata* recruits was not significantly different among pre-conditioned plates and control plates (Fig. 3; Table 1). Although the recruitment was slightly, but not significantly, lower in the pre-conditioned plates from Rib Reef, the recruits on those plates grew significantly more than those in any other treatment. They were 114% larger and 165% wider than recruits from the plates pre-conditioned at Palm Island and from the control plates (Fig. 3; Table 1).



**Fig. 3A–C** Means of density (A), length (B), and width (C) of recruits of *Lobophora variegata* for treatments as in Fig. 2 (except  $n=6$  for B and C)

**Table 1** One-way ANOVAs for the effects of substrate pre-conditioning on the density and sizes of early stages of two brown macroalgae: Fucales spp. and *Lobophora variegata*. R Rib Reef, P Palm Island, C control, n.s. not significant

		Source of variation	df	MS	F	P	Conclusion	
Fucales	Density	Pre-conditioning	2	0.184	1.286	0.295	n.s.	
		Error	24	0.143				
	Length	Pre-conditioning	2	0.021	0.788	0.466		
		Error	24	0.027				
	Width	Pre-conditioning	2	0.036	3.006	0.068		
		Error	24	0.012				
<i>L. variegata</i>	Density	Pre-conditioning	2	0.105	0.812	0.456	n.s.	
		Error	24	0.129				
	Length	Pre-conditioning	2	0.157	8.353	0.004		R > P ≈ C
		Error	14	0.019				
	Width	Pre-conditioning	2	0.232	9.014	0.003		R > P ≈ C
		Error	14	0.026				

*Lobophora variegata* recruits were also frequently observed growing both among algal turfs (between the filaments) and on CCA, as well as on bare substrate (with associated microbial films). There was no significant relationship between the density or sizes of *L. variegata* recruits and the cover of algal turfs (density:  $r^2=0.018$ ,  $P=0.596$ ,  $n=18$ ; length:  $r^2=0.001$ ,  $P=0.918$ ,  $n=11$ ; width:  $r^2=0.002$ ,  $P=0.898$ ,  $n=11$ ). The cover of CCA was not related to density of *L. variegata* recruits ( $r^2=0.073$ ,  $P=0.278$ ,  $n=18$ ), but was moderately and significantly, positively related to growth ( $r^2>0.56$ ,  $P<0.01$ ,  $n=11$  for both length and width).

#### Effects of texture and material on Fucales and *L. variegata* recruits

Comparison of rough and smooth ceramic plates indicated that roughness significantly enhanced the density of Fucales and *L. variegata* recruits (Fig. 2 and Fig. 3). Recruitment was 65% and 177% higher on rough ceramic plates than on smooth ceramic plates for Fucales ( $t=2.97$ ,  $df=16$ ,  $P=0.009$ ) and *L. variegata* ( $t=2.06$ ,  $df=16$ ,  $P=0.055$ ), respectively. No differences were observed in the size of Fucales recruits across abiotic substrates ( $t=-0.61$ ,  $df=16$ ,  $P=0.547$  for length;  $t=-1.07$ ,  $df=16$ ,  $P=0.3$  for width; Fig. 2). In contrast, recruits of *L. variegata* from rougher surfaces were significantly smaller than those from smoother surfaces (Fig. 3;  $t=-3.51$ ,  $df=11.7$ ,  $P=0.005$  for length;  $t=-3.29$ ,  $df=11.4$ ,  $P=0.007$  for width).

Within the dead coral plates, the density of Fucales recruits was not affected by the grooves cut into the rough treatment ( $t=-0.27$ ,  $df=16$ ,  $P=0.791$ ; Fig. 2). The survival of *L. variegata* on roughened dead coral plates was higher (74%) than on ordinary dead coral plates, but the difference was not significant ( $t=1.54$ ,  $df=16$ ,  $P=0.144$ ). No differences were observed in the size of recruits of either taxa between texture treatments of dead coral ( $t$ -test,  $P>0.05$ ; Fig. 2 and Fig. 3). In general, dead coral plates had more recruits of *L. variegata* than ceramic plates (120% higher; Fig. 3).

## Discussion

The nature of the substrate, especially the presence of live coral tissue, had considerable influence on the recruitment success of the two coral reef macroalgae studied. These effects were, however, variable and depended on the type of substrate, the species, and the type of response measured.

#### Algal recruitment onto healthy coral tissue

The most important outcome of this study was the demonstration that algal propagules of Fucales (mainly *Sargassum* spp.) and *L. variegata* did not settle on healthy, live coral tissue (Fig. 2 and Fig. 3), independent of the coral species. Algal recruits were never found on healthy coral tissue of any of the coral species examined, supporting previous findings for massive *Porites* corals from nearby reefs (Diaz-Pulido and McCook 2002). Although we observed occasional recruits of both species growing on small dead tissue areas beside healthy coral tissue, the pattern of dead coral tissue was never consistent with algal recruitment as the cause of coral tissue death, but was generally indicative of physical or other injuries. The strong and consistent contrast between recruitment on live corals and dead coral plates strongly suggests that the absence of recruits on live coral tissue represents defensive exclusion by the coral. The strength of this exclusion is emphasized by the contrast with CCA (and algal turfs), since both taxa were observed growing directly on CCA (and among turfs). Thus the ability of corals to exclude algal recruitment was impressive, not only in comparison to dead substrata, but also in comparison to other organisms, including calcified organisms.

This conclusion has important implications in terms of the competitive interactions between benthic algae and corals, particularly in the context of reef degradation. The replacement of corals by algae may occur by three processes: (1) settlement and growth of algal propagules from the plankton onto healthy coral tissue; (2) competitive vegetative overgrowth from adjacent algal thalli; and (3) coral disturbance, injury,

stress, or tissue mortality, followed by either of the above processes. The mechanism of replacement due to algal settlement from the plankton onto healthy coral tissue seems to be rare for a range of algal groups and forms and coral species (Diaz-Pulido and McCook 2002). The second mechanism, replacement by vegetative overgrowth, has been documented for fleshy macroalgae (including *L. variegata*) and filamentous algal taxa, both on nearby islands of the GBR (Jompa and McCook 2002a; 2002b) and in the Caribbean (Hughes 1994; Littler and Littler 2000). Algal settlement and colonization is a rapid and almost universal consequence of coral tissue death, or even injury or stress (McCook et al. 2001; Diaz-Pulido and McCook 2002). Thus it appears that the replacement of healthy corals by algae is more likely to involve either lateral, vegetative overgrowth by competing algae or coral disturbance and subsequent algal colonization, than settlement of algal propagules directly from the plankton. Given the extent of coral damage and mortality due to disturbances, such as bleaching or coral disease (Wilkinson 2002), and that algal settlement has the potential to colonize large areas much more rapidly than vegetative growth, we suggest that settlement of algal propagules on stressed or dead coral tissue is likely to be the most important mechanism by which corals are replaced by algae.

The mechanisms by which live corals competitively inhibit the settlement or recruitment of algal propagules (i.e. space pre-emption) are not clear from our study. However, likely processes include mucus secretion, cleaning activity of tentacles, allelochemicals, or ingestion of algal propagules (Lang and Chornesky 1990; McCook et al. 2001).

#### Effects of pre-conditioning sites, algal turfs, and CCA

In general, variations in the density of Fucales and *L. variegata* recruits (Fig. 2 and Fig. 3) among pre-conditioning treatments or sites were not significant, notwithstanding the increased growth of *L. variegata* recruits on plates from Rib Reef (Fig. 3). To some extent the lack of significant differences appears to reflect variation within treatments (limiting experimental power). Pre-conditioning treatments are unlikely to have strong effects except those caused by the colonizing biota, and the abundance and height of turf algae in particular varied considerably within treatments. On this basis, the relationships between recruitment and components of the EACs may be more informative than the lack of significant differences among treatments.

The contrasting relationships between CCA and Fucales or *L. variegata* are intriguing. Previous work has generally found that some CCA inhibited the recruitment of algal propagules (Steneck 1997; Keats et al. 1997; Figueiredo et al. 1997; Littler and Littler 1997),

either by epithelial sloughing or enhanced grazing on the surface of the CCA (but see Kendrick 1991; Airoidi 2000 for different effects of CCA on algal turfs). These processes could explain the weak negative relationship between Fucales recruitment and cover of CCA. However, this contrasts markedly with the increased growth of *L. variegata* on plates conditioned at Rib Reef, which presumably reflect the higher abundance of CCA on those plates (Fig. 1A), since there was a clear positive relationship with cover of CCA. The underlying cause of this pattern remains obscure, although Santelices and Varela (1994) found that calcium carbonate facilitated rhizoidal attachment in the fleshy red alga *Gelidium chilense*, perhaps explaining an apparent association between this alga and CCAs.

It is also intriguing to speculate on the contrasting relationships between CCA and Fucales or *L. variegata* and the contrasting distributions of these taxa across the continental shelf. Although the abundance of both taxa is apparently strongly regulated by herbivory (de Ruyter van Steveninck and Breeman 1987; Morrison 1988; McCook 1996; 1997; Jompa and McCook 2002a; 2002b), *Sargassum* spp. are virtually absent from offshore reefs, whereas *L. variegata* is widespread and generally common but low in abundance on offshore reefs (McCook et al. 1997; personal observations). Since CCA are ubiquitous and most abundant on offshore reefs (McCook et al. 1997; Fabricius and De'ath 2001), it may be that the differing distributions of *Sargassum* and *L. variegata* are to some extent due to differing effects of CCA.

The relationships between algal turfs and algal recruitment were also contrasting, being positively related for Fucales, but unrelated for *L. variegata*. Previous experimental studies have shown a range of effects for turf algae on recruitment of Fucales and kelps, including facilitation by both small, filamentous algal turfs (<1 cm height; Ang 1985; McCook and Chapman 1993) and large algal turfs (Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992), and competitive inhibition of survival of macroalgal recruits by algal turfs (Reed 1990; Chapman 1990; Worm and Chapman 1998). The mechanisms mediating the facilitation interaction may include refuges against desiccation, grazing, and water displacement (above references). The presence of a bacterial film has also been suggested to enhance recruitment of marine algae (Ang 1985; Santelices 1990). Although the relationships in our study are only correlative, since we did not directly manipulate algal turfs, causal interpretations are strengthened by the nature of the pre-conditioning, which took place prior to, and in a different place from, the recruitment. It may be that the turfs facilitated attachment of Fucales recruits, with little subsequent inhibition of this taller taxon, but did not competitively inhibit the prostrate *L. variegata* juveniles. Overall, the effects of algal turfs and CCA on algal recruitment cannot be considered to be homogeneous among taxa.

## Effects of texture and material

Substrate rugosity of ceramic plates enhanced the survival of Fucales and *L. variegata* recruits, and inhibited the growth (size) of *L. variegata*. Rougher surfaces had up to 165% more recruits than the smoother surfaces (Fig. 2 and Fig. 3). Among plates made from dead coral, although our attempt to increase rugosity had no effects on Fucales recruitment, there was a large but not significant increase in *L. variegata*. We suggest that the lack of significant effects of rugosity among coral plates reflects the high intrinsic micro-rugosity or porosity of the coral skeleton. Higher survival of macroalgal recruits on rougher textures is consistent with reports in the literature (Harlin and Lindbergh 1977; Norton 1983; Hixon and Brostoff 1985; Fletcher and Callow 1992; Amsler et al. 1992; McCook and Chapman 1993; Johnson 1994; Anderson and Underwood 1994). Rougher textures and porous materials have been suggested to protect algal recruits from dislodgment by wave action, water currents, and grazing activity and to increase the surface area available for settlement and recruitment (references above).

It is interesting that substrate rugosity increased the density but decreased the growth of *L. variegata* recruits (Fig. 3). This may reflect increased competition with other organisms, such as fleshy crustose algae (Fig. 1B), the recruitment of which was also enhanced by the texture. Whatever the explanation, the contrasting effects on density and growth demonstrate that effects on recruitment may vary markedly among different life-history parameters.

Recruitment of *Lobophora variegata* was affected more by rugosity (and perhaps by material) than that of Fucales. This variability may reflect a relationship between propagule size and optimum surface rugosity (Fucales propagules are substantially larger than those of *L. variegata*), or differences in post-settlement mortality, since effects on the two stages cannot be separated in this study (Fletcher and Callow 1992; as discussed by Amsler et al. 1992). However, they again emphasize the variability, this time between taxa.

Although it is not possible to directly compare recruitment on coral and ceramic plates in a factorial analysis, it is worth noting that density of *L. variegata* recruits was significantly less on ceramic plates than on coral plates. Whether this is due to physical or chemical differences in the plates is unclear, although the microporous nature of the coral skeleton did allow the rhizoids of *L. variegata* to penetrate deeper and anchor better than did the ceramic material (personal observations; see also Hardy and Moss 1979 for *Fucus*). Barnes and Topinka (1969) noted enhanced growth of *Fucus* germlings on carbonate substrates, in contrast to our results for both taxa.

In summary, the abiotic and biotic characteristics of the substrate may be important to the recruitment of these two taxa of brown algae. However, the outcomes of these interactions were variable and complex, and

depended on the type of substrate, organisms already present, the species involved, and the life history processes (attachment, survival, or growth). Despite the heterogeneity in outcomes, it is clear that algal settlement via propagule dispersal will rarely occur onto healthy coral tissue. The variability in outcomes is important in terms of subsequent development of algal populations, especially, for example, during putative invasions by *Sargassum* of inshore reefs of the GBR.

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