Contributions to Marine Science 2012: 89–93
Date of Publication: 29 Sep.2012

THE EFFECT OF BENTHIC MACROALGAE ON CORAL SETTLEMENT

Lee Co Sin
*Tropical Marine Science Institute, National University of Singapore,
18 Kent Ridge Road, Singapore 119227.
E-mail: cosin@nus.edu.sg*

Juan Walford
*Tropical Marine Science Institute, National University of Singapore,
18 Kent Ridge Road, Singapore 119227.*

Beverly Goh Pi Lee
*Natural Sciences & Science Education, National Institute of Education, Nanyang Technological University,
1 Nanyang Walk, Singapore 637616
E-mail: beverly.goh@nie.edu.sg*

ABSTRACT. — Benthic macroalgae generally dominate on degraded and disturbed coral reefs. However, little is known about the interactions between benthic macroalgae and coral larvae on tropical reefs. The present study examined the effects of macroalgal species on the settlement success of *Pocillopora damicornis* larvae under aquarium conditions. Coral larvae were exposed to locally common macroalgal species *Bryopsis corymbosa, Halimeda opuntia, Sargassum* sp. and *Padina minor*. The presence of *B. corymbosa, Sargassum* sp. and *H. opuntia* had significant negative effects on larval settlement, while that of *P. minor* had no significant effect. Coral polyp "bail-out" from skeletons was also observed in the experimental tanks containing macroalgae. These results suggest that the presence of some benthic macroalgal species could inhibit coral settlement.

KEY WORDS. — *Pocillopora damicornis*, settlement, macroalgae, coral

INTRODUCTION

Interaction between corals and algae is an important process in coral ecosystem dynamics. In healthy coral reefs, scleractinian corals normally cover natural substrata, while macroalgae are rarely present (McManus & Polsenberg, 2004). However following a disturbance, coral reefs have been reported to shift from an environment that favours coral dominance to one that favours algal dominance (Hughes, 1994; Done, 1999; McManus et al., 2000). Increased nutrient levels, sedimentation, pollution and eutrophication can enhance macroalgae growth and promote succession changes in reef communities (Tomascik, 1991; Belliveau & Paul, 2002; Fabricius, 2005).

Different algal groups have different effects on corals due to their physical, biological and chemical characteristics, as well as environmental factors (Jompa & McCook, 2003). In a review of coral-algal interactions by McCook et al. (2001), six mechanisms for competition between corals and algae were identified: (1) overgrowth, (2) shading, (3) abrasion, (4) allelopathic chemical effects, (5) space pre-emption/recruitment barrier and (6) epithelial sloughing. Previous studies indicated that many benthic algae can either enhance or inhibit coral larval settlement (Kuffner et al., 2006; Birrell et al., 2008). Crustose coralline algae (CCA) species, for example, can induce coral larval settlement and metamorphosis (Morse et al., 1988; Heyward & Negri, 1999). Nugues & Szmant (2006) found that coral larvae of *Favia fragrum* settled on the green macroalga *Halimeda opuntia* in the presence of more suitable settlement substrata. Another macroalga *Lobophora variegata* enhanced coral settlement of *Acropora millepora*, but the closely related macroalga *Padina* sp. inhibited settlement (Birrell et al., 2008). Benthic cyanobacterium *Lyngbya majuscula* had a negative effect on larval recruitment of *Pocillopora damicornis* and survival of *Acropora surculosa* larvae (Kuffner & Paul, 2004). However, the effects of other tropical macroalgae on coral larval settlement have received little attention.

The aim of the present study was to investigate the effects of several common species of benthic macroalgae on larval settlement of the brooding coral *Pocillopora damicornis* under aquarium conditions. *Pocillopora damicornis* is a common species on reefs in Singapore and spawns almost every month. The present study focused on four species of macroalgae: *Bryopsis corymbosa* (Agardh, 1842), *Halimeda opuntia* (Linnaeus, 1816), *Padina minor*(Yamada, 1925) and *Sargassum* sp., which are abundant on Singapore's reefs. The present study hypothesised that these macroalgae could influence coral settlement on Singapore's reefs.

MATERIALS AND METHODS

Identification of macroalgal species. — *Halimeda opuntia, Padina minor* and *Sargassum* sp. were collected from the reefs at St John's Island, Singapore, and *Bryopsis corymbosa* was collected from a coral holding tank set up on St. John's Island. All macroalgae were maintained in a 100 L outdoor tank with a flow-through system until the start of the experiment.

Effect of macroalgae on coral larval settlement. — The study was carried out from June to Oct 2006 at the Tropical Marine Science Institute, Singapore. Four *P. damicornis* colonies of various sizes (approximately 10-25 cm in diameter) were collected from the reefs at Raffles Lighthouse, Singapore, and maintained in aquarium tanks at the Tropical Marine Science Institute. Newly released larvae of *P. damicornis* were collected after the new moon using a 500-μm plankton mesh placed over the container's overflow. Larvae were pooled and randomly selected for each experimental treatment (Lee et al., 2009).

Cement tiles were used as a settlement substratum. The cement tiles were made using one part of Portland cement and one part river sand (Lee et al., 2009). All cement tiles (dimensions: 100 × 100 × 10 mm) were biologically conditioned in a flow-through seawater tank that was seeded with calcareous coralline algae (CCA)-covered rubble. To develop a layer of CCA, treatment tiles were incubated for more than 3 months in a seeding tank until CCA cover was complete. Tiles well covered with CCA were used as settlement substrata in all the treatment and control tanks. About 5 g (total wet weight) of each macroalgal species was attached to both sides of a cement tile using a short length PVC water hose as a C-clamp (Fig. 1). All macroalgae were free of sediments, epiphytes or fouling organisms. To minimise potential chemical contamination, all hoses and polyethylene aquarium tanks were pre-soaked in seawater for at least 1 week before use. One experimental tile on which one of the macroalgal species attached was placed on the bottom of each polyethylene tank filled with two liters of UV-treated seawater, and forty larvae were transferred into each tank. Four replicate tanks were prepared for each macroalgal species and with another four control tanks each containing one tile with CCA but without macroalgae. The total numbers of settled larvae and unsettled larvae were counted at the end of the 10-day experiment. The 10-day experimental period was chosen for the present study because it was observed that settlement decreased 9-10 days after release of the larvae (Lee et al., 2009). The numbers of coral polyp "bail-out" observed in settled larvae were noted daily for each experimental tank.

All the experimental tanks were placed in a large tray with running seawater to keep the temperature between 27°C and 31°C. The experimental tanks were kept in natural light conditions in an indoor aquarium with a glass roof. The water in the tanks was not changed during the entire experiment, but some fresh seawater was added to each tank every 2 days to compensate for evaporation. Mild aeration was supplied to each tank and the dissolved oxygen levels were maintained at more than 6.0mg ml^{-1}. The salinity of the seawater was between 29 and 32 ‰ during the study.

Statistical analysis. — Experimental data were tested for normality and homogeneity of variances. Multivariate analysis of variance (MANOVA) was used to compare larval settlement in the experimental tanks with different macroalgal species. The percentages of the larvae settled on the surfaces of the each tile were calculated by using the numbers of larvae settling on each surface (top, sides or bottom, respectively) of the tile divided by the total number of larvae on the tile. Subsequently, the data were arcsine transformed and were assessed using two-way ANOVA. The Log_{10} (x+1) transformation was applied to the data for polyp "bail-out". Tukey's test was used for the subsequent post-hoc comparison.

RESULTS

Larval settlement of *P. damicornis* was significantly influenced by the presence of different macroalgal species (Wilks's $\lambda_{8,28} = 0.232$, $p < 0.01$). Univariate results showed significant effects on the mean number of larvae settled on tiles ($F_{4,15} = 6.981$, $p < 0.01$) and unsettled larvae ($F_{4,15} = 9.806$, $p < 0.001$), but no significant effect on the mean number of larvae settled on the sides of the tank ($F_{4,15} = 0.561$, $p = 0.694$). At the end of the 10 day experiment, the mean number of larvae settled on the control tiles (CCA-covered tiles) was significantly higher than on the tiles in tanks with *B. corymbos, Sargassum* sp. and *H. opuntia* (Fig. 2). The highest larval settlement was observed on the control tiles.

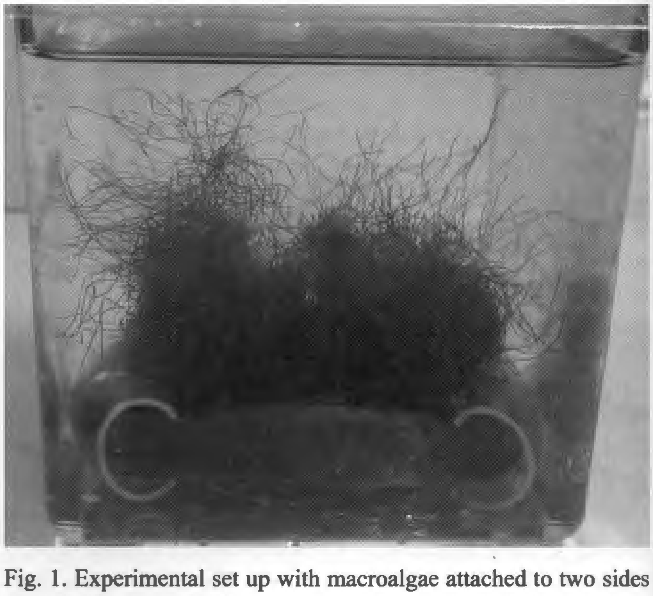

Fig. 1. Experimental set up with macroalgae attached to two sides of each tile using PVC water hose as a C-clamp.

Table 1. Results of 2-way ANOVA on coral settlement density crossed with factors: macroalgal species (*Bryopsis corymbosa*, *Halimeda opuntia*, *Padina minor* and *Sargassum* sp.) and tile surfaces (top, sides or bottom), and results of Tukey's test (*indicates significant treatment effects).

Factors	*df*	*F*	*p*
Macroalgal species	4	0.708	= 0.591
Tile surface	2	201.519	< 0.001*
Macroalgal species × tile surfaces	8	1.124	= 0.366

There was no significant interaction between the macroalgal species and the preferred settlement surfaces (top, sides or bottom) on the tiles (Table 1). Tukey's test revealed significant differences in settlement on the different surfaces of the settlement tiles, but no significant differences in settlement between the control tanks and the tanks containing different macroalgal species (Table 1). Overall, the mean percentage of larvae settling onto the top of the tile was significantly higher than the mean percentage of larvae settling on the sides and bottom of the tile (Fig. 3).

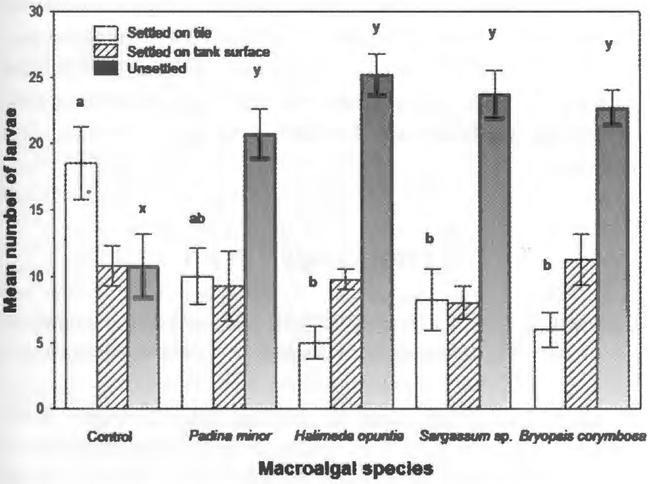

Fig. 2. Mean number of *P. damicornis* larvae observed in the experimental tanks for each treatment with different species of macroalgae and the control at the end of the 10 day experiment; (Error bars show standard error; different letters, a, b, and x, y indicate significant differences between treatments, $p < 0.01$).

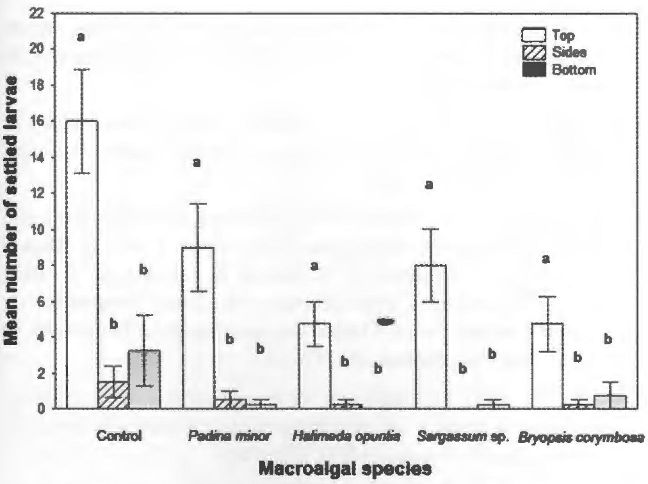

Fig. 3. Mean number of settled *P. damicornis* larvae observed on different surfaces of tiles for each treatment with different species of macroalgae and the control at the end of the 10 day experiment; (Error bars show standard error; different letters, a and b indicate significant differences between treatments, $p < 0.001$).

Coral polyp "bail-out" was observed in treatment tanks containing macroalgae from 3 to 5 days after the start of the experiment, but not in the control tanks. A significant difference ($F_{4,15} = 2.817$, $p < 0.05$) in the mean numbers of polyp "bail-out" was found only between the treatment tanks containing *H. opuntia* and the control (Fig. 4).

DISCUSSION

In the present study, different species of macroalgae were found to have different effects on the numbers of settled *Pocillopora damicornis* larvae. The presence of macroalgae significantly decreased overall larval settlement compared to the controls, except for the tanks containing the brown alga *Padina minor*. Although settlement in the *P. minor* treatment was not significantly different from the control treatment, unsettled larvae were significantly higher than the control treatment. The presence of these macroalgae may potentially reduce the likehood of *P. damicornis* larvae settling in the natural environment.

The larvae of *P. damicornis* in this study clearly preferred to settle on the CCA-covered tiles without the presence of macroalgae (control treatment). CCA is known to induce the metamorphosis and settlement of larvae (Morse et al.,

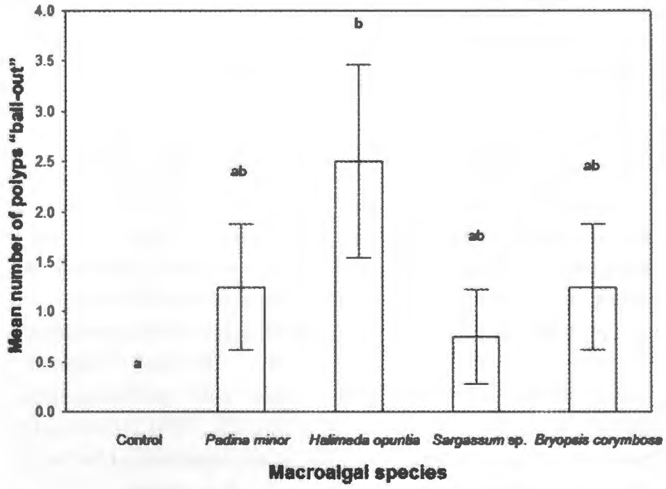

Fig. 4. Mean numbers of polyp "bail-out" observed in treatment tanks containing different macroalgae and the control on Day 5 of the experiment; (Error bars show standard error; different letters, a, b indicate significant differences between treatments, $p < 0.05$).

1996; Heyward & Negri, 1999; Diaz-Pulido et al., 2010). However, the presence of *B. corymbosa, Sargassum* sp., *P. minor* and *H. opuntia* species decreased settlement compared to the CCA tiles without these macroalgae present. The results also showed that more larvae settled on the sides of the experimental tanks than on the CCA-covered tiles in the presence of *B. corymbosa* and *H. opuntia.* Upright fleshy algae *Sargassum muricatum, S. tenerrimum* and *Halimeda discoidea* inhibited larval settlement of *Platygyra daedalea* (Diaz-Pulido et al., 2010). Kuffner et al. (2006) found that significantly more larvae of *Porites astreoides* settled on the chamber side than on the biologically conditioned tile in the *Lyngbya polychroa* treatment, while more larvae settled on the tile compared to the chamber sides in the control treatment. This indicates that the combination of CCA with different benthic macroalgae may influence the pattern and behavior of settlement.

Larvae are known to respond to chemical cues associated with macroalgae. Macroalgae can alter chemical composition of seawater (Walters et al., 2003; Birrell et al., 2008), including pH (McConnaughey et al., 2000) and nutrient and organic carbon levels (Larkum et al., 2003; Kline et al., 2006). Previous studies have shown some evidence of chemical effects from benthic macroalgae on larval settlement (Walters et al., 2003; Birrell et al., 2008). Water-soluble chemicals released by *Padina* sp. reduced coral settlement by 30% compared with substratum controls (Birrell et al., 2008). Maypa and Raymundo (2004) also reported that water-soluble chemicals released by *Sargassum polycystum* killed all unsettled *P. damicornis* larvae within 24 hours. *Halimeda* sp. has been reported to produce high concentrations of the chemicals halimedatrial (α-diterpenoid trialdehyde) and halimediateracetate (α-diterpenoid tetraacetate) at breakage points which can deter herbivores (Pual & Fenical, 1983; Paul & Van Alstyne, 1992). The present study suggests that noxious secondary metabolites from the broken fragments of *H. opuntia* attached to the tiles may have inhibited larval settlement, extended their swimming period, and caused polyp "bail-out". There was no water circulation in the experimental tanks, so these fleshy algae may have released a range of chemicals into the water. This indicates that these macroalgae potentially affect the settlement of *P. damicornis* larvae through waterborne chemical effects.

During the planktonic stage, coral larvae search for a suitable substrate to settle on and settled larvae generally cannot relocate to another substrate (Vermeij & Bak, 2002). In this present study, primary polyps were found to "bail-out" from the primary skeleton and return to a planktonic phase in the water. Similar results have been demonstrated in previous studies when larvae were subjected to unfavourable conditions (Richmond, 1985; Goh, 1991). Polyp "bail-out" frequently occurs when the corals are in contact with macroalgae due to the abrasion effect (River & Edmunds, 2001). Hence, the presence of macroalgae may offer an explanation for the polyp "bail-out" which was observed in *P. damicornis*.

The present study has shown that some locally common macroalgal species influenced larval settlement of *P. damicornis*. Among the macroalgae tested, *Sargassum* and *Padina* have been commonly recorded on the reef slope at Pulau Salu, Singapore, and *Halimeda opuntia* on reef flats (Chou & Wong, 1984). Generally, algae dominated an average 16.9% of the total area on the upper (3m) reef slopes and 22% on the lower (10m) reef slopes in Singapore waters (Goh & Chou, 1991). Since Singapore's reefs are covered by macroalgae, the potential for these algae to reduce coral settlement and recruitment is considerable. The results suggest that the presence of macroalgae might be a key factor inhibiting and delaying larval settlement in the wild. However, more detailed investigations are required to achieve a better understanding of coral-algae interactions.

ACKNOWLEDGEMENTS

We thank Sin Tsai Min, Angie Seow, Michelle Lee and staff from the Tropical Marine Science Institute and Reef Ecology Laboratory, National University of Singapore, for assistance in research and field work. This project was partially funded by the NIE/NTU AcRF Grant, RP5/02 GPL to Beverly Goh of the National Institute of Education, Nanyang Technological University.

LITERATURE CITED

Belliveau, S. A. & V. J. Paul, 2002. Effect of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Marine Ecology Progress Series*, **32**: 105–114.

Birrell, C. L., L. J. McCook, B. L. Willis & L. Harrington, 2008. Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora. Marine Ecology Progress Series*, **362**: 129–137.

Chou, L. M. & F. J. Wong, 1984. A note on the distribution of marine macroalgae at Pulau Salu. *Journal of The Singapore National Academy of Science*, Vol. 13.

Diaz-Pulido, G., S. Harii, L. J. McCook & O. Hoegh-Guldberg, 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs*, **29**: 203–208.

Done, T. J., 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *Integrative and Comparative Biology*, **39**: 66–79.

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletion*, **50**: 125–146.

Goh, B. P. L. & L. M. Chou, 1991. Coral reef-associated flora and fauna of Singapore. In: Alcala, A. C., L. M. Chou, R. Miclat, W. Kastora, M. Fortes, W. K. Gong, A. Sasekumar, R. Bina & S. Tridech (eds.), *Proceedings of Regional Symposium on Living Coastal Areas,* Marine Science Institute, University of the Philippines, Manila. Pp. 47–53.

Goh, B. P. L., 1991. Mortality and settlement success of *Pocillopora damicornis* planula larvae during recovery from low levels of nickel. *Pacific Science*, **45**(3): 276–286.

Heyward, A. J. & A. P. Negri, 1999. Natural inducers for coral larval metamorphosis. *Coral Reefs*, **18**: 273–279.

Hughes, T. P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **265**: 1547–1551.

Jompa, J. & L. J. McCook, 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. *Marine Ecology Progress Series*, **258**: 87–95.

Kline, D. I., N. M. Kuntz, M. Breitbart, N. Knowlton & F. Rohwer, 2006. Role of elevated organic carbon levels and microbial activity in coral mortality. *Marine Ecology Progress Series*, **314**: 119–125.

Kuffner, I. B. & V. J. Paul, 2004. Effects of the benthic cyanobacterium *Lyngbya majuscula* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs*, **23**: 455–458.

Kuffner, I. B., L. J. Walter, M. A. Becerro, V. J. Paul, R. Ritson-Williams & K. S. Beach, 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*, **323**: 107–117.

Larkum, A. W. D., E. M. W. Koch & M. Kuhl, 2003. Diffusive boundary layers and photosynthesis of the epilithic algal community of coral reefs. *Marine Biology*, **142**: 1073–1082.

Lee, C. S., J. Walford & B. P. L. Goh, 2009. Adding coral rubble to substrata enhances settlement of *Pocillopora damicornis* larvae. *Coral Reefs*, **28**: 529–533.

Maypa, A. P. & L. J. Raymundo, 2004. Algae-coral interactions: mediation of coral settlement, early survival, and growth by macroalgae. *Silliman Journal*, **45**: 76–95.

McConnaughey, T. A., W. H. Adey & A. M. Small, 2000. Community and environmental influences on reef coral calcification. *Limnology and Oceanography*, **45**: 1667–1671.

McCook, L. J., J. Jompa & G. Diaz-Pulido, 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, **19**: 400–417.

McManus, J. W. & J. F. Polsenberg, 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography*, **60**: 263–279.

McManus, J. W., L. A. B. Menez, K. N. Kesner-Reyes, S. G. Vergara & M. C. Ablan, 2000. Coral reef fishing and coral-algal phase shifts: implication for global reef status. *ICES Journal Marine Science*, **57**: 572–578.

Morse, A. N. C., K. Iwao, M. Baba, K. Shimoike, T. Hayashibara & M. Omori, 1996. An ancient chemosensory mechanism brings new life to coral reefs. *The Biological Bulletin*, **191**: 149–154.

Morse, D. E., N. Hooker, A. N. C. Morse & R. A. Jensen, 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. *Journal of Experimental Marine Biology Ecology*, **116**: 193–217.

Nugues, M. M. & A. M. Szmant, 2006. Coral settlement onto *Halimeda opuntia*: a fatal attraction to an ephemeral substrate? *Coral Reefs*, **25**: 585–591.

Paul, V. J. & K. L. Van Alstyne, 1992. Activation of chemical defenses in the tropical green algae *Halimeda* spp. *Journal of Experimental Marine Biology Ecology*, **160**: 191–203.

Paul, V. J. & W. Fenical, 1983. Isolation of halimedatrial: chemical defense adaptation in the calcareous reef-building alga *Halimeda*. *Science*, **221**: 747–749.

Richmond, R. H., 1985. Reversible metamorphosis in coral planula larvae. *Marine Ecology Progress Series*, **22**: 181–185.

River, G. F. & P. J. Edmunds, 2001. Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *Journal of Experimental Marine Biology Ecology*, **261**: 159–172.

Tomascik, T., 1991. Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. *Marine Ecology Progress Series*, **77**: 261–269.

Vermeij, M. J. A. & R. P. M. Bak, 2002. Corals on the move: rambling of *Madracis pharensis* polyps early after settlement. *Coral Reefs*, **21**: 262–263.

Walters, L. J., C. M. Smith & M. G. Hadfield, 2003. Recruitment of sessile marine invertebrates on Hawaiian macrophytes: Do pre-settlement or post-settlement processes keep plants free from fouling? *Bulletin Marine Science*, **72**: 813–839.