Coral Reefs (2015) 34:87–96
DOI 10.1007/s00338-014-1230-6

REPORT

Does seaweed–coral competition make seaweeds more palatable?

G. O. Longo · M. E. Hay

Received: 25 June 2014 / Accepted: 13 October 2014 / Published online: 25 October 2014

Abstract Seaweed–coral interactions are increasingly common on modern coral reefs, but the dynamics, processes, and mechanisms affecting these interactions are inadequately understood. We investigated the frequency and effect of seaweed–coral contacts for common seaweeds and corals in Belize. Effects on corals were evaluated by measuring the frequency and extent of bleaching when contacted by various seaweeds, and effects on a common seaweed were evaluated by assessing whether contact with coral made the seaweed more palatable to the sea urchin *Diadema antillarum*. Coral–seaweed contacts were particularly frequent between *Agaricia* corals and the seaweed *Halimeda opuntia*, with this interaction being associated with coral bleaching in 95 % of contacts. Pooling across all coral species, *H. opuntia* was the seaweed most commonly contacting corals and most frequently associated with localized bleaching at the point of contact. Articulated coralline algae, *Halimeda tuna* and *Lobophora variegata* also frequently contacted corals and were commonly associated with bleaching. The common corals *Agaricia* and *Porites* bleached with similar frequency when contacted by *H. opuntia* (95 and 90 %, respectively), but *Agaricia* experienced more damage than *Porites* when contacted by articulated coralline algae or *H. tuna*. When spatially paired individuals of *H. opuntia* that had been in contact with *Agaricia* and not in contact with any coral were collected from the reefs and offered to *D. antillarum*, urchins consumed about 150 % more of thalli that had been competing with *Agaricia*. Contact and non-contact thalli did not differ in nutritional traits (ash-free-dry-mass, C or N concentrations), suggesting that *Halimeda* chemical defenses may have been compromised by coral–algal contact. If competition with corals commonly enhances seaweed palatability, then the dynamics and nuances of small-scale seaweed–coral–herbivore interactions at coral edges are deserving of greater attention in that such interactions could scale-up to have important consequences for coral resilience and the persistence of reef structure and function.

Keywords Coral bleaching · Caribbean · *Halimeda opuntia* · Chemical defenses · Herbivory

Introduction

The global decline in coral cover and increase in macroalgal cover is augmenting the frequency of coral–seaweed competition in areas where seaweeds are no longer controlled by herbivores (Hughes 1994; Mumby and Steneck 2008; Bruno et al. 2009; Bonaldo and Hay 2014). Seaweeds may compete with corals via overgrowth, shading, abrasion, allelopathy, and indirect effects such as vectoring coral pathogens and predators or releasing compounds that destabilize the coral's beneficial microbiome (McCook et al. 2001; Nugues et al. 2004a; Smith et al. 2006; Rasher et al. 2011; Barott and Rohwer 2012; Nelson et al. 2013; Wolf and Nugues 2013; Rasher and Hay 2014).

Communicated by Handling Editor Mark Vermeij

G. O. Longo · M. E. Hay (✉)
School of Biology, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA
e-mail: mark.hay@biology.gatech.edu

Present Address:
G. O. Longo
Programa de Pós-Graduação em Ecologia, Dep. Ecologia e Zoologia, Universidade Federal de Santa Catarina, Campus Trindade, Florianópolis, SC 88040-900, Brazil

The outcomes of coral–seaweed contacts are dependent on the pair of interactors, both because corals differ in their ability to compete with seaweeds and seaweeds differ in the strength and mechanisms of their impact on corals (Jompa and McCook 2003; Nugues and Bak 2006; Rasher et al. 2011; Bonaldo and Hay 2014). As an example, some chemically rich seaweeds are allelopathic to corals with seaweeds differing in allelopathic potency and corals differing in their resistance to these effects (Rasher et al. 2011; Bonaldo and Hay 2014). However, these interactions are not static; seaweeds may also induce greater allelopathic potency following contact with a competing coral (Rasher and Hay 2014), and some corals chemically signal mutualistic fishes to remove allelopathic seaweeds contacting the coral (Dixson and Hay 2012).

The dynamic nature of seaweed–coral interactions and the costs and benefits involved in these interactions are not well investigated (Diaz-Pulido et al. 2009; Venera-Ponton et al. 2011; Bonaldo and Hay 2014; Rasher and Hay 2014) but could be critical for understanding coral to macroalgal phase shifts and for informed management of coral reefs. For seaweeds using allelopathic chemicals to damage corals, enhancing allelopathic potency when in contact with corals could compromise the seaweed's anti-herbivore defenses and leave the seaweed more susceptible to herbivores (Rasher and Hay 2014). However, if the same bioactive metabolites serve both as anti-herbivore defenses and as allelopathic compounds, then seaweeds inducing allelopathy could be even more herbivore resistant and even less likely to be removed by natural biotic processes.

A recent investigation on a Pacific coral reef demonstrated that the allelopathic red seaweed *Galaxaura filamentosa* induces more potent allelopathy following contact with the coral *Porites cylindrica*. However, this induced allelopathy co-occurred with a decline in the seaweed's anti-herbivore chemical defenses, demonstrating that: (1) this seaweed produces different compounds for allelopathy versus anti-herbivore defense; (2) the deployment of these compounds is dynamic and context dependent; and (3) there may be a trade-off between chemically mediated competitive ability and defense against consumers (Rasher and Hay 2014). If such a trade-off is common, then chemically rich seaweeds competing with corals may be more palatable than those not competing. Hence, critical aspects of seaweed–herbivore–coral interactions that are recognized as important for reef structure and function may be occurring most frequently at spatial scales of millimeters or centimeters at coral borders, a spatial scale that has not been sufficiently investigated.

If interactions at small spatial scales near coral borders are of overlooked importance, they might be especially relevant on Caribbean coral reefs where coral loss has been especially great (Gardner et al. 2003; Bruno et al. 2009) and where seaweed–coral interactions appear to have shifted more strongly in favor of seaweeds (Roff and Mumby 2012). Numerous reefs in the Caribbean are currently dominated by chemically rich seaweeds such as species of *Dictyota*, *Halimeda,* and *Lobophora* (Hughes 1994; Shulman and Robertson 1996; McClanahan et al. 1999; Edmunds 2002). With this shift to chemically rich seaweeds, contacts between seaweeds and corals became more common, increasing the importance of understanding the nuances of seaweed–herbivore–coral interactions at coral edges where seaweeds contact corals and where competition (especially, chemically mediated competition) may be most intense (Rasher et al. 2011; Andras et al. 2012; Dixson and Hay 2012).

Our goals in this study were to: (1) determine the most common seaweeds and corals physically interacting via contact on a reef in Belize; (2) determine how frequently seaweed–coral contacts were associated with coral bleaching; (3) compare the effects of different seaweeds on various corals; and (4) determine whether coral–seaweed contacts affected the palatability to herbivores of a common seaweed and whether this might occur due to changes in seaweed nutritional value or via other mechanisms.

Materials and methods

Study area

This study was conducted at Curlew Bank, Belize (16°46′N, 88°04′W), a part of the Mesoamerican Barrier Reef System that runs between Mexico and Honduras (Carter and Sedberry 1997). We investigated interactions in both a shallow area (3–6 m; consisting of patchy coral formations, mainly colonies of *Agaricia tenuifolia* and *Porites astreoides*, separated by flat areas of sand, coral rubble, and octocorals) and a deeper area (10–12 m; consisting of patchy coral formations, mainly *P. astreoides*, *Orbicella* spp. and *Agaricia* spp., separated by sand, coral rubble, and a dense cover of gorgonians). Prominent seaweeds in the shallow area were *Halimeda* spp., articulated coralline algae, and filamentous algal turfs, while in the deep area, *Lobophora variegata*, *Sargassum* sp., and *Halimeda* spp. were most common.

Surveys of seaweed–coral contacts

The frequency of seaweed–coral contacts was assessed with 20 m length video transects ($N = 12$ on the shallow reef; $N = 18$ on the deeper reef). Transects were spaced 2–4 m from each other (with no overlap of surveyed area), and every 2 m colonies of the corals *Agaricia*, *Pseudodiploria*, *Favia*, *Meandrina*, *Montastraea-Orbicella* (*M. cavernosa* and species of the former *M. annularis* complex), *Porites,* and *Siderastrea* were carefully investigated if they occurred within

1 m from each side of the transect tape (as in Barott et al. 2012). These colonies were video recorded from the top and from around the edge to assess the seaweed–coral contacts and determine whether contacts were associated with coral bleaching at the site of contact. When contacts occurred, seaweeds were pulled back from the coral to look for bleaching in areas of contact. Bleaching was noted because it is visually obvious and was a local response immediately adjacent to the area of algal contact; it can be assessed quickly in the field and is well correlated with the coral's photosynthetic efficiency (Rasher and Hay 2010; Rasher et al. 2011). Seaweeds were identified to the lowest taxonomic level possible from the videos. The extent of seaweed–coral contacts was evaluated using a top-view picture of each colony with a scale of known size, obtained from the videos. These images were analyzed with the software Image J (Abramoff et al. 2004) to determine the perimeter and area of contacts relative to the total perimeter and area of the colony (i.e., the proportion of coral perimeter and proportion of coral area in contact with seaweed).

Palatability trials

To evaluate whether coral contact affected seaweed palatability, we collected specimens of the green alga *Halimeda opuntia* growing in contact with the coral *A. tenuifolia* and a separate nearby *H. opuntia* (within 1–2 m) not in contact with any coral or other macro-organism. These species were chosen because they were both abundant and were the most common seaweed–coral pair contacting each other on the reefs. Individuals of the sea urchin *Diadema antillarum* with $\geq$10 cm test diameters (i.e., not including the spines) were collected from a depth of about 1.5 m in the lagoon behind the Smithsonian's Carrie Bow Cay Marine Station (16°48′N, 88°04′W). Sea urchins and seaweeds were collected from different locations because *D. antillarum* were uncommon on the fore-reef. We did, however, observe a few *D. antillarum* co-occurring with *H. opuntia* and *A. tenuifolia* on the reef sites we investigated. Additionally, prior to the large-scale die-off of *D. antillarum* in the early 1980s, *D. antillarum* were common on many reef slopes throughout the Caribbean, with densities varying from <1 to as many as hundred individuals per square meter; their feeding influenced algal abundance, distribution and productivity, coral recruitment, and bioerosion, and they commonly co-occurred with *Agaricia* and *Halimeda* species (Hay 1984; Lewis 1986; Lessios 1988). In the presence of predators, they aggregated around corals as a refuge from attack (Carpenter 1984) and thus potentially concentrated feeding near coral edges.

Both seaweeds and sea urchins were brought into the laboratory and held overnight in separate tanks with constant seawater flow and exposed to natural day–night cycles from the adjacent windows. The following day, clumps of *H. opuntia* that had been in contact with *Agaricia* and not in contact with any other corals were divided into similar sized portions, simultaneously spun in a salad spinner to remove excess water, and wet-weighted. Care was taken to choose clean individuals or to carefully remove epiphytes and fauna associated with the seaweeds before using them in feeding trials.

For feeding trials, one pre-weighed thallus of *H. opuntia* that had been in contact with *Agaricia* was paired with a pre-weighed thallus that had not been in contact; these were each cable tied to a mesh grid, presented to an individual urchin in a 8 liter container of flow-through seawater ($N = 25$). Equivalent portions of these same individual seaweeds were placed in a similar, adjacent container (without an urchin) to control for changes in mass unrelated to urchin consumption. Dividing the same seaweed clump into two pieces ensured that parts of the same seaweed were used in the paired trials (with and without urchins) minimizing individual variance in traits that might affect mass change (e.g., growth or respiration rates). Replicates were checked every 2 h ending within 48 h or as soon as we noticed 50 % consumption of either thallus in a replicate. When a replicate ended, seaweeds, and their paired controls, were spun and weighted following the same procedures used to initiate the experiment. Mass consumed was calculated using the formula $[\mathrm{Ti} \times (C_f/C_i)] - T_f$, where T_i and T_f were the initial and final masses of the seaweed offered to sea urchins, respectively, and C_i and C_f the initial and final masses of the paired control without urchins, respectively (Rasher and Hay 2014).

Seaweed nutritional value

Samples of *H. opuntia* both in contact and not in contact with the coral *A. tenuifolia* were frozen after having any epiphytes or associated fauna carefully removed ($N = 10$ of each type). In the laboratory, samples were dried to a constant mass at 60 °C for 48 h, ground to a fine powder, divided into two portions, and one portion acidified with 10 % HCL to remove carbonate. The non-carbonate carbon and nitrogen concentrations were obtained from acidified and unacidified samples, respectively, using an NC2500 elemental analyzer (Carlo Erba Strumentazione, Milan, Italy) interfaced to a Micromass Optima (Micromass LLC, Manchester, UK) continuous-flow isotope ratio mass spectrometer (CF-IRMS). Ash-free-dry-mass of non-acidified samples were obtained using aliquots from treatment and control samples that were dried, weighted, ashed at 450 °C for 4 h, and re-weighted to obtain percent ash-free-dry-mass.

Data analysis

When data met the assumption of homogeneity of variances (assessed with Levene's test), or could be made to do so via

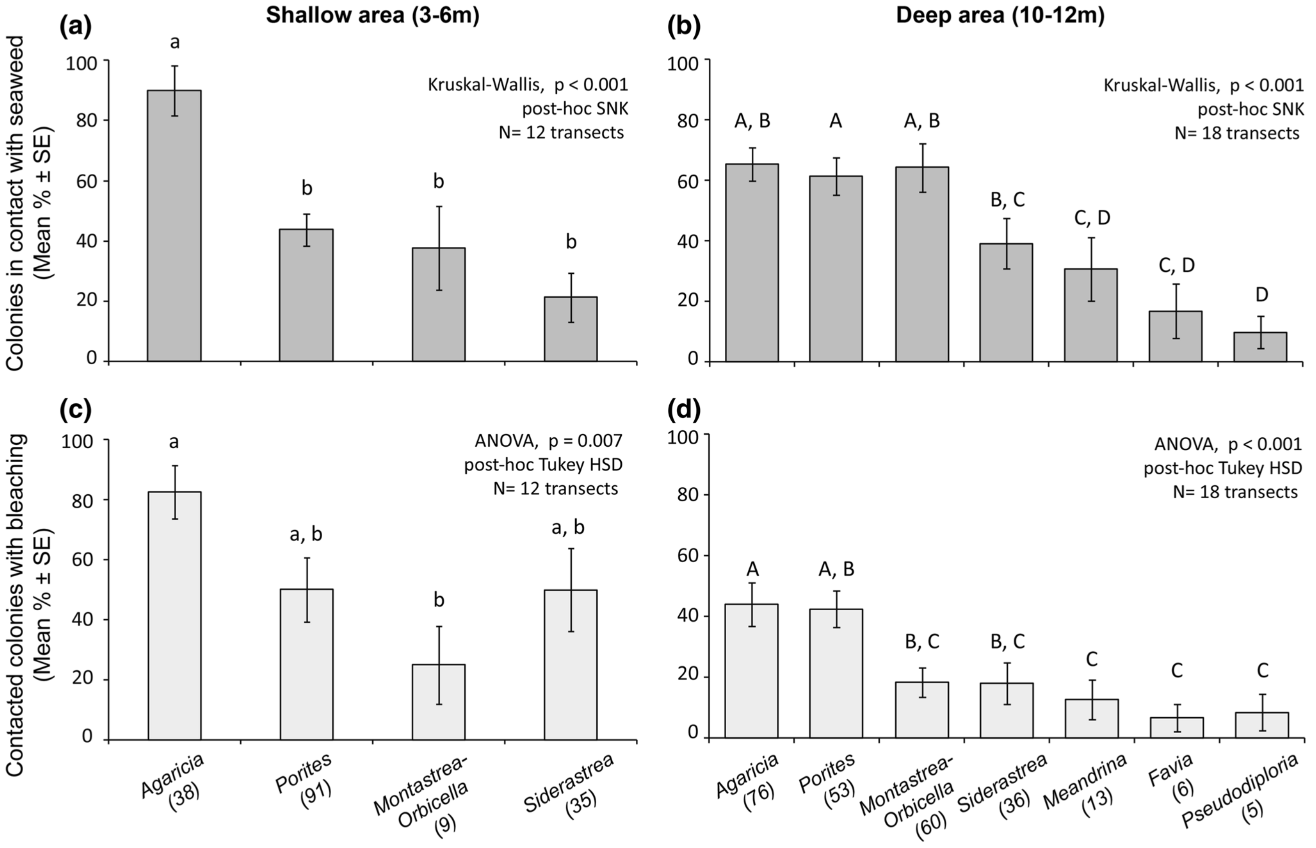

Fig. 1 Frequency of contacts with seaweeds by coral genera (**a**, **b**) and frequency of contacts associated with bleaching by coral genera (**c**, **d**) in transects for the shallow and deep areas (*right* and *left graphs*, respectively). *Lowercase letters above the bars* indicate significant differences within the shallow area and *uppercase* within the deep area. *Numbers* below genus names indicate the total number of colonies assessed

transformation, we employed parametric analyses. When transformed data still violated this assumption, we used nonparametric analyses on non-transformed data. Differences in the frequency of contacts (response variable) between coral genera (grouping variable) were assessed separately for shallow and deep areas with the nonparametric Kruskal–Wallis test. Differences in the frequency of contacts associated with bleaching (response variable) between coral genera (grouping variable) were tested with a one-way ANOVA on square-root transformed data for the shallow areas of the reef, while data for the deep area did not require transformation. Similar procedures were used to investigate differences in the frequency of contacts and contacts associated with bleaching (response variables) by seaweed (grouping variable). A Kruskal–Wallis test was used for the frequency of contacts (response variable) in both shallow and deep areas (grouping variable) and for the frequency of contacts associated with bleaching in the deep area, while a one-way ANOVA on square-root transformed data was used for this response variable in the shallow area.

The extent of seaweed–coral contacts (area and perimeter; response variables) between coral genera (grouping variable) and depth (grouping variable) was investigated using a two-way ANOVA on square-root transformed data, run separately for area in contact and perimeter in contact. A binomial logistic regression model was used to compare the proportion of contacts associated with bleaching (response variable; yes or no) for the most common corals (*Agaricia* and *Porites*), accounting for the interaction between corals (fixed factors) and seaweeds (random factors). Only seaweeds with more than two observations per coral species were included in this test.

Differences in the consumption of *H. opuntia* (response variable) that had been in contact and not in contact with *A. tenuifolia* (grouping variables) were assessed with a paired *t* test. Differences in seaweed nutritional value (ash-free-dry-mass, carbon, and nitrogen concentrations; response variables) between thalli that had been in contact or not in contact with coral (grouping variables) were assessed using *t* tests.

Results

Frequency, extent, and outcomes of seaweed–coral contacts

On the shallow reef, 95 % of *Agaricia* colonies were in contact with some species of macroalgae, and 80 % of these contacts were associated with localized coral bleaching (Fig. 1). For *Porites*, *Montastraea-Orbicella*, and *Siderastrea*, 21–44 % were in contact with seaweeds and 25–50 % of these contacts resulted in localized bleaching. Contact frequency was significantly higher for *Agaricia* than for any other coral species (Kruskal–Wallis, $p < 0.001$; Fig. 1a). On the deeper reef, seaweeds were in contact with 61–65 % of *Agaricia*, *Porites,* and *Montastraea-Orbicella* colonies (Fig. 1b). Contact frequency ranged from 31 to 39 % for *Siderastrea* and *Meandrina* and from 10 to 17 % for *Favia* and *Pseudodiploria*. Contact frequencies were significantly higher for *Agaricia*, *Porites,* and *Montastraea-Orbicella* than for *Meandrina, Favia,* or *Pseudodiploria,* with *Siderastrea* being intermediate between these groups (Kruskal–Wallis, $p < 0.001$; Fig. 1b). On both the deep and shallow reef, 42–83 % of *Agaricia* or *Porites* colonies in contact with seaweeds were bleached at points of contact (Fig. 1c, d).

When evaluating the extent of seaweed contact with corals (area and perimeter in contact), rather than just frequency of contact, proportion of coral colony area in contact with seaweed varied with coral genera, but not with depth, and there were no interactions between coral genus and depth (Fig. 2a; two-way ANOVA, Genera: $F = 5.077$; $p = 0.002$; Depth: $F = 0.030$; $p = 0.861$; Interaction: $F = 0.548$; $p = 0.649$). For perimeter of the coral in contact with seaweed, shallow corals had more contact than deeper corals, but this did not vary with coral genus, and there was no genus by depth interaction (Fig. 2b; Depth: $F = 4.444$; $p = 0.036$; Genera: $F = 0.662$; $p = 0.576$; Interaction: $F = 0.225$; $p = 0.879$). Thus, in terms of the frequency of contact and bleaching (Fig. 1), the area in contact or the perimeter in contact with seaweeds (Fig. 2), *Agaricia* and *Porites* were among the most common corals and the most impacted by seaweeds, with *Agaricia* being more frequently impacted than *Porites* (Fig. 1a).

We identified 14 seaweed species or types commonly in contact with coral colonies (of any species). Five of these seaweeds occurred in the shallow area and 13 in the deeper area (we did not observe Gelidiaceae in contact in deeper areas; Fig. 3). In the shallow area, 60 % of corals were contacted by *H. opuntia* and 96 % of the contacted corals were bleached at the point of contact. Both frequency of contact with and bleaching of corals were greater for *H. opuntia* than for any other seaweed (Fig. 3a and c; Kruskal–Wallis, $p < 0.001$). In deeper areas, contacts were more evenly distributed among seaweeds (Fig. 3b). About 35 % of corals were in contact with *Halimeda tuna.* About 20 % were in contact with *Lobophora, Halimeda goreaui, H. opuntia*, and articulated coralline algae, while filamentous algae and *Sargassum* were in contact with 5–10 % of corals. Another six seaweed species contacted corals, but only infrequently (Fig. 3b). Bleaching at the site of contact was common (50–80 %) for corals contacting *Lobophora,* articulated corallines, and *H. opuntia*. Bleaching occurred in about 20–30 % of contacts with filamentous algae and *H. tuna* and was infrequent for all other algae (<10 %).

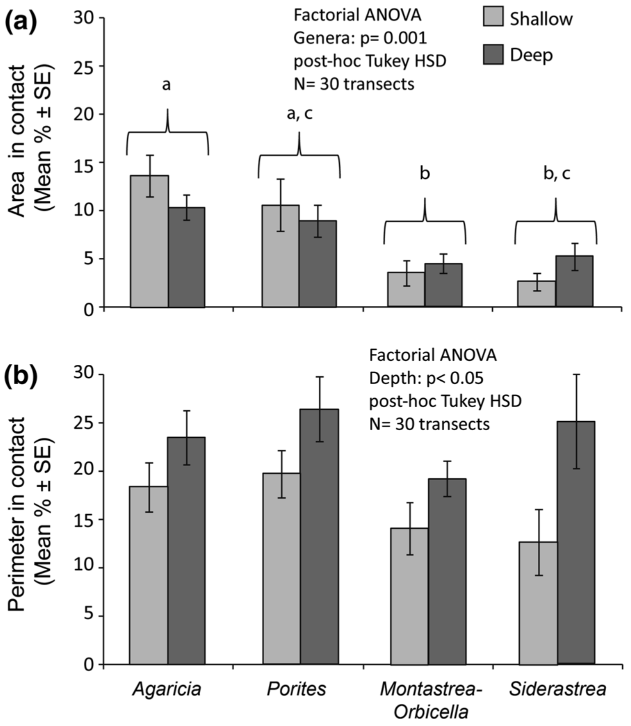

Fig. 2 Proportion of area and perimeter in contact with seaweeds per coral genera and depth. *Lowercase letters* indicate post hoc comparisons within the significant factor genera

Restricting the comparisons to *Agaricia* and *Porites*—the two most common and most contacted corals in terms of area contacted (see Figs. 1, 3)—*H. opuntia* was the most frequent seaweed to contact both genera on the shallow reef (68 and 25 %, respectively; Fig. 4a, b). On the deeper reef, seaweed contact with corals was more evenly distributed across seaweed species for *Agaricia*, while *H. tuna* and *L. variegata* contacts with *Porites* were the most frequent interactions (42 and 43 %, respectively; Fig. 4c, d). Contacts of both corals with each of the three species of *Halimeda* were frequent, ranging from 11–43 % across all coral genera *Halimeda* species pairings (Fig. 4c, d).

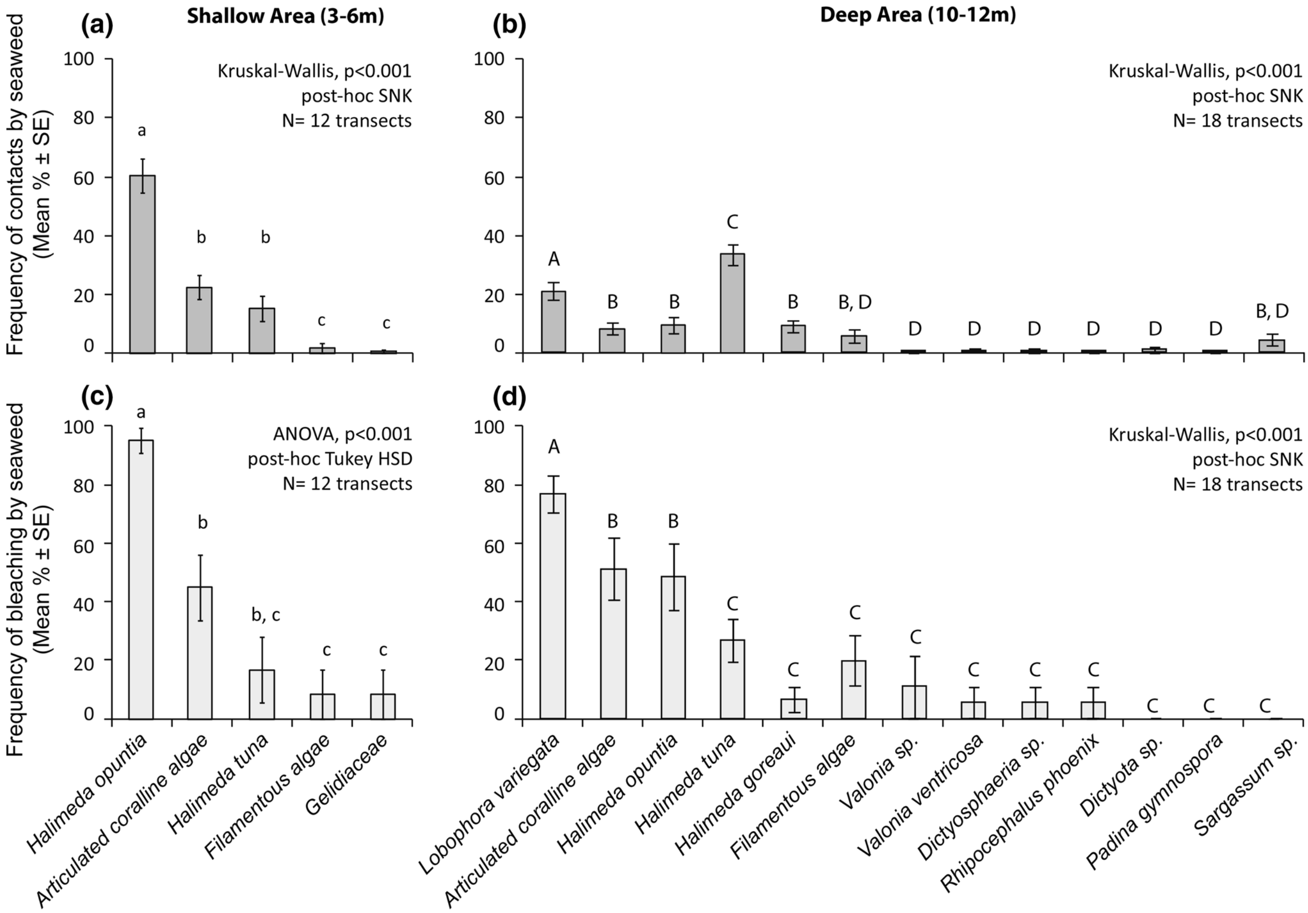

Fig. 3 Frequency of contacts by seaweed (**a**, **b**) and frequency of contacts associated with bleaching by seaweed (**c**, **d**) in the shallow and deep areas (*right* and *left graphs*, respectively). *Lowercase letters above the bars* indicate significant differences within the shallow area and *uppercase* within the deep areas

Contact outcomes differed as a function of coral and seaweed species pairings (Logistic Regression, Interaction $p < 0.001$, Seaweed $p < 0.001$; Coral $p = 0.01$; Table 1). This signal was generated by the differential effects of articulated coralline algae and *H. tuna,* both of which bleached *Agaricia* more frequently than *Porites* colonies (83 and 47 %; 57 and 38 %; respectively). Contacts with *H. opuntia* and *L. variegata* were consistently associated with bleaching (90–94 and 78–79 %, respectively) for both coral genera. Pooling across all seaweeds, contacts with *Agaricia* were more frequently associated with bleaching than were contacts with *Porites*.

Palatability trials and seaweed nutritional value

Diadema antillarum urchins consumed 150 % more *H. opuntia* that had been in contact with the coral *A. tenuifolia* than *H. opuntia* that had not been in contact with this coral (Paired *t* test, $p = 0.035$; Fig. 5). This response was not associated with greater nutritional value of seaweed thalli that had been in contact with corals (Fig. 6). Organic content, carbon concentration, and nitrogen concentration did not vary significantly between *H. opuntia* thalli that had and had not been growing in contact with *Agaricia* (*t* test, Organic matter $p = 0.986$; Carbon $p = 0.223$; Nitrogen $p = 0.521$; Fig. 6).

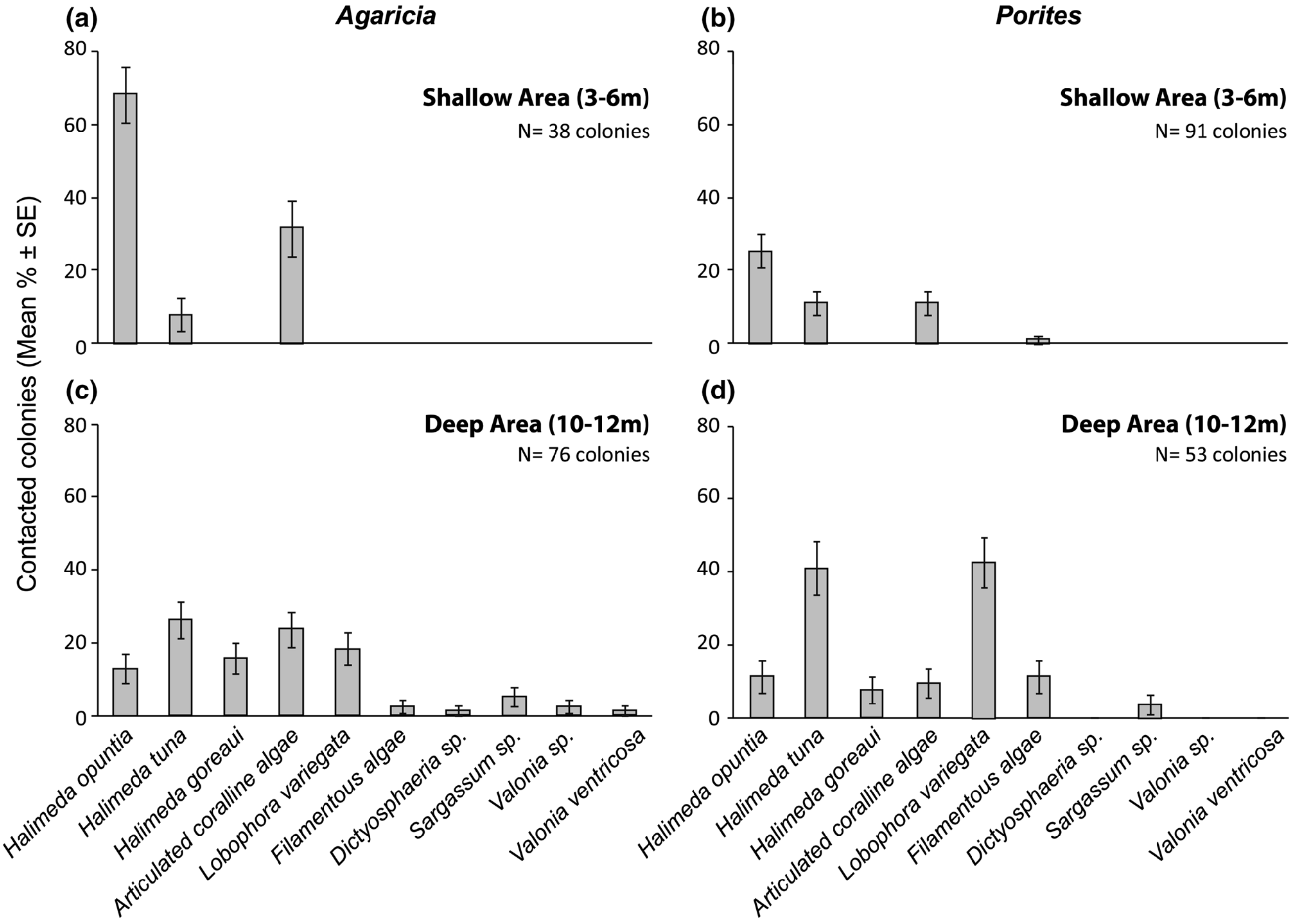

Fig. 4 Proportion of contacted colonies for the two most common coral genera, *Agaricia* and *Porites,* by seaweed in the shallow and deep area (*top* and *bottom* graphs, respectively)

Table 1 Proportion of contacts associated with bleaching per seaweed for the two most common coral genera, *Agaricia* and *Porites*, and depths combined

Seaweeds in contact with corals	*Agaricia* bleached	*Porites* bleached
Articulated coralline algae	**83 %** *(48)*	**47 %** *(15)*
Dictyosphaeria cavernosa	100 % *(3)*	–
Filamentous algae	50 % *(2)*	50 % *(6)*
Halimeda goreaui	59 % *(22)*	25 % *(4)*
Halimeda opuntia	94 % *(47)*	90 % *(29)*
Halimeda tuna	**57 %** *(42)*	**38 %** *(32)*
Lobophora variegata	79 % *(28)*	78 % *(23)*
Sargassum sp.	0 % *(8)*	0 % *(2)*
Valonia sp.	100 % *(2)*	–
Ventricaria sp.	0 % *(1)*	–
All seaweeds combined	**73 %** *(203)*	**60 %** *(111)*

Numbers in italic indicate the total number of contacts with that seaweed. Differential effects detected in the logistic regression are displayed in bold. Only seaweeds with more than two observations per coral species were included in this test

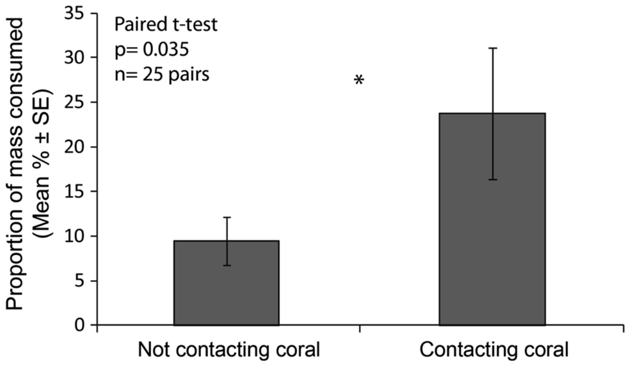

Fig. 5 Mass of *H. opuntia* that had and had not been in contact with the coral *A. tenuifolia* consumed by sea urchins *D. antillarum* when both were simultaneously offered in laboratory feeding trials. *Asterisk* indicate significant differences between the *bars*

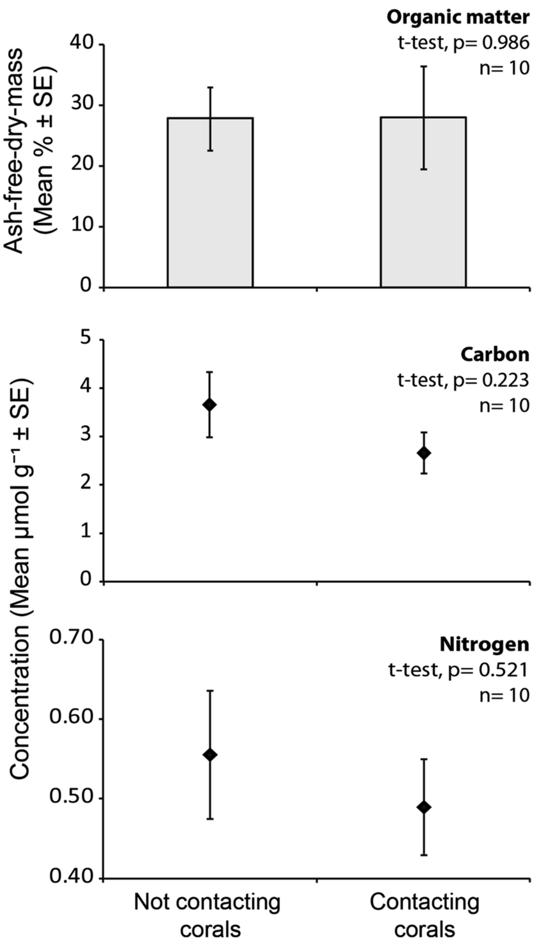

Fig. 6 Nutritional traits of *H. opuntia* thalli collected 1–2 m from *A. tenuifolia* versus thalli growing in contact with the coral

Discussion

Most coral colonies were in contact with seaweeds, and a large portion of these contacts were associated with coral bleaching. Coral–seaweed contacts were particularly frequent between *H. opuntia* and corals in the genus *Agaricia*, with this interaction being associated with bleaching in 95 % of the cases. Although the mechanisms producing bleaching in this study were not investigated, *H. opuntia* is allelopathic to other corals in the Caribbean (Rasher and Hay 2010). This chemically rich seaweed is also chemically defended against Caribbean reef herbivores (Paul and Fenical 1983; Hay et al. 1988). If different chemicals serve as anti-herbivore defenses versus allelopathic compounds and are induced in response to these different challenges, this could impose a trade-off where competing with corals could affect the seaweed's susceptibility to herbivory, as recently demonstrated for an allelopathic and herbivore deterrent red alga in the tropical Pacific (Rasher and Hay 2014). In contrast, if the same compounds serve as both herbivore deterrents and as allelopathic agents, then induction in response to either challenge could make seaweeds more resistant to both. The patterns we found here suggest that competition with corals may in some manner compromise this alga's resistance to herbivory.

Following the decline of acroporid corals throughout the Caribbean, *Agaricia* spp., *Porites* spp., and *Orbicella* spp. (former *Montastraea*) became the dominant corals on Caribbean reefs, which were becoming increasingly dominated by seaweeds in the the genera *Sargassum*, *Dictyota*, *Lobophora*, and *Halimeda* (Hughes 1994;Williams and Polunin 2001; Alvarez-Filip et al. 2009; Jackson et al. 2014). As a result, the most ecologically important coral–seaweed interactions are likely to be concentrated among these genera (McCook et al. 2001). In the present study, *Agaricia, Porites,* and *Montastraea-Orbicella* were the corals most frequently in contact with seaweeds (40–90 % of individuals in contact), but *Agaricia* and *Porites* were consistently among the most contacted and the most frequently bleached at areas of contact.

The coral genus *Agaricia* experienced a severe decline between the 1970s and the 2000s in the Caribbean (Shulman and Robertson 1996; Nugues and Bak 2006). This decline is often associated with the die-off of the sea urchin *D. antillarum* (de Ruyter van Steveninck and Bak 1986). The loss of *Diadema* might have had more important implications for *Agaricia* than are immediately apparent if it selectively attacked seaweeds in contact with corals and thus slowed the impacts of seaweed–coral competition. *Agaricia* corals may be especially dependent on such interactions because they appear to be poor competitors against seaweeds. When the seaweed *L. variegata* was experimentally put in contact with different corals in Curaçao, *Agaricia agaricites* was the only coral not able to reduce algal growth, proving to be a poor competitor (Nugues and Bak 2006).

Corals can respond differently when competing with different seaweeds, which can determine the outcomes of the interaction (McCook et al. 2001). Some corals use microfilaments to damage *H. opuntia*, but colonies of *Montastrea* and *Orbicella* were most effective in comparison to other corals including *Agaricia* and *Porites* (Nugues et al. 2004a). In the present study, contacts between *Agaricia* and articulated coralline algae were more frequently associated with coral bleaching than when this seaweed group contacted *Porites*. These differences could be associated with characteristics of the seaweed (e.g., functional groups) but also with traits or life form of the corals (McCook et al. 2001; Jompa and McCook 2003). Corals with encrusting and plate-like life forms were previously suggested to be more susceptible to competition from seaweeds (Hughes 1989; McCook et al. 2001), which agrees with the greater susceptibility of *Agaricia* than *Porites* to the seaweeds we found contacting these corals in our field surveys. For example, corals with a plate-like form, such as some *Agaricia* species, may generate areas beneath their projecting borders where seaweeds can escape herbivores. In contrast, seaweeds at the border of massive corals, such as *Porites*, appear more exposed to herbivores.

The differences in life forms between *Agaricia* and *Porites* were not associated with differences in their resistance to *H. opuntia*. When either of these corals contacted *H. opuntia*, more than 90 % of the colonies were bleached in areas of contact. The mechanisms leading to this high association with coral bleaching were not investigated, but *H. opuntia* is allelopathic to *Porites porites* in the Caribbean (Rasher and Hay 2010). In addition to being allelopathic to corals, *Halimeda* can harm corals by hosting corallivores that consume coral tissues (Wolf and Nugues 2013) and by vectoring coral diseases (Nugues et al. 2004b). It is also a low preference food for herbivores due to chemical and structural defenses (Paul and Hay 1986; Hay et al. 1988, 1994; Paul and van Alstyne 1988) and to nocturnal growth that allows its most herbivore-susceptible new growth to avoid herbivory until this growth begins to calcify and alter chemical defenses as the sun rises (Hay et al. 1988). *Halimeda*'s productivity may also be enhanced by higher nutrient levels that inhibit some corals (Lapointe et al. 1987; Littler and Littler 2007). The combination of these traits may allow *Halimeda* to be a frequent and extensive competitor of corals on numerous Caribbean reefs.

In the present study, sea urchins consumed ~150 % more *H. opuntia* that had been in contact with the coral *A. tenuifolia* than nearby *H. opuntia* that was not contacting coral, even though no differences in their nutritional values could be detected. This suggests that previous contact with the coral may have compromised the seaweed's anti-herbivore defenses and enhanced susceptibility to herbivory. Given the frequency of these contacts, the vulnerability of *Agaricia* to seaweed damage, and the importance of herbivores in the mediation of coral–seaweed competition (Lewis 1986; Mumby and Steneck 2008; Hughes et al. 2010; Rasher et al. 2013), this could have important implications for ecosystem function. It is well known that resilience of reef function is dependent on herbivores removing seaweeds and preventing reef degradation (Bellwood et al. 2004; Mumby and Steneck 2008; Hughes et al. 2010), but how this feeding activity varies on a small scale is relatively uninvestigated. Corals profit from preventing direct contact with seaweeds (Rasher et al. 2011; Andras et al. 2012), and recent studies of specific interactions have demonstrated that some corals can chemically signal mutualistic fishes to remove competing seaweeds once they contact corals (Dixson and Hay 2012). Additionally, the seaweed *G. filamentosa* has been demonstrated to induce greater allelopathy when in contact with the coral *P. cylindrica*, but this induced allelopathy co-occurs with a compromise in anti-herbivore chemical defenses, making the seaweed more palatable to herbivores when in contact with coral (Rasher and Hay 2014). This potential trade-off could explain the pattern of palatability we observed for *H. opuntia*. If such interactions are common, then coral–seaweed interactions may make competing seaweeds more palatable and slow the rate at which seaweeds damage corals, but on an overlooked scale of millimeters or centimeters instead of at scales of reefs. At present, there are only three instances of this being investigated. The green alga *H. opuntia* (this study) and the red alga *G. filamentosa* are both allelopathic to corals and became more palatable when in contact with a competing coral (Rasher and Hay 2014). In contrast, the brown alga *Sargassum polycystum* is not allelopathic, does not induce allelopathy when contacting coral, but also does not become more palatable following competition with coral (Rasher and Hay 2014). This sample size is still too small to draw general conclusions, but the interaction is worthy of additional investigation.

Acknowledgments We thank C.Dell, S.Weber, and J.Montoya for assistance in the laboratory; the Smithsonian Carrie Bow Cay Field Station staff for logistical support. This work was funded by the Teasley Endowment to the Georgia Institute of Technology and by a scholarship from the National Council for Scientific and Technological Development (CNPq - Brazil) through the program "Science Without Borders" from the Brazilian Government to G.O. Longo. This is contribution 968, Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution.

References

Abramoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics International 11:36–42

Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc Biol Sci 276:3019–3025

Andras TD, Alexander TS, Gahlena A, Parry RM, Fernandez FM, Kubanek J, Wang MD, Hay ME (2012) Seaweed allelopathy against coral: surface distribution of seaweed secondary metabolites by imaging mass spectrometry. J Chem Ecol 38:1203–1214

Barott KL, Rohwer FL (2012) Unseen players shape benthic competition on coral reefs. Trends Microbiol 20:621–628

Barott KL, Williams GJ, Vermeij MJ, Harris J, Smith JE, Rohwer FL, Sandin SA (2012) Natural history of coral-algae competition across a gradient of human activity in the Line Islands. Mar Ecol Prog Ser 460:1–12

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Bonaldo RM, Hay ME (2014) Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. PLoS ONE 9(1):e85786. doi:10.1371/journal.pone.0085786

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90:1478–1484

Carpenter RC (1984) Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. Mar Biol 82:101–108

Carter J, Sedberry GR (1997) The design, function and use of marine fishery reserves as tools for the management and conservation of the Belize barrier reef. Proc 8th Int Coral Reef Symp 2:1911–1916

de Ruyter van Steveninck ED, Bak RPM (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Mar Ecol Prog Ser 34:87–94

Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLoS ONE 4:e5239. doi:10.1371/journal.pone.0005239

Dixson DL, Hay ME (2012) Corals chemically cue mutualistic fishes to remove competing seaweeds. Science 338:804–807

Edmunds PJ (2002) Long-term dynamics of coral reefs in St. John, US Virgin Islands. Coral Reefs 21:357–367

Gardner TA, Côte IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65:446–454

Hay ME, Kappel QE, Fenical W (1994) Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. Ecology 75:1714–1726

Hay ME, Paul VJ, Lewis SM, Gustafson K, Tucker J, Trindell RN (1988) Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory, and chemical versus morphological defenses. Oecologia 75:233–245

Hughes TP (1989) Community structure and diversity of coral reefs: The role of history. Ecology 70:275–279

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hughes TP, Graham NJ, Jackson JC, Mumby PJ, Steneck P (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 11:633–642

Jackson JBC, Donovan MK, Cramer KL, Lam VV (2014) Status and trends of Caribbean coral reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland

Jompa J, McCook LJ (2003) Coral-algal competition: macroalgae with different properties have different effects on corals. Mar Ecol Prog Ser 258:87–95

Lapointe BE, Littler MM, Littler DS (1987) A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. Aquat Bot 28:243–255

Lessios HA (1988) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Annu Rev Ecol Syst 19:371–393

Littler MM, Littler DS (2007) Assessment of coral reefs using herbivory/nutrient assays and indicator groups of benthic primary producers: a critical synthesis, proposed protocols, and critique of management strategies. Aquat Conserv Mar Freshw Ecosyst 17:195–215

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

McClanahan TR, Aronson RB, Pretch WF, Muthiga NA (1999) Fleshy algae dominate remote coral reefs of Belize. Coral Reefs 18:61–62

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

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23:555–563

Nelson CE, Goldberg SJ, Kelly LW, Haas AF, Smith JE, Rohwer F, Carlson CA (2013) Coral and macroalgal exudates vary in neutral sugar composition and differentially enrich reef bacterioplankton lineages. ISME J 7:962–979

Nugues MM, Bak RPM (2006) Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long term perspective. Mar Ecol Prog Ser 315:75–86

Nugues MM, Delvoye L, Bak RPM (2004a) Coral defence against macroalgae: differential effects of mesenterial filaments on the green alga *Halimeda opuntia*. Mar Ecol Prog Ser 278:103–114

Nugues MM, Smith GW, Van Hooidonk RJ, Seabra MI, Bak RPM (2004b) Algal contact as a trigger for coral disease. Ecol Lett 7:919–923

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

Paul VJ, Hay ME (1986) Seaweed susceptibility to herbivory: chemical and morphological correlates. Mar Ecol Prog Ser 33:255–264

Paul VJ, Van Alstyne K (1988) Chemical defense and chemical variation in some tropical Pacific species of *Halimeda* (Halimedaceae; Chlorophyta). Coral Reefs 4:263–269

Rasher DB, Hay ME (2010) Chemically rich seaweeds poison corals when not controlled by herbivores. Proc Natl Acad Sci USA 107:9683–9688

Rasher DB, Hay ME (2014) Competition induces allelopathy but suppresses growth and anti-herbivore defence in a chemically rich seaweed. Proc R Soc B 281:20132615

Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94:1347–1358

Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME (2011) Macroalgal terpenes function as allelopathic agents against reef corals. Proc Natl Acad Sci USA 108:17726–17731

Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. Trends Ecol Evol 27:404–413

Shulman MJ, Robertson DR (1996) Changes in coral reefs of San Blas, Caribbean Panama: 1983 to 1990. Coral Reefs 15:231–246

Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. Ecol Lett 9:835–845

Venera-Ponton DE, Diaz-Pulido G, McCook LJ, Rangel-Campo A (2011) Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. Mar Ecol Prog Ser 421:109–115

Williams ID, Polunin NVC (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358–366

Wolf AT, Nugues MM (2013) Synergistic effects of algal overgrowth and corallivory on Caribbean reef-building corals. Ecology 94:1667–1674