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Competition between corals and algae on coral reefs: a review of evidence and mechanisms

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Abstract Despite widespread acceptance that competition between scleractinian corals and benthic algae is important to the structure of coral reef communities, there is little direct experimental evidence that corals and algae do compete, and very little data on the processes and causality of their interactions. Most available evidence is observational or correlative, with intrinsic risks of confounded causality. This paper reviews and categorises the available evidence, concluding that competition between corals and algae probably is widespread on coral reefs, but also that the interaction varies considerably. Widespread replacement of corals by algae may often indicate coral mortality due to external disturbances, rather than competitive overgrowth, but may lead to competitive inhibition of coral recruitment, with consequences for reef recovery. We list eight specific processes by which corals and algae may affect each other, and suggest life history properties that will influence which of these interactions are possible. We propose a matrix for algal effects on corals, which lists the subset of processes possible for each combination of coral life form and algal functional group. This table provides a preliminary framework for improved understanding and interpretation of coral-algal interactions.

Key words Coral reef algae · Coral-algal competition · Macroalgae · Phase shifts · Overgrowth

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Introduction

Competition is an important process determining the structure and composition of benthic communities on coral reefs (Lang and Chornesky 1990; Karlson 1999). In particular, competition between hard corals and benthic algae is considered fundamental to the overall status of coral reefs, especially during “phase shifts” in which reefs dominated by reef-building corals become dominated by macroalgae (e.g. Littler and Littler 1984; Lapointe 1989; Done 1992; Hughes 1994; Miller 1998). Algae are widely considered to be competing with corals for space (or light), and interactions between the two are frequently interpreted simply in terms of algal competitive superiority, often due to reduced herbivory or increased nutrient availability. Miller (1998) and McCook (1999) showed that competition between corals and macroalgae is a critical step during such reef degradation.

However, there is surprisingly little direct, experimental evidence demonstrating competition between these two groups (Miller 1998; McCook 1999). In this review, we explore the available evidence on interactions between corals and algae, with three specific purposes: (1) to summarise existing information on coral-algal interactions, especially competition, and in particular the processes or mechanisms by which corals and algae interact; (2) to demonstrate the lack of hard data on those mechanisms, or even that corals and algae are generally in competition, and hence the need for caution in assumptions about the processes involved; and (3) to suggest a preliminary conceptual framework for understanding the processes by which algae may affect corals.

The review is limited to interactions between scleractinian corals and macroscopic, free-living benthic algae. We do not discuss the larger scale consequences of coral-algal competition for reef composition and structure, comprehensively reviewed by Miller (1998), nor the context for reef degradation and management (reviewed by McCook 1999). Given the considerable structural and

taxonomic diversity of both corals and algae, their interactions will not be homogeneous, so we include consideration of taxa and functional groups or life forms. Given their importance during reef degradation, we emphasise the competitive effects of algae on corals, and in particular whether algal abundance is necessarily the cause, rather than the consequence, of coral mortality (McCook et al. 1997).

Interactions between corals and algae on coral reefs

Summary of available evidence

Based on the arguments of Connell (1983), Schoener (1983), Underwood (1986) and McArdle (1996), we have classified studies according to the levels of evidence they provide that coral-algal interactions are in fact competitive: that is, the performance of either competitor is reduced by the presence of the other. Specifically, we distinguish between: (1) experiments that directly manipulate abundance of either competitor (Table 1); (2) experiments that manipulate herbivores, and thus are assumed to indirectly manipulate algal abundance (Table 2); (3) "natural experiments" or comparisons and observations of correlations between algal and coral abundances (Table 3); and (4) direct observations of coral-algal interactions, at relatively small scales (Table 4). (Individual papers may include data or evidence in more than one category.) Within each table, we have classified studies by location and region, methods and results, and by the algal taxa and functional group and coral taxa and life form.

Proof of competition requires unequivocal evidence that the performance of the study organism is in some way inhibited by the presence of the competitor. That evidence can only be provided by (properly replicated and controlled) direct manipulation of a competitor, so that the only difference between treatments is the presence or abundance of the competitor, and any difference in response may be assumed due (directly or indirectly) to the competitor (Underwood 1986). All other approaches are *potentially* confounded by other factors; although we include some examples to illustrate possible confounding factors, issues of causality and correlation cannot be argued in detail here (see e.g. previous references, and Strong et al. 1984; Diamond 1986). In particular, without experimental evidence, the replacement or overgrowth of live coral by algae does not prove that the algae have outcompeted the corals: the coral may have been killed by some other, unrelated factor (e.g. bleaching, corallivory, storm damage, eutrophication, disease), potentially unknown to the researcher. The algae may have increased as a consequence of the coral loss, and may have been having little or no inhibitory effect on the corals (e.g. McCook 2001).

We emphasise that recognition of the interpretive limitations of any study in terms of competitive causality does not amount to criticism of the study in its own

right. Many of the studies reviewed were not intended to test the competitive nature of the interaction, or to demonstrate causality, but to document patterns or changes in community structure, or effects of herbivores. Such studies are intrinsically valuable, especially where they include long-term or large-scale data, which are difficult to achieve with manipulative experiments.

Direct experimental tests for competition

Only seven studies were found that directly tested competitive interactions between corals and algae (Table 1), of which two were in temperate systems rather than coral reefs. Most of the experiments tested effects of algae on corals, and only one tested effects of corals on algae (McCook 2001). Only two studies simultaneously tested competitive effects and herbivory, despite the importance of herbivory to algal abundance (Miller and Hay 1996, 1998). Most studies demonstrated negative impacts of algae on corals, but these effects varied in intensity, and in one exceptional case, algae actually *protected* corals from bleaching (Jompa and McCook 1998).

Also relevant are several studies (Table 1) intended to examine coral recruitment or recovery from lesions, but which provide de facto tests of the effects of corals on algae. The induction of coral metamorphosis by coralline algae (Heyward and Negri 1999) provides a second example of algae *enhancing* coral success. In the lesion studies, experimental damage to coral tissue (with control, undamaged areas) was followed initially by algal colonisation, but in general the corals regenerated, overgrowing and thereby outcompeting the algae. Algae did not colonise the control areas, and appeared to inhibit but rarely prevent coral recovery in damaged areas, indicating competitive superiority of the corals. Larger lesions persisted for longer periods, often leading to colonisation by more robust and competitively successful algal forms (Meesters and Bak 1993; Meesters et al. 1994, 1997).

Some differences in competitive potential may be discerned between algal groups, such as canopies of large, leathery algae that shade or whiplash corals, and smaller algae that directly contact or smother corals. However, these studies together still provide very limited coverage of different combinations of algal functional groups and coral life forms, and so provide a very limited basis for generalisations about coral-algal competition. Further, most manipulations were inevitably at relatively small scales (~0.1 to <10 m), although several did involve more than one reef or large-scale transplantations.

Indirect experiments using herbivore manipulations

Indirect experimental evidence for competitive effects of algae on corals comes from experimental herbivore manipulations (Table 2). Only nine such studies were found to include data on coral abundance, and most

Table 1 Comparison of studies which directly test effects of algae and corals on each other. Summary table of key aspects of published experimental studies of coral-algal competition (see text; studies are organised by type of study or evidence, and then chronologically). Impacts are summarised as *A* impact of corals and *C* impact of algae; in each case impacts are summarised as: – negative (competitive); 0 no impact; + facilitatory or beneficial. Note that both corals and algae will often be mutually inhibitory, but many studies did not consider impacts of corals on algae, so impacts represent a biased sample. Methods and evidence listed are only those relevant to this table. Any limitations noted refer only to the interpretative context of this table, and are therefore not to be taken as criticisms of the studies (in most cases limitations were unavoidable and acknowledged by authors). *Final rows* summarise studies of coral recruitment or recovery from experimental lesions, which we have reinterpreted in terms of competition. Algal functional groups are modified from Steene and Dethier (1994): *Filament* Filamentous; *Cort Foliose*, creeping or upright; *Cort Macro* corticated macrophytes; *Leathery* leathery macrophytes; *Artic Calc* articulated calcareous; *Crustose* crustose. Creeping and upright corticated foliose algae refer to growth habit, often variable within a genotype. *CCA* Crustose coralline algae; *GBR* Great Barrier Reef

Reference	Location, region	Impacts, methods and evidence		Comments	Algal taxa/functional group	Coral taxa/life form
		A	C			
Hughes (1989)	Rio Bueno, Jamaica, Caribbean	–	Macroalgal removal treatment and natural encounters; coral bleached or dead where in contact with macroalgae; macroalgae outcompeted coral by overgrowth	Experiment design not specified but results clear-cut	Unspecified/“Fleshy algae”	<i>Agaricia</i> spp. + 20 spp. listed/ most forms
Coyer et al. (1993)	California, temperate Pacific rocky kelp bed	–	Coral transplantation to different algal abundance; overgrowth of corals after 1 year; corals damaged by brushing; 10 years	Temperate location; non-reef building coral; results clear cut	<i>Cystoseira</i> ; <i>Dictyota</i> ; CCA; kelp holdfast/Leathery; Cort Foliose; Crustose	<i>Balanophyllia</i> /Solitary (small)
Tanner (1995)	Heron Island, GBR	–0	Algal removal treatment and natural encounters; energetic cost to corals from algal contact; algae reduced cover, growth and fecundity of some corals but not all, and, importantly, did not affect survival	Clear-cut experiment, limited by low cover of both algae and coral – may underestimate effects	Various ^a /Artic Calc; Crustose; Filament; Leathery; Cort Macro; Cort Foliose	<i>Acropora brueggemannia</i> ; <i>Acropora cuneata</i> ; <i>Pocillopora damicornis</i> / Branching
Miller and Hay (1996)	North Carolina, temperate Atlantic; inshore-offshore gradient	–	Algal removal, coral transplantation, herbivore exclusion, and nutrient enrichment; algae inhibited growth and recruitment of coral, due to shading or abrasion	Temperate location; non-reef-building coral; results clear cut	Various ^b /Leathery; Cort Foliose; Filament; Cort Macro	<i>Oculina arbuscula</i> / Branching; recruits
Miller and Hay (1998)	Florida, Caribbean	–	Corals transplanted to herbivore exclusion cages with and without algae present; coral growth reduced in presence of algae	Coral growth rate differences may be slightly confounded by different predator bite rates on corals	Various ^c /Cort Foliose; Artic Calc; Cort Macro; Filament	<i>Porites porites</i> / Branching

Jompa and McCook (1998)	Inshore, central GBR; 2 sites, 2 reefs: inshore-offshore gradient	+	Canopy algal removal; algal canopy protected corals from bleaching damage (shading?)	Demonstrates variable impacts of macroalgal beds	<i>Sargassum</i> /Leathery	Diverse/Diverse
McCook (2001)	Inshore, central GBR	0	Removal of massive corals or turf algae along gradient of terrestrial runoff: corals inhibited turf growth more than vice versa; coral success not related to nutrient or sediment inputs.		Various (listed)/Filament	<i>Porites lobata</i> /Massive
Recruitment study: Heyward and Negri (1999)	Lizard Island, GBR and Ningaloo, Western Australia	+	Calcified red algae induced metamorphosis/settlement of coral larvae	Demonstrates positive impacts of algae on coral. Not intended to address competition	<i>Lithophyllum</i> ; <i>Hydroolithon</i> ; <i>Neogoniolithon</i> ; <i>Amphiroa</i> ; <i>Mesophyllum</i> ; <i>Peyssonnelia</i> /Crustose; Arctic Calc	<i>Acropora millepora</i> ; various/Recruits
Lesion studies: Bak et al. (1977)	SW Curacao, Caribbean	-	Algal turfs which initially colonised experimental lesions on corals were overgrown by coral	Not intended to address coral-algal competition but demonstrates coral overgrowth of colonising algae	Unspecified/Filament	<i>Agaricia agaricites</i> ; <i>Montastrea annularis</i> / Foliose and massive
Meesters and Bak (1993); Meesters et al. (1994, 1997)	Curacao, Caribbean	-	Colonisation of experimental lesions by algae influenced but did not generally prevent coral overgrowth of algae. Duration and type of algal colonisation affected recovery	As above	Unspecified/Filament	<i>Montastrea annularis</i> ; <i>Porites astreoides</i> ; Massive
van Woesik (1998)	Okinawa, Japan	-	As above	As above	Unspecified; <i>Padina</i> /Filament; Cort Foliose	<i>Porites</i> spp./Massive

^a*Halimeda*, *Peyssonnelia*, *Chlorodesmis fastigiata*, *Turbinaria*, *Sargassum*, *Amphiroa*, *Caulerpa*, *Hypnea*, *Enteromorpha*, *Padina*

^b*Sargassum*, *Lobophora*, *Dictyota*, *Dictyopteris*, *Zonaria*, *Ectocarpus*, *Chondria*, *Hypnea*

^c*Dictyota*, *Halimeda*, *Laurencia*, *Coelothrix*, *Galaxaura*, *Amphiroa*, *Styopodium* and filamentous reds

Table 2 Comparison of experiments which indirectly examine coral–algal competition using herbivore manipulations. Impacts, methods, evidence, comments, functional groups and abbreviations as for Table 1. Note that impact summaries (*column A*) assume that

effects on coral are direct results of increased algae, in turn resulting from herbivore manipulations, and ignore potential confounding factors (see text). As such experiments cannot expect to detect impacts of corals on algae, these are not summarised

Reference	Location, region	Impacts, methods and evidence	Comments	Algal taxa/functional group	Coral taxa/life form	
		A				
Vine (1974) ^a	Harvey Reef, Red Sea	–	Settlement plates caged, uncaged and in damselfish territories; observed that invertebrate (incl. coral) recruitment was reduced where algae abundant	No data given for corals; Damselfish effects confound herbivore exclusion with other effects ^a	Unspecified/ Filament	Unspecified/ Recruits
Sammarco (1980, 1982)	Discovery Bay, Jamaica, Caribbean	–0	<i>Diadema</i> density manipulations and removals; no effect of algae on coral recruitment but some effect on survival of recruits and cover of adults; coral recruits overgrew CCAs	Differences among and between taxa in competitive outcomes; <i>Diadema</i> removal alone led to increased coral abundance	32 spp. listed/ Filament; Artic Calc; Crustose	<i>Agaricia</i> spp.; <i>Porites</i> spp. + 15 spp. listed/ Branching; Massive; Foliose; Sub-massive; Recruits
Sammarco and Carleton (1981) ^a	Britomart, GBR	–0	Settlement plates inside and outside territories and cages; coral recruits shaded by filamentous algae, but no effect of caging on recruitment	Damselfish effects confounded ^a	<i>Palmophyllum</i> ; <i>Polysiphonia</i> ; <i>Ceramium</i> ; <i>Gracilariopsis</i> / Crustose (not calcified); Filament	<i>Acropora</i> and <i>Seriatopora</i> + 10 spp. listed/ Recruits
Fitz et al. (1983)	St. Croix, Caribbean	–0	Caged and exposed settlement panels; algal growth in cages reduced coral settlement in one size class, but not in two others	Variable effects	Unspecified/Variou	<i>Agaricia</i> and <i>Porites</i> spp./Recruits
Hay and Taylor (1985)	St. Thomas, Caribbean	–?	<i>Diadema</i> removal; decreased cover of “benthic invertebrates” following algal growth	Coral cover initially low	<i>Dictyota</i> /Cort Foliose	Unspecified/ Unspecified
Lewis (1986)	Carrie Bow, Belize, Caribbean	–	Herbivore reduction by fences; increased algal biomass killed and bleached corals	Although significant, decline in coral cover only 2%	<i>Padina</i> ; <i>Dictyota</i> ; <i>Turbinaria</i> ; <i>Gelidiella</i> + 26 spp. listed/Cort Foliose (Creep; Upright); Leathery; Cort Macro; Filament	<i>Porites astreoides</i> / Massive
Stachowicz and Hay (1999)	North Carolina, temperate Atlantic	–	Removal of symbiotic herbivorous crab led to algal overgrowth (and invertebrates)	Temperate, non-reef-building coral	<i>Sargassum</i> ; <i>Dictyota</i> ; <i>Oculina arbuscula</i> / <i>Codium</i> ; <i>Ectocarpus</i> / Leathery; Cort Foliose; Cort Macro; Filament	Branching
Lirman (2001)	Florida, Caribbean	–	Algal additions and cages led to inhibition and polyp retraction in corals	Algal addition treatment unclear	<i>Halimeda</i> and <i>Dictyota</i> /Artic Calc; Cort Foliose	<i>Montastrea faveolata</i> ; <i>Porites astreoides</i> ; <i>Siderastrea siderea</i> / Massive

^a Comparisons using damselfish territories as herbivore reductions are confounded by complex effects of damselfish on composition of algae, coral injury, coral recruitment, nutrient conditions, etc. (e.g. Kaufman 1977; Russ 1987)

Table 3 Comparison of evidence for coral–algal competition based on natural experiments and correlations in abundance. Studies are organised chronologically within approach or theme. Although more studies could be included, list has been limited to those that specifically invoke coral–algal competition, have been cited in that context, or that we consider noteworthy. “Natural experiment” refers to studies with a specific comparison, but where treatments were not allocated or applied by researchers; in some cases they are human impacts such as fishing pressure or eutrophication. In most cases, *Diadema* die-off occurred against a background of overfishing. Where possible, outcome (O) of interaction is summarised as: A Algae overgrew corals; B no change; C corals overgrew algae; impacts are not summarised as causality is intrinsically confounded (see text). Methods, evidence, comments, functional groups and abbreviations as for Table 1. Most natural experiments also include or imply negative correlations in abundance of corals and algae. Except where noted, all correlation studies listed indicate inverse relationships between cover of algae and corals, although not necessarily identified as such by authors

Reference	Location, region	Outcomes, methods and evidence	Algal taxa/functional group	Coral taxa/life form
O				
Natural experiment (Algae): Crossland (1981)	H. Abrolhos, Western Australia	Algae present or absent; coral growth reduced when algae present	<i>Sargassum</i> and <i>Turbinaria</i> ; <i>Eucheuma</i> and <i>Laurencia</i> / Leathery; Cort Macro	<i>Acropora</i> and <i>Pocillopora</i> spp./Branching
Natural experiments (Herbivory): Potts (1977) ^a	Heron Island, GBR	A B	Unspecified/Filament	<i>Acropora palifera</i> / Branching
de Ruyter van Steveninck and Bak (1986)	Curacao, Caribbean	A	<i>Lobophora</i> ; <i>Dictyota</i> ; <i>Halimeda</i> ; <i>Valonia</i> ; <i>Wrangelia</i> ; turfs/Cort Foliose; Artic Calc; Filament; Crustose	<i>Agaricia agaricites</i> +21 spp. listed/Foliose; Massive; Branching; Encrusting
Liddell and Ohlhorst (1986)	Jamaica, Caribbean	B	<i>Diadema</i> die-off; cover before and after, along depth gradient; changes in coral cover variable, even increased.	Unspecified; <i>Acropora</i> / Branching
Littler and Littler (1997a)	Great Astrolabe Reef, Fiji	A C	High and low fishing pressure; coral recruits could overgrow turfs, but turfs could also exclude recruits; temporal and spatial correlation, cover	<i>Acropora</i> / Branching?; Recruits
Natural experiments (herbivory and disturbance): Hughes (1989, 1994, 1996)	Rio Bueno, Jamaica	A	<i>Diadema</i> die-off and hurricane: temporal and spatial negative correlations in algal and coral cover, and coral recruitment. Effects variable with coral life form <i>Diadema</i> die-off, hurricane, eutrophication (review); algae increased with coral decreases	<i>Agaricia</i> spp. + 20 spp. listed/Most forms
Goreau (1992)	Jamaica, Caribbean	A	<i>Dictyota</i> ; <i>Padina</i> ; <i>Halimeda</i> ; <i>Lobophora</i> ; and others/ Filament; Crustose; Cort Foliose (Creep, Upright); Artic Calc; Leathery <i>Lobophora</i> ; <i>Ceramium</i> ; <i>Dictyota</i> ; <i>Chaetomorpha</i> ; <i>Halimeda</i> ; <i>Sargassum</i> / Cort Foliose; Filament; Artic Calc; Leathery	55 spp. listed/Most forms

Table 3 (Continued)

Reference	Location, region	Outcomes, methods and evidence		Algal taxa/functional group	Coral taxa/life form
			O		
Steneck (1994)	Discovery Bay, Jamaica; St. Croix, Caribbean	A B	<i>Diadema</i> die-off, hurricane; temporal and spatial negative correlations in cover of varying strength, also recruits	<i>Dictyota</i> ; <i>Laurencia</i> ; <i>Lobophora</i> /Cort Foliose; Cort Macro; Crustose	8 spp. listed/Branching; Massive; Foliose
Shulman and Robertson (1996)	Panama, Caribbean	A	<i>Diadema</i> die-off, bleaching; temporal negative correlation of cover of corals and algae over 7 years; some corals no change	<i>Dictyota</i> ; <i>Halimeda</i> /Cort Foliose; Artic Calc	<i>Agaricia agaricites</i> ; <i>Agaricia tenuifolia</i> ; <i>Porites</i> spp.; <i>Millepora</i> spp./Foliose; Massive; Digitate
Rogers et al. (1997)	Virgin Islands, Caribbean	A	Hurricane, herbivorous fish; decrease in corals and increase in algae over 7 years	<i>Dictyota</i> ; <i>Liagora</i> /Cort Foliose; Cort Macro	<i>Montastrea annularis</i> ; <i>Agaricia agaricites</i> ; <i>Siderastrea siderea</i> ; <i>Montastrea cavernosa</i> /Massive; Foliose
Natural experiments (disturbance): Banner (1974)	Kaneohe Bay, Hawaii	A	Eutrophication gradient: categorisation of algal and coral abundances, showing inverse relationship	<i>Dictyosphaeria cavernosa</i> /Foliose	<i>Porites compressa</i> /Digitate
Birkeland (1977)	Panama, Pacific		Oligotrophic and upwelling areas; survival of recruits higher with less algae; filamentous algae trap sediments which kill corals	Unspecified/Filament	Unspecified/Recruits
Smith et al. (1981)	Kaneohe Bay, Hawaii	A	Eutrophication gradient and before-after diversion: algal biomass, cover of corals and algae. Little relevant data included	<i>Dictyosphaeria cavernosa</i> /Foliose	<i>Porites compressa</i> /Digitate
Wittenberg and Hunte (1992)	Barbados, Caribbean		Eutrophication gradient; higher coral juvenile size and survival where algae and sediments less abundant	Unspecified	<i>Porites</i> ; <i>Diploria</i> ; <i>Agaricia agaricites</i> /Massive; Foliose
Hunter and Evans (1994)	Kaneohe Bay, Hawaii	A C	Natural experiment; spatial and temporal correlations, cover; several reversals in abundance; coral not inversely related to algae at some sites	<i>Dictyosphaeria cavernosa</i> /Foliose	5 spp. listed/Most forms
Genin et al. (1995)	Gulf of Eilat, Red Sea		Eutrophication gradient; coral condition inversely related to abundance of algal bloom	<i>Enteromorpha</i> /Filament	^b /Branching; Massive
Miller and Hay (1996)	North Carolina, Atlantic		Inshore-offshore gradient; temperate; algal cover inversely related to coral abundance	See Table 1	See Table 1
Connell et al. (1997)	Heron Island and Jamaica	A	Cyclones; very long term (30 years), negative correlations in algal and coral cover and coral recruitment	Unspecified	Unspecified + Recruits
Spatial and temporal correlations: van Den Hoek et al. (1978)	Curacao, Caribbean		Spatial correlation in cover: depth, etc. gradients	Various (all listed)/All groups	Various (all listed)/Most forms

Author (Year)	Location	Spatial correlation in cover: reef flat zones	Various (all listed)/All groups	Various (all listed)/Massive; Foliose; Branching; Various/ Branching; Massive
Morrissey (1980)	Inshore, central GBR	Spatial correlation in cover; among 9 locations	Unspecified	Massive; Foliose; Branching
Benayahu and Loya (1981)	Gulf of Eilat, Red Sea	Spatial and temporal correlations in cover	<i>Dictyota</i> ; <i>Lobophora</i> ; <i>Sargassum</i> /Cort Foliose; Leathery	Various/ Branching; Massive
Coles (1988)	Arabian Gulf	Spatial correlation in cover, along stress gradient	<i>Sargassum</i> ; <i>Turbinaria</i> ; <i>Hormophysa</i> /Leathery	5 spp. listed/ Branching; Massive
Sheppard (1988)	Red Sea, Arabian Sea, the Gulf	Spatial correlation in cover	<i>Dictyosphaeria cavernosa</i> /Foliose	46 spp. listed/ Most forms
Stimson et al. (1996)	Kaneohe Bay, Hawaii	Spatial correlation in cover: coral cover <i>not</i> inversely related to algal canopy within or between reefs	<i>Sargassum</i> /Leathery	<i>Porites compressa</i> /Digitate
McCook (1999)	Inshore, central GBR			Various

^a Comparisons using damselfish territories are confounded (see Table 2)

^b *Stylophora pistillata*, *Acropora* spp., *Pocillopora verrucosa*, *Favia*, *Favites*, *Porites* spp., *Fungia granulosa*, *Fungia horrida*, *Ctenactis echinata*

indicated declines in corals, presumably in response to the general increase in algal abundance following herbivore exclusion. However, the effects on corals were often variable, or relatively minor. For example, two of the most cited papers in this context are Sammarco (1982), in which removal of *Diadema* alone led to *increased* coral abundance, and Lewis's (1986) classic herbivore exclusion experiment, in which the resulting decline in coral cover was only about 2% (coral abundance was initially relatively low). Inevitably, most of these experiments were relatively small scale and short term, and thus involved smaller, faster growing algal taxa (filamentous and corticated macrophytes).

Importantly, herbivore experiments (and natural experiments involving herbivore changes) are fundamentally tests for herbivore effects, not competition (and are intended as such by their authors). Although effects of algae on corals are generally the most or even the only reasonable interpretation, alternative explanations remain possible. For example, the herbivore exclusion procedure may produce artifacts detrimental to corals (e.g. shading, reduction in flow; not all experiments included procedural controls). Declines in corals could also result from the incidental exclusion of predators that would otherwise restrict corallivores (e.g. gastropods).

"Natural experiments" and correlative studies

Considerably more evidence comes from the numerous comparisons of coral and algal abundance during "natural experiments" or along gradients, or simple inverse relationships between coral and algal abundance in space or time (Table 3). Many of these comparisons have the advantage of wider generality than direct, planned experiments, due to larger spatial or temporal scales. However, as stated previously, causality is intrinsically more ambiguous, since the correlations observed may be coincidental or consequential, rather than causal.

For example, Crossland's (1981) comparison of coral growth in the presence and absence of canopy-forming algae provides valuable and widely cited evidence for competitive inhibition by shading. However, separation of corals into shaded and unshaded was retrospective, since algae appeared in some plots and not others. Further, there was no evidence that the differences were caused specifically by shading, rather than, for example, abrasion by the algae, or by other unknown factors. Algal shading was assumed to be the cause of reduced coral growth, with the differences in algal growth unexplained, but there is no a priori evidence that causality might not be reversed (algal growth reduced as a consequence of coral growth, in turn due to unknown factors), common (same factor/s cause increased algal growth and decreased coral growth), or even coincidental (unrelated factors cause coral and algal differences). Thus, other unmeasured differences between plots, such as variations in light, nutrient,

Table 4 Comparison of direct observations of coral-algal interactions or contacts. Studies that provide relatively detailed and small-scale descriptions or photographs of coral-algal interactions. Methods, evidence, comments, functional groups and abbreviations as for Table 1, outcomes (O) as for Table 3

Reference	Location, region	Methods and evidence	Algal taxa/functional group	Coral taxa/life form
Fishelson (1973)	Eilat, Red Sea	(Photograph) Coral regeneration by overgrowth of areas colonised by algae	Various; esp. <i>Dichotrix</i> ; <i>Sphacelaria</i> ; <i>Lobophora</i> /Filament; Cort Foliose (Creep)	^a /Branching; Massive
Banner (1974)	Kaneohe Bay, Hawaii	(Photograph) Algal overgrowth of corals	<i>Dictyosphaeria cavernosa</i> /~Foliose	<i>Porites compressa</i> /Digitate
Birkeland (1977)	Panama, Pacific	(Photograph) Algae reduce recruit survival and trap sediment	Unspecified/Filament	Unspecified/Recruits
Bak and Engel (1979)	Curacao, Caribbean	(Photograph) Algal overgrowth of 20% recruits	<i>Porolithon</i> and unspecified/ Crustose; Filament	<i>Agaricia agaricites</i> + 21 spp. listed/Recruits
Lewis (1986)	Belize, Caribbean	(Photograph) See Table 2	See Table 2	See Table 2
Hughes et al. (1987); Hughes (1994)	Jamaica, Caribbean	(Photograph) Algal overgrowth of corals	See Table 3	See Table 3
de Ruyster van Steveninck et al. (1988b)	Curacao, Caribbean	(Photograph) Algal growth reduced in close proximity to corals	<i>Lobophora</i> /Cort Foliose (Creep)	<i>Agaricia</i> ; <i>Meandrina</i> ; <i>Mycetophyllia</i> ;
James et al. (1988)	Bahamas, Atlantic; St. Croix, Barbados, Antilles, Caribbean	(Photograph) <i>Peysosmellia</i> overgrows and kills corals	<i>Peysosmellia</i> /Crustose	<i>Stephanocoenia</i> /Foliose; Massive; Encrusting
Lapointe (1989)	Caribbean	(Photograph) Algal overgrowth of coral	<i>Cladophoropsis</i> ; <i>Cladophora</i> /Filament	<i>Acropora cervicornis</i> ; <i>Acropora palmata</i> ; <i>Montastrea annularis</i> /Branching; Massive Unspecified
Stimson et al. (1996)	Kaneohe Bay, Hawaii	(Photograph) Algal overgrowth of coral	<i>Dictyosphaeria cavernosa</i> /Foliose	<i>Porites compressa</i> /Digitate
Keats et al. (1997)	Indo-Pacific	(Photograph) CCA overgrowth of coral	<i>Pneophyllum conicum</i> /Crustose	<i>Porites</i> spp./Massive
Littler and Littler (1997a)	Great Astrolabe Reef, Fiji	(Photograph) Coral recruits overgrew turfs; turfs overgrew adult corals	See Table 3	See Table 3
Littler and Littler (1997b)	Caicos Island, Caribbean	(Photograph) Algae killed coral tissue allelochemically	<i>Dasyopsis spinuligera</i> /Filament or Cort Macro?	<i>Madracis decactis</i> /Digitate
Antonius (1999)	Belize +?; Caribbean	(Photograph) Crust overgrowth of coral	<i>Metapeyssonmellia corallepida</i> /Crustose	<i>Millepora complanata</i>
Finckh (2004)	Funafuti Atoll, Pacific	Algal overgrowth of corals	<i>Lithothamnion</i> /Crustose	<i>Pocillopora</i> ; <i>Heliopora</i> ; <i>Porites</i> /Branching
Smith et al. (1981)	Kaneohe Bay, Hawaii	Algal overgrowth of corals	<i>Dictyosphaeria cavernosa</i> /Foliose	<i>Porites compressa</i> /Digitate
Chadwick (1988)	Kaneohe Bay, Hawaii	Algal overgrowth of coral	<i>Dictyosphaeria cavernosa</i> and CCA/Foliose; Crustose	<i>Fungia scutaria</i> /Mushroom
Wittenberg and Hunte (1992)	Barbados, Caribbean	Algal overgrowth of juvenile corals	Unspecified	<i>Porites astreoides</i> ; <i>Agaricia agaricites</i> ; <i>Diploria</i> spp./Massive; Foliose
Tanner (1995)	Heron Island, GBR	Contact with algae reduced coral growth	See Table 1	See Table 1
Shulman and Robertson (1996)	Panama, Caribbean	Bleaching of corals underneath algae	See Table 3	See Table 3
Lirman (2001)	Florida, Caribbean	Polyp retraction and overgrowth near algae	See Table 2	See Table 2

^a*Stylophora pistillata*, *Pocillopora danae*, *Acropora*, *Favia favaus*, *Platygyra lamellina*, *Favites* spp., *Goniastrea pectinata*, *Lobophyllia corymbosa*, *Millepora dichotoma*, *Porites lutea*

sediment or herbivory regimes, may have contributed to the differences in both algal abundance and coral growth rates.

Similarly, in Potts' (1977) demonstration of reduced coral growth inside damselfish territories, corals were not randomly allocated to treatments, but selected by the damselfish, presumably non-randomly (territory boundaries also changed during the study, so that some corals changed treatments). The damselfish may have selected less vigorous corals, or even have damaged the corals directly (Kaufman 1977). Further, aside from algal abundance, damselfish modify numerous aspects of their territories, including nutrient regime and algal composition (Russ 1987), which may modify coral growth rates. Thus, although valuable, these results should not be taken uncritically as evidence that the algae inhibited coral growth.

Importantly, even where abundant algae have replaced formerly abundant corals, the major cause of coral mortality may be external disturbances, rather than direct competition from the algae (e.g. fresh-water kills in Kaneohe Bay: Smith et al. 1981; Kinsey 1988; Hunter and Evans 1994; hurricane at Discovery Bay: Hughes 1994). Thus, although corals and algae may be competing for space, and competition may explain the algal bloom when corals are removed, the algae may not have directly outcompeted the corals.

Particular caution is required in interpreting causality in studies based on correlations in cover of algae and corals (Table 3). Despite the general assumption that the inverse correlations are caused by competition (e.g. Benayahu and Loya 1981), the patterns may simply reflect coincident differences in other factors influencing their distributions, or causality may even be reversed. For example, offshore to inshore reversals in coral and algal abundance could be due to coral intolerance of inshore turbidity and algal susceptibility to the abundant herbivores on offshore reefs (coincident causality; e.g. McCook 1996, 1997). The same pattern could also arise because corals are killed by inshore sediment loads, allowing algae to persist (Umar et al. 1998).

Several of the other studies listed (Table 3) warrant particular mention. The relatively long time span of temporal comparisons by Shulman and Robertson (1996; 7 years), Connell et al. (1997; 30 years), Rogers et al. (1997; 7 years) and the long time span and broad coverage of some of the *Diadema* die-off studies (e.g. Hughes et al. 1987; Hughes 1989, 1994, 1996; 17 years; Steneck 1994; 9 years), make them particularly valuable, especially since most include considerable background data and evidence for the competitive nature of the changes documented. Historical synthesis of coral and algal abundances and terrestrial runoff in Kaneohe Bay suggest that changes in reef composition involve complex and uncertain interactions between fresh-water kills, eutrophication, sedimentation and coral–algal competition (Hunter and Evans 1994; 20 years; in contrast Smith et al. 1981 and Banner 1974 include little hard data on coral or algal abundances).

Direct observations of apparent competition

Finally, evidence for coral–algal competition comes from numerous direct observations of small-scale interactions, many supported by photographs (Table 4; Fig. 1), in which corals appear to be overgrown by algae. Although convincing, such observations do not necessarily prove that the algae are killing the coral. Any area of coral tissue killed by other causes (e.g. corallivorous fish or invertebrate feeding, temporary sediment burial, bleaching) will generally be rapidly colonised by algae, whereas adjacent healthy coral tissue may continue to vigorously defend itself from algal recruitment or vegetative overgrowth. Thus, close matches between coral tissue damage and algal overgrowth may not indicate algal competitive success, but rather the successful competitive exclusion of algal growth from areas of healthy coral tissue (de Ruyter van Steveninck et al. 1988b; McCook 2001), unless experimental evidence is also available.

Several of the listed observations illustrate the variability of coral–algal interactions. Littler and Littler (1997a) provide contrasting photographs of coral recruits apparently overgrowing filamentous turf algae, and of filamentous turfs apparently killing adult corals. Littler and Littler (1997b) appear to demonstrate algae overgrowing and killing healthy coral tissue by means of allelochemicals, a process otherwise undocumented (but see also Fig. 1D; de Nys et al. 1991 for soft corals). De Ruyter van Steveninck et al. (1988b) document inhibition of algal growth rates by proximity to corals, the only detailed demonstration of coral effects on algae. Finally, Coyer et al. (1993) and Lirman (2001) noted polyp retraction in response to algal brushing, providing otherwise scarce evidence for the mechanisms of competition.

Discussion of evidence: general points

Overall, there is little evidence that unambiguously demonstrates competition between corals and reef algae, and very little demonstrating competitive overgrowth of corals by algae. Only 7 of the 57 papers reviewed provided direct experimental tests for competition. Much of the available evidence is indirect, anecdotal or correlative, and provides little understanding of the processes by which algae may replace corals. Interpretations of algal competitive superiority are frequently justified by citing one of a limited number of specific studies (in particular, Birkeland 1977; Potts 1977; Crossland 1981; Smith et al. 1981; Sammarco 1982; Lewis 1986), many of which were not designed to test competition. In some cases papers have been cited that have no relevant first-hand evidence, but merely refer to other studies (usually one of the above), or that include no more than passing speculation about the process.

Nonetheless, competition between corals and algae generally seems the most realistic explanation of most of the available evidence. Despite the limitations of that evidence, the breadth and range of observational

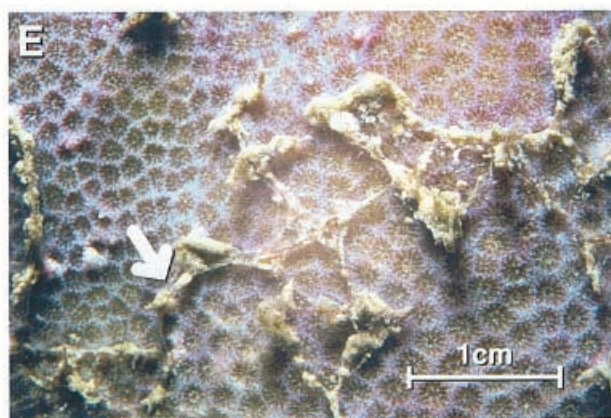
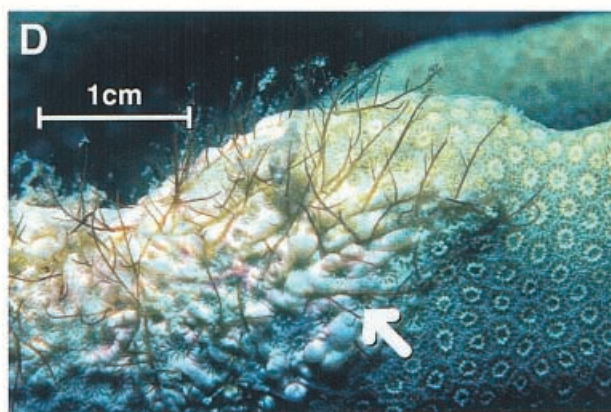
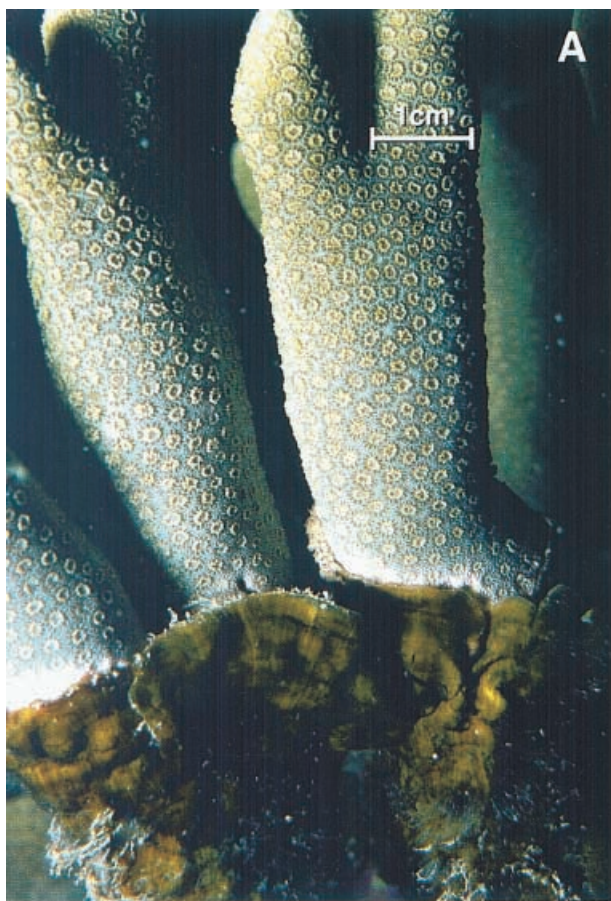


Fig. 1 Coral–algal interactions: examples of a range of interactions between corals and algae. **A** Overgrowth of coral (*Porites cylindrica* in this case) by the brown alga *Lobophora variegata*, a widespread phenomenon, especially on Caribbean reefs. **B** Same coral showing bleached tissue after removal of algae. Experimental removals of either coral or algae near boundary showed that both algae and corals inhibit each other's growth (inshore GBR; Jompa and McCook, unpublished data). **C** Shading by *Sargassum* canopy protected corals from bleaching damage during 1998 mass bleaching: right side of *Porites lobata* shown was underneath the *Sargassum* canopy, and was not bleached, whereas left side was not shaded and was bleached (inshore GBR; experimental removal of canopy demonstrated causality: Jompa and McCook 1998). **D** Coral tissue death following overgrowth by filaments of the red alga *Corallophila huysmansii*, possibly due to chemical effects (*P. cylindrica*, inshore GBR); arrow shows swollen coral tissue around algal filaments. **E** Substantial amounts of sediments and mucus adhering to individual filaments of *Anotrichium tenue* (arrow; Ceramiales, Rhodophyta) overgrowing *P. lobata* (inshore GBR). It appears that coral mucus production could effectively remove settling sediment particles except where they were trapped by algal filaments. This secondary effect of algae appeared to significantly increase damage to underlying coral tissue

and correlative studies are consistent with coral–algal competition as a widely general structuring process.

However, the interaction is also highly variable in mechanism and outcome, and the detailed processes and mechanism of coral–algal competition warrant careful scrutiny. Many of the studies listed showed variable effects or outcomes not limited to inhibitory effects of algae on corals (~16 of 43 studies in Tables 1, 2 and 3). Corals can inhibit algal growth (de Ruyter van Steveninck et al. 1988b; McCook 2001) or even overgrow and kill the algae (e.g. Meesters and Bak 1993; Meesters et al. 1994, 1997). Algae may have no effects or even positive effects on corals (Jompa and McCook 1998; Heyward and Negri 1999) and overgrowth may not lead to coral death. Many areas experience seasonal blooms of ephemeral brown algae (e.g. *Dictyota*, *Hydroclathrus*, *Chnoospora*, *Colpomenia*) which entangle and overgrow corals for weeks to months, without causing significant harm to the coral population (Coles 1988, personal observations). Competitive superiority is by no means fixed: turf algae may be both aggressive to or overgrown by live corals (Potts 1977 c.f. Fishelson 1973; Bak et al. 1977) and may exclude or be overgrown by coral recruits under different circumstances (Littler and Littler 1997a). Crustose corallines appear relatively invasive and aggressive to corals (Table 4), but may also facilitate coral settlement (Heyward and Negri 1999).

In particular, evidence for algal overgrowth as the direct cause of coral mortality is very limited. Algal replacement may be confounded with algal competitive superiority at the scales of both populations and polyps (previous sections). Coral mortality for any reason is generally followed by colonisation by algal turfs, indicating that corals widely inhibit algal cover. Where algae are found overgrowing dead coral (polyps or populations), it cannot be assumed that the algae are the cause, not simply the consequence, of coral mortality (without experimental evidence, e.g. Hughes 1989; Coyer et al.

1993 in Table 1). The interaction is apparently competitive, since the algae have been released from competitive inhibition by the corals, but the corals may have been the superior competitor (in the absence of disturbance). It is likely that external disturbances and competition will interact: stressed corals will probably be less successful competitors, or algae may colonise outward from patches killed by external events. It is also important to distinguish between competitive abilities of established and recruiting corals. Even if competitively inferior to established corals, algae, once established by disturbance, may successfully pre-empt space and inhibit coral recruitment, preventing recovery from disturbances (such as bleaching, storms or crown of thorns; Hughes 1996; Connell et al. 1997). These distinctions among different competitive processes may have important consequences in terms of management of reef degradation (McCook 1999).

It is important that algal replacement of corals be viewed in the context of herbivore effects on algal abundance. Much of the evidence for algal effects on coral come from studies of herbivore reductions (herbivore exclusions, *Diadema* die-off and overfishing and damselfish studies). Herbivory is a key factor mediating the effects of algae on corals, since the standing crop or biomass (per unit area) of algae is largely controlled by herbivores (reviews by Hatcher 1983; Steneck 1988; Carpenter 1997; McCook 1999) and the ability of algae to compete will depend on the accumulation of sufficient biomass to overgrow corals (Miller and Hay 1996, 1998).

However, it is also noteworthy that algal replacement of corals does not necessarily require reductions in herbivory (various papers in Table 3). The area occupied by algae can increase dramatically and rapidly in response to coral death without significant changes in herbivory (e.g. Williams 1986 for crown of thorns starfish damage, Diaz-Pulido and McCook unpublished data for coral bleaching). The role of substrate availability is significant in the context of the relative roles of nutrients and herbivory during phase shifts (Lapointe 1997; Hughes et al. 1999). Although herbivores may control algal abundance in terms of biomass per unit area, area occupied is also controlled by disturbance and competitive inhibition by corals. Nutrients can only affect algal growth, which may or may not accumulate as increased biomass, depending on herbivory rates. Herbivory can only affect algal standing crop or biomass (per unit area), although this may lead to changes in algal area by increased vegetative or sexual colonisation. Substrate availability, determined by competitive inhibition by corals and disturbance, will affect algal areal abundance, with potential subsequent competitive effects on coral recovery (Miller 1998; McCook 1999).

The geographic coverage of the evidence is patchy, even if observational and correlational studies are included. Studies from the Caribbean are prevalent (27 + 3 from temperate west Atlantic), with a few from the Pacific (10), GBR (4), Red Sea/Arabian Sea/Gulf (6), and a single study from Japan. We found only three relevant studies

from the Indian Ocean and none from Southeast Asia, where coral diversity is greatest. Even within the regions covered, a few specific locations dominate (e.g. Discovery Bay, Jamaica). Notwithstanding the various limitations of the data, there is no indication of geographic differences in the nature of coral–algal interactions.

Taxonomic coverage is inevitably very limited, but, more critically, a large proportion of studies do not specify the competitors, even to functional groups (none of the studies reviewed noted lodging of herbarium specimens of algal taxa involved). Thus only a few, limited generalisations about the variability in processes or mechanisms of interactions are possible.

In general, few algal taxa appear able to actually overgrow healthy corals by direct contact. Records of overgrowth predominantly involve *Lobophora* (Fig. 1A, B), *Dictyota*, *Halimeda*, *Dictyosphaeria* and crustose coralline algae, as well as a few specific, filamentous red algae (Table 4). However, this may simply reflect the relative abundance of these taxa, since the first three genera are particularly abundant in the Caribbean (refs. in Diaz-Pulido and Diaz 1997). With the exceptions of a few, apparently allelopathic species (Littler and Littler 1997b; Fig. 1D) and of blue-green algae that induce coral diseases (e.g. Antonius 1988), we propose that filamentous algae and large, leathery algae can rarely colonise healthy coral tissue, and that observations of such overgrowth often result from prior coral injury or death.

Mechanisms of competitive inhibition between corals and algae

Few studies have explicitly considered the mechanisms or processes by which algae and corals compete, beyond widespread reference to “overgrowth” or “metabolic costs”. These processes will inevitably vary with circumstances such as disturbance history, herbivory, nutrients, etc., and especially with the life history and structure of both corals and algae. A coral competing for space on a reef will be subject to very different stresses in response to overgrowth by a creeping, foliose alga (e.g. *Lobophora*; Fig. 1A, B) or a large, canopy-forming alga (e.g. *Sargassum* species with a small attachment holdfast and no vegetative dispersal; Fig. 1C). The ability of corals to compete with algae also varies significantly among coral life forms. Hughes (1989) observed that encrusting or platelike (foliose) *Agaricia* was more susceptible to algal smothering than massive colonies (also Shulman and Robertson 1996).

As a first step toward a framework for understanding the variability in mechanisms of these interactions, we list the possible processes by which algae can inhibit corals and vice versa (Table 5, derived from Schoener 1983; Carpenter 1990; Lang and Chornesky 1990; Olson and Lubchenco 1990; Karlson 1999), and then consider the circumstances under which these processes can take place (Table 6). It can be assumed that space and light

are the limiting resources for which corals and algae compete (Carpenter 1990), since other resources, such as nutrients, are unlikely to be significantly depleted by competitors. There are six distinct mechanisms, listed in Table 5, by which algae are able to directly compete with corals for space or light. A number of studies refer to energetic or metabolic costs of interactions as a competitive process (leading to e.g. reduced growth or reproduction), but we consider these costs are actually consequences of the interaction, not a kind of competition. Although not discussed here, it is worth emphasising that corals and algae may have numerous indirect effects on each other. Such effects may increase the impact of the interaction (e.g. sediment trapping shown in Fig. 1E).

Clearly, different species of coral and algae will be differently capable of, or susceptible to, the different mechanisms listed in Table 5, depending on factors such as size, structure, shape, growth form, growth patterns, polyp and tentacle size, and sexual and vegetative reproductive mechanisms, as well as environmental factors such as nutrients, herbivory and light levels. Where feasible, coral–algal interactions should therefore be considered on a case by case basis, and this approach may be effective where a few key species are especially important. For example, on Caribbean reefs, interactions between a limited set of corals (e.g. *Montastrea* spp., e.g. *M. annularis*, *Agaricia agaricites*, *Acropora tenuifolia*, *Acropora palmata* and *Porites astreoides*) and algae (e.g. *Dictyota* spp., *Lobophora variegata* and *Halimeda* spp., e.g. *H. opuntia*) may account for most of the significant interactions in terms of shifts in reef status.

Overall, however, a species-by-species (or even genus-by-genus) approach is unlikely to yield effective summary of the possible interactions, for several reasons. Firstly, the enormous species (or genus) diversity of both corals and algae (approx. 330 and 500 spp. respectively for the GBR) means that a species-by-species (or even genus-by-genus) approach is simply not practical. Further, some species of both corals and algae have highly plastic growth forms with distinctly different competitive potential (e.g. *Lobophora*, an alga widely important in coral overgrowth, may have crustose, creeping, leafy or upright, bushy habits, depending on grazing regimes, etc: de Ruyter van Steveninck et al. 1988a; Littler et al. 1989; Diaz-Pulido and Bula-Meyer 1997). Finally, many species of algae are impractical to identify and quantify at relevant scales for ecological studies, since they occur as assemblages (e.g. turfs), rather than as clearly distinguishable taxa.

We propose that algal effects on corals can be effectively considered in terms of algal functional groups, based on those of Littler (1980), Littler and Littler (1984) and Steneck and Dethier (1994), and coral life forms (de Vantier 1986). By considering each combination of algal functional group and coral life form, a limited subset of the six mechanisms can be seen to be possible or likely (Table 6). This interaction matrix provides a preliminary but useful basis for structuring

Table 5 Mechanisms for competition between corals and algae. Adapted from Schoener (1983); Carpenter (1990), Olson and Lubchenco (1990), Lang and Chornesky (1990) and Karlson (1999), modified for corals and algae specifically

Algal inhibition of corals	Coral inhibition of algae	Includes:	Categories
Overgrowth	Overgrowth	Smothering;	Direct, interference, overgrowth (Fig. 1A, B)
Shading ^a	Shading	Overtopping;	Indirect, exploitative, consumptive (Fig. 1C)
Abrasion	Abrasion	Whiplash ^b ;	Direct, interference, encounter
	Stinging, etc.	including sweeper tentacles and polyps, mesenterial filaments	Direct, interference, encounter
Chemical ^c	Chemical	Allelopathy	Direct, interference, chemical (Fig. 1D?)
Pre-emption/ Recruitment barrier ^d	Space pre-emption		Direct, exploitative, consumptive
Epithelial sloughing ^e	Mucus secretion		Defensive mechanism

^aShading or overtopping may include establishment of dense canopy, with numerous effects on the chemical and physical conditions, hydrodynamics, etc

^bWhiplash, often cited as damaging corals, will generally also be very detrimental to the softer algal tissue

^cAllelopathic chemical effects have been demonstrated on soft corals (de Nys et al. 1991) and hard corals (Littler and Littler 1997b); see our Fig. 1D

^dCanopy-forming macrophytes will actually occupy little of the substrate, but may still form an effective barrier to coral settlement

^eEpithelial sloughing and mucus secretion are defence mechanisms against epibiotic colonisation, rather than mechanisms for expansion (Lang and Chornesky 1990; Littler and Littler 1999; personal observations)

the variability in effects of algae on corals, with several immediate general implications. For example, a comparison of the variation between algal groups (rows) and between coral life forms (columns) in Table 6 suggests that potential competitive processes are more dependent on the properties of the algae than the corals. There

are apparently significant qualitative differences among algal groups in terms of their potential competitive interactions. Thus research into algal overgrowth of corals would benefit from more detailed identification and description of the algae, at least to functional groups.

Table 6 Matrix of competitive interaction mechanisms by functional group and life form. Proposed mechanisms for algal effects on corals, based on algal functional group (as for Table 1) and coral life forms. Each cell contains two rows, top row indicating the competitive mechanisms we propose are probable or common processes, second (italicised) row indicating processes we suggest occur but are less important or common; entries are intended to be

representative not exhaustive, and amount to hypotheses, not literature review. *O* Overgrowth; *S* shading; *A* abrasion; *C* chemical; *P* pre-emption; *R* recruitment barrier; *SI* epithelial sloughing; – no mechanism applicable. *Superscripts* indicate references for examples; * indicates mechanisms suggested by our own observations or unpublished data

Algal functional groups	Coral life forms							
	Branching	Digitate	Tabulate	Encrusting	Foliose	Massive	Mushroom	Recruits
Microalgae	O ¹ ; C ²	O; C ²	O; C ²	O; C ²	O*; C	O ^{3,4} ; C	–	O; C
Filamentous	–	–	–	–	–	–	<i>O; C</i>	–
Foliose	<i>O^{1,5,6,7,8,9}; C*</i>	<i>O; C¹⁰</i>	<i>O; C</i>	<i>O; C</i>	<i>O¹¹; C</i>	<i>O^{8,11}; C</i>	–	<i>O¹²</i>
Upright corticated foliose	<i>O^{14,15}</i>	<i>O</i>	<i>O</i>	<i>O</i>	<i>O^{17,19,20}</i>	<i>O^{17,19}</i>	<i>O¹⁶</i>	<i>O; S; P^{17,22}</i>
Creeping corticated foliose	<i>O^{7,17,18}; A⁶</i>	<i>O; A</i>	<i>O</i>	–	<i>A</i>	<i>A</i>	<i>O²¹; A²¹</i>	–
Corticated macrophytes	<i>O^{7,18}</i>	–	–	O*	<i>O^{17,19}</i>	–	–	<i>O; S; P¹⁷</i>
Leathery macrophytes	–	<i>O</i>	<i>O*</i>	–	–	<i>O^{8,17,19,24}</i>	<i>O</i>	–
Articulated calcareous	<i>O²³; A</i>	<i>A</i>	<i>A</i>	<i>A</i>	<i>A</i>	<i>A</i>	<i>A</i>	<i>O; A; P/R²²</i>
Crustose	<i>S⁶</i>	<i>S*</i> ;	<i>S*</i> ;	<i>S*</i> ; A	<i>S*</i> ; A	<i>S*</i> ; A*	<i>S*</i>	<i>R; A</i>
	<i>O^{9,23}; A⁶</i>	<i>A</i>	<i>A*</i>	<i>O*</i>	–	<i>O*</i>	–	–
	–	<i>O</i>	<i>O</i>	<i>O</i>	–	–	–	<i>O; S; P²⁴</i>
	<i>O^{8,9}</i>	<i>O</i>	<i>O</i>	–	<i>O¹⁷</i>	<i>O^{8,17}</i>	<i>O</i>	–
	<i>O^{18,25,26}</i> ;	–	–	<i>O</i>	–	–	–	<i>O¹²; SI²⁸</i>
	<i>S^{25,26}</i>	<i>O</i>	<i>O</i>	–	<i>O</i>	<i>O^{26,27}</i>	<i>O¹⁶</i>	–

¹Littler and Littler (1997a); ²Antonius (1988); ³Kuta and Richardson (1997); ⁴Santavy and Peters (1997); ⁵Potts (1977); ⁶Miller and Hay (1996); ⁷Stachowicz and Hay (1999); ⁸Goreau (1992); ⁹Tanner (1995); ¹⁰Littler and Littler (1997b); ¹¹Sammarco (1980); ¹²Bak and Engel (1979); ¹³Birkeland (1977); ¹⁴Banner (1974);

¹⁵Smith et al. (1981); ¹⁶Chadwick (1988); ¹⁷Hughes (1996); ¹⁸Hughes et al. (1987); ¹⁹Lewis (1986); ²⁰Shulman and Robertson (1996); ²¹Coyer et al. (1993); ²²Steneck (1994); ²³Crossland (1981); ²⁴Hughes (1994); ²⁵Finckh (1904); ²⁶James et al. (1988); ²⁷Keats et al. (1997); ²⁸Littler and Littler (1999)

In contrast, comparison of the coral life forms suggests that the differences between adult life forms are largely quantitative: similar mechanisms are involved, but different life forms are more or less vulnerable. For example, massive corals may be more vulnerable than branching corals to whiplash by larger algal fronds, since the algae may become entangled in a branching coral, resulting in more damage to the algae than the coral. Within life forms, there is also likely to be considerable quantitative variation with both colony size and polyp size. Larger colonies are less liable to overgrowth or shading, and corals with larger polyps (or tentacles) may generally be able to better defend themselves against algae. Importantly, however, there are considerable qualitative differences between adult life forms (collectively) and coral recruits. Coral recruits appear vulnerable to more forms of algal competition than established corals.

The different combinations of interaction type and functional groups will have distinctly different consequences for the viability of coral populations. Few corals will survive direct overgrowth by creeping, prostrate algae, whereas many could adapt to shading by canopy-forming leathery algae, or could increase mucus production to shed recruiting filaments. Algal impacts on coral recruits may have severe consequences for the long-term maintenance of sustainable coral populations, even where the algae have little impact on adult corals (previous section).

We emphasise that Table 6 is not intended as complete or final, but as an initial attempt to organise the possible variability in the interaction. The lists indicate which processes we consider conceptually relevant to a particular combination of coral and algal types, with illustrations from the literature where possible. The paucity of detailed research means that many of the possible combinations have not been documented and Table 6 is not a literature summary. Entries are intended to be generally relevant, rather than exhaustive, and exceptions will occur. There are also several limitations to a scheme based on functional groups and life forms (Table 6). It does not directly incorporate the variation due to coral colony size or polyp size, nor the supply-side ecology of both algae and corals. For example, an algal canopy may serve as a barrier to release and settlement of broadcast spawning corals, but have little impact on recruitment of corals which brood planula larvae. Algal ability to colonise or overgrow corals will be enhanced for taxa which can spread and attach vegetatively, or which have wide dispersal and rapid growth. In contrast, algae that require large size and sexual reproduction for dispersal, or have limited dispersal distances (e.g. some species of *Sargassum*) will have limited opportunity to colonise substrate made available by disturbances. Such properties are only partly accounted for by the functional groupings.

Algal functional groups may also be inadequate summaries of algal properties under some competitive circumstances. During algal blooms or outbreaks, mas-

sive standing crops of ephemeral algae may accumulate (e.g. Banner 1974; Genin et al. 1995). These may create chemical and physical conditions (Raffaelli et al. 1998) for underlying corals that are not indicated by the functional group of the component algal taxa. Similarly, algae may often interact with corals as complex assemblages of taxonomically and structurally diverse algae, rather than as distinct taxa or functional groups. Examples of such assemblages include closely adherent creeping mats (~0.2–1 cm thick), tough, interwoven, turf mats (~2–10 cm thick), thick tangles of more delicate ephemerals (~20–50 cm thick), and distinct algal canopies (~10–200 cm high). In such cases it may be more appropriate to describe the assemblage than the component algae. Algal assemblage canopy height at least should be estimated and reported.

In terms of structuring the potential effects of corals on algae, coral polyp and tentacle size and colony size appear important, whereas we found the functional form/life form approach was less successful. Coral life form does influence competitive ability and some generalisations are possible. For example, tabulate corals will be more likely to shade competitors than encrusting or massive taxa (Hughes 1989). However, several of the mechanisms by which corals affect competitors (Table 5) are not related to life form, but to polyp and tentacle size, which may vary considerably within groups. The ability of coral recruits to settle on and overgrow different algal groups (crusts and turfs especially) will be important. The more complex matrix required to organise these effects is beyond the scope of this review. Corals will also have important indirect effects on algae, including in particular the provision of habitat for herbivorous fishes.

Conclusions

In summary, there is surprisingly little known about the causality and processes by which corals and algae interact, especially about the effects of algae on corals. There is little experimental evidence available, and most evidence is correlative or based on simple observations. The weight of that evidence suggests that competition between algae and corals is widespread on coral reefs, and largely mediated by herbivory. However, there is little evidence that where algae have replaced corals, algae are generally the cause, and not simply the consequence, of coral mortality.

Research into coral–algal interactions, especially algal overgrowth of corals, will benefit from more explicit consideration of the mechanisms by which the organisms interact, and the properties that influence those interactions. The potential impacts of algal overgrowth on recruiting corals deserve particular attention, as they may be critical to coral population viability. There is a need for improved description of algal competitors, particularly their taxonomy (as far as feasible) and structure including functional group, but ideally in-

cluding indications of standing crop and canopy structure (e.g. height). The consequences of this emphasis would include more meaningful understanding of the processes taking place, their variability, and hence their consequences in terms of severity of impact, and long-term community structure. This understanding should in turn improve our ability to interpret, predict and manage "phase shifts" in which abundant corals are replaced by algae (McCook 1999), with severe ecological, environmental, and economic consequences.

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