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Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*

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ABSTRACT: Recovery of degraded reefs is dependent on the settlement of coral larvae into habitats typically dominated by benthic algae, so that benthic algae may play pivotal roles in coral settlement and reef recovery. Here we demonstrate that waterborne influences of macroalgae could affect coral settlement before larvae contact reef substrata and that such effects vary between macroalgae. We tested for waterborne effects of algae on both pre-settlement behaviour and settlement of larvae of the coral *Acropora millepora* onto live fragments of the crustose coralline alga *Hydrolithon reinboldii*. Treatments comprised seawater collected from aquaria that had previously contained 1 of 3 macroalgae common on degraded reefs. The foliose brown macroalga, *Lobophora variegata*, enhanced coral settlement by 40% relative to substratum control treatments. In contrast, the filamentous green macroalga *Chlorodesmis fastigiata* ('turtle weed'), hindered coral settlement by delaying settlement of larvae, although final settlement was similar to that in control treatments. *Padina* sp., a foliose brown macroalga closely related to *L. variegata*, reduced coral settlement by 30% compared with substratum controls. The demonstration of waterborne effects suggests that macroalgae can influence coral settlement before larvae reach reef substrata, even on a crustose coralline alga known to induce settlement, and even where the immediate settlement location is free of macroalgal cover. These results demonstrate the complexity in the mechanisms underlying the effects that overabundant macroalgal growth may have on reef recovery. These effects have critical implications for the ecological resilience of coral reefs, especially as climate change increases the frequency and severity of disturbances to reefs.

KEY WORDS: Coral · Macroalgae · Recruitment · Resilience · Settlement · Allelopathy

INTRODUCTION

Globally, degradation of coral reefs is increasingly generating algal dominated environments (Hughes et al. 2003, 2005), particularly as climate change increases the frequency of reef decline. The ecological resilience of reefs relies on the ability of corals to recruit or recover successfully in environments dominated by various forms of benthic algae (Diaz-Pulido & McCook 2002, Hughes et al. 2007, McCook et al. 2007). The period during which larvae settle and metamorphose is a critical but vulnerable stage in the early life history of corals, linking the processes of dispersal and larval supply to the survival and growth of benthic juveniles. Successful settlement depends on how coral larvae respond to and are affected by influences from the physical environment and benthic biota (Harrison & Wallace 1990, Pawlik 1992, Abelson & Denny 1997, Birrell et al. 2008). Since fleshy or turfing algae invariably dominate degraded and disturbed coral reefs, they potentially exert a controlling influence on coral settlement, which may restrict reef recovery and significantly undermine the ecological resilience of these reefs (Done 1992, Hughes 1994, Connell 1997,

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McCook 1999, McCook et al. 2001, 2007, Hughes et al. 2007, review by Birrell et al. 2008). In addition to the physical pre-emption of space and changes to the character of settlement surfaces through processes such as sediment trapping (Birrell et al. 2005), benthic algae also contribute significantly to the chemical environment confronting larvae during the settlement process (Jensen 1977, Amsler et al. 1992, McCook et al. 2001, Birrell et al. 2008). However, the potential for macroalgae to affect settlement of coral larvae through allelochemical processes has received little attention (Maypa & Raymundo 2004, Kuffner et al. 2006, review by Birrell et al. 2008).

Emerging evidence indicates that a range of benthic algae can have chemical effects, which either enhance (Morse 1991, 1992, Pawlik 1992, Hadfield & Paul 2001) or deter the settlement of marine invertebrate larvae (Steinberg et al. 2001, 2002, Walters et al. 2003, review by Birrell et al. 2008). Besides producing or harbouring secondary metabolites that can have direct effects on larvae (Steinberg & de Nys 2002, Gross 2003, Walters et al. 2003), benthic algae may chemically alter the settlement environment, for example by modifying the seawater pH (McConnaughey et al. 2000) or by altering dissolved nutrient concentrations as a result of metabolic processes such as photosynthesis, respiration and calcification (Carpenter et al. 1991, Larkum et al. 2003). Such chemical changes may affect habitat selection and settlement by coral larvae, which display chemotaxis or orientate in response to chemical gradients (Harrison & Wallace 1990, Pawlik 1992).

Such algal effects on coral larvae and the environment larvae encounter are undoubtedly important to reef resilience, but demonstrations of macroalgal effects on coral replenishment processes are scarce (McCook et al. 2007, Birrell et al. 2008). Recent studies have demonstrated that effects of algae and cyanobacteria on invertebrate larvae, including corals, can range from settlement cues and inducers to lethal antifouling compounds, and also have shown that the outcomes of macroalgal chemical interactions with larvae vary among taxa (e.g. Walters et al. 1996, Baird & Morse 2004, Kuffner & Paul 2004, Maypa & Raymundo 2004, Kuffner et al. 2006, review by Birrell et al. 2008).

However, much of the previous work has focused on coral species with brooding planulae (and limited dispersal) or has considered settlement onto artificial (e.g. glass, terracotta) or unidentified substrata (e.g. assemblages of different crustose coralline algae), thereby confounding effects of algae with effects of settlement substrata, or has focused on effects of chemicals bound to algal surfaces (e.g. chemicals bound to crustose coralline algae on which corals may settle) (Morse et al. 1988, 1994, 1996, Pawlik 1992, Maypa & Raymundo 2004, Kuffner et al. 2006, reviewed in Birrell et al. 2008). Steinberg et al. (2001) and Steinberg & de Nys (2002) highlight the potential for water-soluble chemicals from macroalgae to signal sites for invertebrate settlement, suggesting that inducers of larval settlement are most likely to be primary metabolites (e.g. polysaccharides, amino acids, peptides) because these are typically present in higher concentrations than are secondary metabolites and are readily exuded or leaked from macroalgae into seawater.

This study explored the effects of water-soluble chemicals released from benthic macroalgae on the settlement of larvae from the coral, *Acropora millepora* (Ehrenberg). Specifically, we investigated water-borne effects of 3 common macroalgae, *Lobophora variegata* (Lamouroux), *Padina* sp. and *Chlorodesmis fastigiata* (C. Agardh 'turtle weed'), on pre-settlement behaviour and larval metamorphosis in the presence of a crustose coralline alga, *Hydrolithon reinboldii* Weber-van Bosse & Foslie, known to induce settlement of *Acropora* larvae (Morse et al. 1988, 1994, 1996). The macroalgae tested are common and widespread, especially on degraded reefs (Done 1992, Hughes 1994, McCook 1999). Importantly, we investigated settlement to a standardised substratum that was more likely to represent natural settlement substrata on reefs, than on artificial or unrealistic substrata.

MATERIALS AND METHODS

Experimental approach and design. To investigate potential water-soluble chemical effects of macroalgae on coral settlement, coral larvae were placed in seawater collected from aquaria that had contained either 1 of 3 algae or control treatments. Larvae of the coral *Acropora millepora* were produced and raised in aquarium facilities at Lizard Island Research Station using established procedures (Babcock & Heyward 1986, Willis et al. 1997) and presented with live surfaces of the crustose coralline alga *Hydrolithon reinboldii* for settlement.

The experimental design tested 5 levels of seawater treatment: (1 to 3) seawater collected from tanks holding one of the macroalgae *Lobophora variegata*, *Chlorodesmis fastigiata*, or *Padina* sp.; (4) seawater collected from a tank holding pieces of reef substrata (substratum control); and (5) plain seawater control. Each level of treatment was replicated in 10 petri dishes, with each petri dish containing a piece of *Hydrolithon reinboldii*. Treatments were randomly assigned to petri dishes.

Experimental treatments and procedures. To create the different seawater treatments, live, whole and intact thalli of *Lobophora variegata*, *Chlorodesmis fastigiata* and *Padina* sp. were placed in tanks of still seawater under shaded natural light. For each treatment, 6 l of seawater were conditioned for 90 min with 250 g (± 25 g wet weight) of each macroalga. This treatment was chosen to approximate macroalgal density and water residence within macroalgal assemblages on an inshore or degraded reef habitat. Macroalgae, chosen to have minimal epiphytes or fouling organisms, were collected from fringing reefs surrounding Lizard Island (14° 41′ S, 145° 28′ E) on the Australian Great Barrier Reef. Importantly, to avoid the release of injury-activated stress compounds into seawater treatments, macroalgae were maintained intact, attached to pieces of substratum, during collection and experimental procedures, and any damaged specimens were discarded. Because macroalgae remained attached to substratum, a reef substratum treatment was included to control for potential influences from biofilms or other microbiota associated with the substratum. To create the substratum control, pieces of reef substratum similar to those used in the algal treatments were treated in the same manner as for the algal treatments (approximately 100 ± 10 g wet weight of reef substratum). Substratum pieces (with or without algae) were stabilised for approximately 20 h to minimise and standardise any effects of boring organisms, but were used within 24 h to avoid degeneration of the algae. To control for the potential presence of waterborne chemicals in seawater used in the experimental treatments, a final 'seawater control' treatment used plain seawater with no algal or substratum addition.

Assays for waterborne algal effects on larval settlement were replicated in 10 plastic petri dishes, each containing 40 ml of the appropriate seawater treatment, a live fragment of *Hydrolithon reinboldii*, and 20 competent coral larvae. Larval development and settlement competency were assessed microscopically prior to the experiment using random subsamples of larvae at daily intervals after fertilisation (see Willis et al. 1997 for fertilisation protocols). Colonies of *Hydrolithon reinboldii* were collected from fringing reefs surrounding Lizard Island within 24 h of the experiment and fragmented into pieces of equal surface area (1.0 ± 0.1 cm^2) with approximately equal volumes of attached substratum (0.5 ± 0.05 cm^3). Coral larvae were counted as they were added to petri dishes using a glass pipette. Replicates were maintained at a constant temperature of 26°C with moderate levels of natural light.

Data and analysis. As the primary response variable, the number of coral larvae that settled and metamorphosed on *Hydrolithon reinboldii* surfaces was recorded after 48 h, and expressed as a percentage of the 20 larvae added to each replicate. These observations were made using a stereo dissection microscope and accounted for all 20 larvae originally placed in each petri dish. These observations confirmed that, of those that settled, larvae exclusively settled on live *H. reinboldii* surfaces and not on the petri dish or surfaces attached to *H. reinboldii* fragments. Data analysis of treatment effects on coral settlement involved a 1-way ANOVA followed by *a priori* comparisons of algal treatments with substratum controls. Data were tested for homogeneity of variance using Cochran's *C*-test, and for normality of residuals graphically and for kurtosis and skewness (Systat 8.0^{TM}).

As secondary response variables, 3 measures of larval behaviour were used: (1) substratum testing, for activities in which larvae touched surfaces with their aboral end repeatedly and occasionally attached, but without necessarily metamorphosing; (2) swimming, for visibly motile larvae; and (3) stressed, for larvae observed to be motionless or floating at the water surface, presumably including dead larvae (Harrison & Wallace 1990, Raimondi & Morse 2000). The percentage of larvae expressing each category of behaviour was recorded when initially added to each petri dish, and 2, 10 and 24 h later. Larval behaviour was observed using a magnifying glass to avoid moving the petri dishes and disturbing either settled or unsettled larvae. Data are presented for substratum testing and stressed behaviours only, as results for swimming closely mirrored those for substratum testing; data are presented graphically and are not analysed statistically owing to the confounding effects of non-independence between the 3 behavioural measures, and between repeated measures on the same samples.

RESULTS

Effects of water-soluble influences on coral settlement

Mean settlement of *Acropora millepora* larvae was nearly 1.4 times greater in seawater that had been collected from tanks containing the macroalgae *Lobophora variegata* (mean ± SE, 76 ± 4.6% of larvae settled) than in the substratum control treatment (55 ± 6.0% settled), and about twice that in the unconditioned seawater control (37 ± 4.6% settled; Fig. 1, Table 1). In contrast, larval settlement in seawater collected from tanks holding the closely related alga *Padina* sp. (39 ± 6.7%), was nearly one-third less than in the substratum control. Final settlement in the *Chlorodesmis fastigiata* treatment (46 ± 4.6%) was slightly, but not significantly, less than in the substratum control (Table 1). Interestingly, larval settlement in the seawater control treatment (37 ± 4.6%) was the least of all treatments, and markedly less than in the substratum control treatment.

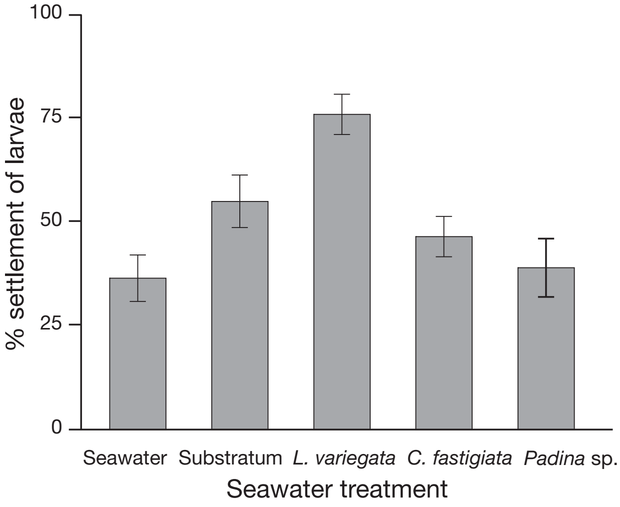

Fig. 1. *Acropora millepora.* Mean percentage (±1 SE) of larvae from the coral *A. millepora* settled on live surfaces of the crustose coralline algae *Hydrolithon reinboldii* after 48 h in seawater and substratum controls and macroalgal treatments (*Lobophora variegata*, *Chlorodesmis fastigiata*, *Padina* sp.). Means for each treatment are calculated from 10 repli-cates, which each contained 20 coral larvae

Table 1. Results of ANOVA tests comparing the effects of waterborne influences of macroalgae on larval settlement (*Acropora millepora*) among the macroalgal treatments (*Lobophora variegata*, *Chlorodesmis fastigiata*, *Padina* sp.) and controls (substratum and seawater). Cochran's *C*-test indicates homogeneity of variance (*C* critical value = 0.307). Data are not transformed

Source of variation	df	MS	*F*	p
Treatment	4	101.47	8.434	<0.001
Error	45	12.031		
Cochran's *C* = 0.295				
A priori comparisons with substratum control				
L. variegata				0.010
C. fastigiata				0.279
Padina sp.				0.045
Seawater control				0.021

Effects of water-soluble influences on larval behaviour

There was a dramatic difference in initial behaviour of coral larvae when added to the different treatments (Fig. 2). In all but one treatment, namely *Chlorodesmis fastigiata*, most larvae immediately began testing the coralline algal substrata, and continued to do so for 24 h, and very few larvae appeared stressed throughout this period. In contrast, in the *C. fastigiata* treatment, almost no *Acropora millepora* larvae were observed to display substratum testing behaviour at the start of treatment (2.5 ± 1.3%) and most appeared stressed. However, within 2 h, the mean percentage of larvae testing substrata in this treatment increased by over 20-fold (to 71 ± 3.8%) and subsequently remained approximately constant (65 to 70%) for the first 24 h. Nonetheless, consistently fewer larvae (by 10 to 15%) were observed to test substrata after 2, 10 and 24 h in the *C. fastigiata* treatment compared with other treatments.

Compared with other treatments, larvae in the *Lobophora variegata* treatment showed consistently

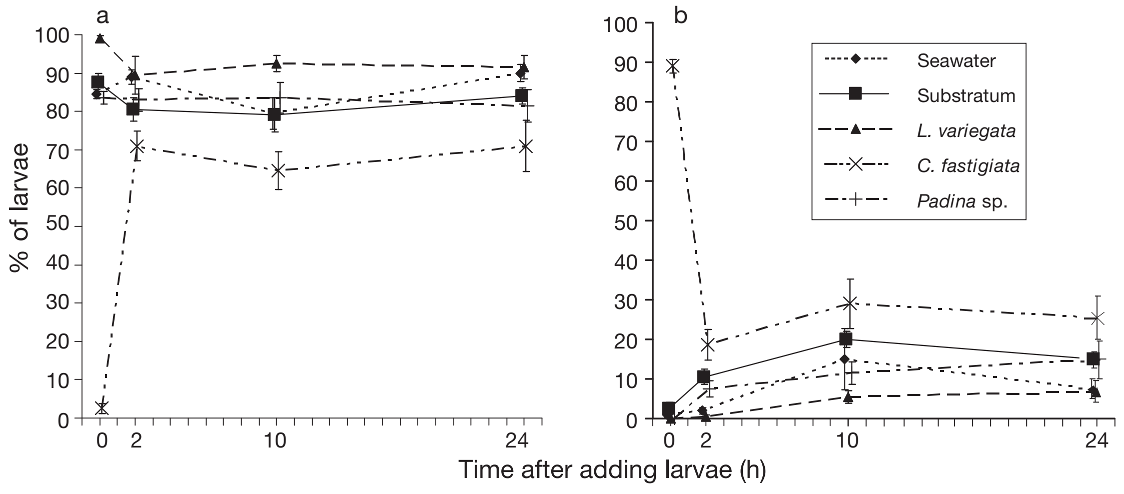

Fig. 2. *Acropora millepora.* Mean percentage (±1 SE) of *A. millepora* larvae displaying the behavioural responses defined as (a) testing substratum and (b) stressed, in seawater and substratum controls and macroalgal treatments (*Lobophora variegata*, *Chlorodesmis fastigiata*, *Padina* sp.). Means for each treatment are calculated from 10 replicates, which each contained 20 coral larvae. The response of larvae in *C. fastigiata* treatments is unlikely to promote settlement in the vicinity of this macroalgae

higher levels of substratum testing (initially 99 ± 0.7%), and lower levels of stressed behaviour. Larval behaviour in the *Padina* sp. treatment was generally similar to that in the 2 control treatments, with around 75 to 85% of larvae testing substrata throughout the 24 h of observation.

DISCUSSION

The results of this study are significant to understanding recruitment and recovery of corals on degraded reefs for several reasons. Firstly, they demonstrate that some macroalgae may influence the settlement of coral larvae by means of water-soluble chemical influences, the first such demonstration for a broadcast spawning coral. On Indo-Pacific reefs, recruitment is dominated by broadcast spawning corals (e.g. Hughes et al. 1999) and recruitment of spawning corals on degraded, algal dominated reefs requires dispersal through algal beds. In contrast, the larvae of brooding corals are released into the benthic boundary layer and are negatively buoyant, keeping them close to suitable substrata and sites for settlement (Harrison & Wallace 1990). This highlights an overlooked mechanism of coral–algae interaction with serious implications for coral recruitment on disturbed or degraded reefs.

Secondly, the results demonstrate that different species of macroalgae can have markedly different waterborne effects on the behaviour and settlement of *Acropora millepora* larvae. Water from the foliose brown macroalga *Lobophora variegata* enhanced coral settlement by approximately 40% relative to the substratum control treatment. In contrast, settlement was inhibited by water from the closely related *Padina* sp., and the filamentous green macroalga *Chlorodesmis fastigiata* delayed settlement responses of larvae. Although final settlement in the *C. fastigiata* treatment was not significantly different from the control treatment, in nature such delays may reduce the likelihood of coral larvae settling in the vicinity.

Thirdly, demonstrations of waterborne effects on coral settlement suggest that macroalgae potentially affect coral settlement before larvae reach reef substrata, even if the immediate settlement area is free of macroalgal cover. In particular, macroalgae may affect coral replenishment beyond the immediate spatial scale of the physical space occupied by algae to surrounding and down-current areas, and coral replenishment may be affected in reef areas even if there is relatively low macroalgal cover and sufficient favourable settlement surfaces. The extent of these effects will vary considerably, depending on factors such as the amount of algae and dilution due to conditions such as turbulence and currents. There is a need for further research on the extent of algal chemical effects in different natural conditions (i.e. reefs dominated by fleshy algae or turfing and crustose forms). However, it seems likely that large beds of fleshy algae will have the most significant effects.

Fourthly, the results demonstrate that waterborne influences from macroalgae affect the settlement of corals even on a substratum considered to be important for inducing coral settlement in the field. For example the crustose coralline algae *Hydrolithon reinboldii* is known to induce settlement of larvae from a variety of corals, particularly acroporids, and has a widespread distribution on the Great Barrier Reef (Morse et al. 1996, Harrington 2004, Harrington et al. 2004, R. Steneck & L. Harrington unpubl. data). Thus, coral settlement may be affected by the combination of different benthic macroalgae present in an assemblage (e.g. both fleshy and crustose algae) and not solely by the calcareous red algae reported to induce coral settlement (e.g. Morse et al. 1988, 1996, Heyward & Negri 1999). Interestingly, Nugues & Szmant (2006) showed that larvae of *Favia fragrum* settled on the green alga *Halimeda opuntia* even when another substratum more suitable for settlement was present, although they suggested this may result from high abundance of larvae. In contrast, all settled larvae settled on the coralline algae in our study.

Chemical effects of macroalgae on settlement

In general, the settlement, behaviour and survival of coral larvae are known to be influenced by chemical and physical properties of the marine environment (Harrison & Wallace 1990, Pawlik 1992, Maida et al. 1995a,b, Raimondi & Morse 2000), and algae are known to release a range of chemicals into the surrounding water (Amsler et al. 1992, Walters et al. 2003), so it is not surprising that macroalgae affect coral settlement through waterborne chemical effects. Only recently, however, has there been evidence for such effects from macroalgae or benthic cyanobacteria. Kuffner & Paul (2004) reported allelopathic reduction of larval survival of the broadcast spawning coral *Acropora surculosa* and recruitment of the brooding coral *Pocillopora damicornis* in response to the cyanobacterium *Lyngbya majuscula*. Kuffner et al. (2006) found reduced overall recruitment, or settlement at distance, for the brooding coral *Porites astreoides* in response to the macroalgae *Dictyota pulchella* and *Lobophora variegata*, as well as the cyanobacteria *L. majuscula*, *L. polychroa* and *L. confervoides*. Water-soluble chemicals released by *Sargassum polycystum* killed all unsettled *Pocillopora damicornis* larvae within 24 h and all settled larvae within 10 d (Maypa & Raymundo 2004). Similarly, all unsettled larvae died within 24 h in *Laurencia papillosa* treatments, whereas larvae that did settle displayed 100% survival. *Halimeda opuntia* and *Peyssonnelia rubra* had no deleterious effects on settled or unsettled larvae (Maypa & Raymundo 2004). In contrast to our results, Baird & Morse (2004) report reduced survival of larvae of both the brooding corals, *Stylophora pistillata* and *Acropora palifera*, in response to treatments containing fragments of a *Lobophora* sp.

More generally, macroalgal influences on the chemistry of seawater (Amsler et al. 1992, Walters et al. 2003), include primary and secondary metabolites (Steinberg et al. 2001), pH (McConnaughey et al. 2000), and nutrient and organic carbon levels (Carpenter et al. 1991, Larkum et al. 2003, Kline et al. 2006, review by Birrell et al. 2008). Macroalgae have both surface-bound and waterborne chemical effects on the larval settlement of other invertebrates, including both deterrence and induction (Pawlik 1992, Steinberg et al. 2001, 2002, Steinberg & de Nys 2002, Walters et al. 2003). For example, on Hawaiian coral reefs, the release of water-soluble chemicals by some macroalgal species (*Ulva* sp. and *Sphacelaria* sp.) inhibited settlement, and others (*Dictyota* spp.) even killed larvae of the fouling bryozoan *Brugula neritina* and the polychaete *Hydroides elegans*. In contrast, water-soluble chemicals released by *Padina* sp. enhanced settlement of *H. elegans*, whereas *Sargassum* spp. had no effect on *B. neritina* larvae (Walters et al. 1996).

Although our results provide clear evidence that macroalgae affected coral settlement through waterborne chemicals, the nature of the chemical influences is unclear. Compounds known to induce invertebrate larvae to settle are generally primary metabolites such as carbohydrates, peptides or even nutrients and are commonly water soluble, whereas deterrents are usually secondary metabolites that are insoluble (Steinberg et al. 2001). There is limited information available on chemical effects of the algae used in our experiment. *Chlorodesmis fastigiata* is known to produce a cytotoxic diterpenoid, chlorodesmin, a secondary metabolite that deters herbivores (Wylie & Paul 1988, Hay et al. 1989, Paul et al. 1990). *Lobophora variegata* produces a variety of secondary metabolites, such as phlorotannins (Stern et al. 1996, Arnold & Targett 1998, 2000) and bromophenols (Chung et al. 2003), which may deter herbivores, along with other chemicals (e.g. orcinol, phloroglucinol, salicylic acid, usnic acid; Walters et al. 2003 and references therein). Seawater passing over *Lobophora variegata* attracted *Diadema antillarum* (Solandt & Campbell 2001), which feeds preferentially on the macroalga (Tuya et al. 2001). *Padina* has also been reported to contain secondary metabolites (e.g. alginic acid) with herbivore deterrent and cytotoxic capacity (Renaud et al. 1990, Walters et al. 1996, Ktari & Guyot 1999, Chung et al. 2003, Walters et al. 2003). However, even closely related macroalgal taxa may contain different chemical compounds and have different chemical effects on the settlement of invertebrate larvae (Steinberg et al. 2001, 2002, Steinberg & de Nys 2002, Walters et al. 2003).

It is also possible that bacteria, microflora or ephiphytes associated with the surfaces of the macroalgae contribute to the observed effects, although algal samples were chosen to minimise epiphytes. There is evidence that the induction of invertebrate settlement by calcareous and coralline algae is at least partially mediated by bacteria associated with the algae (Johnson et al. 1991, 1997, Morse & Morse 1991, Johnson & Sutton 1994, Negri et al. 2001, Harder et al. 2002, Webster et al. 2004). The surfaces of *Lobophora variegata* support diverse bacterial communities (Jensen et al. 1996), which may produce biologically active compounds capable of affecting invertebrates (Jiang et al. 1999). Distinguishing between allelochemical effects of macroalgae and those from associated organisms warrants further research.

Implications for reef resilience

The enhancement of coral settlement by *Lobophora variegata* is of particular interest for 2 reasons. Firstly, this macroalga is particularly widespread on disturbed and degraded reefs around the world, including the recent massive overgrowth of bleached corals in the southern Great Barrier Reef (Diaz-Pulido & Diaz 1997, McClanahan et al. 2001, L. J. McCook unpubl. data). Secondly, there is an emerging body of evidence showing contrasting effects of *Lobophora* spp. on corals, and the current study emphasises that a particular species of alga may have different effects on different life history stages or demographic processes. Consistent with the positive effects found in the present study, are the promotion of first stage elongation of larvae from 7 acroporid corals (Morse et al. 1996) and the results of a survey of benthic biota surrounding coral recruits on inshore reefs of the Great Barrier Reef (Birrell 2003), which found *L. variegata* was more frequently present and more abundant in close proximity to coral recruits than in background communities. However, in contrast to these positive effects, Kuffner et al. (2006) reported avoidance of *L. variegata* by larvae of *Porites astreoides* and Baird & Morse (2004) reported deleterious effects on coral larvae by *Lobophora* sp., although they also noted that injury to the algae tissue may have stimulated release of stress compounds. Several reports have shown that *L. variegata* actively competes with corals, overgrowing and killing both recruits and mature colonies (De Ruyter van Stevenick et al. 1988, Hughes 1994, Littler & Littler 1997, Jompa & McCook 2002a,b, Nugues & Bak 2006, authors' pers. obs.), although the corals also defend themselves. It remains unclear to what extent these variable results reflect experimental differences, or biological, geographic or other variations (e.g. Paul et al. 2001), but it seems probable that, overall, reef overgrowth by *L. variegata* has detrimental effects on coral populations.

The implications of these small-scale experimental results for processes on reefs at large are also limited by several additional factors. In this experiment, larvae were tested over very small scales (10 cm) and were confined to relatively small areas (petri dishes), and so had limited options for settlement. In nature, coral larvae actively search the reef benthos before settling and can delay settlement to maximise the chance of finding a suitable microhabitat (Harrison & Wallace 1990, Pawlik 1992, Raimondi & Morse 2000). However, if larvae fail to encounter suitable microhabitats, evidence exists that they can metamorphose in suboptimal conditions, even without a surface to settle on (reviewed in Harrison & Wallace 1990), and inhibition of invertebrate settlement by algal secondary metabolites may decrease as larvae mature (Gribben et al. 2006 for the algae *Delisea pulchra* and *Dilophus marginatus*). Thus, more coral larvae may have settled under the deleterious effects of *Chlorodesmis fastigiata* in this experiment than would settle close to the macroalga in nature, because they lacked alternative microhabitats in the experimental treatments. This could explain the reversal of larval behaviour in the *Chlorodesmis* treatment. Secondly, there was no water circulation in experimental treatments, whereas water flow and hydrodynamics in nature can disperse, dilute and mix different waterborne chemicals (Pawlik 1992, Maida et al. 1994, 1995a,b, Abelson & Denny 1997). Thus, chemical conditions in this experiment are likely to have been more homogenous than under natural conditions and the effects more consistent. It is likely that algal effects may operate differently between microhabitat scales on the order of centimetres and larger scales that are relevant to reef-wide algal dominance. The use of experimental systems incorporating flow dynamics would help to bridge this gap.

Summary

In summary, this study demonstrates that macroalgae can influence larval settlement of a broadcast spawning coral by means of waterborne chemical effects, and that such effects vary considerably among algal taxa and include both enhancement and inhibition of larval settlement. This emphasises an overlooked effect of benthic algae on coral recruitment that is particularly relevant to disturbed or degraded reefs typically dominated by benthic macroalgae. The results suggest that abundant fleshy macroalgae could affect coral settlement before larvae reach the reef substratum, even on surfaces of a crustose coralline alga known to induce coral settlement, and even where the immediate settlement area is free of macroalgal cover. Thus, the nature of algal cover on reefs may have complex and previously unrecognized effects on coral recruitment, and, hence, on the recovery of coral assemblages following disturbance. As human effects, especially mass bleaching of corals due to climate change, become more frequent, large-scale algal dominance of reefs will also become more frequent (Diaz-Pulido et al. 2007), making such chemical effects potentially critical to the long-term resilience of coral reefs.

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