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Effects of algal turfs and sediment on coral settlement

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Abstract

Successful settlement and recruitment of corals is critical to the resilience of coral reefs. Given that many degraded reefs are dominated by benthic algae, recovery of coral populations after bleaching and other disturbances requires successful settlement amidst benthic algae. Algal turfs often accumulate sediments, sediments are known to inhibit coral settlement, and reefs with high inputs of terrestrial sediments are often dominated by turfs. We investigated the impacts of two algal turf assemblages, and of sediment deposits, on settlement of the coral *Acropora millepora* (Ehrenberg). Adding sediment reduced coral settlement, but the effects of different algal turfs varied. In one case, algal turfs inhibited coral settlement, whereas the other turf only inhibited settlement when combined with sediments. These results provide the first direct, experimental evidence of effects of filamentous algal turfs on coral settlement, the variability in those effects, and the potential combined effects of algal turfs and trapped sediments.

Keywords: Algal turfs; Coral settlement; Sediment; Resilience

1. Introduction

Degradation or even simple disturbance of coral reefs, whether caused by terrestrial run-off, crown-of-thorns starfish outbreaks, over-fishing, or mass-bleaching events, generally involves increased dominance by benthic algae (Hughes, 1994; McCook, 1999; McClanahan et al., 2001; Diaz-Pulido and McCook, 2002; Wilkinson, 2002). Increasingly it is becoming recognized that the process of degradation involves a failure to recover from acute disturbances (Hughes, 1994; Connell, 1997; Done, 1999; McCook, 1999; Hughes et al., 2003). The successful settlement and recruitment of corals is critical to the recovery of coral populations after disturbance, and hence a fundamental aspect of overall reef resilience (Hughes, 1996; Hughes and Tanner, 2000). However, settlement and recruitment of corals occurs amidst algal assemblages, and this will be increasingly so as climate change leads to increasingly frequent mass bleaching (Hoegh-Guldberg, 1999; Hughes et al., 2003), followed by algal colonisation (Diaz-Pulido and McCook, 2002). It is therefore surprising that very little is known about the effects of benthic algae on coral settlement and recruitment (McCook et al., 2001).

Filamentous algal turfs in particular are likely to have critical effects on coral settlement and recruitment. A recent survey of coral recruits on a range of inshore reefs on the Australian Great Barrier Reef found that coral recruits were more often found in close proximity to filamentous algal turfs than any other major benthic group, more so than predicted by overall abundance in the habitats surveyed (Birrell, 2003). Turf algae rapidly colonise the surfaces of dead corals, and may persist for several years (Price, 1975; Diaz-Pulido and McCook, 2002), particularly when herbivores maintain low biomass of large, upright macroalgae (McCook, 1999). Benthic algae, predominantly algal turfs, comprised up to 90% of benthic cover across large areas of the Great Barrier Reef, particularly the inshore regions, after

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disturbances by mass-bleaching events and regional outbreaks of crown-of-thorns starfish (Sweatman et al., 2000, 2001). Similarly, algal turfs dominated reefs in Kenya on the East coast of Africa, following the 1998 mass-bleaching event (McClanahan et al., 2001).

Terrestrial run-off has been shown to have numerous impacts on reefs, including serious impacts on coral reproduction, settlement and recruitment (Rogers, 1990; Gilmour, 1999; Fabricius et al., 2003). In particular, sediments deposited on the reef substratum have been shown to inhibit the settlement of coral larvae and to smother newly settled juveniles (Babcock and Davies, 1991; Babcock and Mundy, 1996). However, previous studies have not placed these effects in the context of community dominance by benthic algae, especially algal turfs, although sediment trapping and accumulation by algae, and algal turfs in particular, is widely observed (Eckman et al., 1989; Steneck, 1997; Airoldi, 1998; Purcell, 2000). Algal assemblages reduce the flow of water in the boundary layer, enhancing sediment deposition and reducing resuspension (Eckman et al., 1989; Carpenter and Williams, 1993; Vogel, 1994), and can also physically trap sediment, preventing resuspension (Purcell, 2000). Sediment accumulation in algal turfs has been shown to enhance the ability of these assemblages to smother and overgrow other benthic biota, such as crustose coralline algae (Steneck, 1997). Clearly, there is potential for algal turfs and sediments to act in combination to hinder coral settlement, especially on degraded or disturbed inshore reefs subject to high inputs of sediments.

This study provides a preliminary exploration of the effects of filamentous algal turfs, and algal turfs combined with sediments, on the settlement of coral larvae. We tested whether the presence of algal turfs and/or sediments on dead coral substrata can reduce larval settlement of the hard coral, *Acropora millepora* (Ehrenberg).

2. Materials and methods

2.1. Experimental design

To test the hypotheses that algal turfs hinder coral settlement and that sediments accumulated in algal turfs enhance this effect, we manipulated the presence of algal turfs and sediments on dead coral substrata, and compared the number of corals that settled in six different treatments. Importantly, to explore potential variability in the impact of the turfs, we used two different algal turf assemblages. Thus, the experimental design included three main factors: *Algal turf type* (two levels: Turf 1 and Turf 2), *algal turf presence* (two levels: with and without; fixed factor), and *sediment presence* (two levels: with and without; fixed factor). Within each combination of these treatments, we used three tanks (nested within each combination of main factors) and inside each tank placed six settlement surfaces (replicates).

2.2. Experimental substrata, treatments, and larval settlement procedures

Experimental settlement surfaces consisted of 5 cm × 5 cm pieces of dead, tabulate *Acropora* colonies that had well-established algal turf assemblages. For treatments without algal turfs, we carefully removed most algae, using a wire brush. Sediment addition treatments involved addition to each tank of 50 cm^3 of sediment, which was allowed to settle on the coral settlement surfaces. Sediment was obtained by filtering (15 μm) seawater from the reef crest in front of the Orpheus Island Research Station (18°36.5′ S, 146°29.4′ E).

The first turf assemblage ("Turf 1") was established de novo on settlement surfaces that had been cut from a dead colony of tabular *Acropora* coral, cleaned with a high-pressure water hose, exposed to sunlight for one week, and then re-immersed for six weeks, to allow algal turfs to recolonise. The settlement surfaces were suspended from buoys one metre below the sea surface and 100 m offshore from the reef crest at Orpheus Island (18°36.4′ S, 146°29.4′ E), where herbivore abundance was low (pers. obs.).

The second turf assemblage ("Turf 2") was a well-established community on an in situ dead colony of tabular *Acropora*, collected from shallow water (1–3 m depth) on the North–East (exposed) corner of Orpheus Island (18°37.0′ S, 146°29.4′ E) and cut into settlement surfaces. Orpheus Island reefs were extensively bleached in 1998, resulting in the death of up to 90% of *Acropora* corals (Berkelmans and Oliver, 1999; Marshall and Baird, 2000), which were subsequently colonised by algal turfs (Diaz-Pulido and McCook, 2002), suggesting the assemblages in this treatment were approximately 2.5 years old.

The two algal turfs and associated substrata were quite different in several respects. Turf 1 (5–8 mm) was generally higher than Turf 2 (less than 3 mm), presumably due to grazing of Turf 2. Turf 1 algal assemblages were less dense, more variable (at 1 cm scale) and covered a smaller percentage of the settlement surfaces (85%) compared to Turf 2 algal assemblages (93%), reflecting the recent recolonisation of Turf 1. Turf 1 appeared to have a simpler, less developed species composition, but detailed comparisons were beyond the scope of the present study. Perhaps as a result of the less dense filamentous algae, Turf 1 algal mats generally had more underlying crustose coralline algae than the Turf 2 algal mat (6.5% and 2.0% respectively). The topography of the settlement surface used to grow the Turf 1 algal assemblage was more irregular, and loosely branched than that of the Turf 2 algal assemblages.

The experiment was conducted in the outdoor aquarium facilities at the Orpheus Island Research Station. Tanks (9 litre volume, opaque plastic rectangular buckets) were placed in a shaded, outdoor raceway, each supplied continuously with 25–30 l per hour of filtered running seawater (15 μm), and temperature maintained between 28 and 30 °C by circulating seawater around the outsides of tanks. Overflow from each tank occurred through a hole covered by plankton mesh, so as not to lose coral larvae. To encourage larvae to settle on the upper surfaces of substrata, light levels were reduced using 70% shade cloth over the entire setup, with experimental substrates on the bottom of each tank (see Mundy and Babcock, 1998).

Larvae were obtained from *A. millepora* (Ehrenberg) using procedures in Willis et al. (1997) to spawn and fertilise gametes and raise the larvae during the mass coral spawning in December 2001. *A. millepora* is common on Orpheus Island reefs, easily maintained in aquaria and spawns predictably (Willis et al., 1985). Larval supply was standardised to 5000 (±500) competent larvae per tank and larvae allowed to settle for four days. Larval settlement and metamorphosis was confirmed by examining randomly selected surfaces under a dissecting microscope. Experimental settlement surfaces were submerged in seawater at all times.

2.3. Data collection and analysis

Coral settlement was measured as the number of metamorphosed coral larvae (hereafter referred to as *recruits*) on each experimental settlement surface. Recruits were counted with a dissecting microscope and a 1 cm × 1 cm grid placed over the experimental settlement surfaces.

The mean number of coral recruits in each treatment combination was compared using nested ANOVA, followed by post-hoc Student–Newman–Keuls (SNK) comparisons. Because the initial differences between the two turf assemblages were so marked, resulting in a significant 3-way interaction, we did not compare the two turf types statistically, but analysed each as a separate experiment. Data were examined for homogeneity of variance (Cochran's *C* test), outliers, and independence and normality of residuals, and on that basis were logarithmically transformed $\log_{10}$(number of recruits + 0.01).

3. Results

There were considerable differences in the effects of the two algal turf assemblages on coral settlement, resulting in a significant 3-way interaction between algal turf type, algal turf presence and sediment presence (Fig. 1, Table 1). In particular, the turfs differed in effects on larval settlement, depending on whether or not sediment had been added to the experimental treatment.

For Turf 1, the presence of either, or both, of ungrazed, newly established algal turfs (SNK, $p < 0.05$), or sediments (SNK, $p < 0.05$) reduced coral settlement to extremely low levels, most often to zero. In the absence of both algae and sediments, mean settlement was 5–50 times greater. There was some variation between tanks within treatment combinations, although this nested factor was not statistically significant.

In contrast, the effects of older, grazed turf assemblages (Turf 2) on settlement of coral larvae were smaller and not statistically significant ($p = 0.863$, Table 1, Fig. 1), whereas sediment deposits uniformly reduced larval settlement ($p = 0.046$, Table 1) and this impact was consistent whether the turf assemblage was present or absent ($p = 0.359$, Table 1). Although algal effects were not significant, coral settlement tended to be lower

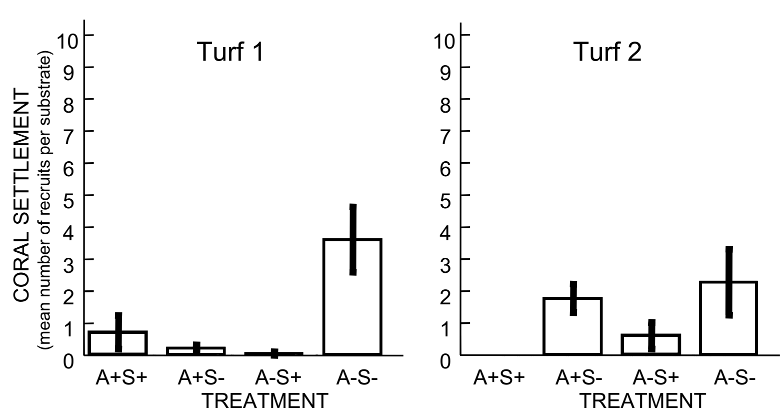

Fig. 1. Average number of settled *A. millepora* larvae (±1 SE) on experimental settlement surfaces with two different algal turfs: Turf 1 and Turf 2. Treatments are combinations of algal turfs present (A+) or removed (A−), and sediments added (S+) or not (S−). No coral larvae settled in the A+S+ treatment of Turf 2. Presence of sediment reduced coral settlement, but the effects of algal turfs varied, in one case significantly reducing settlement (Turf 1; SNK $p < 0.05$); in the other settlement inhibition was only significant in combination with sediments (Turf 2; Table 1).

Table 1
Analysis of variance comparing effects of algal turf assemblages (A) and sediment (S) on larval settlement of the coral *A. millepora*

Analysis	Source of variation	MS	df	*F*-ratio	*P*
Turf 1 and Turf 2	T × A × S	13.834	1	5.503	0.032
	Tank (T × A × S)	2.514	16	3.395	<0.001
	Residual	0.741	123		
Turf 1	Algae (A)	6.693	1	4.438	–
	Sediment (S)	16.034	1	10.632	–
	A × S	11.801	1	7.825	0.023
	Tank (A × S)	1.508	8	2.077	0.052
	Residual	0.726	60		
	Cochran's *C*	0.2051			
Turf 2	Algae (A)	0.111	1	0.032	0.863
	Sediment (S)	19.510	1	5.543	0.046
	A × S	3.329	1	0.946	0.359
	Tank (A × S)	3.520	8	4.844	<0.01
	Residual	0.727	60		
	Cochran's *C*	0.2315			

3-Way ANOVA, including two levels of algal turf type (Turfs 1 and 2) as the third factor, algal turf type (T), is shown, as well as 2-way ANOVAs for effects of algae and sediment within each type of algal turf. Data are log transformed ($x' = \log_{10}$(number of recruits + 0.01)). Cochran's critical $C_{p<0.05} = 0.3029$. SNK results are reported in the text.

in the presence of algae and was uniformly zero in the presence of both sediments and algae, suggesting the differences to Turf 1 are a matter of degree, and reflect in part reduced power due to greater variation among tanks (the denominator mean square in this comparison). Maximum coral settlement occurred where both sediments and algae were absent (A-S-, 6.3 recruits ±2.3 SE). There was considerable and significant variation among tanks within treatment combinations. Together, these observations raise the possibility that the lack of significant interactions between sediments and grazed, older algal assemblages may reflect high within-treatment between-tank variability and decreased power of the comparison, as well as the smaller effects of algae.

4. Discussion

The results of this study provide several useful pointers in terms of coral settlement in the context of recovery of reefs from degradation and disturbance. Firstly, they provide the first direct, experimental evidence that some algal turfs reduce coral settlement in their own right (McCook et al., 2001). When coral settlement surfaces colonised by ungrazed, newly established (<6 week old) algal turfs were presented (Turf 1 treatment), coral larvae settled almost exclusively on surfaces that were cleaned of algal turfs and without sediments. Secondly, the differences in effects of algal Turfs 1 and 2 demonstrate the considerable variability in effects, even among filamentous algal turfs. Thus, the effects of algal assemblages on coral recovery and resilience post-bleaching can not be ignored, nor assumed uniform.

The reduced settlement in the presence of sediment is consistent with previous studies (Babcock and Davies, 1991). Importantly, however, the combined results for Turfs 1 and 2 demonstrate that the effects of sediment deposits may depend on the presence and nature of algal assemblages present on the substratum. This effect is likely to be much more pronounced in the field (but more difficult to test), where the trapping of sediments by algal turfs is known to be important (Steneck, 1997; Purcell, 2000). The flow regime in our tanks was such that the presence of algae did not dramatically enhance the persistence of sediment deposits. Unfortunately, it would be very difficult to design a fully factorial experiment which sustained differences in algae and sediments and realistic flow conditions. The demonstration of interactions between sediments and algal turfs is significant in particular, because previous experiments have only tested sediments in isolation. Such single factor experiments may seriously under-estimate the threats of human impacts, such as sediment run-off, by ignoring the full context of their effects (Fabricius et al., 2003).

The results of this study suggest that coral recovery may be delayed on reefs dominated by algal turfs, particularly those stressed by high sedimentation, through reduction and even inhibition of coral settlement. This is a particular concern for inshore reef areas which are vulnerable to terrestrial run-off and high sediment inputs from developed catchments, especially on the inshore Great Barrier Reef (Bryant et al., 1998; Wilkinson, 2002; Wachenfeld et al., 1998; Fabricius et al., in press). For example, coral recruitment was much lower on reefs influenced by terrestrial run-off from developed catchments (Wet Tropics or Cairns to Innisfail region) compared to a relatively undeveloped catchment area (Princess Charlotte Bay region; Birrell, 2003; Fabricius, pers. comm.). Reefs in the Cairns to Innisfail region (developed catchment) were subject to significantly higher inputs of terrestrial sediments, and are dominated by algal turfs (Fabricius et al., in press), following high coral mortality during crown-of-thorns starfish outbreaks during the mid to late 1990s (Engelhardt et al., 1997) and the mass-bleaching event of 1998 (Berkelmans and Oliver, 1999; Sweatman et al., 2000, 2001). Thus our results are consistent with large-scale correlations between algal turf abundance, sediment load, and reduced reef resilience, although the differences in recruitment between the two regions are likely due to a number of factors.

The significance of these effects should not be underestimated, given impending increases in frequency and severity of coral mortality, especially in the context of climate change: as many as 3–4 mass-bleaching events per decade have been predicted (Hoegh-Guldberg, 1999; Hughes et al., 2003). Algal turf assemblages have been observed to dominate dead coral surfaces for more than one and a half years after crown-of-thorns starfish outbreaks (Price, 1975) and more than two and a half years after mass-bleaching (McClanahan et al., 2001; Diaz-Pulido and McCook, 2002). In both of these examples, algal turf dominance potentially spanned two or more coral spawning seasons, and thus could contribute to reduced coral recovery also for at least 2–3 years. Given that coral stress and mortality in these scenarios will also result in reduced fecundity, there is a risk of synergistic impacts on overall coral replenishment and reef resilience.

This study also demonstrates that benthic algal assemblages that may not be competitively superior to established corals, can still have negative impacts on coral populations by affecting coral settlement. Algal turf assemblages generally do not out-compete mature corals but rather colonise dead coral surfaces (Price, 1975; McCook, 2001; Diaz-Pulido and McCook, 2002, 2004; Jompa and McCook, 2003a,b). Just as the effects of algae may be more severe for coral recruits than for larger established corals (Hughes and Jackson, 1985; Hughes, 1989, 1996; McCook et al., 2001), different types of algal assemblage are likely to have different effects on settling coral larvae compared to settled recruits. Thus our conceptual framework for understanding the role of coral–algal competition in the degradation of coral reefs must recognize that competition varies between life history stages of corals, and between algal assemblages, with the potential to generate very different outcomes.

The differences between the two algal turfs, and the considerable variation between tanks within the same treatment combinations are difficult to attribute to specific causes without further experimentation. However, it is likely that height and density of the turf affect the settlement of corals, and it is significant that the more strongly grazed turf had higher coral recruitment (Steneck and Dethier, 1994; McCook et al., 2001). This serves to emphasise the potential importance of protecting herbivores in order to enhance reef resilience. However, the observed differences may also reflect differences in heterogeneity of substrates (Harrison and Wallace, 1990) or differences in the taxonomic composition of the turfs, or the bacteria or other benthic biota (e.g., crustose coralline algae) associated with the substrates and algal turf assemblages, all of which can affect coral settlement (Morse et al., 1988; Johnson et al., 1991; Johnson et al., 1997; Negri et al., 2001; Baird et al., 2003). In particular, many algae have chemical influences on the settlement of invertebrate larvae (Steinberg et al., 2001; Steinberg and de Nys, 2002), and although little is known about the chemical effects of algae on coral settlement, Jompa and McCook (2003a,b) suggested that allelopathy by a filamentous alga killed established *Porites* coral tissue. Finally, on conceptual grounds, fine filamentous algal turfs are likely to be relatively innocuous for coral settlement, in comparison to thicker, corticated algal turfs or thick stands of larger fleshy and leathery macroalgae (Jompa, 2001). This is supported by the observation that coral recruits were more commonly observed in the proximity of filamentous algal turfs than other groups of macroalgae (Birrell, 2003).

In summary, sediment deposits reduced coral settlement, but the effects of different algal turfs varied, from relatively little effect of a well established and grazed turf, to serious inhibition by a newly established (<6 week old) algal turf with greater canopy height. Thus algal colonisation of reefs after disturbance may inhibit coral settlement, slowing recovery and reducing the long-term resilience of these reefs. These effects are likely to be exacerbated if the reefs are also stressed by sediment deposition.

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References

Airoldi, L., 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79, 2759–2770.

Babcock, R., Davies, P., 1991. Effects of sedimentation on settlement of *Acropora millepora*. Coral Reefs 9, 205–208.

Babcock, R., Mundy, C., 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinian corals. Journal of Experimental Marine Biology and Ecology 206, 179–201.

Baird, A.H., Babcock, R., Mundy, C.P., 2003. Habitat selection by larvae influences the depth distribution of six common coral species. Marine Ecology Progress Series 252, 289–293.

Berkelmans, R., Oliver, J.K., 1999. Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs 18, 55–60.

Birrell, C.L., 2003. Influences of benthic algae on coral settlement and post-settlement survival: implications for the recovery of disturbed and degraded reefs. M.Sc., James Cook University, Townsville, 131 pp.

Bryant, D., Burke, L., McManus, J., Spalding, M., 1998. Reefs at risk: a map-based indicator of the threats to the worlds coral reefs. World Resources Institute, International Center for Living Aquatic Resources Management, World Conservation Monitoring Centre, and United Nations Environment Programme, Washington DC.

Carpenter, R.C., Williams, S.L., 1993. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnology and Oceanography 38, 687–694.

Connell, J.H., 1997. Disturbance and recovery of coral assemblages. Coral Reefs 16, S101–S113.
Diaz-Pulido, G., McCook, L.J., 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. Marine Ecology Progress Series 232, 115–128.
Diaz-Pulido, G., McCook, L.J., 2004. Effects of live coral, epilithic algal communities and substrate type on algal recruitment. Coral Reefs 23, 225–233.
Done, T.J., 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. American Zoologist 39, 66–79.
Eckman, J.E., Duggins, D.O., Sewell, A.T., 1989. Ecology of an understory kelp environment: I. Effects of kelps on flow and particle transport near the bottom. Journal of Experimental Marine Biology and Ecology 129, 173–187.
Engelhardt, U., Miller, I., Lassig, B.R., Sweatman, H., Bass, D., 1997. Crown-of-thorns starfish (*Acanthaster planci*) populations in the Great Barrier Reef World Heritage Area: status report 1995–1996. In: State of the Great Barrier Reef World Heritage Area Workshop, Townsville, pp. 158–184.
Fabricius, K., De'ath, G., McCook, L.J., Turak, E., Williams, D., in press. Changes in inshore algae, coral and fish communities along water quality gradients on the Great Barrier Reef. In: Hutchings, P.A., Haynes, D. (Eds.), Proceedings of Catchment to Reef: Water Quality Issues in the Great Barrier Reef Region Conference. Marine Pollution Bulletin.
Fabricius, K.E., Wild, C., Wolanski, E., Abele, D., 2003. Effects of transparent exopolymer particles (TEP) and muddy terrigenous sediments on the survival of hard coral recruits. Estuarine Coastal and Shelf Science 57, 613–621.
Gilmour, J., 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. Marine Biology 135, 451–462.
Harrison, P.L., Wallace, C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky, Z. (Ed.), Coral Reefs: Ecosystems of the World, vol. 25. Elsevier, Amsterdam, 133–207 pp.
Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50, 839–866.
Hughes, T.P., 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70, 275–279.
Hughes, T.P., 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551.
Hughes, T.P., 1996. Demographic approaches to community dynamics: a coral reef example. Ecology 77, 2256–2260.
Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. Ecological Monographs 55, 141–166.
Hughes, T.P., Tanner, J.E., 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81, 2250–2263.
Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J.A., Marshall, P.A., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.
Johnson, C.R., Muir, D.G., Reysenbach, A.L., 1991. Characteristic bacteria associated with surfaces of coralline algae: a hypothesis for bacterial induction of marine invertebrate larvae. Marine Ecology Progress Series 74, 281–294.
Johnson, C.R., Lewis, R.E., Nichols, D.S., Degnan, B.M., 1997. Bacterial induction of settlement and metamorphosis in marine invertebrates. In: Proceedings of the 8th International Coral Reef Symposium, Panama, pp. 1219–1225.
Jompa, J., 2001. Interactions between macroalgae and scleractinian corals in the context of reef degradation. Ph.D., James Cook University, Townsville, 147 pp.
Jompa, J., McCook, L.J., 2003a. Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but are killed by the red alga *Anotrichium tenue*. Marine Ecology Progress Series 258, 79–86.
Jompa, J., McCook, L.J., 2003b. Coral–algal competition: macroalgae with different properties have different effects on corals. Marine Ecology Progress Series 258, 87–95.
Marshall, P.A., Baird, A.H., 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19, 155–163.
McClanahan, T.R., Muthiga, N.A., Mangi, S., 2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. Coral Reefs 19, 380–391.
McCook, L.J., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18, 357–367.
McCook, L.J., 2001. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs 19, 419–425.
McCook, L.J., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19, 400–417.
Morse, D.E., Hooker, N., Morse, A.N.C., Jensen, R.A., 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. Journal of Experimental Marine Biology and Ecology 116, 193–217.
Mundy, C., Babcock, R., 1998. Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement. Journal of Experimental Marine Biology and Ecology 223, 235–255.
Negri, A.P., Webster, N.S., Hill, R.T., Heyward, A.J., 2001. Metamorphosis of broadcast spawning corals in response to bacteria isolated from crustose algae. Marine Ecology Progress Series 223, 121–131.
Price, I.N., 1975. The development of algae on the skeletons of reef-building corals. In: Proceedings of the Crown-of-Thorns Starfish Seminar. Australian Government Publishing Service, Canberra, pp. 181–191.
Purcell, S.W., 2000. Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. Bulletin of Marine Science 66, 199–214.
Rogers, C.S., 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series 62, 185–202.
Steinberg, P.D., de Nys, R., 2002. Chemical mediation of colonization of seaweed surfaces. Journal of Phycology 38, 621–629.
Steinberg, P.D., de Nys, R., Kjelleberg, S., 2001. Chemical mediation of surface colonization. In: McClintock, J.B.B. (Ed.), Marine Chemical Ecology. CRC Press, Boca Raton, Florida, pp. 355–387.
Steneck, R.S. 1997. Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients. In: Proceedings of the 8th International Coral Reef Symposium, pp. 695–700.
Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69, 476–498.
Sweatman, H., Cheal, A., Coleman, G., Fitzpatrick, B., Miller, I., Ninio, R., Osborne, K., Page, C., Ryan, D., Thompson, A., Tomkins, P., 2000. Long-term monitoring of the Great Barrier Reef, Status Report 4. Australian Institute of Marine Science, Townsville, Australia.
Sweatman, H., Cheal, A., Coleman, G., Delean, S., Fitzpatrick, B., Miller, I., Ninio, R., Osborne, K., Page, C., Thompson, A., 2001. Long-term monitoring of the Great Barrier Reef, Status Report 5. Australian Institute of Marine Science, Townsville, Australia.
Vogel, S., 1994. Life in Moving Fluids: The Physical Biology of Flow, second ed. Princeton University Press, Princeton, NJ, 467 pp.

Wachenfeld, D.R., Oliver, J.K., Morrissey, J.I., 1998. State of the Great Barrier Reef World Heritage Area. Great Barrier Reef Marine Park Authority, Townsville Australia.

Wilkinson, C.R., 2002. Status of Coral Reefs of the World: 2002. Australian Institute of Marine Science, Townsville.

Willis, B.L., Babcock, R., Harrison, P.L., Oliver, J.K., Wallace, C.C., 1985. Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. In: Proceedings of the 5th International Coral Reef Symposium, Tahiti, pp. 343–348.

Willis, B.L., Babcock, R.C., Harrison, P.L., Wallace, C.C., 1997. Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. Coral Reefs 16, S53–S65.