Competitors as accomplices: seaweed competitors hide corals from predatory sea stars

Cody S. Clements and Mark E. Hay

School of Biology and Aquatic Chemical Ecology Center, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA

Indirect biotic effects arising from multispecies interactions can alter the structure and function of ecological communities—often in surprising ways that can vary in direction and magnitude. On Pacific coral reefs, predation by the crown-of-thorns sea star, *Acanthaster planci*, is associated with broad-scale losses of coral cover and increases of macroalgal cover. Macroalgal blooms increase coral–macroalgal competition and can generate further coral decline. However, using a combination of manipulative field experiments and observations, we demonstrate that macroalgae, such as *Sargassum polycystum*, produce associational refuges for corals and dramatically reduce their consumption by *Acanthaster*. Thus, as *Acanthaster* densities increase, macroalgae can become coral mutualists, despite being competitors that significantly suppress coral growth. Field feeding experiments revealed that the protective effects of macroalgae were strong enough to cause *Acanthaster* to consume low-preference corals instead of high-preference corals surrounded by macroalgae. This highlights the context-dependent nature of coral–algal interactions when consumers are common. Macroalgal creation of associational refuges from *Acanthaster* predation may have important implications for the structure, function and resilience of reef communities subject to an increasing number of biotic disturbances.

1. Introduction

Indirect biotic interactions can strongly impact the structure and function of ecological communities, but the mechanisms and circumstances controlling their relative importance is incompletely understood [1–4]. Indirect biotic effects occur when the impact of one species on another is mediated by the presence of a third [2]. This commonly entails modifying the density (i.e. density-mediated indirect interactions) or traits (e.g. behaviour, morphology, life history) of one species, which goes on to influence subsequent interactions among other species [5–7]. These effects are ubiquitous across ecological systems and are known to influence a myriad of species interactions (e.g. competition, predation, mutualism), as well as community- and ecosystem-level processes [5,8–10].

A substantial body of work has highlighted the role of indirect effects in competitive interactions between species, including situations in which the strength or qualitative sign of competitive effects on one species can be altered when its competitor ameliorates the negative impacts of an extrinsic stressor, such as predation by a third species (i.e. ‘associational refuge’) [11–14]. A better understanding of context-dependency is needed for both modelling indirect interactions and for building robust management strategies for ecosystems subject to increasing disturbances [13,15].

Coral reefs provide a good example of the needs for, and values of, understanding indirect interactions. Reefs are in worldwide decline because of a variety of natural and anthropogenic disturbances [16–19], with declines in coral cover commonly accompanied by increases in benthic macroalgae [19–21]. Macroalgae use a variety of physical (e.g. shading, abrasion, overgrowth) and/or chemical (i.e. allelopathy) mechanisms to directly reduce coral recruitment,
growth, survival and fecundity [22–25]. Coral–algal interactions may also suppress corals indirectly by promoting virulent bacteria [26,27], or by stressing corals in ways that attract corallivores that further damage competing corals [28]. Alternatively, despite being competitors, seaweeds may hide susceptible corals from fish consumers [29,30] or buffer stressful physical conditions [31]. The direct and indirect effects of macroalgae on corals, coupled with the increasing prevalence of macroalgal–coral competition, may impact the current and future function of coral reefs, but the relative cost versus possible benefits of macroalgae to corals remains poorly understood, as does how this may vary as a function of local biotic context [19,28–31].

On Pacific coral reefs, coral consumption by the crown-of-thorns star, *Acanthaster planci*, is a major driver of coral loss [18,32]. During *Acanthaster* outbreaks, reef corals can be devastated over large areas, resulting in cascading losses of other species, and decline of reef resilience and function [33,34]. If macroalgal competitors sheltered corals from *Acanthaster* predation, they could have a net positive impact on corals despite being important competitors. Such an associational refuge could alter *Acanthaster* feeding preferences, with implications for reef community composition and local persistence of coral species favoured by *Acanthaster*. Assessing the context-dependent nature of these interactions requires a greater understanding of the relative costs (e.g. competition) versus benefits (e.g. potential associational refuge) for corals in contact with benthic macroalgae.

Here we explored the direct negative and indirect positive effects arising from competitive interactions between corals and macroalgae. Using a combination of manipulative and observational field experiments, we investigated the effects of a common brown macroalga, *Sargassum polycystum*, on the coral *Montipora hispida*, and how costs and benefits for the coral may vary because of *Acanthaster* feeding and *Sargassum* abundance. *Sargassum* is a canopy-forming macroalga that blooms on degraded reefs worldwide [35–37], while *Montipora* is a common coral that frequently contacts *Sargassum* on overfished or degraded reefs [38]. *Montipora* is also a favoured prey of *Acanthaster*, which is common on both healthy and degraded reefs in Fiji [39,40], and is regularly observed feeding on *Montipora* (C. Clements 2013, personal observation). We hypothesized that at sufficient densities, *Sargassum* not only would reduce coral growth, but also might provide *Montipora* with an associational refuge from *Acanthaster*. For the latter, this included testing whether the probability of *Acanthaster* attacking *Montipora* declined with *Sargassum* density, as well as whether the preference of *Acanthaster* for *Montipora* over *Porites cylindrica* (a low-preference prey) would reverse if *Montipora* was competing with high densities of *Sargassum*.

2. Material and methods

(a) Study site

This study was conducted within a no-take marine protected area paired with an adjacent fished area on the reef flat (1.5–2.5 m deep) at Votua Village along the Coral Coast of Viti Levu, Fiji (18°13.049’S, 177°842.968’E). All manipulative experiments were conducted within the reserve, where corals on hard substrates were abundant (approx. 55% cover) and macroalgae were uncommon (approx. 2% cover), while the field survey of *Acanthaster* feeding on corals as a function of natural macroalgal cover was conducted in the fished area where macroalgae were abundant (91%) and corals were uncommon (approx. 5% cover) [37].

(b) Influence of *Sargassum* on *Montipora* growth

We conducted a manipulative experiment within Votua’s no-take reserve during December 2013–March 2014 to test whether prolonged contact with *Sargassum* affects *Montipora* growth rates, and whether these effects vary with the density of surrounding *Sargassum*. We collected five branches of *Montipora* of similar size (approx. 3.5–4.5 g) from each of 20 colonies (100 branches total) located on the reef flat of the reserve and attached them individually to cut-off necks of inverted plastic bottles using epoxy (Emerkit). Each bottle portion and respective coral was then screwed individually into a bottle cap embedded within the substrate. The five *Montipora* branches collected from each colony were then surrounded by one of five algal treatments: 0, 2, 4, 6 or 8 fronds of the brown alga *S. polycystum* (length = 15–20 cm; n = 20 per treatment; figure 1). All *Sargassum* was collected from the adjacent fished area. To manipulate coral–algal contact, two 5 cm nails were embedded into the substrate on opposite sides of the bottle cap so that a three-stranded rope could be slipped over the nail head to hold the seaweed in contact with the coral. All corals and surrounding macroalgae were caged with 1 cm²-grid metal screening to exclude herbivorous fishes, and all cages were brushed at least once every 9 days to remove fouling organisms. During routine maintenance, any *Sargassum* displaced from the ropes (e.g. because of wave action) was replaced.

Coral growth was assessed monthly by weighing corals and their respective bottle-top/epoxy to determine the change in mass from initial measurements. Corals were weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container mounted to a tripod holding it above the water. Bottle tops and epoxy were brushed clean of fouling organisms within 24 h before each weighing session, and were gently shaken 30 times to remove excess water immediately prior to weighing. At the end of the experiment, each coral was separated from its bottle-top/epoxy base, and both were weighed separately to determine by subtraction the per cent change in coral mass alone. Data on percentage change in mass violated parametric assumptions, so analyses were by Kruskal–Wallis ANOVA on ranks followed by Wilcoxon pairwise comparisons corrected for multiple contrasts.

(c) Influence of seaweed on *Acanthaster* feeding preference field survey

To assess whether the presence of *Sargassum* influenced *Acanthaster* foraging in the field, we surveyed *Acanthaster* attacks on corals with varying levels of algal contact found within Votua Reef’s fished area during July–August of 2013. We used the fished instead of the protected area because macroalgae were more common here and gave a larger range of algal–coral contacts to evaluate; in the protected area, seaweeds were too uncommon to allow this evaluation. We searched for *Acanthaster* that had recently attacked a *Montipora* colony by locating corals with characteristic *Acanthaster* feeding scars, which are white in coloration, not yet showing colonization by diatoms or filamentous algae, and thus indicative of recent predation events [33]. Each recently attacked colony (n = 22) was then photographed, along with the five nearest-neighbour *Montipora* colonies (all neighbouring colonies were within 2 m of the primary colony; 132 colonies in total; 15 of the nearest-neighbour colonies had also been attacked to some extent). Colony photographs were then analysed for the percentage cover of macroalgae (with the vast majority being *Sargassum*) using CORAL POINT COUNT [41]. The program randomly placed 40 points on each photo, and the organism beneath each point was identified.
To evaluate the relationship between the percentage of each Montipora colony covered by macroalgae and the percentage of each colony eaten by Acanthaster, we used Spearman’s rank correlation because data did not meet normality assumptions. Logistic regression analysis was used to determine whether macroalgal cover (primarily Sargassum) influenced the probability of a colony being either attacked or not attacked. We also pooled all surveyed corals that had been either attacked or not attacked by Acanthaster and compared the average percentage cover of macroalgae (mostly Sargassum) on attacked versus non-attacked colonies. We evaluated these data using a Wilcoxon signed-rank test because the data violated parametric assumptions.

(d) Feeding experiments
To experimentally evaluate the impact of seaweed presence on Acanthaster feeding, we conducted a series of feeding choice experiments during July–August 2012 and June 2013 on the reef flat of Votua Village’s no-take marine reserve. Feeding trials conducted during July–August 2012 entailed placing individual sea stars within 1.5 m field enclosures \( n = 10 \) and offering them a choice of either Montipora surrounded by fronds of Sargassum (length = 15–20 cm) or Montipora that lacked surrounding Sargassum. For each series of feeding trials, sea stars were collected from Votua Reef and held within separate enclosures for at least 5 days before the experiment. We also collected paired branches (6–8 cm each) of Montipora from colonies on Votua Reef within 24 h of each respective trial. Pairs of corals, each cable tied to a small piece of PVC pipe (3 cm) embedded in the substrate, were transplanted 0.5 m from each other in each enclosure. Sargassum contact with one coral in each cage was manipulated by placing Sargassum in three-stranded rope and securing the ends of this rope to small nails driven into the substrate near the treatment coral. This allowed us to manipulate seaweed density in a manner mimicking natural contacts seen in the fished area of the reef. Sea star predation on corals was monitored over the following 24–36 h, noting the first colony to be attacked and consumed. Four feeding choice experiments were conducted with Sargassum at densities of 2, 4, 6 or 8 fronds near the treatment coral and compared with a coral lacking adjacent Sargassum. To test whether physical structure alone could alter Acanthaster feeding preference, four parallel experiments were simultaneously conducted using biologically inert Sargassum mimics (plastic aquarium plants) in place of live Sargassum.

Following the above trials, additional choice experiments were conducted using fronds of reduced length (approx. 5 cm) to determine whether adjacent Sargassum suppressed Acanthaster feeding despite a substantial reduction in algal canopy height. Sea stars were offered a choice between Montipora surrounded by 6 fronds of shorter Sargassum (5 cm height) and Montipora without surrounding Sargassum \( n = 10 \) pairs. A parallel experiment was simultaneously conducted using plastic Sargassum mimics (length = ~5 cm) in the place of live seaweed \( n = 10 \) pairs. For each feeding experiment, we used a Fisher’s exact test to assess the number of replicates in which the control (no nearby Sargassum) versus the treatment (Sargassum adjacent) was attacked first. At the end of each feeding trial, uneaten corals were returned to the reef and sea stars were sacrificed (at the request of the village environmental committee).

We conducted an additional feeding experiment in June 2013 that followed the same procedures. In this experiment, individual sea stars were offered a choice between M. hispida and P. cylindrica that both lacked surrounding Sargassum \( n = 10 \), or a choice between Montipora surrounded by 8 fronds of Sargassum (length = 15–20 cm) and Porites that lacked surrounding Sargassum \( n = 10 \) pairs. Porites cylindrica is a common coral on both healthy and degraded reefs in Fiji [38], and is typically avoided by Acanthaster [42,43]. Sea star predation on corals was monitored over the following 1–10 days, noting the first colony to be attacked and consumed. For each feeding trial, differences in the instances of Montipora versus Porites being attacked first were tested using a Fisher’s exact test.
3. Results

Montipora growth decreased linearly with increasing Sargassum density (Kruskal–Wallis ANOVA on ranks: $H = 53.4$, d.f. = 4, $p < 0.001$; figure 2); control corals without Sargassum grew approximately 2.7 times more than corals surrounded by 8 Sargassum fronds. Although Sargassum suppressed Montipora growth (figure 2), it also provided protection from Acanthaster predation (figure 3). In field surveys, extent of Acanthaster predation on Montipora was negatively correlated with macroalgal cover (Spearman’s rank correlation: $r_s = -0.655$, $p < 0.001$; figure 3). Of the 132 colonies of Montipora we surveyed, 35 had been attacked and 97 had not. Attacked colonies had an average macroalgal cover of 8%, while the unattacked colonies had an average cover of 55% macroalgae (Wilcoxon signed-rank test: $z = -7.235$, $p < 0.001$; figure 3). The 132 colonies of Montipora were surveyed, 35 had been attacked and 97 had not. Attacked colonies had an average macroalgal cover of 8%, while the unattacked colonies had an average cover of 55% macroalgae (Wilcoxon signed-rank test: $z = -7.235$, $p < 0.001$; figure 3). The logistic regression model corroborated these findings by showing that the probability of Acanthaster predation on Montipora decreased with increasing cover of macroalgae (likelihood ratio test: $X^2 = 70.373$, d.f. = 1, $p < 0.001$; figure 4). Probability of being attacked dropped to approximately 0% once macroalgae covered about 40–60% of the coral surface.

In feeding experiments, coral colonies surrounded by 8, 6 or 4 Sargassum fronds were rarely, if ever, attacked, while paired corals without Sargassum were uniformly consumed (figure 5). Attack frequency on corals with two adjacent Sargassum fronds was 50% less than corals with no adjacent Sargassum, but this difference was not significant ($p = 0.174$). Much of the defensive value of Sargassum appears to derive from physical structure alone; corals surrounded by plastic Sargassum mimics also were significantly less susceptible to Acanthaster attack (figure 5 b,d,f,h). In 9–10 of the 10 replicates in each experiment, a coral was attacked and consumed within the initial 24–36 h.

In the feeding experiments using short (length = 5 cm) Sargassum fronds, coral colonies surrounded by Sargassum were never attacked first, while paired corals lacking Sargassum were uniformly attacked and consumed (figure 6a). Similarly, corals surrounded by plastic Sargassum mimics of reduced height were attacked and consumed significantly less than colonies that lacked mimics (figure 6b). In every replicate, a coral was attacked and consumed within the initial 24–48 h.

When offered corals alone, Acanthaster always preferred Montipora to Porites ($p < 0.001$; figure 7a). If Sargassum was placed around Montipora, the preference reversed, with Acanthaster selectively consuming Porites in 9 of 10 replicates ($p < 0.001$; figure 7b). Additionally, in assays where one Montipora colony was not surrounded by Sargassum, 9 of the 10 replicates fed within 24–36 h. By contrast, when Montipora was surrounded by Sargassum and paired with Porites, attacks on 9 of 10 replicates did not begin until days 8–10 of the experiment, indicating the low preference of Porites, but also the even lower preference of Montipora when associated with Sargassum.

4. Discussion

Coral–macroalgal interactions are fundamental to coral reef community dynamics [21], but research to date has mostly emphasized the many negative effects of macroalgae on corals [22,23,28,44,45]. In this study, we demonstrate that indirect positive effects may offset some of the direct negative effects of macroalgae on corals. Our findings underscore the need to consider the complex matrix of indirect effects that arise when species interact not as pairs but within a diverse biotic matrix involving scores of additional species. It is not uncommon for interactions that are negative in some situations to become positive in other circumstances [13,14]. Because coral–macroalgal interactions are critical in structuring modern, human-disturbed reefs [17,19,21], gaining a better understanding of how environmental context alters these interactions is important for both fundamental ecology and effective management.

Sargassum commonly blooms on reefs where herbivorous fishes have been excluded or overfished [35–37], and Montipora growth declined substantially with increasing Sargassum density. The mechanism(s) by which Sargassum reduced Montipora growth were not addressed, but may be physical (e.g. shading, abrasion, sediment trapping) and/or chemically or microbially mediated [23,24,26,46–49]. Prior studies conducted on these same reefs detected no evidence that Sargassum, its lipid-soluble extracts or inert Sargassum mimics caused bleaching or visible damage to common corals [24,25,38,44], but previous assays did not evaluate effects on coral growth. Our findings are consistent with earlier studies that report reductions in coral growth because of competition with Sargassum sp. [29,50], and suggest that effects of Sargassum on corals may be subtle, take time to manifest and be expressed as effects on growth rather than short-term bleaching or survivorship.

Despite the adverse effects of Sargassum on Montipora growth, Sargassum can provide an unappreciated benefit to corals by producing an associational refuge from Acanthaster predation, which is a significant driver of coral decline on Pacific reefs [32]. Our field survey of Acanthaster feeding indicated that the frequency of sea star attacks on Montipora declined as association with seaweeds increased. Additionally, corals that were attacked suffered less damage as the cover of Sargassum increased. Thus, Sargassum has the potential to decrease the risk of Acanthaster attack, as well as the extent of colony damage to those corals that are attacked. The latter not only gives corals an opportunity to survive and recover but may also allow for induced defences among corals that have this ability [51].
Previous investigations on this reef flat found that about 65% of the corals in the fished area were in contact with macroalgae, that about 40% of their perimeter was in contact with macroalgae, and that corals were more frequently in contact with *Sargassum* and the brown seaweed *Turbinaria* than would be expected by chance [38]. These patterns might be explained by our findings that contact with these non-allelopathic, but competing macroalgae might provide a net benefit to corals by alleviating *Acanthaster* predation, and possibly other biological or physical stressors (e.g. ultraviolet radiation or fish predators) [30,31]. Given the context-dependent nature of *Montipora–Sargassum* interactions, the extent of similar benefits for other corals will probably vary as a function of coral palatability, macroalgal allelopathy, tolerance for macroalgal contact and intensity of *Acanthaster* predation. For example, *Sargassum* contact may provide a net positive effect for corals favoured by *Acanthaster* (e.g. *Acropora* or *Montipora* sp.) when sea star density is low to intermediate, while corals typically avoided by *Acanthaster* (e.g. *Porites* sp.) may benefit only when sea star density is high and preferred prey have been extirpated. 

The relevance of our field survey (which assessed cover by all macroalgae) was further supported by the feeding choice experiments demonstrating that *Sargassum* by itself was capable of providing an associational refuge from *Acanthaster* predation. Interestingly, the only density of *Sargassum* (i.e. 2 fronds) that did not effectively deter *Acanthaster* was also the only density that did not significantly reduce coral growth, suggesting that the density of *Sargassum* necessary to effectively deter *Acanthaster* predation may necessarily entail coral–algal competition sufficient to reduce *Montipora* growth. Judging by the similar effects of both *Sargassum* and plastic *Sargassum* mimics on *Acanthaster* feeding, deterrence of *Acanthaster* may be explained by the physical presence of a non-food species alone. Other researchers have documented instances where structural refuge provided by competitors (e.g. corals) or epibionts (e.g. amphipods) can reduce predation on associated corals by hindering *Acanthaster*’s ability to detect, access and/or efficiently feed on potential prey [52–55]. *Sargassum* is a tough, abrasive, canopy-forming macroalga that often occurs in dense stands capable of surrounding or covering coral colonies; thus physical effects alone could be mediating coral–sea star interactions. However, our data do not preclude some aspects of chemical interference as well. *Acanthaster* feeding preferences, both within and among coral species, play an integral role in determining the effects of *Acanthaster* on coral communities [33,56]. Additional choice feeding experiments revealed that the deterrent effects of *Sargassum* were not only capable of influencing
Acanthaster's intraspecific feeding preference for Montipora but also between Montipora and P. cylindrica. Previous studies document that Montipora is a preferred prey and Porites among the least preferred foods of Acanthaster [42,43,54,56,57]. In our assays, sea stars overwhelmingly preferred Montipora when given a choice between Montipora and Porites without surrounding seaweeds, but this preference reversed when offered Porites alone versus Montipora surrounded by Sargassum. In this experiment, Acanthaster also delayed all feeding for several days before finally accepting Porites. These results are a striking demonstration of Sargassum's ability to facilitate a trait-mediated indirect interaction by modifying Acanthaster feeding behaviour (i.e. TMII, sensu Abrams [58]).

Our results provide a novel example of how the indirect effects of coral–algal competition can potentially cascade to affect the wider coral community; however, the community-level effects of these processes are difficult to predict because of the context-dependent nature of the outcomes. The associational refuge provided by Sargassum appears to be predominantly physical in nature and is probably capable of providing comparable benefits with other coral species in close contact with this macroalga. There is no evidence that Sargassum is associated with certain coral species more than others, but recent work suggests that a broad range of coral genera show a mild positive association with Sargassum in the field on the reefs we studied [38]. Interspecific indirect effects such as prey switching may therefore not become prevalent until preferred coral species that lack algal contact have been depleted. Sargassum could then facilitate short-term apparent competition [59] between remaining preferred corals and less preferred species that lack macroalgae via increased Acanthaster predation on the latter.

Figure 5. The number of Montipora colonies without or with (a,c,e,g) Sargassum or (b,d,f,h) Sargassum mimics that were attacked and consumed by Acanthaster, as a function of decreasing (top to bottom) Sargassum/Sargassum mimic density.
Figure 6. The number of Montipora colonies with or without shorter (5 cm) (a) Sargassum or (b) Sargassum mimics that were attacked and consumed by Acanthaster.

Figure 7. (a) The number of Montipora or Porites colonies without Sargassum that were attacked and consumed by Acanthaster. (b) The number of Montipora colonies with Sargassum, or Porites colonies without Sargassum, that were attacked and consumed by Acanthaster. Analysed by Fisher’s exact test.

Our findings complicate community-level predictions for reef systems composed of mosaics of healthy and degraded coral reef habitats, such as healthy reefs in reserves that are surrounded by fished and degraded areas along Fiji’s Coral Coast. For the reefs we studied, macroalgal cover and contact with corals is higher, and coral cover lower, in fished areas that are degraded than in neighbouring reserves [37,38]. Low prey availability can intensify Acanthaster foraging behaviour [60] and is expected to result in hunger-mediated directional movement of individuals from areas of depleted coral cover to neighbouring locales with higher coral cover [33,61,62]. Extensive contact between corals and fleshy macroalgae like Sargassum may exacerbate this behaviour by restricting access to corals that would otherwise be available, potentially leading sea stars to increase their density and predation intensity on corals in nearby MPAs if Acanthaster selectively migrate to, and accumulate in, habitats with more corals and limited macroalgae. Thus, while the indirect effects of macroalgal contact may provide fitness advantages to individual colonies in degraded areas, they could also compromise adjacent coral communities composed of preferred prey species if coral predators preferentially immigrate to these areas because of the greater availability and accessibility of preferred coral prey [33]. Our argument contrasts with previous findings documenting decreased frequency of Acanthaster outbreaks in no-take zones on the Great Barrier Reef [63]. We suspect that such patterns may vary with reserve size or outbreaks in no-take zones on the Great Barrier Reef [63].

This study highlights how interactions between corals and benthic macroalgae can be diverse and can change in direction and magnitude of effect with changing ecological context. While the negative effects of algal competition have been extensively documented [23,24,38,64], our understanding of the dynamic and context-dependent nature of these interactions when coupled with other disturbances, such as corallivory, remains limited [28–30,65]. This is especially true for corallivorous species as influential as Acanthaster, which is capable of drastically reducing the functioning and productivity of reef ecosystems [33], and is considered to be a primary driver of long-term coral decline in locales across the Indo-Pacific [18,32]. The ability of macroalgae to act as an associational refuge by altering Acanthaster predation is an unforeseen effect that may impact reef structure, function and resilience.

Ethics. Experiments were performed in accordance with the ethical regulations of the Georgia Institute of Technology and Fijian law.

Data accessibility. Datasets used in this study are available online from the Dryad repository (http://dx.doi.org/10.5061/dryad.6324j).

Authors’ contributions. C.S.C. and M.E.H. conceived the study. C.S.C. conducted the research with minor help from M.E.H. C.S.C. carried out the data analysis, and C.S.C. and M.E.H. wrote the paper.

Competing interests. We declare that we have no competing interests.

Funding. Financial support provided by NSF grant no. OCE-0929119, NIH ICBG grants U01-TW007401 and U19TW007401, and the Teasley Endowment to Georgia Tech.

Acknowledgements. We thank the Fijian government and the Korolevu-i-Wai district elders for collection and research permissions, V. Bonito for logistical support, and D. Rasher, D. Beatty and D. Gibbs for assistance in the field. We also thank two anonymous reviewers for their constructive comments.
References


