Competition induces allelopathy but suppresses growth and anti-herbivore defence in a chemically rich seaweed

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Many seaweeds and terrestrial plants induce chemical defences in response to herbivory, but whether they induce chemical defences against competitors (allelopathy) remains poorly understood. We evaluated whether two tropical seaweeds induce allelopathy in response to competition with a reef-building coral. We also assessed the effects of competition on seaweed growth and seaweed chemical defence against herbivores. Following 8 days of competition with the coral Porites cylindrica, the chemically rich seaweed Galaxaura filamentosus induced increased allelochemicals and became nearly twice as damaging to the coral. However, it also experienced significantly reduced growth and increased palatability to herbivores (because of reduced chemical defences). Under the same conditions, the seaweed Sargassum polycystum did not induce allelopathy and did not experience a change in growth or palatability. This is the first demonstration of induced allelopathy in a seaweed, or of competitors reducing seaweed chemical defences against herbivores. Our results suggest that the chemical ecology of coral–seaweed–herbivore interactions can be complex and nuanced, highlighting the need to incorporate greater ecological complexity into the study of chemical defence.

1. Introduction

Many organisms induce defences against natural enemies following direct attack or attacks on nearby conspecifics [1]. Induction of defences can increase fitness in environments where attacks are unpredictable, attack cues are reliable and defences are costly but effective [2,3]. Induction may also slow the counter-adaptation of natural enemies by creating variance in defences that represent a moving evolutionary target [4]. It is therefore not surprising that many seaweeds and terrestrial plants induce chemical defences in response to herbivory [2,5]. However, whether seaweeds also have the ability to induce chemical defences against competitors (i.e. allelochemicals) remains unknown [6]. Because seaweeds frequently interact not only with herbivores but also with competitors and pathogens, a better understanding of how processes other than herbivory affect the expression of seaweed defences is needed.

The extent to which seaweeds induce allelopathy against competitors may depend on whether their chemical defences serve single versus multiple functions. Some seaweeds produce allelopathic compounds that act as a broad-spectrum defence [7,8]; these allelochemicals could potentially be induced by competitors, herbivores or pathogens [9,10]. However, induction of allelopathy in such seaweeds could be constrained by ecological pressures (e.g. herbivory) that are rapid and/or fatal, thus mandating constitutive expression of broad-spectrum defences [8]. It is likely that multiple ecological processes interactively shape the expression and fitness costs of multi-function defensive molecules [11]. By contrast, seaweeds that produce multiple types of defensive molecules, each with differing functions, may be more capable of fine-tuning chemical defences against competitors via induction. However, this strategy could impose trade-offs if production of more allelopathic compounds reduces growth [12] or the production of compounds that function against other natural enemies [13–15]. Investigations exploring the defence strategies of, and chemical constraints within, marine
organisms are few [7,8,16,17] but are needed to understand the causes and consequences of induced allelopathy in seaweeds. Understanding the effects of competition on seaweed growth and chemical defence becomes increasingly important as humans impact marine communities and shift them between states of consumer versus competitor control [18]. For example, the community structure and strength of ecological processes are shifting dramatically on some coral reefs. Historically, herbivory controlled the structure and function of coral reef algal communities [19]. Rapid grazing by herbivores maintained non-coral substrates in early successional states, thereby preventing the establishment of seaweeds and promoting the dominance of corals [19]. However, reefs worldwide have recently experienced major losses of coral due to a host of human impacts [20,21] and many of these coral-poor reefs, especially those in the Caribbean, have undergone a ‘phase shift’ to seaweed dominance, because herbivores were overharvested or lost to disease and rates of herbivory have become insufficient to control algal growth [22,23]. Reduced herbivory allows competition between seaweeds and corals to intensify [24–26], increasing the importance of seaweed–coral competition versus herbivory in governing reef dynamics [22].

On coral reefs, phase shifts to seaweed commonly involve the proliferation of brown seaweeds, such as Sargassum, Turbinaria, Dictyota, Lobophora and Padina or calcified green seaweeds like Halimeda [27–30]. As these seaweeds become abundant, they reduce the growth, survival and reproduction of corals [24–26]. Among those that proliferate, seaweeds in the genera Dictyota, Lobophora and Halimeda are chemically rich and some may use chemical warfare against coral competitors (allelopathy) to maintain dominance [28,31–33]. However, it remains unknown whether coral–seaweed competition affects the concentration of allelochemicals or herbivore deterrents in seaweeds, and the effects of competition on seaweed growth remain inadequately described. Some chemically rich seaweeds fluctuate with season or disturbance, possibly limiting their impact on corals [34]; however, if they induce allelopathy in response to competition, then even brief interactions could result in significant damage to corals. The ability of chemically rich seaweeds to induce allelopathy could affect the rate at which these seaweeds proliferate on degraded reefs and form ecological feedbacks that prevent the recovery of reef-building corals [22].

In this study, we evaluated the effects of seaweed–coral competition on the strength of allelopathic versus anti-herbivore chemical defences in the seaweeds Sargassum polycystum and Galaxaura filamentos. These seaweeds are common to abundant on degraded reefs in Fiji, but differ in taxonomy, morphology and secondary chemistry. We asked: does competition with a common coral (i) induce allelopathy, (ii) affect seaweed growth or (iii) affect the palatability or effectiveness of anti-herbivore chemical defences within either seaweed?

2. Material and methods

(a) Study site and organisms

Our study was conducted in May–December 2011 on an approximately 1.5–2.5 m deep reef flat within a no-take marine reserve at Votua Village, Viti Levu, Fiji (18°13.049′ S, 177°42.968′ E). Within the reserve, reef-building corals are abundant (approx. 55% cover) and seaweeds are uncommon (approx. 2% cover); in adjacent areas subject to artisanal fishing, seaweeds are abundant (approx. 91% cover) and corals are rare (approx. 5% cover) [30]. Upon reserve establishment (2004), both areas were coral depauperate and reef dominated [35]. Recent coral recovery in the reserve and continued seaweed domination outside the reserve appear to be driven by fishing-induced changes to herbivory; herbivorous fishes are now abundant and diverse within the reserve but are scarce outside and as a result herbivory remains low outside the reserve [30,31].

We studied the brown seaweed S. polycystum and the red seaweed G. filamentos (hereafter, referred to by genus names) because they: (i) are common (Galaxaura) to abundant (Sargassum) on degraded reefs outside the reserve [30], (ii) are regularly observed in contact with corals in degraded habitats (D. B. Rasher, 2010 and 2011, personal observation), (iii) differ in taxonomy and morphology and (iv) differ in their palatability to herbivores (Sargassum, high; Galaxaura, low) and allelopathic effects on corals (Sargassum, benign; Galaxaura, harmful) [30–32]. We used the coral Porites cylindrica (hereafter ‘Porites’) because it (i) is common to both healthy and degraded reef flats in Fiji, (ii) is regularly observed in contact with seaweeds in degraded habitats (D. B. Rasher, 2010 and 2011, personal observation) and (iii) responds differentially to competition with different seaweeds, but is more resistant to seaweed effects than other co-occurring corals [31,32]. All seaweed palatability and chemical defence assays were conducted with herbivorous fishes in the field because they control algal community structure on Pacific reefs [19,26] and are, therefore, likely to be the herbivores against which seaweed anti-herbivore defences evolved [36].

(b) Coral induction of seaweed allelochemicals

In a previous study, Galaxaura was allelopathic to the four common coral species investigated, while Sargassum showed no allelopathic effect [31,32]. Here, we conducted field experiments to test whether competition with the coral Porites induces greater allelopathy in Galaxaura or any allelopathic activity in Sargassum. To create replicate corals, we collected 100 branches of Porites (6–8 cm length) from numerous colonies within the reserve, epoxied each branch into a cement cone [31] and deployed them on a metal rack in the reserve (depth = 1 m) to allow for acclimation and growth. After 24 months, this created 100 multi-branched coral colonies approximately 12–15 cm in height. To create experimental controls, we removed half of the corals (n = 50), submerging them in commercial bleach (3–6% sodium hypochlorite) for 4 days, rinsed and dried them to remove all traces of bleach and interspersed the skeletons among the 50 living corals on the rack. These skeletons served as controls, allowing us to differentiate the effects of seaweed contact with a living competitor from those due to contact with a physically equivalent, but non-living, object.

Following interspersion of corals and skeletons on the rack, we collected 25 individuals of both Sargassum and Galaxaura (Sargassum = 18–20 g wet mass, approx. 25–30 cm height; Galaxaura = 33–36 g wet mass, 12–15 cm height) from within the same area outside the reserve. We split each alga into a two similar-sized portions, using one for the treatment and the other for the control. This standardized initial seaweed chemical traits between treatments and controls. We then uniformly spun each pair in a salad spinner to remove excess water, weighed each seaweed, inserted each into a 20 cm length of 3-stranded rope, and attached one thallus from each pair to a cone holding a living Porites (‘treatment’) and the remaining thallus to a cone holding a Porites skeleton (‘control’). Each seaweed was attached by slipping the ends of the 3-stranded rope over nails embedded 180° apart on the upper surface of the cone. This design resulted in a 2 cm gap between the seaweed and coral, allowing seaweed movement and seaweed–coral contact comparable to interactions observed in nature (n = 25 treatment−1 species−1).
To simulate the low herbivory experienced by these seaweeds outside the reserve [31], we caged the rack with wire mesh (1 cm² openings). The experiment ran for 8 days. Some thalli of each species detached during the 8-day study; these replicates and their autogenic pairs were excluded, resulting in n = 15 treatment –1 species –1.

To assess allelochemical induction in Sargassum and Galaxaura after 8 days of competition with coral, we generated hydrophobic extracts [31,32] from treatment and control thalli and tested their allelopathic effects on new Porites in the field. We previously identified two allelopathic compounds produced by G. filamentosa—both terpenoid loliolide derivatives [32]. Although these two molecules may be involved in the induction of allelopathy in Galaxaura, monitoring changes in their concentrations pre-versus post-competition to evaluate induction would be insufficient and potentially misleading, because they represent only two of at least six compounds in an allelopathic mixture produced by Galaxaura (see fig. 4 in [32]). The other allelopathic compounds remain unidentified due to their low yield and/or instability following isolation [32]. Given that multiple compounds within Galaxaura act together to produce its allelopathic effect and that most of these compounds cannot be identified and thus quantified, the only rigorous way to evaluate induction was to assess the allelopathic strength of the extract from seaweeds that had competed with corals versus those that had not. We assessed this for hydrophobic crude extracts because previous studies demonstrated that hydrophilic fractions produced no allelopathic effect and the effect of the whole seaweed was reproduced by the hydrophobic extract alone [31,32].

For each seaweed species, we created bulk extracts by removing a small portion of thallus from each seaweed and grouping them by treatment or control. We determined the volumetric displacement of the grouped thalli from each species, exhaustively extracted each in 100% methanol, and dried each by rotary evaporation. We then partitioned each extract between water and ethyl acetate, and retained the hydrophobic (ethyl acetate) fraction of each for testing its allelopathic effects on Porites. To test its effects on Porites, hydrophobic extracts from treatment and control thalli were re-suspended in solvent and incorporated at natural volumetric concentration into a series of approximately 1 cm² Phytagel (Sigma-Aldrich, USA) squares (n = 10 extract –1 species –1) hardened on window screen backing [37,38]. We also prepared squares with solvent but no seaweed extract as controls for the effects of the Phytagel, solvent and backing (n = 10; ‘Phytagel control’). Phytagel squares with and without seaweed extracts differed in colour and clarity but because the bioactivity of Sargassum extract squares (dark) and Phytagel control squares (light) did not differ (figure 1), nor did severalpigmented seaweed extract versus Phytagel contrastst in previous assays [32], we assumed that colour did not affect pulse-amplitude-modulated (PAM) readings to a detectable degree and thus avoided the use of dyes (with unknown effects) to standardize colour/clarity.

Phytagel squares were wrapped and cable-tied at mid-height on individual branches of Porites (6–8 cm height, planted as above) and were interspersed on an un-caged rack in the reserve. After 24 h, we assessed the effects of seaweed extracts versus Phytagel controls on coral photophysiology by taking a single PAM fluorometry measurement (fibre-optic diameter = 5.5 mm, distance = 9–10 mm, angle = perpendicular) under the centre of each square (see below for detailed methods).

To confirm that induction of allelochemicals by Galaxaura increases coral damage under field conditions, we conducted an 8-day Galaxaura–Porites manipulation as before, but then placed the thalli (instead of extracts) of Galaxaura that had been in contact with Porites (‘treatment’) into competition with new Porites fragments (6–8 cm branches, planted as above; n = 15) and assessed the impacts of these seaweeds on corals relative to thalli that had been in contact with Porites skeletons (‘controls’; n = 15). We evaluated the effects of treatment and control seaweeds on the photophysiology of these new corals after 2, 4 and 12 days. We also deployed Porites without seaweed contact as environmental controls (‘environmental control’; n = 15). At each sampling interval, we took a single PAM fluorometry measurement (as above) on each coral at the most damaged location experiencing seaweed contact along the mid-point of the branch (i.e. excluding extremities). Environmental controls were sampled at the most damaged location along the mid-point using identical protocol. We caged the rack to prevent grazing by large herbivores.

(c) Pulse-amplitude-modulated fluorometry

We used PAM fluorometry (Diving-PAM, Walz, Germany) to assess changes in the photosystem II (PSII) quantum yield of zooxanthellae living within Porites, following contact with seaweed thalli or extracts. PAM fluorometry is commonly used to assess PSII function within the coral holobiont in response to biotic or abiotic stressors, and to investigate the processes leading to coral bleaching [38–40]. Measurements of light-adapted corals (i.e. effective quantum yield (ΦPSII)) theoretically range from 0.0 to approximately 0.83. Empirical studies suggest that measurements of approximately 0.50–0.75 are indicative of a healthy coral and measurements of approximately 0.00–0.25 are indicative of coral bleaching and mortality [38–40]. Effective quantum yield (ΨPSII) values are highly correlated with visual assessments of coral bleaching for Porites and other corals at our study site [31,32].

We wanted to assess coral responses in nature with minimal disturbance of the test corals, so we sampled them in the field between 09.00 and 13.00 h. We interspersed readings for treatments and controls through time to prevent confounding seaweed effects with in situ temporal changes in non-photochemical quenching (i.e. temperature and UV). Coral fragments were (i) collected from colonies adjacent to our experimental rack (i.e. the same depth and local condition), (ii) allowed to acclimate on the rack for 1–24 months prior to experiments and (iii) haphazardly interspersed among treatments and controls to homogenize...
initial variance in zooxanthellae density and diversity among replicates. We avoided self-shading while sampling.

(d) Effects of competition on seaweed growth, palatability and anti-herbivore defence

In addition to allelochemical induction, we evaluated whether competition affected the growth of either seaweed or changed their susceptibility to herbivory. To assess growth, we measured the spun wet mass (g) of each treatment and control pair before and after the 8-day competition period. To evaluate changes in palatability, we then conducted paired feeding assays in the field using a portion of each autogenic treatment and control pair. We removed four branches from each treatment seaweed, spun them uniformly in a salad spinner to remove excess water, weighed the branches and inserted them 5 cm apart on a 60 cm section of 3-stranded rope. Ropes holding control seaweeds were assembled identically (n = 15 rope pairs species⁻¹). Furthermore, a single branch of each seaweed from each pair was spun, weighed and inserted into a 20 cm segment of 3-stranded rope to be deployed as a caged control to assess changes in seaweed mass unrelated to herbivory.

Within the reserve, we deployed autogenic pairs of treatment and control seaweed in a network of pools accessible to herbivorous fishes at both low and high tide. We deployed pairs within approximately 0.50–0.75 m of each other, and caged controls within 1 m of each pair. Replicates were spaced by 5–7 m. We recollected pairs when approximately 50% of the total biomass (within pairs) was consumed; thus, tests for Sargassum lasted 2–24 h and tests for Galaxaura lasted 5–7 days. Following assays, seaweeds were bagged in situ and returned to the laboratory, where they were spun and re-weighed. We calculated the mass of each seaweed consumed using the formula:

\[ \text{mass consumed} = \frac{(T_i - T_f) \times n}{(C_i - C_f) \times n} \]

where \( T_i \) and \( T_f \) were the initial and final masses (respectively) of a seaweed exposed to herbivory, and \( C_i \) and \( C_f \) were the initial and final masses (respectively) of its autogenic caged control protected from herbivory.

To test the hypothesis that an increase in the palatability of Galaxaura following competition was owing to changes in anti-herbivore defensive chemistry, we tested the deterrent effects of hydrophobic extracts from treatment versus control Galaxaura against herbivorous fishes in the field. These extracts were the same as those used to assess induction of allelopathy in Galaxaura. To test extract deterrence against herbivorous surgeonfish (Naso lituratus and Naso unicornis), we re-suspended each extract in ether, coated each at a natural volumetric concentration on five blades (a 2.04 ± 0.03 ml volumetric equivalent, mean ± s.e.; \( n = 10 \)) of blotted dry and pre-weighed Padina borga (a preferred prey of N. lituratus and N. unicornis [30], hereafter ‘Padina’), allowed the ether to evaporate, inserted each set of blades 5 cm apart on their own 60 cm section of 3-stranded rope (\( n = 12 \) ropes extract⁻¹), and deployed pairs of treatment and control ropes in the field (as described earlier).

Because feeding on Padina was rapid (approx. 10 min pair⁻¹), we deployed one pair at a time, monitored feeding and re-collected pairs when approximately 50% of the total biomass within each pair was consumed. We observed only N. lituratus and N. unicornis feeding on the Padina. Following assays, seaweeds were bagged in situ and returned to the laboratory, where they were blotted dry and re-weighed. Given the duration of each assay and our visual assessment that seaweed tissues were not being lost to processes other than herbivory, we did not deploy caged controls.

To test extract deterrence against other herbivores, we re-suspended the same Galaxaura extracts in ether, coated each at a natural volumetric concentration on three branches (a 0.74 ± 0.02 ml volumetric equivalent) of blotted dry and pre-weighed Amphipora crassa (a heavily calcified seaweed avoided by Naso spp. but consumed by the parrotfish Chlorurus sordidus [30], hereafter ‘Amphipora’), allowed the ether to evaporate, inserted each set of branches 3 cm apart on their own 60 cm section of 3-stranded rope (\( n = 12 \) ropes extract⁻¹), and deployed paired treatment and control ropes in the field (as described earlier). We also coated Amphipora only with ether and deployed them as caged controls within 1 m of each pair to control for changes in seaweed mass unrelated to herbivory. Grazing on Amphipora was low (only five pairs received detectable grazing) and assays lasted 3–5 days. We calculated the mass of Amphipora consumed among the five pairs with detectable grazing using the formula described earlier.

(e) Statistical analyses and data deposition

Treatments and controls were created using autogenic pairs of seaweed and feeding assays were deployed as spatial pairs in the field; thus, data regarding seaweed growth, palatability and chemical deterrence were evaluated with paired t-tests (and in one instance a Wilcoxon signed-rank test when data could not be transformed to meet parametric assumptions). We analysed data regarding the allelopathic potency of seaweed chemical extracts with a one factor ANOVA. Data regarding the effects of induced Galaxaura thalli were analysed with a two factor, repeated measures ANOVA. We further evaluated significant ANOVA results with Tukey post-hoc tests. All statistical analyses were performed using SIGMASTAT (v. 3.5, Systat Software Inc.). Datasets used in this study are available online from BCO-DMO data system (http://bco-dmo.org/).

3. Results

(a) Coral induction of seaweed allelochemicals

When extracts of Sargassum were generated following 8 days of contact with a living coral (treatment) or coral skeleton (control) and were tested for allelopathic effects in the field, neither treatment nor control Sargassum extracts affected Porites relative to Phytagel controls (figure 1). By contrast, both extracts from Galaxaura significantly suppressed Porites \( \Phi_{PSII} \) (ANOVA: \( F_{4,45} = 36.676, p < 0.001 \)), with extracts from treatment Galaxaura being a significant 44% more allelopathic than extracts from control Galaxaura (figure 1). Galaxaura is always allelopathic but induced greater allelopathy following competition with Porites.

When Galaxaura thalli were grown next to Porites (treatment) or a Porites skeleton (control) for 8 days and then placed in contact with new Porites, treatment thalli were a significant 37% more damaging to Porites than control thalli on day 2, confirming prior induction in the treatment seaweeds and demonstrating their impact under field conditions (figure 2 and table 1). However, by day 4, both treatment and control thalli exhibited a similar and significant suppression of Porites \( \Phi_{PSII} \) relative to environmental controls (figure 2 and table 1).

Thus, induction of allelopathy in Galaxaura occurs within 4 days of competition with Porites. Effects of treatment Galaxaura on corals did not differ between days 2 and 12 (table 1). By contrast, effects of control thalli increased significantly with time, consistent with an induction of allelochemicals in response to new contact with living coral (table 1). Quantum yield values of Porites that served as environmental controls did not change significantly during the study (table 1), indicating a minimal effect of the environment or our sampling schedule on our \( \Phi_{PSII} \) measurements.
defence focus on plant–herbivore interactions in isolation [42,43]. The roles of other enemies, such as competitors, in eliciting plant chemical responses remain less explored [9,44,45], particularly in marine systems [6]. In our study, the chemically rich seaweed *Galaxaura* induced greater allelopathy in response to competition with the coral *Porites* (figures 1 and 2; table 1). To our knowledge, this is the first demonstration of induced allelopathy in seaweeds.

When competing with *Porites*, *Galaxaura* also became more palatable to herbivores (figure 3), with this increased palatability caused by a weakening of its anti-herbivore chemical defences, or possibly a production of feeding stimulants (figure 4). Thus, *Galaxaura* produces different chemical defences to combat competitors versus herbivores. Some seaweeds and sponges produce a single molecule or suite of molecules that serve as a broad-spectrum defence [7,8,16], and this defence strategy has allowed certain seaweeds to invade new ecosystems because a single defence makes them both competitively superior and resistant to herbivores [46,47]. However, *Galaxaura* produces different compounds to combat different types of natural enemies, a phenomenon better described among terrestrial plants (e.g. [13,15]). Such a strategy may allow organisms to respond to divergent ecological threats with defences fine-tuned to each threat. This could be advantageous in ecosystems that flip between states of consumer versus competitor control or that display a spatial mosaic of selective pressures. At our study site, *Galaxaura* lives both deeply embedded between corals, where competition with coral would be high and herbivory low, and on open substrates exposed to herbivores. Thus, individuals in this population experience different ecological pressures within the same reef habitat; this mosaic of threats may select for *Galaxaura* to maintain an arsenal of different defences that can be adjusted within each microhabitat.

While *Galaxaura* experienced reduced growth and increased palatability owing to competition with *Porites*, *Sargassum* did not (figures 1–3). The mechanisms underlying these differing patterns are unknown. *Porites* may deploy defences (e.g. allelochemicals) against seaweeds in a species- or threat-specific manner, or *Galaxaura* and *Sargassum* may differ in their susceptibility to the same coral defence. *Porites* cylindrica can directly suppress the growth of some chemically rich seaweeds (e.g. *Lobophora variegata* [25]); these coral defences might have reduced the growth and compromised the effectiveness of anti-herbivore defences in *Galaxaura*. In contrast to direct effects, it is equally plausible that *Porites* indirectly altered the growth and palatability of *Galaxaura* by triggering a trade-off between the induction of allelopathy and growth, or the production of herbivore deterrents [14]. Regardless of the mechanism responsible, coral competitors can alter the growth of chemically rich seaweeds and their susceptibility to herbivory. Such nuanced phenomena are rarely considered, but could be important components of coral–seaweed–herbivore interactions on tropical reefs.

Although competition can suppress seaweed chemical defence against herbivores (figure 4), the consequences of this phenomenon may be context-dependent. It may create little cost to seaweeds on severely degraded and overfished reefs—the situation in which coral–seaweed interactions might be most frequent and induced allelopathy most prevalent. In this ecological scenario, the loss of anti-herbivore defences with competition likely would not decrease seaweed fitness because seaweed browsers are scarce on overfished reefs.

### 4. Discussion

#### (a) Competition can change seaweed allelopathy, growth and anti-herbivore defence

In nature, organisms interact with, and are simultaneously challenged by, numerous types of natural enemies [41]. Despite this, most studies and theories of plant chemical interactions have focused almost exclusively on the plant–herbivore interaction (e.g. [42,43]). The roles of other enemies, such as competitors, in eliciting plant chemical responses remain less explored [9,44,45], particularly in marine systems [6]. In our study, we demonstrated that the chemically rich seaweed *Galaxaura* induced greater allelopathy in response to competition with the coral *Porites* (figures 1 and 2; table 1). To our knowledge, this is the first demonstration of induced allelopathy in seaweeds.

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weeds can increase their damage to corals by inducing
unknown, but our findings reveal that some chemically rich sea-
induce allelopathy in response to competition remains
recruitment [28,31,33]. Whether these Caribbean seaweeds
allelochemicals that reduce coral survival, reproduction and
[27,28,34]), and several species in these genera produce
the spatial dominants on many degraded fore-reefs (e.g.
Table 1.
Dictyota, Lobophora
vering from these shifts [20,22,23,50]. Seaweeds in the genera
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Our results have implications for plant defence para-
digms. The effectiveness of plant chemical defences and its cost to the plant are often evaluated by studying pair-
wise herbivore–plant interactions in a relatively controlled
setting [2,5]. Yet, in a natural setting with multiple types of
enemies [41], plant responses to herbivores may be less pre-
dictable if multiple ecological processes interact to affect the
expression of defence metabolites [11,13,15,44]. In our
study, the addition of a single competitor caused a dramatic change in the palatability of Galaxaura and the effectiveness of
its chemical defences against herbivorous fishes (figures 3
and 4). These findings highlight the notion that ecologically
simplified studies may inadequately evaluate the effective-
ness of plant chemical defences in nature, and reinforce the
call to incorporate greater complexity into defence studies
to better evaluate the utility of plant defence theories [48,49].
but primarily in the austral winter when
periodically blooms and covers the heavily fished reefs that
esiana, which can bleach and kill small corals [31,32],
commonly bloom first and remain dominant on
reefs in the Pacific if certain seaweed browsers are missing
Caribbean [31] and the frequent interactions between seaweeds
and corals on many Caribbean reefs (e.g. [51]), coral induction of seaweed allelopathy could play an underappreciated role in
generating the low resilience of corals in the Caribbean [50].

Despite their low palatability [30,31] and potential ability to induce allelochemicals (figures 1 and 2), chemically rich
seaweeds rarely dominate shallow reef flats in Fiji [30]. Instead, it is non-allelopathic, palatable brown seaweeds
such as Sargassum, Turbinaria and Padina that occupy the majority of space following reef degradation and reductions
in herbivory [30,31,52]. Chemically defended seaweeds are
spatially or temporally patchy on degraded reef flats outside
the reserve. The allelopathic brown seaweed Dictyota bartayr-
esiana, which can bleach and kill small corals [31,32],
periodically blooms and covers the heavily fished reefs that
we study, but primarily in the austral winter when Sargassum
Other allelopathic species (e.g. Galaxaura, Chlorodesmis)
are common but patchily distributed [30]. Why allelopathic
seaweeds are not dominant in reef flat habitats is unknown.
Increased palatability in response to competition, as seen in
Galaxaura (figures 3 and 4), is unlikely to be a major factor con-
sidering that the seaweeds that dominate outside the reserve are
highly palatable, yet experience little herbivory because brows-
ing herbivores are overfished outside the reserve [30,31]. Given
that non-allelopathic seaweeds such as Sargassum, Turbinaria
and Padina commonly bloom first and remain dominant on
Pacific reef flats following the exclusion of herbivores [26,52],
a parsimonious explanation may be that rapid recruitment and
space pre-emption by these poorly defended seaweeds
prevent allelopathic species from proliferating.
(b) Implications for reef ecology and conservation
In recent decades, reefs throughout much of the Caribbean have
shifted from coral to seaweed dominance, with few reefs reco-
vering from these shifts [20,22,23,50]. Seaweeds in the genera
Dictyota, Lepeophora and Halimeda have together become
the spatial dominants on many degraded fore-reefs (e.g.
[27,28,34]), and several species in these genera produce
allelochemicals that reduce coral survival, reproduction and
recruitment [28,31,33]. Whether these Caribbean seaweeds
induce allelopathy in response to competition remains
unknown, but our findings reveal that some chemically rich sea-
weeds can increase their damage to corals by inducing
allelopathy. Given the prevalence of allelopathic species in the

<table>
<thead>
<tr>
<th>source of variation</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p-value</th>
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<td>treatment</td>
<td>2</td>
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<td>1.314</td>
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<td>replicate (treatment)</td>
<td>42</td>
<td>0.755</td>
<td>0.018</td>
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<tr>
<td>day</td>
<td>2</td>
<td>0.152</td>
<td>0.076</td>
<td>5.952</td>
<td>0.004</td>
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<tr>
<td>treatment × day</td>
<td>4</td>
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<td>0.107</td>
<td>8.407</td>
<td>&lt;0.001</td>
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<tr>
<td>residual</td>
<td>84</td>
<td>1.072</td>
<td>0.013</td>
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<tr>
<td>total</td>
<td>134</td>
<td>5.037</td>
<td>0.038</td>
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</table>

<table>
<thead>
<tr>
<th>Tukey post-hoc test results (p-values)</th>
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</thead>
<tbody>
<tr>
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<tr>
<td>day 2</td>
</tr>
<tr>
<td>treatment thalli versus environmental control</td>
</tr>
<tr>
<td>control thalli versus environmental control</td>
</tr>
<tr>
<td>treatment thalli versus control thalli</td>
</tr>
<tr>
<td>day 4</td>
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<tr>
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</tr>
<tr>
<td>control thalli versus environmental control</td>
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<tr>
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<td>day 12</td>
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<td>treatment thalli versus environmental control</td>
</tr>
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<tr>
<td>treatment thalli versus control thalli</td>
</tr>
<tr>
<td>day 2 versus 4</td>
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<tr>
<td>treatment thalli versus environmental control</td>
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<tr>
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<tr>
<td>day 4 versus 12</td>
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<tr>
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<tr>
<td>treatment thalli versus control thalli</td>
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<tr>
<td>day 2 versus 12</td>
</tr>
</tbody>
</table>
Thus, managing for a diverse guild of reef herbivores, containing both species capable of removing non-allelopathic and allelopathic seaweeds, appears necessary to prevent and reverse seaweed domination on Pacific reefs [22,30].

5. Conclusion

Similar to plants in terrestrial systems, secondary chemistry plays an important role in the interactions between seaweeds and their natural enemies [53,54]. However, the extent to which seaweeds mediate multiple ecological interactions via chemical defences, or how multiple ecological pressures interactively shape the expression of seaweed defensive molecules, remains inadequately understood. Our study provides new insights into the complexity of chemically mediated coral–seaweed–herbivore interactions. We found that competition can induce increased allelopathy, but also decrease the growth and increase the palatability of a chemically rich seaweed. These findings highlight the need to incorporate greater ecological complexity into investigations of the ecology and evolution of chemical defences [41,48,49] and their cascading effects on ecosystems [54].

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