# Chemically rich seaweeds poison corals when not controlled by herbivores

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**Coral reefs are in dramatic global decline, with seaweeds commonly replacing corals. It is unclear, however, whether seaweeds harm corals directly or colonize opportunistically following their decline and then suppress coral recruitment. In the Caribbean and tropical Pacific, we show that, when protected from herbivores, ~40 to 70% of common seaweeds cause bleaching and death of coral tissue when in direct contact. For seaweeds that harmed coral tissues, their lipid-soluble extracts also produced rapid bleaching. Coral bleaching and mortality was limited to areas of direct contact with seaweeds or their extracts. These patterns suggest that allelopathic seaweed-coral interactions can be important on reefs lacking herbivore control of seaweeds, and that these interactions involve lipid-soluble metabolites transferred via direct contact. Seaweeds were rapidly consumed when placed on a Pacific reef protected from fishing but were left intact or consumed at slower rates on an adjacent fished reef, indicating that herbivory will suppress seaweeds and lower frequency of allelopathic damage to corals if reefs retain intact food webs. With continued removal of herbivores from coral reefs, seaweeds are becoming more common. This occurrence will lead to increasing frequency of seaweed-coral contacts, increasing allelopathic suppression of remaining corals, and continuing decline of reef corals.**

allelopathy | competition | coral–seaweed–herbivore interactions | marine chemical ecology | marine protected area

As foundation species, corals promote marine biodiversity, support a multitude of ecosystem functions, and provide goods and services critical to human societies (1, 2). However, coral reefs are in global decline, with reefs commonly converting from species-rich and topographically complex communities dominated by corals to species-poor and topographically simplified communities dominated by seaweeds (3–7). In the Caribbean, average cover of hard corals has declined by ~80% in the last 3 decades (5) and more than 30% of the world's coral species face elevated risk of extinction (6). Monitoring (7), field experiments (8–10), and a meta-analysis (11) all indicate that herbivory is critical in preventing seaweed replacement of corals. However, the extent to which seaweeds drive these shifts by outcompeting adult corals in the absence of herbivory, or proliferate only after coral mortality is triggered by other causes (such as disease or bleaching) is debated (12–15). To compound this uncertainty, studies addressing seaweed-coral competition have: (*i*) produced variable results, (*ii*) rarely been conducted using numerous species-pairings, (*iii*) varied in experimental techniques (complicating comparisons), and (*iv*) sometimes been conducted in laboratory settings lacking ecologically realistic conditions (e.g., flow and turbulence). Thus, the general importance of competition between established seaweeds and corals remains uncertain. An understanding of mechanisms determining the outcomes of seaweed-coral interactions, and of how herbivory mediates these interactions, is needed if reefs are to be better managed, especially with the continuing harvest of reef herbivores (12, 15, 16).

The importance of physical vs. chemical mechanisms affecting seaweed-coral interactions is also unclear (13). Although smothering, shading, and abrasion by a limited number of seaweeds have been shown to negatively (13, 17–19) or positively (20) affect corals, chemically-mediated competition between adult corals and seaweeds has received limited attention. Numerous marine benthic organisms produce secondary metabolites that function to deter consumers or suppress competitors (21). In field studies, seaweed secondary metabolites have been proposed as likely agents affecting coral mortality (17, 22), but only one investigation has demonstrated seaweed allelopathy (against a soft coral) under ecologically realistic field conditions (23). In contrast, laboratory-based studies of multiple seaweed-coral pairings suggest that release of seaweed primary metabolites (i.e., sugars and carbohydrates) can indirectly mediate coral mortality through effects on coral-associated microbes (24). These laboratory-based effects have yet to be documented under field conditions, and a recent field study found no effect of nearby seaweeds on the severity and dynamics of a microbe-generated coral disease, suggesting that natural hydrodynamic conditions may limit the impacts of algal generated metabolites in the field (25). Thus, the relative frequency, intensity, and general ecological effects of seaweed allelopathy against corals remain unknown, as do the chemical nature and mechanisms of allelopathy between seaweeds and corals (e.g., the activity of primary vs. secondary metabolites and the role of direct poisons vs. indirect effects on microbes).

Here, we describe field experiments in the Caribbean and tropical Pacific designed to assess the outcomes and mechanisms involved in seaweed-coral competition across multiple seaweed species and functional groups. Throughout these 20-d experiments, we monitored effects of seaweeds on coral bleaching, death, and photosynthetic efficiency using photographic image analysis and in situ pulse-amplitude modulated (PAM) fluorometry, respectively. To assess the most plausible mechanism for the patterns we observed in our experiments, we then tested the effect of lipid-soluble extracts from each seaweed on corals (Fig. 1). These seaweeds were then transplanted onto reefs to determine how herbivory may mediate seaweed-coral competitive interactions by limiting seaweed abundance. Our results indicate that several common seaweeds produce lipid-soluble metabolites that damage corals when seaweeds and corals come into direct contact.

## Results

**Seaweed Effects on Corals.** When the coral *Porites porites* (Panama) was placed in direct contact with seven common seaweeds for 20 d, *Ochtodes secundaramea*, *Dictyota bartayresiana*, *Lobophora variegata*, *Halimeda opuntia*, and *Amphiroa fragillisima* caused significant bleaching relative to controls ($P < 0.001, n = 9$) (Fig. 2*A*), while *Padina perindusiata* or *Sargassum* sp. did not. Because visual assessments of coral bleaching and mortality can be subjective (26), we also analyzed the effects of seaweeds on coral photo-

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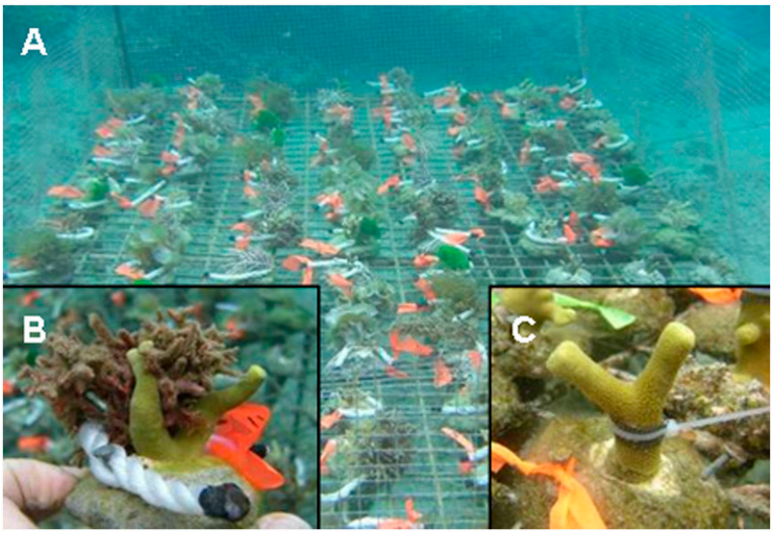


**Fig. 1.** Experimental design. (*A*) A rack holding experimental corals in cones. (*B*) A coral replicate showing a seaweed transplanted against a coral. (*C*) A coral replicate wrapped with a gel containing the lipid-soluble extract of a seaweed.

synthetic efficiency (effective quantum yield) using in situ PAM fluorometry, a method that quantifies coral health in response to environmental stressors (24, 26). Symbiont photosynthetic efficiency was highly correlated with bleaching ($r^2 = 0.92$, $P < 0.001$) (Fig. 3). Paralleling patterns of bleaching and mortality, *O. secundaramea*, *D. bartayresiana*, *L. variegata*, *H. opuntia*, and *A. fragillisima* suppressed photosynthetic efficiency of *P. porites* by 52 to 90% relative to controls ($P < 0.001$, $n = 9$) (Fig. 2*C*), while *P. perindusiata* and *Sargassum* sp. had no effects. Corals in contact with the most harmful seaweeds had effective quantum yields indicative of severe bleaching and mortality (ref. 24, and references within). Neither visual bleaching, nor suppression of photosynthetic efficiency occurred on the sides of corals away from seaweed-coral contact (5–10 mm from seaweed contact; $P = 0.358$, $n = 9$). Thus, seaweeds damaged corals only in areas of direct contact.

Results for tests with *Porites cylindrica* (Fiji) were similar to those from Panama. When *P. cylindrica* was in contact with eight common seaweeds for 20 d, *Chlorodesmis fastigiata* and *Galaxaura filamentosa* caused significant visual bleaching, relative to controls ($P < 0.001$, $n = 11$) (Fig. 2*B*), while *Padina boryana*, *Liagora* sp., *Amphiroa crassa, Sargassum polycystum*, and *Turbinaria conoides* caused no significant visual coral bleaching. *Dictyota bartayresiana* caused appreciable visual bleaching, but did not statistically differ from controls by posthoc analysis. *P. cylindrica* bleaching correlated with photosynthetic efficiency ($r^2 = 0.86$, $P < 0.001$) (Fig. 3), and corals in contact with harmful seaweeds had effective quantum yields indicative of severe bleaching/mortality ($P < 0.001$, $n = 11$) (Fig. 2*D*). In contrast, *S. polycystum*, *T. conoides*, and *A. crassa* had no effect on coral bleaching or photosynthetic efficiency. The seaweeds *P. boryana* and *Liagora* sp. caused slight, but significant suppression of *P. cylindrica* photosynthetic efficiency (Fig. 2*D*) relative to controls, despite not generating significant visual bleaching (Fig. 2*B*). Contact with these seaweeds produced stress unrecognizable by visual assessments alone. As with *P. porites* in Panama, no significant visual bleaching, nor suppression of photosynthetic efficiency, occurred on the far sides of *P. cylindrica* away from seaweed contact ($P = 0.794$, $n = 11$). Thus, Fijian seaweeds also caused bleaching only in areas of direct contact.

Seaweeds could have affected corals via abrasion, shading, or lipid-soluble allelopathic compounds transferred by direct contact rather than via dissolution into the water. When inert models designed to mimic the shading and abrasion of bladed species, like *Padina*, and filamentous species, like *Chlorodesmis*, were placed in direct contact with *P. cylindrica* for 16 d in the field, *Padina* mimics (0% bleaching, Y: $0.661 \pm 0.011$) and *Chlorodesmis* mimics (0% bleaching, Y: $0.595 \pm 0.027$) caused no bleaching or effects on photosynthetic efficiency ($P > 0.999$ and $P = 0.149$ for bleaching and photosynthetic efficiency, respectively, $n = 10$), relative to controls (0% bleaching, Y: $0.587 \pm 0.066$) (Fig. S1). Thus, physical effects of abrasion and shading were not detectable in our experiment.

**Extract Effects on Corals.** When lipid-soluble extracts from each Panamanian seaweed were embedded at natural volumetric concentration in Phytagel strips and placed in direct contact with *P. porites* for 24 h in the field (27) (Fig. 1*C*), effects of extracts paralleled effects of direct seaweed contact; *O. secundaramea, D. bartayresiana, L. variegata, H. opuntia,* and *A. fragillisima* caused significant coral bleaching and suppression of photosynthetic efficiency in assays using both intact seaweeds ($P < 0.001$, $n = 9$) (Fig. 2*C*) and chemical extracts ($P < 0.001$, $n = 10$) (Fig. 2*E*). *Padina perindusiata* and *Sargassum* sp. caused no significant bleaching in either assay.

In Fiji, extracts from *C. fastigiata*, *D. bartayresiana*, *G. filamentosa*, and *Liagora* sp. caused bleaching and suppression of photosynthetic efficiency of *P. cylindrica* relative to controls ($P < 0.001$, $n = 10$) (Fig. 2*F*); extracts of *P. boryana*, *A. crassa, S. polycystum*, and *T. conoides* did not. With the exception of *P. boryana*, effects of Fijian seaweeds in assays using intact plants (Fig. 2*D*) were mirrored by effects of lipid-soluble extracts (Fig. 2*F*). *Padina* was unusual in that it suppressed effective quantum yield by 25% in whole-seaweed assays, but its extract produced no rapid allelopathic effect. It is possible that its extract acts slowly, or that the modest effect of *P. boryana* that we detected in our 20-d whole-plant assay was a mild effect of shading or abrasion.

The effects of extracts were produced by extracting entire algal thalli. This could be unrealistic if the allelopathic metabolites we detected were in, but not on, seaweeds where they could be transferred to corals. When lipids were extracted from only the surfaces of four Fijian seaweeds (28), incorporated into Phytagel strips, and placed in contact with *P. cylindrica* for 24 h in the field, surface extracts of *C. fastigiata*, *D. bartayresiana*, and *G. filamentosa* caused bleaching and suppression of photosynthetic efficiency relative to controls ($P < 0.001$, $n = 10$) (Fig. 4). In contrast, surface extracts of *A. crassa*, which had no effect in whole-plant assays, had no sig-

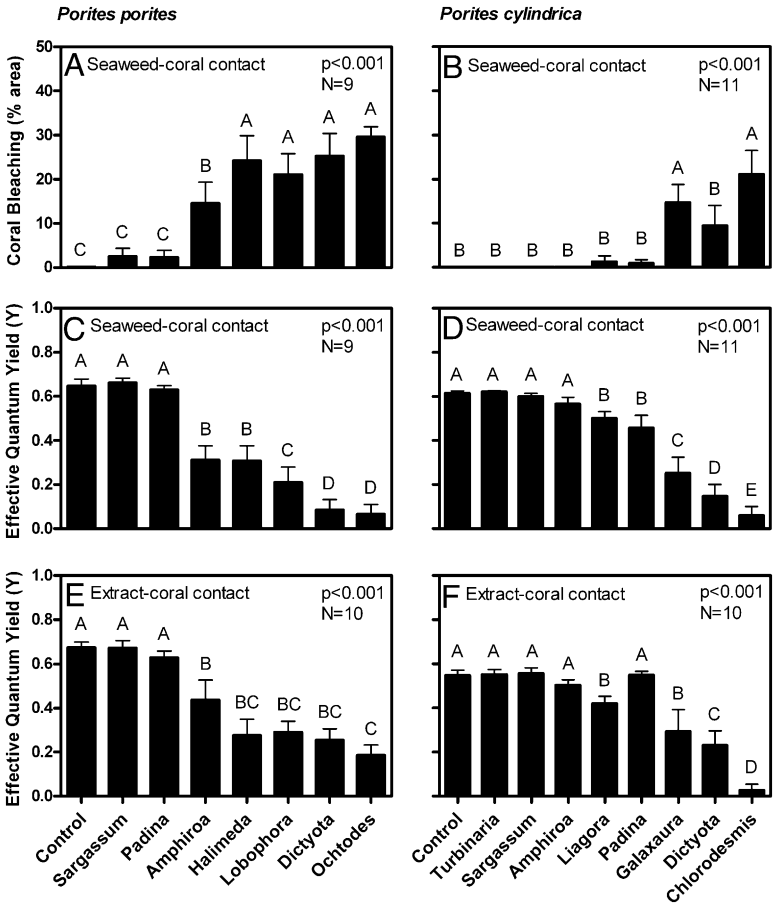


**Fig. 2.** Effects of intact seaweeds and extracts on coral health. (*A* and *B*) Visual coral tissue bleaching (percent 2D area; mean ± SEM) and (*C–F*) photosynthetic efficiency (Y; mean ± SEM) of the corals *Porites porites* in Panama and *Porites cylindrica* in Fiji when in contact with intact seaweeds for 20 d (*A–D*: $n$ = 9–11), or in contact with gel strips containing lipid-soluble extracts from the same seaweeds for 24 h (*E* and *F*: $n$ = 10). Analyzed by Kruskal-Wallis ANOVA on Ranks. Letters indicate homogeneous subgroups by posthoc Student-Newman-Kuels tests.

nificant effects. Thus, effects of surface extracts, of whole-plant extracts, and of assays using intact plants all indicate that lipid-soluble allelopathic metabolites occur on algal surfaces and damage adjacent corals following direct contact.

**Herbivore Effects on Seaweeds.** Our experiments were performed in a marine protected area (MPA) of Votua Village's reef flat, Fiji. In this MPA, coral cover is high (57 ± 3%; mean ± SEM) and macroalgal cover is low (3 ± 1%). In contrast, the adjacent reef flat 300 m west of the MPA is heavily fished and has low coral (3 ± 2%) and high macroalgal cover (47 ± 5%). Cover of both corals and macroalgae differ between sites ($P < 0.001$, $P < 0.001$, respectively, $n = 10$).

In 2008, when we transplanted all macrophytes used in our caged competition study into both sites, losses over 24 h in the MPA were 40 to 100% for all species; losses in the fished area were 0 to 40% (Fig. 5*A*). For all species but *Chlorodesmis*, rates of grazing in the MPA were significantly higher than on the fished reef flat. When repeated in 2009, trends were similar. Six

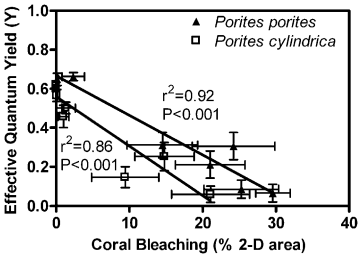


**Fig. 3.** Linear correlation between coral bleaching and photosynthetic efficiency for both corals. Values determined for corals in direct contact with seaweeds for 20 d (mean ± SEM; $n$ = 9–11 per seaweed-coral treatment). Analyzed by Pearson's correlation coefficients.

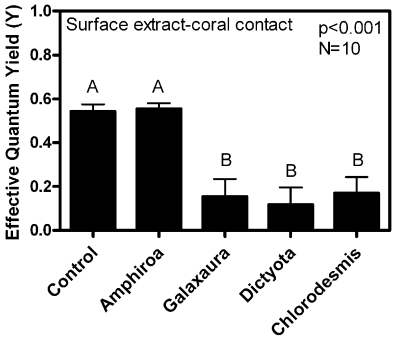


**Fig. 4.** Effects of seaweed surface extracts on coral health. Photosynthetic efficiency (Y; mean ± SEM) of *Porites cylindrica* in direct contact for 24 h with gel strips containing lipid-soluble extracts from the surfaces of seaweeds ($n$ = 10). Analyzed as in Fig. 2.

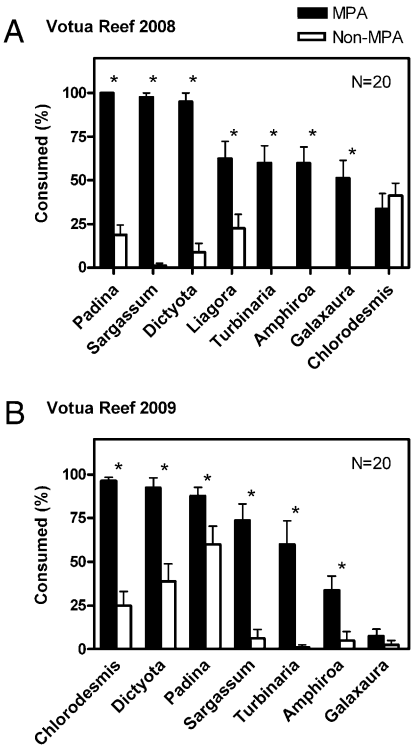


**Fig. 5.** Consumption of seaweeds in a marine protected area (MPA) and adjacent fished reef. Seaweeds consumed (percent; mean ± SEM) by herbivores during a 24-h feeding assay on a protected ($n$ = 20) and fished ($n$ = 20) reef (~300 m apart) in 2008 (*A*) and 2009 (*B*). Stars indicate differences in the consumption of a seaweed between reefs, within a year, by Mann-Whitney U tests.

of the seven species were consumed significantly more in the MPA; *Galaxaura* was minimally consumed in both sites (Fig. 5*B*).

## Discussion

In both the Caribbean and tropical Pacific, contact of seaweeds with *Porites* corals commonly caused bleaching, lowered photosynthetic efficiency, and in several cases death of coral tissues in areas of contact. These patterns were reproduced when corals were in contact with only the lipophilic extracts of these seaweeds, suggesting that seaweeds damaged corals via chemical mechanisms. Our inert algal mimics produced no detectable effects on corals, also indicating chemical instead of physical effects.

In Panama, five of seven seaweeds (71%) caused bleaching of *P. porites*; in Fiji, three of eight species (38%) caused bleaching of *P. cylindrica*. We commonly observed these *Porites* spp. in contact with seaweeds at our field sites, suggesting that this genus may be relatively tolerant of contacts, potentially making these data conservative relative to other corals. As reefs are increasingly depleted of herbivores that suppress seaweeds (4, 7, 12, 15, 16), coral-seaweed contacts will increase in frequency, enhancing the damage that corals may experience from allelopathic seaweeds. Thus, in addition to suppressing recruitment and growth of new corals (29), several common seaweeds (Fig. 2) can damage adult corals using allelochemicals.

To date, the few demonstrated allelopathic interactions among reef species all rely on transfer of metabolites via direct contact rather than via transmission through the water (23, 27, 30), suggesting that allelopathic metabolites are lipid- rather than water-soluble and that their effects are generated by contact rather than proximity alone. The primacy of lipids as allelopathic agents makes evolutionary and energetic sense given the ocean's potential to dilute and advect water-soluble metabolites.

Although the activity of lipid extracts matched patterns from intact algae in 93% of the interactions we investigated, physical mechanisms, such as shading or abrasion, may be important for some seaweed-coral interactions or for interactions lasting longer than 20 d. However, patterns of coral bleaching did not correlate well with seaweed structure that should affect abrasion; seaweeds that caused bleaching commonly had a soft non-abrasive thallus (e.g., *Ochtodes*, *Chlorodesmis*, *Dictyota*), while tougher, more abrasive species like *Turbinaria* and *Sargassum* did not damage corals. Additionally, some of the most chemically active seaweeds in Fiji (*Chlorodesmis* and *Dictyota*) produced obvious bleached areas after only 2 d of contact; algal mimics designed to cause abrasion and shading had no effect after 16 d (Fig. S1). Moreover, assays using extracts from algal surfaces alone demonstrated that allelopathic metabolites are at sufficient surface concentrations to damage corals. Recent studies show that multiple seaweeds deploy secondary metabolites on their surfaces where they could play allelopathic roles (31, 32).

Although numerous seaweeds associated with degraded reefs (e.g., *Lobophora*, *Halimeda*, *Dictyota*, *Amphiroa*) bleached corals in our study, a few seaweeds that are common following herbivore removal (*Sargassum*, *Turbinaria*, *Padina*) did not rapidly damage corals. To avoid confounding density and species effects, we deployed one seaweed thallus per replicate in our field experiments. It is possible that our results are conservative and that seaweeds like *Sargassum*, *Padina*, and *Turbinaria* may need to grow in greater abundance or for greater lengths of time to produce impacts on coral health. Indeed, some studies have detected effects of *Sargassum* on *Porites* growth (via abrasion) in < 20 d using greater seaweed abundance in treatments (18), and have found large stands of *Sargassum* to be associated with increased *Porites* mortality and decreased coral recruitment within experimental fish exclosures over longer time periods (9).

Seaweeds like *Dictyota* that both bloom on overfished reefs (33) and are strongly allelopathic (Fig. 2) may be especially damaging to corals, although *Dictyota* species appear variable in their allelopathic activities (34). Fortunately, other strongly allelopathic species, like *Chlorodesmis*, *Galaxaura* and *Ochtodes*, rarely become abundant on reefs. However, our observations of fishes feeding on our algal transplants in Fiji indicated that a single herbivorous fish (*Siganus argenteus*) was responsible for all grazing on *C. fastigiata* (see also ref. 35), suggesting that suppression of even a single herbivore species in this diverse community could elevate risk of coral degradation via algal allelopathy.

Recent studies found that water-soluble leechates from seaweeds caused rapid coral mortality in the laboratory via effects on coral-associated microbes and suggested this was because of microbial stimulation by dissolved organic carbon (24). Our results were consistent with seaweeds damaging corals via lipid-soluble allelochemicals transferred during contact; we detected no near-contact effects (i.e., on opposite side of corals just millimeters away from seaweed contact) that might be expected if water-soluble primary metabolites were damaging corals. Whether lipid-soluble secondary metabolites act as direct coral poisons or via effects on coral-associated microbes (24, 36) was not tested, but the lack of an impact that spread beyond areas of direct contact may be most parsimoniously explained as a direct allelochemical effect. Regardless of mode of action, direct contact between corals and several seaweeds produced allelopathic interactions that damaged corals. Seaweed primary (dissolved organic carbon) and secondary metabolites might also interact synergistically to harm corals, with the importance of differing metabolites varying under different conditions.

We conducted our competition studies using a caged design that excluded herbivores, simulating modern reef conditions where herbivorous fishes have been over-harvested (12, 16). When seaweeds from our Fijian competition study were placed in the field within a MPA and 300 m away in a fished area, most seaweeds were

rapidly consumed in the MPA (Fig. 5) hosting a diverse herbivore guild (37), but consumed much more slowly or at undetectable rates on an adjacent reef subject to fishing. Several of the seaweeds consumed in our feeding assays demonstrated potent allelopathic activity against corals, and are known to be rich in secondary metabolites that deter some reef herbivores (e.g., *Dictyota*, *Chlorodesmis*, *Ochtodes*, *Halimeda*). Thus, even modest harvesting of those fishes that consume chemically rich seaweeds (10, 38) could lead to increases in some of the most chemically damaging seaweeds and to increasing allelopathic impacts on reef corals. Moreover, these findings indicate that feeding complementarity (10) and high grazing rates typical of healthy, less-fished reefs (7, 9, 15, 16), should suppress allelopathic damage to corals by limiting seaweed abundance, and thus seaweed-coral contacts.

Our results show that numerous seaweeds can damage corals via allelochemicals. Such chemical effects could produce the suppression of coral fecundity and recruitment noted by previous investigators (references within ref. 29; 39) and could produce negative feedbacks, making reef recovery less likely as seaweed abundance increases (15). Chemically mediated seaweed-coral competition may limit recovery of present-day coral reefs, regardless of the factors causing initial coral decline. This will be especially true where local factors (e.g., overfishing) interact with global factors (e.g., climate change) to change reef community structure over large spatial scales that limit the ability of herbivores to control seaweed abundance. Information on which seaweeds damage corals and which herbivore species best limit these seaweeds may prove useful in better managing reef resilience to facilitate recovery (4, 9, 10, 40).

## Materials and Methods

**Experimental Design and Study Organisms.** We assessed the outcomes of, and mechanisms involved in, seaweed-coral competition by assaying the effects of common seaweeds in the Caribbean (Coco Point Reef, Bocas del Toro, Panama; 9°18.019′N, 82°16.350′W, June–July 2008) and tropical Pacific (Votua Reef, Viti Levu, Fiji; 18°13.049′S, 177°42.968′E, August–September 2008) on a common *Porites* species coral from each location. To create standardized units of seaweed-coral contact in the same environmental setting, we collected 6- to 8-cm branches of *P. porites* (Panama) and *P. cylindrica* (Fiji) and glued them individually into small cement cones (Fig. 1) with underwater epoxy (Emerkit). In each cement cone, we embedded 4-cm nails on opposite sides of the upper surface so that the ends of a three-strand rope holding a seaweed could be slipped over each nail head, to hold the seaweed in contact with the coral. We used representative-sized individuals of seaweeds that were common at each site. Intact, whole thalli were used to avoid stress compounds that might be released if seaweeds were clipped. Control corals received a rope without macroalgae. Our transplant procedures allowed for seaweed-coral contact representative of natural contacts observed in the field.

We interspersed treatment and control replicates ($n$ = 10–12 for each species) haphazardly (15 cm apart in all directions) across five racks made of PVC (Panama) or welded metal (Fiji) frames holding metal mesh into which the bases of the cones could be placed (Fig. 1). In Panama, the racks were secured on a coral-dominated reef, holding corals at 4 m depth. In Fiji, racks were secured on a coral-dominated reef flat, holding corals at 1 m depth at low tide. *Porites* species were common around our racks in both sites. We caged racks with 1-cm$^2$-grid metal screening to exclude large herbivores, and brushed cages every 2 d to remove fouling organisms. During routine maintenance, we visually noted bleaching of corals and replaced any seaweeds lost because of wave action (happened infrequently and only in Fiji). After 20 d, we assessed the effects of seaweed contact on coral tissue bleaching, relative to controls, using photographic surveys. Corals with bleaching were photographed with an underwater digital camera held perpendicular to the coral fragment. Using an in-frame scale, 2D percent-area bleaching of each replicate was quantified using ImageJ (1.40, NIH) photo analysis software. Because visual assessments of coral bleaching/mortality can be subjective (26), we also quantified the effects of seaweed contact on coral bleaching after 20 d using in situ PAM fluorometry. Measurements were taken at the most damaged location of seaweed-coral contact and at the same height on the opposite side of the coral branch. These latter measurements assessed effects on coral tissues only millimeters away from affected tissues, but not in direct physical contact with seaweeds. We sampled control corals in the same manner (at a similar height on the side with the control rope and on the side opposite the rope).

In these field experiments, we used the corals *P. porites* (Caribbean Panama) and *P. cylindrica* (Fiji) because this is a pan-tropical genus common to both sites and used in other investigations of coral-seaweed competition (8, 17–19, 22). The seaweeds we used were (*i*) common-to-abundant on these Poritid-dominated reefs, (*ii*) observed in contact with corals, and (*iii*) representative of a range of taxonomic and morphological forms.

**Algal Mimic Study.** We also tested possible effects of abrasion and shading alone using inert algal mimics. We constructed a foliose mimic of *Padina* by cutting opaque fronds from black plastic bags and grouping them with cable-tie "holdfasts" (Fig. S1*C*); a filamentous mimic of *Chlorodesmis* was made by cutting 60 loops of Dacron line (White River Fly Shop Magibraid Flyline Backing) into filaments and grouping them with a cable-tie "holdfast" (Fig. S1*D*). Algal mimics ($n$ = 10 per treatment) were then inserted into segments of three-strand rope and attached to fragments of *P. cylindrica* on racks at Votua Reef, Fiji (see experimental design, above). Control corals ($n$ = 10) were also deployed with rope segments lacking an algal mimic (Fig. S1*E*). Effects of algal mimics or controls on coral bleaching were assessed after 16 d using photographic surveys and in situ PAM fluorometry as described above (Fig. S1 *A* and *B*).

**Allelochemical Bioassays.** We exhaustively extracted whole tissues (20-mL displacement volume) of each alga with 100% methanol, filtered the extract, and removed the solvent by rotary evaporation. We resuspended each extract in 15 mL of ethyl acetate, added it to 200 mL of water and an additional 200 mL of ethyl acetate in a 1-L separatory funnel, and obtained the lipid-soluble fractions of each alga by collection of the ethyl acetate layer. This was repeated three times for each sample to assure efficient partitioning. Each lipid-soluble extract was dried by rotary evaporation and stored at −5 °C for 2 to 3 d until bioassay preparation.

For bioassays, we resuspended lipid-soluble extracts in 1 mL methanol and added them at appropriate volumetric concentration to Phytagel (Sigma-Aldrich) bioassay strips (1 cm$^2$) that were formed on window screen (modified methods of ref. 27). Control gels were created in the same manner, including the addition of methanol, but lacking seaweed extract. Gels were refrigerated for 7 to 10 h until deployed in the field. For deployment, a strip ($n$ = 10 for each treatment) was wrapped around a coral branch and held in place by a cable tie (Fig. 1*C*). After 24 h, we removed each strip and took a PAM fluorometry reading under the center of each treatment and control strip.

We also extracted lipophilic metabolites from the surfaces of four Fijian seaweeds (three allelopathic, one not) using the hexane dip method (28) to test if allelopathic metabolites were on seaweed surfaces at ecologically-relevant concentrations that could produce the allelopathic effects we observed in our whole-tissue allelochemical bioassays. Samples (20-mL displacement volume) were collected from the field, excess water was removed in a salad-spinner, and the alga was extracted with 100% hexanes for 30 s while vortexing (28). We then dried each lipophilic extract under rotary evaporation, resuspended them in 500 μL of hexanes, and added them at natural volumetric concentration to Phytagel strips as described above. Controls were created in the same manner, including the addition of hexanes, but lacking seaweed extract. Treatment and control gel strips ($n$ = 10 per extract) were deployed and assayed in the same manner as the whole-tissue allelochemical bioassays.

**PAM Fluorometry.** PAM fluorometry was used in situ to assess the effects of seaweeds and their extracts on coral health (effective quantum yield). PAM fluorometry provides a more rigorous and quantifiable measure of coral bleaching compared to visual assessments alone (24, references within ref. 26). Effective quantum yield is a measure (unitless, ranging from 0.0–1.0) of the efficiency of photosystem II within light-adapted photosynthetic organisms (i.e., under ambient field conditions) (24, 26). Values for healthy corals typically range from 0.5 to 0.7 (i.e., maximum potential quantum yield), depending on coral species and depth (26). Values of ∼0.0 to 0.2 are indicative of severe bleaching and mortality (24).

We took all PAM fluorometry readings between 0900 and 1400 h, and interspersed readings for all treatments and controls in time so that readings for a treatment would not be confounded by time (and associated variance in light or temperature). We observed low within-treatment variance (Fig. 2) for all of our treatments and controls, indicating minimal variance because of time of sampling.

**Seaweed Palatability Assays.** To assess how herbivory might impact seaweeds and thus the probability of seaweed-coral contacts, we conducted field feeding assays in both September 2008 and August 2009 using the seaweed species from our 20-d field competition study in Fiji. *Liagora* sp. was not included in 2009 assays because of its scarcity at that time. We conducted these studies in Fiji because of close proximity of protected and fished reefs (∼300 m apart), which allowed us to

assess the survivorship of each seaweed species in the presence and absence of a diverse herbivore guild (37). We collected each seaweed species from the same location that we collected seaweeds for our competition study and chemical extractions. Each year, standardized thalli of each seaweed (8–9 cm height) were inserted 3 to 5 cm apart on a 60-cm length of three-strand rope, and deployed at intervals of ~5 m across a protected and fished reef ($n$ = 20 per site) (*Methods* of ref. 41). After 24 h, we visually scored seaweeds on each rope in situ as 0, 25, 50, 75, or 100% consumed, based on changes in seaweed height. Ropes at both sites were scored by the same individual to prevent observer bias. Caged controls were not deployed, as both sites within each location had similar topography and hydrodynamic conditions, and seaweeds that were 100% consumed still had basal remnants in the rope that showed grazing marks from fishes. If we pulled seaweeds from ropes (as a wave might), the entire seaweed thallus pulled free rather than breaking off at the base; thus, we could detect no evidence of loss to processes other than fish feeding.

**Benthic Survey.** We quantified benthic cover of macrophytes and hard corals in the Votua MPA and 300 m west of the MPA by running 30-m transect surveys ($n$ = 10 per site). In the middle of each site, we deployed the first transect according to a randomly generated compass bearing, and ran subsequent transects parallel to this initial transect. Perpendicular distances between each transect were randomly assigned. Macrophytes and hard corals were scored (presence/absence) at 1-m intervals along each transect to determine percent cover.

**Statistical Analysis.** Data from our field competition and allelochemical bioassays violated parametric assumptions, so we evaluated them using Kruskal-Wallis ANOVA on Ranks. When some replicates lost seaweeds or were missed during final scoring, we randomly excluded replicates from other treatments (1, 2) to equalize sample sizes and allow more powerful posthoc tests that require balanced sample sizes. The algal mimic assay results were analyzed by one-factor ANOVAs. Differences among subgroups were analyzed for all ANOVAs using Student-Newman-Kuels posthoc tests. Herbivory assays produced ordinal data, so they were analyzed by Mann-Whitney U tests (42). We analyzed transect data using a $t$ test (for hard coral cover) and a Mann-Whitney U test (for macroalgal cover).

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