Coral–algal competition: macroalgae with different properties have different effects on corals

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ABSTRACT: Competition between hard corals and macroalgae is a key ecological process on coral reefs, especially during reef degradation, which often involves a 'phase-shift' from coral- to alga-dominated reefs. However, there are relatively few published studies exploring the variability in this interaction. This paper expands the range of documented coral–algal interactions by comparing the mechanisms and outcomes of interactions involving 3 different algal species, as well as general, mixed algal turfs. Mixed filamentous turfs had relatively minor effects on corals. However, the turfing filamentous red alga *Corallophila huysmansii* provided a dramatic exception to this pattern, being able to settle on, overgrow and kill live coral tissue, perhaps due to allelochemical production by the alga, although this was not directly demonstrated. The larger filamentous alga *Chlorodesmis fastigiata* ('Turtle Weed'), which is conspicuous and abundant on Indo-Pacific reefs, caused polyp retraction but had little other noticeable effect on coral tissue. A corticated red alga *Hypnea pannosa*, frequently observed living within colonies of the branching coral *Porites cylindrica*, did not have a major impact on underlying coral tissue, even over a period of 1 yr, apparently because its relatively translucent and porous thallus structure does not strongly inhibit coral tissue functions. Together, the results demonstrate the considerable potential variability in both the process and outcome of coral–algal competition. This variability can be effectively interpreted in terms of the limited number of mechanisms by which algae can affect corals, with these mechanisms depending largely on the properties (physical, biological, chemical) of the algae. Given the central importance of coral–algal competition to the process of coral reef phase-shifts, understanding the variability and complexity in such competition will have important implications for the prediction and consequences of such phase-shifts.

KEY WORDS: Coral–algal competition · Algal functional groups · Filamentous algal turfs · Corticated algae · Life-history traits · *Porites* spp. · *Corallophila huysmansii* · *Chlorodesmis* spp.

INTRODUCTION

Competition is a key process determining the structure and composition of benthic communities on coral reefs (Lang & Chornesky 1990, Karlson 1999). In particular, competition between hard corals and benthic algae is fundamental to the overall status of coral reefs, especially during reef degradation. Coral reef degradation commonly involves a so-called phase-shift from reefs dominated by corals to reefs dominated by benthic algae (Done 1992, Hughes 1994, McCook 1999).

There has been considerable recent controversy over the relative importance of bottom-up processes, such as eutrophication (e.g. Lapointe 1997, 1999), and top-down control by herbivores (Hughes 1994, Hughes et al. 1999, Aronson & Precht 2000) in contributing to these changes, particularly in the context of declines in Caribbean reefs. According to the bottom-up model, excess nutrient supply results in an increased growth of benthic algae (e.g. Hanisak 1979, Lapointe 1997, Schaffelke & Klumpp 1998, Schaffelke 1999), leading to overgrowth of corals and consequent reef degrada-

tion (Smith et al. 1981, Pastorok & Bilyard 1985, Bell 1992, Naim 1993, Lapointe 1999). The top-down model argues that algal biomass is predominantly controlled by herbivore consumption (e.g. Hay 1981, 1984, Lewis 1985, 1986, Hughes 1994, McCook 1996, 1997, Russ & McCook 1999) and that phase shifts are often the result of declines in herbivores, with consequent increases in algal abundance and competitiveness.

However, it is important to recognise that competition between corals and algae is a critical step in both models of reef degradation, since both bottom-up and top-down perspectives assume that increased algal abundance will lead to decreased coral abundance, by altering the competitive balance between corals and algae. However, there is relatively little direct experimental evidence that algae do compete, either directly or indirectly, and little information on the relative roles of direct competition and other interactions. Further, it is often assumed that the competitive interactions between corals and algae are relatively uniform, with algae generally competitively superior (Miller 1998, McCook 1999, McCook et al. 2001). However, the available evidence suggests that different types of algae may have very different effects on corals, and much of this variation may be related to properties of the algae, including physical (e.g. size, structure, growth form), biological (e.g. sexual or vegetative mechanisms) and even chemical (allelopathic or secondary metabolites) characteristics. Many of these properties may be effectively summarised in terms of algal functional groups (Littler 1980, Littler & Littler 1984, Steneck & Dethier 1994, discussion in McCook et al. 2001).

This study aimed to broaden the range of documented coral–algal interactions, by comparing the effects on corals of 3 different types of macroalgae chosen to represent a range of effects and processes, and of taxonomies. The algae examined include a small, turfing, filamentous red alga *Corallophila huysmansii* (Ceramiaceae, Ceramiales, Rhodophyta), the larger, filamentous but non-turfing green algae *Chlorodesmis* spp. (Udoteaceae, Bryopsidales, Chlorophyta), and a corticated red alga *Hypnea pannosa* (Hypneaceae, Gigartinales, Rhodophyta). Each of these algae were commonly observed living on or in direct contact with live corals and therefore might have negative impacts on the coral tissue. Although work elsewhere has shown filamentous algae to contribute to the death of coral recruits (Birkeland 1977), previous work on our study reefs has suggested that most filamentous, turfing algal species are unable to overgrow live coral tissue (McCook 2001). In contrast, *C. huysmansii* was observed apparently overgrowing live tissue of the branching coral *Porites cylindrica* (Fig. 1), with considerable associated damage to the coral tissue. We com-
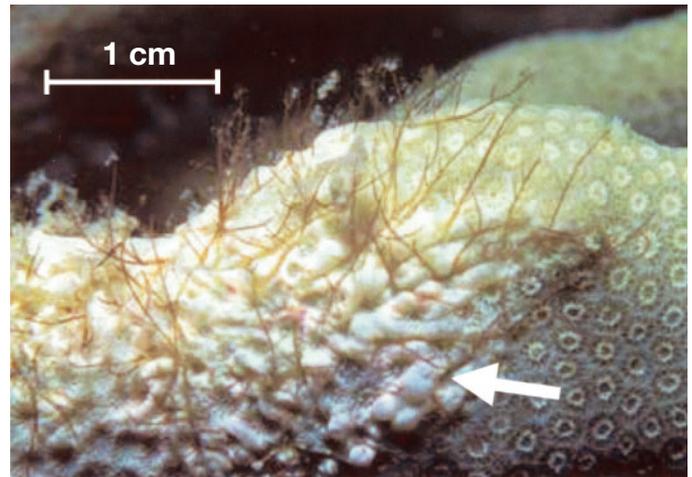
Fig. 1. *Corallophila huysmansii*. Tissue death of coral *Porites cylindrica* following overgrowth by filaments of red alga *C. huysmansii*. Arrow shows swollen coral tissue around algal filaments. Severity of tissue response to such sparse and fine filaments suggests that responsible mechanism may involve allelochemical effects, as the symptoms do not appear consistent with any of the other mechanisms by which algae may affect corals (McCook et al. 2001)

pared the extent to which *C. huysmansii* and general turf algae were able to invade live coral and damage the coral tissue.

Chlorodesmis spp., commonly known as turtle-weed, are bright green, upright (i.e non-turfing), filamentous algae which are widespread and conspicuous on Indo-Pacific reefs, growing as thick tufts or patches, often surrounded by live coral tissue (Fig. 2), commonly of massive *Porites* spp. Although common, the algae are rarely if ever abundant or extensive, with patches rarely growing larger than 20 to 30 cm in diameter. Despite being highly conspicuous, *Chlorodesmis* spp. patches appear able to persist even in areas with relatively high levels of herbivory, apparently because the filaments contain high levels of a secondary metabolite with herbivore-deterrent properties (Ducker 1976, Paul et al. 1990, Craig et al. 1997). Given this herbivore resistance, it was of interest to explore why the algae do not overgrow larger areas of coral and achieve more extensive patches.

Hypnea pannosa is one of a number of fleshy algae commonly observed growing as mats within the branches of *Porites cylindrica* colonies (Fig. 3), but with distinctly different structure and growth form than *Corallophila huysmansii* and *Lobophora variegata* (Jompa & McCook 2002a,b), both of which grow on the same coral species. Although technically a corticated alga (i.e. with a differentiated external cell layer, generally resulting in a more robust thallus), *H. pannosa* grows as a reticulate mass, and is relatively brittle,
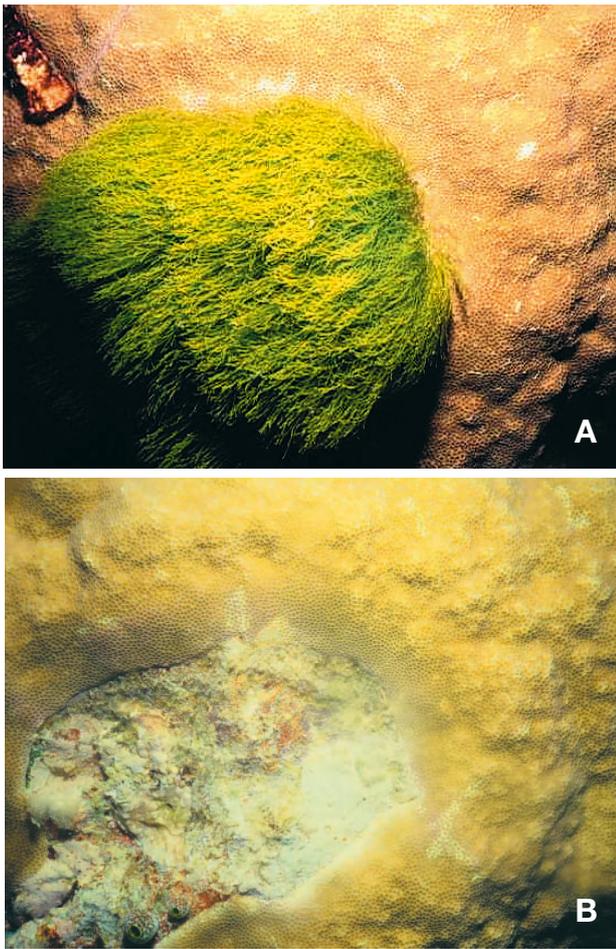
Fig. 2. *Chlorodesmis fastigiata* ('Turtle Weed') growing amidst live coral on Rib Reef, mid-shelf central GBR. Highly conspicuous tufts apparently deter herbivores by means of secondary metabolites, but nonetheless remain as small patches and do not grow into extensive beds. (A) *C. fastigiata* plot (February 1999, patch is approximately 10 cm in diameter); (B) same plot 2 mo later (April 1999) showing seasonal dieback of alga, which died-back and reappeared repeatedly in same plots (see 'Results')

porous and translucent, in contrast to the delicate turfing habit of the filamentous *C. huysmansii* and the robust, creeping and adherent foliose morphology of the brown foliose alga *L. variegata*. *H. pannosa* has been observed in this growth habit on branching corals over wide latitudinal and cross-shelf ranges on the Great Barrier Reef (GBR), and on SE Asian reefs (L. J. McCook unpubl. data). This growth habit, of clumps or mats within branching coral colonies, is relatively common for a range of coral reef algae, including *H. pannosa*, *L. variegata*, *Amansia rhodantha* (Ceramiales, Rhodophyta) and various species of *Laurencia* (Ceramiales, Rhodophyta; L. J. McCook pers. obs.). The *H. pannosa–P. cylindrica* interaction there-

fore provides both useful contrasts to other documented interactions and an example of a coral–algal interaction with wide geographic relevance.

MATERIALS AND METHODS

Study species and sites. The first study, on the interaction between *Corallophila huysmansii* and *Porites cylindrica*, was conducted on the reef slope (7 to 8 m
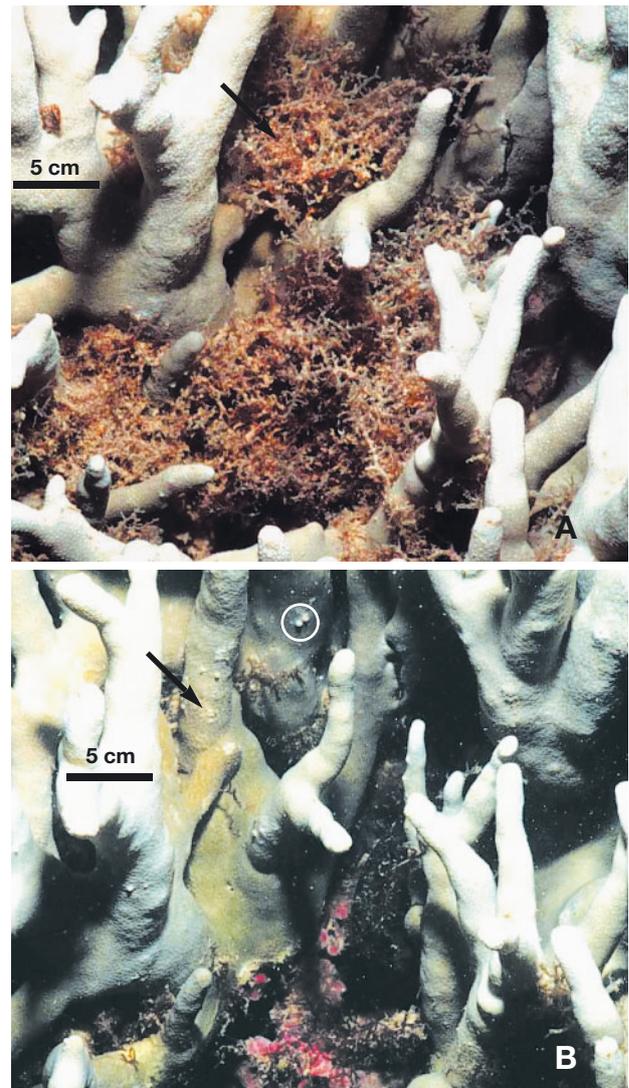
Fig. 3. *Hypnea pannosa*, a corticated red alga commonly observed growing within branches of *Porites cylindrica*. Structure of coral branches probably provides refuge for this alga from herbivory (Jompa & McCook 2003). Coral tissue seemed relatively unaffected by presence of this alga. (A) *H. pannosa* growing within coral branches. (B) Same branches as in (A) a few months later, after manually removing the alga. Arrows indicate coral tissue previously covered by the alga in relatively healthy condition, although darker in colour; minor tissue lesions (e.g. circled in B) were sometimes observed

depth) at Cannon Bay (18° 41.0′ S, 146° 35.2′ E), Great Palm Island, inshore GBR, Australia, close to the site used by McCook (2001). The site was dominated by large colonies of *P. cylindrica* (~65% cover, based on four 20 m line-intercept transects), of which many had fleshy macroalgae, especially *Lobophora variegata*, growing as mats around the bases of branches. During a survey of the site, a number of colonies were found to have the filamentous turfing species *C. huysmansii* growing on live tissue of *P. cylindrica*, usually as relatively small patches (~20 cm^2), but occasionally completely overwhelming and killing patches of *P. cylindrica* up to 1 m in diameter. Nonetheless, *C. huysmansii* was not abundant, with estimated overall cover at this site less than 2%, and few observations at other sites.

The effect of *Hypnea pannosa* on *Porites cylindrica* was investigated on the reef crest (3 to 5 m) at Little Pioneer Bay (18° 36.0′ S, 146° 29.3′ E), Orpheus Island, inshore GBR. *P. cylindrica* was also abundant at this site, but, in contrast to Cannon Bay, the dominant macroalga growing within the coral branches at this site was *H. pannosa*. Patches of the alga varied in size, from about 20 cm^2 to 2 m^2, with mats generally between 5 to 10 cm thick, and in much greater abundance than *Corallophila huysmansii*.

The interaction between *Chlorodesmis* spp. and corals was monitored at a reef-flat site (1 to 2 m; 18° 28.5′ S, 146° 52.7′ E) and a reef slope site (8 to 10 m; 18° 28.4′ S, 146° 52.8′ E) on Rib Reef, a mid-shelf reef on the central GBR. The algae occupied small patches amidst live tissue of massive *Porites* spp. (predominantly *P. lobata*) and *Favites* spp., and encrusting *Montipora* spp. *Chlorodesmis* spp. filaments were in direct contact with surrounding coral tissue. Although most of the *Chlorodesmis* patches studied were *C. fastigiata*, several of the reef slope patches were comprised of *C. major*. However, as their effects on corals were indistinguishable, both species are treated together as *Chlorodesmis* spp. *Chlorodesmis* spp. do have basal rhizomes, but these do not form the extensive horizontal filaments seen in typical turfing morphologies (e.g. *C. huysmansii*, see Price & Scott 1992 for details). The *Chlorodesmis* spp. patches were very common (and easily noticed), but relatively small, so that overall abundance was low.

Expt 1: *Corallophila huysmansii.* To examine the ability of *C. huysmansii* to colonise and kill live coral tissue, we compared the effects of this alga on mortality of coral tissue with the effect of other mixed turfing and crustose coralline algae. We did this by attempting to 'infect' or induce colonisation of healthy *Porites cylindrica* branches with either *C. huysmansii* or with general mixed algal turfs. Using a small hand-saw, we carefully removed 9 live branches of *P. cylindrica* (approx. 2 cm thick and 6 cm long) with *C. huysmansii*

present and attached them to 9 randomly selected healthy coral branches using cable ties (*C. huysmansii* infection treatment). Similarly, 9 other dead coral branches, overgrown by general mixed algal turfs and coralline algae, were attached to healthy coral branches ('mixed algal infection'), adjacent to (~30 cm apart) 1 of the branches infected by *C. huysmansii* (mixed turfs did not occur on live coral tissue). Experimental branches were approximately 2 m apart. The effect of the algae on the coral was estimated as the area (mm^2) of coral tissue mortality associated with the algal infection, measured with vernier callipers every 5 to 8 wk for 6 to 7 mo. The experiment was run at 2 different times of the year to assess temporal or seasonal variability in the interaction. The first period was from August 1998 to March 1999, the second from May to November 1999.

Algal overgrowth in these experiments was generally relatively short-lived (3 to 4 mo). To investigate whether this reflected intrinsic seasonality or senescence of the alga, a number of *Corallophila huysmansii*-overgrown branches were collected to determine their longevity in aquaria. Branches were anchored by glueing to clay tiles, transplanted, and maintained under running seawater at the James Cook University aquarium. Algal condition was regularly observed for 6 mo (concurrently with the second experimental period in May to November 1999).

Expt 2: *Hypnea pannosa.* The effects of *H. pannosa* on *Porites cylindrica* were assessed by comparing coral growth and mortality in quadrats in which the alga was naturally present or experimentally removed. We marked 16 plots (50 × 50 cm) within *P. cylindrica* colonies that had extensive mats of *H. pannosa* alga growing within the coral branches. The alga was removed from 8 randomly selected plots (*H. pannosa* removal treatment) and was left intact on the other 8 plots as controls (*H. pannosa* present).

To compare coral growth and tissue mortality between treatments, 4 individual branches were randomly chosen within each plot and marked with plastic labels attached by cable ties onto the basal part of the branch. Coral tissue mortality was estimated for the tagged coral branches as the change in area (mm^2) of dead coral tissue, using callipers (as for Expt 1). Coral growth was estimated as linear skeletal extension measured from the marker (cable tie) to the tip of each coral branch. This experiment ran for 1.5 yr from April 1998 to October 1999.

Expt 3: *Chlorodesmis* spp. The potential effects of the filamentous green algae *Chlorodesmis* spp. on surrounding corals were investigated by monitoring *Chlorodesmis* spp. patches, to identify any apparent stresses or impacts. On both the reef flat and reef slope at Rib Reef, we marked 15 small permanent quadrats

(14.5 × 21.5 cm) containing patches of *Chlorodesmis* spp. completely surrounded by live coral tissue, and monitored them photographically. Quadrats were photographed using a Nikonos V camera with 28 mm lens and close-up kit; algal filament heights were measured manually, and qualitative observations of coral condition were noted every 2 to 3 mo for 18 mo, from September 1998 to March 2000.

Data analyses. Data analyses for Expts 1 and 2 involved a simple 1-way ANOVA (using data from end of each experiment) and a nested ANOVA with plots nested within treatments, respectively. All data were tested for homogeneity of variance (Cochran's test), outliers, and independence and normality of residuals. Based on these tests, data transformation was unnecessary for Expt 2. Data for Expt 1 were log-transformed because temporal changes differed by orders of magnitude between treatments, resulting in heteroscedasticity in the untransformed data. Qualitative observations of *Chlorodesmis* spp. effects only are presented, since no significant coral tissue mortality was recorded for these algae.

RESULTS

Expt 1: *Corallophila huysmansii*

Corallophila huysmansii was able to colonise and overgrow live *Porites cylindrica* tissue, and overgrowth by even relatively sparse filaments of *C. huysmansii* appeared to cause considerable damage to underlying and adjacent coral tissue (e.g. Fig. 1). Coral tissue became bleached and swollen even up to several millimetres away from algal filaments, and subsequently died; this only occurred adjacent to algal filaments, and was not observed in coral tissue adjacent to areas of live *P. cylindrica* branches without the alga present. The results provide strong evidence that overgrowth by *C. huysmansii* was the direct cause of coral tissue death. Coral tissue mortality was significantly higher in the *C. huysmansii* infection treatment than on corals infected by mixed algal turfs, during both periods (Fig. 4, Table 1). About 1 mo after *C. huysmansii* branches had been placed in contact with healthy coral branches, the alga had colonised and overgrown the healthy coral tissue. Although only a little coral tissue actually died within that time, the rest of the overgrown tissues were clearly severely stressed (Fig. 1). Coral tissue mortality appeared to generally follow overgrowth, but with a delay of up to several months; dead coral tissue was subsequently occupied by mixed-species, filamentous algal turfs. Thus, although Fig. 4 shows an increase in coral mortality toward the end of both experimental periods, algal colonisation

Table 1. *Corallophila huysmansii*. ANOVAs of effects of 'infection' by either *C. huysmansii* or mixed filamentous turfs on coral tissue mortality. Data are transformed to $\log_{10}(x+1)$, and analyzed independently for the first and second periods using data from final measurements for each period

Source	df	MS	F	p
First period (Aug 98 to Mar 99)				
Treatment	1	38.0	46.2	<0.001
Residual	16	0.8		
Second period (May to Nov 99)				
Treatment	1	24.7	22.7	<0.001
Residual	16	1.1		

had generally ceased by that time, and only very few coral branches still had small amounts of *C. huysmansii* filaments growing on live coral tissue. Algal overgrowth of new live coral tissue generally ceased within 2 to 6 mo. Comparison of the 2 experimental periods suggests that the time course of colonisation
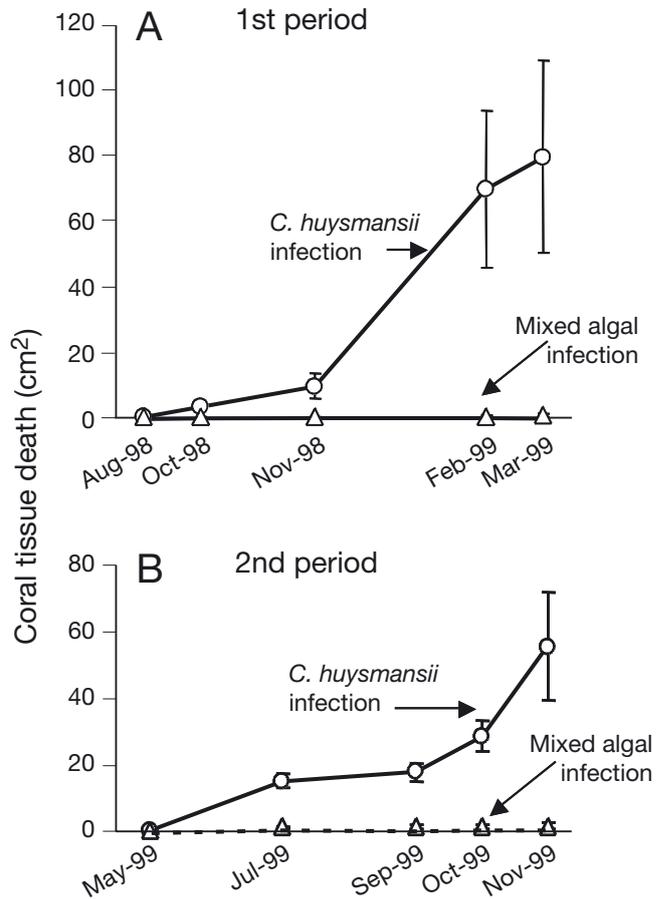
Fig. 4. *Corallophila huysmansii*. Coral tissue mortality of branches 'infected' by *C. huysmansii* and mixed algal turfs. Data are means (±SE) of total coral-tissue death (cm²) for 9 replicates

was similar at both times of year, with little seasonal difference (Fig. 4). Interestingly, in contrast to the field experiments, *C. huysmansii* transplanted to aquaria continued to grow well over new coral substrate for up to 6 mo, and attained upright filament heights longer than those in the field.

In contrast to the *Corallophila huysmansii* treatment, the mixed algal turfs and crustose corallines were relatively poor competitors with healthy *Porites cylindrica*. Coral branches in the mixed algal treatment showed only minor tissue mortality during the first month, and otherwise generally remained healthy throughout the study periods. In a few cases, coral tissue even grew from the healthy coral branch over the mixed algal communities on the experimentally attached, dead coral branches.

Expt 2: *Hypnea pannosa*

The presence of *Hypnea pannosa* had minimal effects on both coral tissue mortality and growth during this experiment. Coral tissue mortality in both treatments was minimal, indicating that *H. pannosa* had not caused significant damage to underlying coral tissue. Coral tissue underneath the algal mat was generally healthy, although a little darker in colour, with only a few minor tissue-lesions (Fig. 3). Quantitative results are not given because tissue mortality was insufficient to quantify. Although growth (or linear skeletal extension) of *Porites cylindrica* branches was very slightly higher in the absence of *H. pannosa* than in plots with the alga present, this difference was very small and not significant (Fig. 5, Table 2).
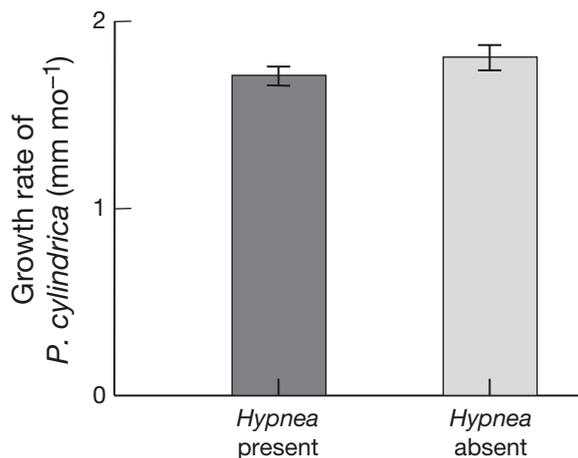
Table 2. *Hypnea pannosa*. ANOVA of effect on growth rate of *Porites cylindrica*. Homogeneity of variance test shown as Cochran's *C*, critical value of *C* here is 0.26; data are untransformed

Source	df	MS	*F*	p
Treatment	1	0.15	1.37	0.261
Plot (treatment)	14	0.11	0.97	0.492
Residual (n = 4)	48	0.11		
Cochran's *C* = 0.24				

Expt 3: *Chlorodesmis* spp.

Coral tissue in direct contact with *Chlorodesmis* spp. filaments showed minimal tissue damage even after 18 mo of monitoring. Direct observations showed that longer algal filaments (5 to 10 cm in length), although very soft, would constantly brush adjacent coral tissue as the filaments moved with water motion, with the frequent consequence that coral polyps in the vicinity of the filaments were retracted, and the tissue showed minor stress symptoms such as pale colouration or a pink speckled appearance.

Both photographic monitoring and filament height measurements showed that *Chlorodesmis* spp. patches undergo a dramatic cycle in standing crop, with a periodic loss and reappearance or regrowth of most macroscopic filaments. Although the periodicity of this cycle is difficult to determine from intermittent photographs/visits, and appeared to vary between patches, it appears that individual patches can undergo at least 1 complete cycle within 4 to 6 mo (e.g. Fig. 2). Of the 15 *Chlorodesmis* spp. patches initially marked in each zone, after 18 mo, 12 were still present on the reef flat and 6 on the reef slope.

DISCUSSION

The results in this paper, taken together with those of several other recent studies (Table 3), considerably extend the range of taxa, algal and coral types, and outcomes of documented coral–algal interactions. They also further illustrate the considerable variation possible in both processes and outcomes of these interactions (Miller 1998), and provide an opportunity to review the ideas about variability in mechanisms and outcomes proposed by McCook et al. (2001). This 'mechanisms approach' argues that there are a limited number of mechanisms by which corals can affect algae, and vice versa, and that consideration of the properties of the algae provides useful clues as to which of those mechanisms may be relevant (e.g. sparse filamentous algae are unlikely to have strong

Fig. 5. *Hypnea pannosa*. Growth rate of *Porites cylindrica* in plots with *H. pannosa* present or experimentally removed. Data are means (±SE) of coral growth rate of 32 replicates averaged over 4 plots

Table 3. Comparison of recent studies demonstrating range of competitive effects of algae on corals and potential mechanisms and apparent effects of different types of algae on corals. Algal properties clearly provide valuable indications of potential competitive mechanisms and consequent effects. Many of those properties are effectively summarized by the functional groups, with the clear exception of allelochemical properties. (This table provides an update to Tables 1 to 4 in McCook et al. 2001)

Algae	Functional group	Potential mechanism	Effect on corals	Source
Mixed algal turfs	Filamentous (turf)	Vary	No major effect	McCook (2001), Jompa & McCook (2003, this volume), present study
Corallophila huysmansii	Filamentous (turf)	Allelochemical?	Coral tissue mortality	Present study
Anotrichium tenue	Filamentous (turf)	Allelochemical? (+ sediment trapping)	Coral tissue mortality	Jompa & McCook (2003, this volume)
Chlorodesmis spp.	Filamentous (non-turf)	Abrasion	No major effect	Present study
Lobophora variegata	Creeping corticate foliose	Overgrowth	Coral tissue mortality	Jompa & McCook (2002a,b)
Hypnea pannosa	Corticated macrophyte	Shading and/or overgrowth	No major effect/ minor tissue damage	Present study
Sargassum spp. *Cystoseira* spp. + *Turbinaria* spp.	(Canopy-forming) Leathery macrophytes	Shading and/or abrasion and/or physical barrier	Reduced coral bleaching	Jompa & McCook (1998, unpubl. data)

shading effects; see also Fig. 1 of present paper). The different algal taxa examined in this study demonstrate strongly contrasting effects on corals, with 1 filamentous taxon (*Corallophila huysmansii*) causing severe coral tissue damage even at some distance from the filaments, and others (general mixed algal turfs, *Hypnea pannosa* and *Chlorodesmis* spp.) causing negligible damage.

It appears that much of this variation can be interpreted in terms of the properties of the algae, and the consequent mechanisms by which they affect the adjacent coral tissue by direct overgrowth, shading, abrasion or chemical effects (or by pre-emption of space and recruitment inhibition: McCook et al. 2001). Thus, although corticated algae are generally more robust than filamentous taxa, *Hypnea pannosa* is a relatively fragile example of the corticated functional group (Littler 1980, Steneck & Dethier 1994), and its relatively porous, reticulate structure and translucent thallus apparently do not limit water flow (with associated gas and nutrient exchange) or light availability sufficiently to seriously inhibit coral growth or survival. *Chlorodesmis* spp., although generally longer and more robust than *Corallophila huysmansii*, do not have a turfing growth habit, and have limited ability to vegetatively overgrow and colonise new substrate. Although they appear to cause polyp retraction, the effect is minor, perhaps because their filaments are relatively soft, or because the seasonal dieback provides adjacent coral with an opportunity to recover, or because the coral colony is able to subsidise the areas with retracted polyps by translocation of metabolites.

In contrast, the relatively delicate filaments of *Corallophila huysmansii* can very effectively colonise and kill healthy coral tissue. The turfing growth habit of *C. huysmansii* allows it to rapidly invade new substrate, but this alone cannot explain its ability to colonise live coral tissue, as many of the taxa present in the (relatively harmless) mixed filamentous turfs have similar growth habits. Thus, whatever factor provides *C. huysmansii* with the ability to colonise live coral tissue is critical to the competitive effectiveness of this taxon.

The relatively short life-span of *Corallophila huysmansii* in the field experiments is intriguing. Its greater longevity in aquaria, along with the occasional occurrence of large patches of *Porites cylindrica* overgrown by *C. huysmansii*, suggests that its dieback in the field is not due to intrinsic seasonality or senescence, but to other factors. Although the longevity of *C. huysmansii* in aquaria may reflect competitive advantages conferred by the lack of herbivores or elevated nutrient conditions, this remains strictly speculative without further evidence.

The apparent ability of *Corallophila huysmansii* to kill coral tissue relatively distant from its fine filaments (Fig. 1) raises the possibility of allelochemical effects (see e.g. de Nys et al. 1991 for details of algal effects on soft coral). Although we do not have direct chemical evidence, it is difficult to explain the nature of the effect by any of the other mechanisms by which algae are known to inhibit corals (McCook et al. 2001): the pattern of tissue death apparent in Fig. 1 is hard to reconcile with overgrowth (smothering), shading, or abrasion (pre-emption and epithelial sloughing are not relevant here). Thus the mechanisms approach

(McCook et al. 2001) is able to suggest an explanation for the strength of effects of *C. huysmansii* on *Porites cylindrica* interaction without direct evidence.

This approach is also effective for results from other studies. Like *Hypnea pannosa*, the foliose brown alga *Lobophora variegata* also grows amidst the basal branches of *Porites cylindrica* colonies, but in contrast to *H. pannosa*, *L. variegata* occurs in an adherent, creeping form and has a relatively robust and opaque foliose thallus which effectively blocks light and water flow. The apparent consequence is that, again in contrast to *H. pannosa*, *L. variegata* can overgrow and kill *P. cylindrica* (Jompa & McCook 2002a,b). Large, canopy-forming leathery macrophytes had relatively minor effects on understory corals, even apparently protecting them from bleaching damage by shading (Jompa & McCook 1998). Such algal canopies are unlikely to smother corals, as their small holdfasts occupy relatively little primary substrate; however, their extensive canopies can shade or abrade corals. Further illustrations of this approach for other published studies (e.g. Fishelson 1973, Potts 1977, Hughes 1994, Tanner 1995, Miller & Hay 1996) are reviewed by McCook et al. (2001).

Interestingly, of the interactions documented in Table 3 and McCook et al. (2001), smothering and the putative chemical effects appear relatively lethal to corals, whereas shading and abrasion effects appear less severe. Note also that chemically mediated interactions constitute a limitation to the functional group approach suggested for coral–algal competition by McCook et al. (2001): although much of the variability in coral–algal interactions can be explained by algal properties that are effectively summarised by accepted functional groups (Littler 1980, Steneck & Dethier 1994), allelochemical effects are not predicted by these groups.

In summary, the present results expand the range of documented coral–algal interactions, and emphasise the potential variability in both processes and outcomes of those interactions. Importantly, that variability can be effectively interpreted in terms of the properties of the algae, and the potential mechanisms by which they can affect the corals. Better interpretation and understanding of the variability in coral–algal interactions could enable more effective prediction of the outcomes and consequences of coral–algal dynamics under varying circumstances, with significant consequences in the context of reef degradation.

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