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REPORT

Epibiotic mutualists alter coral susceptibility and response to biotic disturbance through cascading trait-mediated indirect interactions

G. S. Bergsma

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Abstract Biotic disturbances are important drivers of community structure, but interactions among community members can determine trajectories of response and recovery. On coral reefs in French Polynesia, epibiotic amphipods induce the formation of branch-like "fingers" on flat colonies of encrusting *Montipora* coral. The fingers form as coral encrusts the amphipods' tubes and lead to significant changes in colony morphology. I tested whether the induced morphological changes affect *Montipora's* susceptibility to predation by pincushion (*Culcita novaeguineae*) and crown-of-thorns sea stars (*Acanthaster planci*). *Montipora* with fingers were less likely to be attacked and more likely to survive attack than colonies without fingers. Furthermore, the presence of fingers altered *A. planci* prey preference. Sea stars preferred *Montipora* without fingers over other common coral genera, but preferred other genera when *Montipora* had fingers. Amphipods indirectly affected *Montipora*'s resistance and resilience to predation, and the susceptibility of other coral genera to predation, through induced morphological changes. Such trait-mediated indirect interactions likely play an important role in determining how species respond to periodic sea star outbreaks.

Keywords Trait-mediated indirect interaction (TMII) · Disturbance · Mutualism · Coral morphology · Acanthaster planci · Montipora

Introduction

Corals are a foundation species, providing essential habitat structure and primary productivity on tropical reefs, and disturbances that affect coral survival and growth may impact entire tropical reef communities. For example, periodic outbreaks of echinoderm predators, particularly crown-of-thorns sea stars (*Acanthaster planci*), have dramatic effects on coral reef community composition (Porter 1972; Keesing 1992).

The effects of echinoderm outbreaks, and the potential for recovery, may be influenced by factors that affect sea star prey preference. Sea star prey preference, in turn, may be mediated by species interactions. For example, the presence of epibiotic invertebrate symbionts in coral colonies can alter sea star prey selection (Devantier and Endean 1988; Pratchett 2001) and, therefore, affect coral survival and community structure following a crown-of-thorns sea star outbreak. While the protective role of invertebrate epibiotic symbionts on corals has been well-studied, researchers have mostly explored the effects of direct interactions (i.e., defensive behaviors of the epibionts). Indirect effects of symbionts, such as induced phenotypic changes that alter coral's susceptibility to predation, may be equally important.

Organisms that induce phenotypic changes in other species create the potential for trait-mediated indirect interactions (Abrams 1995; Werner and Peacor 2003) and

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G. S. Bergsma (✉)
Department of Ecology, Evolution and Marine Biology,
University of California, Santa Barbara, CA 93106, USA
e-mail: bergsma@lifesci.ucsb.edu

G. S. Bergsma
Division of Science and Environmental Policy, California State
University Monterey Bay, Seaside, CA 93955, USA

may play critical roles in determining community responses to disturbance. Because corals are an important structure-forming species, changes in coral morphology may affect entire reef communities. Therefore, induced phenotypic changes involving the morphology of corals may have particularly important community-wide effects.

In Moorea, French Polynesia, corals in the genus *Montipora* host gammaridean amphipods that form tubes on the surface of the colony, altering colony morphology (Bergsma 2009; Electronic Supplemental Material, ESM Fig. S1a). The tubes are overgrown by the coral, forming long, branch-like “fingers” on plating or encrusting colonies that result in increased coral growth and survival (Bergsma and Martinez 2011). Echinoderm outbreaks are one of the major disturbances impacting the coral community on Moorea (Faure 1989; Berumen and Pratchett 2006), and *Montipora* are favored prey. Any effect the amphipods have on *Montipora’s* susceptibility to predators could affect the community response to these biological disturbances.

This study aims to determine the effect of symbiotic amphipods on the susceptibility of the coral community to biotic disturbance and the potential for recovery. I test two hypotheses: (1) amphipod-induced fingers alter *Montipora*’s ability to resist and recover from sea star attack, and (2) changes in morphology alter sea star preference for *Montipora* relative to other coral genera, indirectly affecting the susceptibility of other corals to attack.

Methods

Study sites and species

I conducted experiments and surveys at the UC Berkeley Gump South Pacific Research Station and in the northern lagoon of Moorea, French Polynesia (Fig. 1). A description of the sites and the species studied are included in an appendix (ESM).

Susceptibility of *Montipora* to predation

Laboratory study

I measured the fingers’ effect on *Montipora’s* susceptibility to predation in the laboratory. I collected five pin-cushion sea stars (PCS) and five crown-of-thorns sea stars (COTS) from the lagoon and kept each species separately in two large (1.5 m by 2.5 m, with 0.75 m water depth) outdoor tanks with flow-through seawater. Because of limitations in the number and size of tanks available for the study, I used all five individuals of each species together in each set of trials. This served both to increase the number of corals attacked during the trials and to create constant experimental conditions across trials. I arranged six cement blocks along the perimeter of each tank as platforms to present pairs of corals to the predators; blocks were spaced at least 1 m apart to ensure that sea stars could not simultaneously access two blocks. The sea stars typically hid within the blocks during the day and emerged to feed at night, so experiments were timed to take advantage of these discrete nocturnal feeding bouts.

I collected *Montipora* sp. colonies ranging from 15 to 45 cm in maximum basal diameter from the lagoon. Fingered colonies, which had at least 50% of their surface covered with fingers greater than 5 cm in length, were paired with non-fingered colonies of similar basal area, so that they were equally likely to be discovered by searching sea stars. I placed one pair of colonies on each block, with colonies in each pair spaced approximately 5 cm apart. Because of the size of the sea stars relative to the size of the colonies, this allowed sea stars feeding on one colony to touch and detect the other (e.g., ESM Fig. S1b). I introduced colonies to the tanks at midday and checked them every 24 h. If either coral in a pair was damaged by predation, I replaced the pair to ensure that the proportion of each coral type presented to the predators was constant throughout the experiment.

I observed the tanks regularly in the evening and verified that all sea stars were observed foraging and feeding during the experiment. Individual sea stars typically fed on a single colony pair over the course of the night, with 1–2 PCS and 3–4 COTS observed feeding each night. All corals were either attacked or removed from the tank within several days of being introduced to the predators. In total, 21 colony pairs were attacked by PCS and 48 by COTS.

For each colony in attacked pairs, I noted the presence of damage, as indicated by discoloration and loss of living tissue. Colonies were categorized as attacked if there was any damage or undisturbed if there was no damage. I calculated the proportion of corals with and without fingers that were attacked and tested differences between colonies with and without fingers in the proportion of corals attacked using Pearson’s chi-square tests.

I also visually estimated the percent of each colony’s surface that had been consumed and calculated the difference in percent consumed between paired corals. Colonies that were attacked often had most of their surface consumed, while corals that were avoided generally had no damage, resulting in a bimodal distribution in the data. Differences in the percent consumed were, therefore, tested using a paired Wilcoxon signed rank test.

Finally, I noted the presence of living tissue for individual corals that had been attacked. Remaining tissue could continue to grow, so colonies with tissue were considered to have survived, whereas colonies that had been completely consumed were considered dead. I calculated the proportion of corals surviving attack and tested

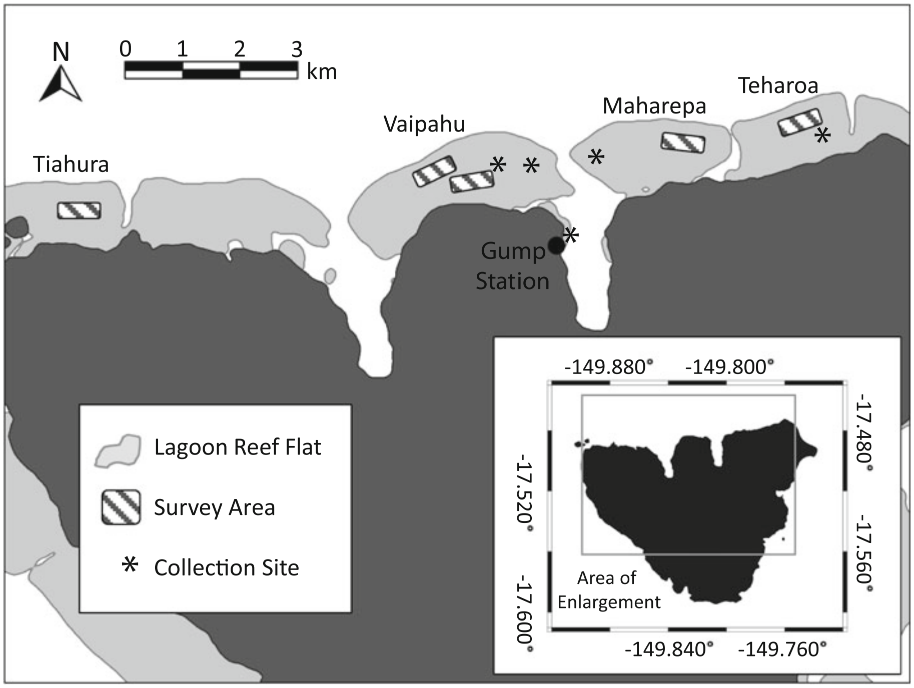

Fig. 1 Map of the north shore of Moorea, French Polynesia, indicating study locations

differences in survival between colonies with and without fingers using a Pearson's chi-square test for COTS. For PCS, the assumptions for contingency testing were not met due to the low number of fingered corals that were attacked, so a Fisher's exact test was used instead.

To be sure that patterns observed did not arise due to the inedibility of some colonies, I retained all of the undamaged corals and reintroduced them to the sea star tanks for a week following the experiment. By the end of the week, all the coral colonies had been completely consumed, indicating that all the colonies used were palatable.

Field study

I surveyed corals in the lagoon to document the impact of crown-of-thorns on *Montipora*. Snorkelers searched for COTS in areas with a high density of *Montipora* corals exhibiting symbiont-induced fingers and identified colonies of *Montipora* that had been attacked within 5 m of each sea star. I estimated each attacked colony's basal area as an ellipse. I also categorized *Montipora* colonies as having either high relief (more than two fingers greater than 5 cm in length), low relief (fingers shorter than 5 cm), or no fingers. I estimated the percent of each colony's surface area that was attacked and recorded the presence of living tissue following an attack using the same criteria as the laboratory experiment. I tested differences in the percent of the colony attacked among colonies with high relief, low relief, or no fingers using a mixed-effect ANCOVA accounting for finger state and colony size, with individual COTS modeled as a random variable, and a post hoc least squares means Tukey test when differences were found. I calculated the average probability of corals with high, low, or no fingers being completely consumed for each COTS encountered and tested differences in the probability of being completely consumed using paired Wilcoxon signed rank tests, with sequential Bonferroni corrections to adjust for simultaneous comparisons.

To measure the relative preference of COTS for *Montipora* with or without fingers, I measured the proportion of coral area with and without fingers in the surrounding environment. I surveyed three 10 m × 1 m band transects placed at random headings away from each COTS encountered. I estimated the area of each *Montipora* colony found on transects and recorded finger presence and relief in the manner described above. The surface area of all colonies on the transects with high, low, or no fingers, and the surface area of colonies that had been attacked by sea stars, was used to calculate COTS selectivity using Chesson's Electivity Index (α; Chesson 1978). I then compared the α values for different morphologies to the value of α obtained if COTS were selecting colonies randomly ($\alpha_{\mathrm{rand}} = k^{-1}$, where $k =$ the number of different prey types available) to determine whether different morphologies were preferred or avoided.

Effects of fingers on prey preference

Laboratory study

To test whether the presence of fingers altered COTS prey preference, I used a laboratory experiment to compare consumption of *Montipora* with *Acropora*. I collected colonies of *Acropora digitifera* and *Montipora* sp. with and without fingers, ranging in size from 20 to 50 cm in maximum diameter from the lagoon. I paired each *Acropora* colony with a *Montipora* colony of similar size. The *Montipora* used in half of the pairs had fingers, while half did not. I conducted feeding trials with COTS using the same procedures as the previous laboratory experiment. I also observed the corals over the first few hours following nightfall to record which species was first attacked in each pair. In total, 46 pairs with fingered *Montipora* and 49 pairs with unfingered *Montipora* were attacked. For attacked pairs, I recorded whether the *Montipora* colony had fingers and the percent of each colony's surface that was consumed. I then calculated the difference between the percent of the *Montipora* and the percent of the *Acropora* that was consumed for each pair.

The difference in the frequency that each species was attacked first was tested using a Pearson's chi-square test. Differences between *Montipora* and *Acropora* in the percent of the colony attacked were tested using paired Wilcoxon signed rank tests for pairs of colonies with and without fingers. The mean difference between *Montipora* and *Acropora* in the percent attacked for pairs containing *Montipora* with fingers was then compared to the mean difference for pairs containing *Montipora* without fingers using a Wilcoxon rank sum test.

Field study

I surveyed areas of high coral diversity within the lagoon to document COTS' preference among common coral genera. I used thirty-three randomly placed 25-m point-contact transects, with points spaced every 0.5 m, to record the percent cover of algae, coral, and non-living substrate. I identified living and recently killed corals to genus and noted colonies attacked by COTS. I used the percent cover of corals and the percent cover of corals attacked by COTS to calculate COTS selectivity using Chesson's Electivity Index (α). Again, I compared α values for different coral genera to the value of α obtained if COTS were selecting prey randomly to determine whether different corals were preferred or avoided.

Results

Susceptibility of *Montipora* to predation

The presence of fingers altered *Montipora's* susceptibility to echinoderm predation in the laboratory. For COTS, 81% of colonies without fingers were attacked, while 50% of colonies with fingers were attacked ($X^2_{1,n=96} = 10.39$, $P = 0.0013$; Fig. 2a). For PCS, 100% of colonies without fingers were attacked, while only 14% of colonies with fingers were attacked ($X^2_{1,n=42} = 31.50$, $P < 0.0001$; Fig. 2b). For pairs of colonies that were attacked, colonies without fingers suffered twice the amount of tissue loss as colonies with fingers for COTS ($W_{+n=48} = 433.5$, $P < 0.0001$; Fig. 2c) and four times the amount for PCS ($W_{+n=21} = 95$, $P < 0.0001$; Fig. 2d). Among individual colonies that were attacked, there was also a significant difference between colonies with and without fingers in the frequency with which colonies were completely consumed by COTS ($X^2_{1,n=63} = 7.32$, $P = 0.0068$), but not by PCS (Fisher's exact test, $n = 24$, $P = 1.00$). The lack of a significant difference for PCS is likely due to a lack of statistical power arising because only 3 colonies with fingers were attacked by PCS. No colonies with fingers were ever completely consumed by either predator, whereas 21% of colonies without fingers were completely consumed by COTS, and 24% were completely consumed by PCS (Fig. 2e, f).

The laboratory results were mirrored in the field. Thirty-six COTS were observed that attacked 180 colonies with high-relief fingers, 99 colonies with low-relief fingers, and 393 colonies with no fingers. COTS have a higher selectivity for *Montipora* colonies without fingers than for colonies with either high-relief or low-relief fingers (Fig. 3a), and there were significant differences among corals with high, low, and no fingers in the percent of colony area consumed ($F_{2,73.17} = 66.18$, $P < 0.0001$). A post hoc test indicated that corals with no fingers had over 30% more of their total area consumed than colonies with either high- or low-relief fingers, but there was no difference between corals with high- and low-relief fingers (Fig. 3b). Similarly, corals without fingers were significantly less likely to survive an attack than corals with either high-relief ($W_{+n=25} = 105$, Bonferroni adjusted $P = 0.0003$) or low-relief ($W_{+n=25} = 104.5$, Bonferroni adjusted $P = 0.0003$) fingers, but there was no difference between corals with high- and low-relief fingers ($W_{+n=25} = 0.5$, Bonferroni adjusted $P = 0.9999$). Only 2% of colonies with high-relief fingers and 3% of colonies with low-relief fingers were completely consumed, while 25% of colonies with no fingers were completely consumed (Fig. 3c).

Effects of fingers on prey preference

Fingers also appeared to affect COTS consumption of *Montipora* relative to *Acropora*. There was a significant difference in the proportion of each species that was first attacked between pairs of colonies with and without fingers ($X^2_{1,n=54} = 6.075$, $P = 0.0137$). When no fingers were present on *Montipora*, both species were attacked first with almost equal frequency, indicating no preference by the COTS. However, when fingers were present on *Montipora*, *Acropora* was attacked first almost four times as often,

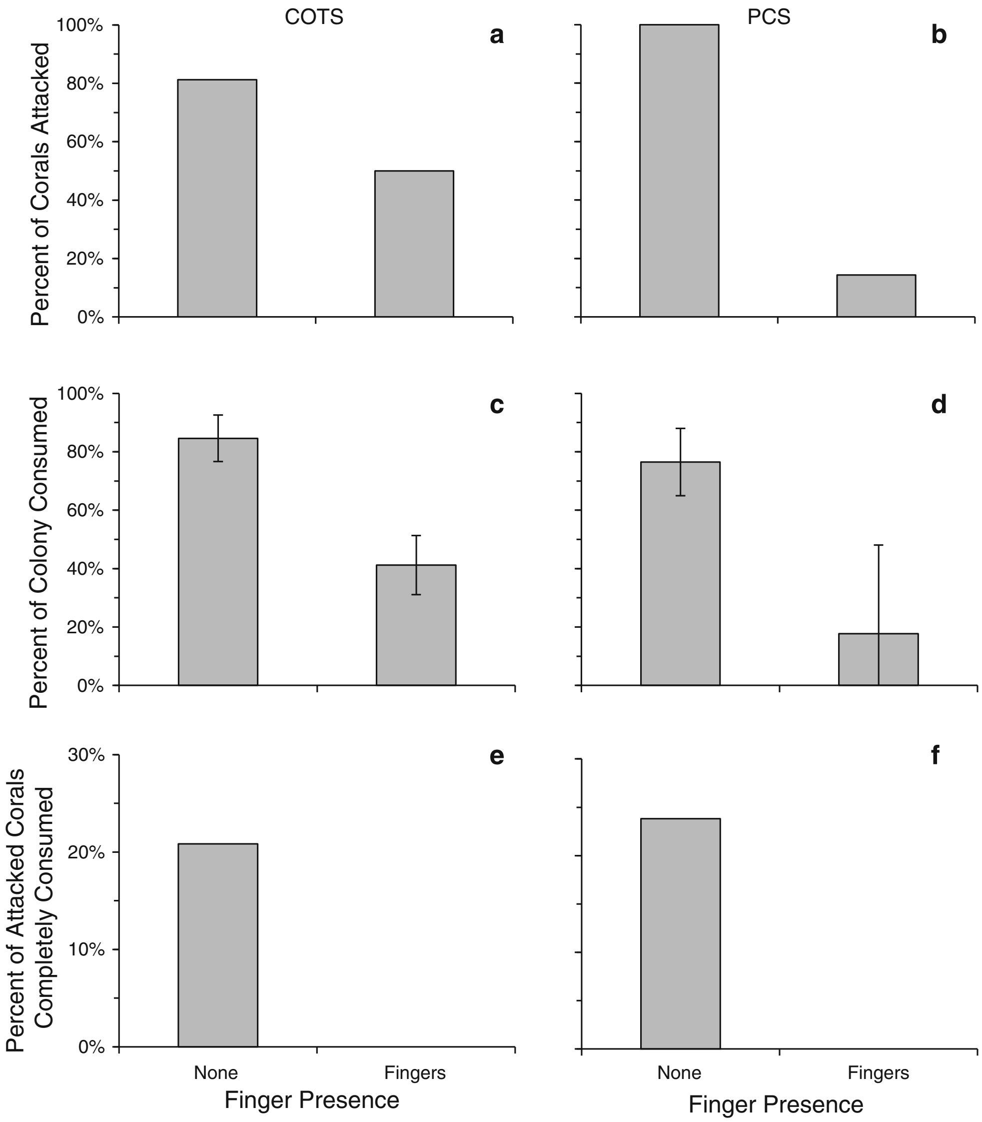

Fig. 2 The percent of *Montipora* colonies with and without fingers that were attacked by **a** crown-of-thorns ($N = 48$ attacked pairs) or **b** pin-cushion ($N = 21$ attacked pairs) sea stars. The mean percent (±95% CI) of each colony's surface area consumed by **c** crown-of-thorns or **d** pin-cushion sea stars for all fingered and unfingered colonies in attacked pairs. The percent of fingered and unfingered *Montipora* colonies that were completely consumed by **e** crown-of-thorns or **f** pin-cushion sea stars for individual colonies that had been attacked

indicating a preference for *Acropora* (Fig. 4a). Similarly, there was no difference in the percent consumed between *Acropora* and *Montipora* with no fingers ($W_{+n=49} = 49$, $P = 0.2178$), but *Acropora* had 30% more area consumed than *Montipora* with fingers ($W_{+n=46} = -285.5$, $P < 0.0001$; Fig. 4b). The absolute difference in the percent consumed between *Montipora* and *Acropora* was also significantly greater for pairs of colonies with fingers than for pairs without fingers ($S_{n1=49,n2=46} = 1576$, $P < 0.0001$), indicating that fingers altered COTS' preference for the two species.

Field surveys found that COTS preferentially selected *Montipora* without fingers, *Acropora* and *Pocillopora*, but avoided *Porites* and *Montipora* with fingers (Fig. 5). Interestingly, COTS had a higher selectivity for *Montipora* colonies without fingers and a lower selectivity for *Montipora* colonies with fingers than all other common coral genera. This indicates that the presence of fingers leads crown-of-thorns in Moorea to switch preference for *Montipora* relative to other coral genera.

Discussion

The laboratory results indicate that amphipods enhance *Montipora's* resistance and resilience to echinoderm

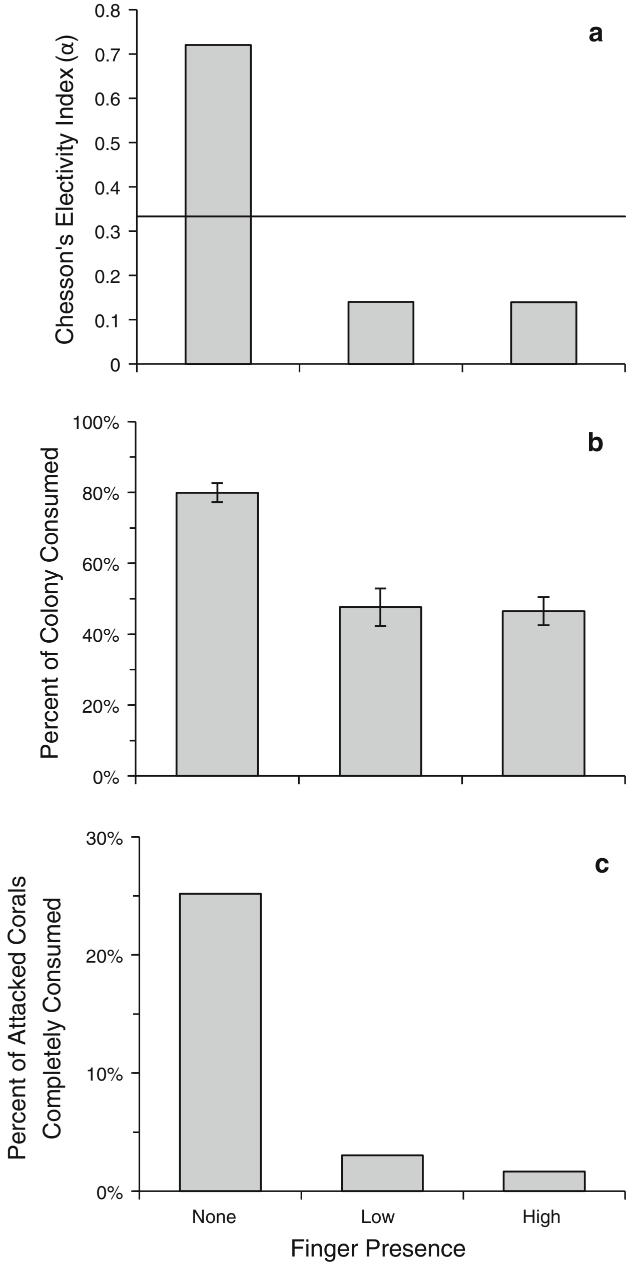

Fig. 3 **a** Chesson's electivity indices (α) for crown-of-thorns preying on *Montipora* with either no, low-, or high-relief fingers. The *horizontal bar* represents the α level where prey are selected randomly (k^{-1}, where k = number of prey types available); growth forms with indices above the line are preferred, while those below are avoided. **b** The mean percent surface area (±95% CI) of *Montipora* colonies consumed and **c** the percent of colonies that were completely consumed when attacked by crown-of-thorns sea stars in the field

predation. Fingered corals were less likely to be attacked and more likely to retain living tissue following attacks (Fig. 2). Because all of the sea stars of each species were used together in the laboratory experiments and so few unique sea stars were used, one weakness of this study is that the results may be driven by the feeding preferences of

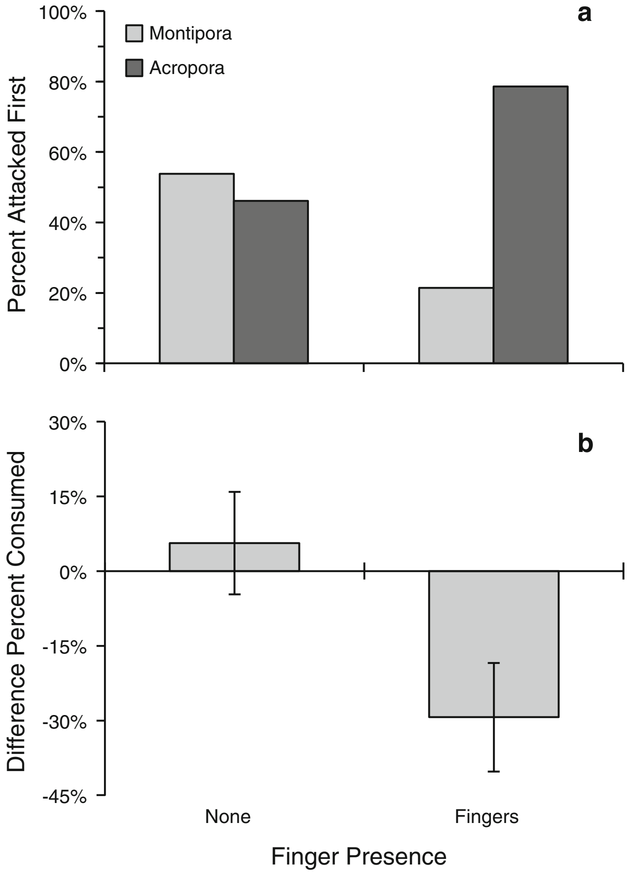

Fig. 4 **a** The percent of *Acropora* and *Montipora* that were selected as initial prey (i.e., they were attacked first) for pairs of corals where *Montipora* did (N = 46 pairs) nor did not (N = 49 pairs) have fingers. **b** The mean difference (±95% CI) between *Acropora* and *Montipora* in the percent of colony surface area consumed for pairs of corals where *Montipora* did or did not have fingers. Positive values indicate that a greater percent of *Montipora* was consumed; negative values indicate that a greater percent of *Acropora* was consumed

only a few active sea stars. However, the field surveys also found that fingered corals are less likely to be attacked and completely consumed by COTS (Fig. 3), corroborating the laboratory results and indicating that amphipods increase coral survival and potential for recovery. Partial predation of a colony induces increased defenses in corals (Gochfeld 2004), so increased rates of survival could further strengthen the defensive benefits of harboring amphipods if surviving colonies are less palatable to sea stars in the future.

Many epibiotic crustaceans are known to affect prey selection and repel coral predators (Pratchett 2001), but this mechanism of protection is unique. Amphipods appear to provide a refuge by enhancing physical structure rather than by active defense. Sea stars avoided sections of colonies with fingers (ESM Fig. S1c, d), but readily consumed corals that harbored amphipods that had not yet formed long fingers. PCS only consumed coral tissue along

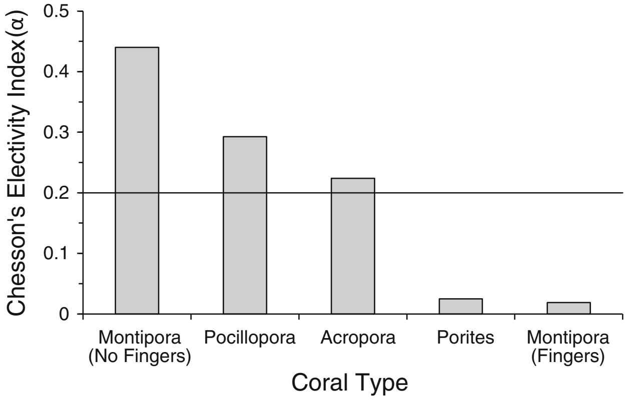

Fig. 5 Chesson's electivity indices (α) for crown-of-thorns sea stars preying on four common coral genera, with *Montipora* divided by fingered and unfingered forms. The *horizontal bar* represents the α level where prey are selected randomly (k^{-1}, where k = number of prey types available); taxa with indices above the line are preferred, while those below are avoided

fingered colonies' edges, and when COTS attacked fingered colonies, they commonly consumed the tissue near the tips of the fingers where the amphipods reside, leaving patches of living tissue in recesses between fingers. On many colonies, tissue between fingers or deep in crevices was all that survived, suggesting that physical relief provides refuge from predation regardless of amphipod presence.

This is consistent with sea stars' mode of feeding. Sea stars consume coral by pressing their everted stomach against the coral's surface. High physical relief could potentially reduce the ability of a sea star to conform its stomach to the coral's surface, effectively reducing the area of contact and reducing feeding efficiency. This is evident in the difference in the results for COTS and PCS; COTS are more flexible and better able to conform to the surface of the coral than PCS, explaining why COTS are able to consume fingered corals better than PCS (Fig. 2).

Interestingly, this mechanism contradicts the conclusions of Keesing (1990), who suggested that COTS prefer pocilloporids and acroporids because their increased structural complexity increases feeding efficiency. Other studies investigating the effect of coral morphology on COTS prey preference have had mixed results. De'ath and Moran (1998) found that COTS preferred tabular and branching morphologies over encrusting and massive morphologies within the *Acropora*, suggesting that complex morphologies are preferred, but Pratchett (2007) found no preferences for specific morphologies. De'ath and Moran (1998) treated corals at the generic level, whereas Pratchett (2007) identified corals to species, so it is possible that the preferences observed by De'ath and Moran were the result of differing preference for certain coral species confounded with their morphology. Because this study examines differences in morphology within the same morphospecies, it suggests that increased structural complexity actually deters COTS predation.

Enhanced survival via changes in morphology is a unique example of a mutualist-induced predator defense. Most inducible defenses are directly induced by consumers (e.g., Relyea 2001; Callaway et al. 2003), but any organism that alters traits in other species could alter those species' susceptibility to predation (e.g., Offenberg et al. 2006). The amphipod–*Montipora*–echinoderm interaction is, therefore, a trait-mediated indirect interaction (TMII, sensu Abrams 1995), where the amphipods, by inducing changes in morphology of the coral, indirectly affect the interaction between corals and their predators. TMIIs can drive population dynamics and community structure (Peacor and Werner 2000), but have been predominantly examined through non-consumptive predator–prey interactions (e.g., Trussell et al. 2003; Madin et al. 2010). This study demonstrates that TMIIs occur outside of the traditional top-down vs. bottom-up framework and that mutualistic, commensal, parasitic, or competitive interactions that affect plastic traits should be considered when attempting to understand how TMIIs structure communities. Studies of TMII have also largely investigated behavioral trait plasticity (Lima 1998; Dill et al. 2003), whereas a full understanding of TMIIs requires integrating morphological, physiological, and biochemical traits as well (Werner and Peacor 2003).

While the presence of amphipods benefits *Montipora*, the effect of the amphipods' presence on the coral community is less clear. The laboratory results show that the presence of fingers on *Montipora* alters COTS preference for *Acropora* or *Montipora* (Fig. 4), and the electivity indices from the field surveys indicate that finger presence may alter prey preference among a number of coral genera relative to *Montipora* (Fig. 5). The morphology of *Montipora* alters COTS behavior, which in turn affects survival of neighboring corals, an example of a behaviorally mediated indirect interaction. This system, therefore, is a novel example of cascading trait-mediated indirect interactions, whereby amphipods indirectly alter COTS prey preference, affecting the wider coral community's susceptibility to predation.

The amphipods appear to have indirect negative effects on other coral genera. Where multiple prey species share a common predator, numerical responses leading to satiation or induced defenses leading to prey switching may be common mechanisms by which prey species indirectly affect one another (Abrams and Matsuda 1996). In this case, the indirect linkage between *Montipora* and other coral genera could function like apparent competition (Holt 1977), whereby increased abundance of fingered forms of *Montipora* could negatively affect competitors by increasing COTS predation. However, the presence of avoided forms of *Montipora* could also lead to associational defenses (Hay 1986; Levenbach 2008), similar to the refuge provided by *Porites* to other coral genera during a recent COTS outbreak in Moorea (Kayal et al. 2011).

The effects of the *Montipora*–amphipod association on the reef community as a whole are, therefore, difficult to predict; amphipods increase *Montipora's* resilience and resistance to echinoderm predation, but may yield greater mortality for neighboring corals. A similar effect has been observed with corals that harbor guard crabs and is hypothesized to lead to changes in the relative abundance of coral species following COTS outbreaks (Colgan 1987; Glynn 1987). The overall effect of the amphipods likely depends on the nature of the disturbance. In cases where there is a persistent, low level of COTS predation, COTS structure communities by consuming preferred corals (Keesing 1992). In such a scenario, the presence of fingers may shift the coral community away from dominance of *Pocillopora* or *Acropora* and promote dominance of *Montipora*. Branching *Pocillopora* and *Acropora* provide refuge and settlement habitat for many reef fish and invertebrates, so such a shift could be detrimental to the overall abundance and diversity of these organisms. During large outbreaks, however, COTS quickly consume preferred corals, switch to non-preferred prey, and ultimately kill almost all corals (Pratchett 2007). Under these conditions, the increased ability for *Montipora* to survive attack would reduce the loss of coral cover, hasten coral regrowth, and allow faster recovery. In either case, the trajectory of the community response to disturbance is altered by the presence of amphipods, suggesting that trait-mediated indirect interactions may be important in determining an ecosystem's resistance and resilience to biotic disturbances.

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