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Species and size diversity in protective services offered by coral guard crabs

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Abstract

Coral guard crabs in the genus *Trapezia* are well-documented defenders of their pocilloporid coral hosts against coral predators such as the Crown-of-Thorns seastar (*Acanthaster planci* complex). The objectives of this study were to examine the protective services of six species of *Trapezia* against corallivory, and the extent of functional diversity among these *Trapezia* species.

Studies conducted in Mo'orea, French Polynesia showed the *Trapezia* – coral mutualism protected the host corals from multiple predators through functional diversity in the assemblage of crab symbionts. Species differed in their defensive efficacy, but species within similar size classes shared similar abilities. Smaller *Trapezia* species, which were previously thought to be ineffective guards, play important defensive roles against small corallivores.

We also measured the benefits of this mutualism to nearby coral species in the midst of an *Acanthaster* outbreak that reduced the live coral cover on the fore reef to less than 4%. The mutualism positively affects the reef coral demography and potential for recovery during adverse predation events through shelter of multiple species of small corals near the host coral. Our results show that some *Trapezia* species may be functionally equivalent within the same size class, decreasing the threat of gaps in coral protection caused by absence or replacement of any single *Trapezia* species.

Key Words: Functional Diversity, Functional Equivalence, Mutualism, *Trapezia*, *Pocillopora*, *Acanthaster*, Associational Refuge, Complementarity, Symbiosis, Partner Benefits

Introduction

Mutualistic symbioses stabilize and increase biodiversity in an ecosystem by: 1) reducing antagonism between host and symbiont, eliminating arms races that could result in extinction; 2) increasing the resistance of each species to stressors external to the relationship; and 3) enhancing survival benefits for many species in complementary assemblages of mutualists and mutualistic networks. Mutualisms often occur with more than one species providing benefits to a host species, and community diversity within symbiotic suites has been largely overlooked (Howe 1984). High mutualist diversity may confer greater survival benefits to the host species than a single mutualist (Stachowicz and Whitlatch 2005; Baskett et al. 2009), especially if functional diversity exists in the system. Whole communities may have net beneficial effects for a shared host that can be considered mutualistic in nature (Bracken et al. 2007; Stachowicz et al. 2008). Studies on the interactions between mutualist species are underrepresented in the literature (Morris et al. 2007), but relevant and central to understanding diverse systems (McKeon et al. 2012). Mutualist diversity within symbiotic suites drives variation in partner benefits, strongly impacting the extent and strength of these ecological partnerships (Schemske and Horvitz 1984; Addicott 1986; Meunier et al. 1999; Correa and Baker 2009).

Functional diversity and equivalence in ecological roles of similar species have become focal points in our understanding of community structure and the generation and maintenance of biodiversity (Harris 1995; Loreau et al. 2002; Loreau 2004). Diversity has been simplified into ecological units of 'functional groups', but studies testing the equivalence of species within functional groups have shown mixed results (Chalcraft and Resetarits 2003). The few studies to date comparing ecological function of closely related species under the same environmental conditions have supported the idea that functional diversity, rather than equivalence, may be the

norm (Resetarits and Chalcraft 2007). Despite this evidence, the assumptions of functional equivalence underlying the construction of functional groups have remained a central premise in much of theoretical ecology, from Neutral Theory (Hubbell 2005) to Food Web Theory (Menge and Sutherland 1987; Leibold and McPeek 2006).

Testing for functional diversity and equivalence is most tractable and applicable in clades of closely related or morphologically similar species (Leibold and McPeek 2006). Crabs of the genus *Trapezia* differ in size but exhibit few other morphological differences. *Trapezia* are defensive mutualists of coral hosts in the family Pocilloporidae (Pearson and Endean 1969; Glynn 1976, 1987). These crabs have been implicated in providing a number of ecological services to their host corals: repulsion of corallivores (Glynn 1987; Pratchett 2001), removal of sediment (Stewart et al. 2006), and alleviation of the impacts of vermetid snails (Stier et al. 2010). The functional differences between different species of this well-known marine mutualist genus have not yet been examined in detail.

Trapezia are part of an assemblage of specialized associates of pocilloporid corals. *Pocillopora* make up a large percentage of reef cover in lagoonal and fore reef systems in the Central Pacific. Thirteen of the 21 described *Trapezia* species occur in French Polynesia. Symbiont community composition varies with coral species, growth form, reef zone, and community membership (Odinetz 1983). The maximum size of *Trapezia* is constrained by host interbranch width (Adams et al. 1985; Huber and Coles 1985). A single mating pair of a given *Trapezia* species typically occupies each coral colony, although each colony can host multiple species and additional juveniles. Larger coral colonies may host pairs of up to five species of *Trapezia*, while smaller coral colonies may only shelter a single species. The benefits to the

Trapezia include shelter and nutrition in the form of lipids sequestered in the tips of the polyp tentacles, which the crabs graze (Stimson 1990).

The objectives of this study were: 1) to evaluate the services of multiple *Trapezia* species to their host corals; 2) to make interspecific comparisons of functional roles in *Trapezia*; 3) to assess the effect of symbiont size on functional role; and 4) to assess the impact of the symbiosis on the surrounding reef community. We compared the defensive efficacy of several species and size classes of *Trapezia* against two corallivores in lab experiments. We also examined the role of the *Pocillopora-Trapezia* mutualism in mitigating the effects of *Acanthaster planci*, the Crown-of-Thorns sea star, during a natural outbreak event.

Methods

<u>Study Locations</u>

Corallivore defense studies were conducted in Mo'orea, French Polynesia, at the Richard B. Gump Research Station of the University of California, utilizing the flow-through seawater system and a fore reef field site.

<u>Study Organisms</u>

Pocillopora species make up a large percentage of reef cover in lagoonal and fore reef systems in the Central Pacific. The bulk of this is composed of coral colonies with morphologies in three coarse groupings. The *Pocillopora verrucosa – P. meandrina* group, referred to in this manuscript as *"Pocillopora verrucosa"*, are mid-sized pocilloporids, rarely exceeding 15 cm in colony height and typically occupied by small- to medium-sized *Trapezia* species. A second morphological group, the *P. eydouxi – P. woodjonesi* group (hereafter *"Pocillopora eydouxi"*), is larger in stature, commonly exceeding 60 cm in colony height, and has substantially broader interbranch widths. These corals host the entire size range of *Trapezia* species; from the smallest

at branch junctures and the colony's base, to the largest, which actively transit the openings between branches. The third morphological grouping is composed of species currently assigned to *Pocillopora damicornis*, a finely branched morphotype that exhibits extreme environmental variation across reef microhabitats (Veron and Pichon 1976).

Species-level distinctions across the geographic range of *Pocillopora* remain unresolved at morphological, genetic, and taxonomic levels (Veron and Pichon 1976, Veron 2000, Combosch et al. 2008). As such, we chose to use internally consistent morphological groupings in the experiments, but do not have further identification of the entities involved.

We investigated *Trapezia* defense against three corallivores: the Crown-of-Thorns seastar *Acanthaster "planci"* (Linnaeus 1758), a species complex (Vogler et al. 2008); the seastar *Culcita novaeguineae* Müller & Troschel 1842*; and the muricid gastropod *Drupella cornus* (Röding 1798). For simplicity, we will refer to these species by their generic name only hereafter.

These species are the most common coral predators on Central Pacific reefs. *Acanthaster* often occurs in high densities during population booms (Birkeland 1989). *Acanthaster* is capable of consuming all reef corals, but does exhibit feeding preferences (Pratchett 2007; Pratchett et al. 2009). *Culcita* is a generalist predator of sessile organisms, including corals (Glynn and Krupp 1986). *Drupella* is a specialized corallivore whose impact on reef corals is second only to *Acanthaster* (Turner 1994). The three species feed on corals nocturnally, and leave visible 'scars' of exposed coral tissue in the course of a single feeding event.

Experiments on defense utilized single reproductive pairs of *Trapezia punctimanus* Odinetz 1984 (a small species); *T. bidentata* (Forskål, 1775) and *T. serenei* Odinetz, 1984

(medium sized species); and *T. flavopunctata* Eydoux & Souleyet, 1842 (a large species). Small CW pairs of *T. serenei* were also used as a 'small' species in the experiments with *Drupella*, as crabs of this species reach sexual maturity at much smaller sizes when living within small coral colonies. The first author identified the crabs to species, relying on Castro et al. (2004), the original species descriptions, and molecular data (M[c]Keon 2010) from voucher specimens deposited at the Florida Museum of Natural History.

Experimental Design

Four species of *Trapezia* were used in experiments evaluating defense against the three corallivores. The differences in size between the three species of corallivore allowed for evaluation of the impact of size of both predator and defender in the defensive efficacy of species of *Trapezia*. The extreme difference in size among corallivore, coral host, and crabs necessitated different experimental approaches to assess the range of defensive behaviors. Large individuals of *Acanthaster* in particular were unreliable predators in lab feeding trials, but were easy to track during field experiments, while *Culcita* and *Drupella* would readily attempt feeding during a single night in the lab chambers, but were difficult to trace in the field.

During 2008 and 2009, Mo'orea experienced an outbreak of *Acanthaster*, allowing field manipulations to test the effect of *Trapezia* defense on *Acanthaster* predation. By September 2008, the majority of live coral had been eaten, with the notable exception of *Pocillopora eydouxi* Milne Edwards & Haime 1860, which occurs on the forereef and hosts pairs of *T. flavopunctata* as well as a suite of other symbiotic species. A closely related species, *Pocillopora damicornis* Linnaeus, 1758 is a highly favored food in the diet of *Acanthaster*

(Pratchett 2007). Smaller *Pocillopora verrucosa* (Ellis & Solander 1786) had been consumed in near totality, and least-favored taxa such as *Porites* and soft corals were also being eaten.

Drupella cornus

Two sets of experiments tested the defensive efficacy of two size classes of *Trapezia serenei* (small adult crabs 4-6 mm carapace width [CW], and medium adult crabs 9-10 mm CW) and one size class of *T. punctimanus* (small – 4-6 mm CW) against the corallivorous snail *Drupella cornus*. Two 135 L aquaria equipped with flowing seawater served as experimental chambers. *Pocillopora verrucosa* colonies were gathered from the back reef environment on the day of the experiments. Small coral colonies had a mean volume of 260 ± 136 cm³, and the larger coral colonies had a mean volume of 3706 ± 1057 cm³. Exosymbionts and other animals were removed from the corals using wooden skewers, as described above.

Experimental treatments for the small size class (4-6 mm CW) of crabs were: all symbionts removed (n = 22), small *T. serenei* (n = 22), and *T. punctimanus* (n = 22). Experimental treatments for the larger size class (9-10 mm CW) only included *T. serenei* and a removal treatment, because *T. punctimanus* does not occur in an equivalent size range. Both experiments were conducted as described below.

Forty *Drupella* with 15-17 mm aperture lengths were collected from the fore reef, housed in a glass aquarium with a flow-through sea water system and starved for a minimum of 72 hours prior to use in experiments. We placed one *P. verrucosa* colony from each of the three treatments into the center of three assigned tanks. Three *Drupella* individuals were lined up on the bottom downstream rear edge of each aquarium to ensure the availability of a chemosensory signal from the coral to the snails. Three *Drupella* were used in each treatment so that a measurable feeding scar would be produced during the experimental period of 19-24 hours. The experiment was

repeated each night with a new set of corals and symbionts, with treatments alternating between tanks each day. *Drupella* were reused after a 72 hour starvation period, and a new cohort of *Drupella* was collected after ten days and starved as above.

After each experiment, the length, width, and height of corals were measured. We recorded the number of snails found on the coral and measured the size of any feeding scars. Measurements of the amount of tissue consumed in an irregular three-dimensional branching coral are difficult and contentious. We chose to use proxies of coral volume and feeding scars calculated as the volume of an ellipsoid using the formula: $V = 4/3\pi abc$, where a, b, and c are radii following McKeon et al. (2012). After each trial the aquaria were scrubbed, rinsed, drained and refilled.

The defensive efficacy of the crab treatments was compared to appropriately sized control corals; the differences in host size does not allow for direct comparison of the efficacy of small crabs in small corals and larger crabs in larger corals.

Culcita novaeguineae

Experiments testing defense against *Culcita* by two species of *Trapezia* were conducted in flow-through plastic pools of approximately 2,670 L volume. *P. verrucosa* were gathered from the back reef environment on the same day of the experiments. Two sets of experiments were conducted with two size classes of corals. Experiments using the large size-class of coral colonies (mean volume of 3354±979 cm^3) had treatments as follows: pairs of *T. serenei* (n = 20, CW = 9-11 mm), pairs of *T. bidentata* (Forskål, 1775) (n = 20, CW = 9-11 mm), and all symbionts removed (n = 20). The second set of experiments used a smaller size-class of coral (mean volume 519±175 cm^3) included pairs of smaller *T. serenei* in smaller corals (n = 9, CW =

4-6 mm) and a set with all symbionts removed (n = 8). As above, the desired experimental symbiont community was established through manual removal of symbionts and other coral-associated animals.

Culcita novaeguineae were collected from the back reef (n = 37, mean body diameter 16 cm) in Cook's Bay, Mo'orea, held in large plastic pools with flowing seawater, and were starved for at least 48 hours before experimental use. Corals were positioned in the middle of the plastic pools, and a single *Culcita* was placed directly on top of each experimental coral at sundown. Predation was evaluated the following morning, after approximately 15 hours. Coral volume and feeding scar dimensions were estimated as noted above.

Acanthaster planci

Several studies have suggested that *Trapezia* may be able to repel *Acanthaster* corallivory (Glynn 1987; Pratchett 2001). These studies have either been observational or conducted as lab experiments. A large outbreak of *Acanthaster* on Mo'orea beginning in 2008 allowed field assessment of the defensive capabilities of *Trapezia flavopunctata* Eydoux & Souleyet 1842, the largest species of *Trapezia*. We chose a spur and groove fore reef site off the northern shore of Mo'orea and conducted experiments from October to November of 2008. We manually removed *Trapezia flavopunctata* from 45 haphazardly selected *Pocillopora eydouxi* colonies, and selected a second set of 45 coral colonies with pairs of *T. flavopunctata* allowed to remain in the coral. The removals were maintained for one month. Other symbiotic species, including fish, arthropods, and smaller species of *Trapezia*, were left in the coral colonies. Control corals were disturbed in a manner similar to that used to remove *T. flavopunctata*. Every 48 hours all corals were checked for tissue loss (feeding scars), and measured as described previously.

Additional surveys were conducted around 90 live and 90 dead *P. eydouxi* for live coral survival in the immediate proximity of *P. eydouxi* colonies. Decomposition of dead colonies of *P. eydouxi* was evaluated using a 1 − 10 scale for the loss of surface features and depth of bioerosion on mid-branch cross-sections. While we cannot rule out other sources of mortality, all of the *P. eydouxi* used in the study were in the same stage of decomposition, and had died within the last year, suggesting the recent *Acanthaster* outbreak. *Pocillopora eydouxi* is a large arborescent species on the fore reef, and grows as a canopy over neighboring smaller corals. Living coral colonies encountered under the canopy and to 1/2 of colony diameter beyond the canopy margin were counted and identified to genus.

Results

Drupella cornus

Frequency of predation was significantly higher in corals with symbionts removed (22/22) than in corals containing a small size-class *T. serenei* pair (8/22; Fisher's Exact Test, p = 0.0003). Mean tissue loss during predation events was significantly higher in corals with symbionts removed (n = 22, 13.9 cm^3, 8.7% total coral volume proxy [TCVP]), than in corals containing small *T. serenei* pairs (n = 8, 7.94 cm^3, 1.3% TCVP; Student's T-Test p = 0.003, Figure 1). Neither predation frequency nor mean tissue loss differed significantly between corals containing the larger size-class of *T. serenei* and the matched set of corals with symbionts removed (predation frequency: Fisher's Exact Test, p > 0.05; mean tissue loss: Student's t-test, p > 0.05).

In trials with corals containing *T. punctimanus*, predation frequency differed significantly between corals with crab pairs present and removed (Fisher's Exact Test, p = 0.0009). Mean tissue loss during predation events was also significantly higher in corals with symbionts

removed (n = 20, 22.9 cm^3, 5.7% of TCVP), than in corals with *T. punctimanus* pairs present (n = 9, 0.61% of TCVP; Student's t-test p = 0.00001; Fig. 1).

Culcita novaeguineae

The differences in defense provided to the coral host by the medium size-class of *T. serenei* and *T. bidentata* were evaluated using ANOVA. Mean tissue loss differed significantly among treatments: 19% of TCVP in corals containing *T. serenei* pairs (n = 5), 37% of TCVP in corals containing *T. bidentata* pairs (n = 10), and 49% of TCVP in corals with symbionts removed (n = 20; ANOVA: p < 0.01, Fig. 2). There was also a significant difference in tissue loss when the data were analyzed as presence or absence of crab pairs, ignoring species differences (Tukey's HSD, p < 0.001). Small corals with the small size-class of *T. serenei* present (n = 9) and removal treatments (n = 8) were completely consumed by *Culcita*, so no statistical test was needed.

Acanthaster planci

Live coral cover on the fore reef of Mo'orea from 2000-2006 varied from 41-51%, and was dominated by species of *Pocillopora*, *Porites,* and *Acropora* (Adjeroud et al. 2009). Photos made in 2006 of our immediate study area provided estimated coral cover of about 80%. By September 2008, coral cover had plummeted in northern Mo'orea as a result of a population outbreak of *Acanthaster planci*. In our study area, total living coral cover had decreased to 3.4% (se = 0.97, n = 45) as calculated from quadrat surveys, and most of the coral recorded during the survey were *P. eydouxi*. Living coral cover changed little by October 2009; with estimated cover at 3.2% (se = 0.75, n = 45), and *Pocillopora eydouxi* remained the most abundant coral species on the reef.

Removal of *T. flavopunctata* from remaining live *P. eydouxi* led to an increased rate of attack and tissue loss in hosts. Over the two-week experimental period, 64% (29/45) of corals with symbionts removed were attacked, compared with 18% (8/45) of corals with *T. flavopunctata* pairs present (Binomial Proportions Test, p < 0.005; Electronic Supplemental Material [ESM] 1A). Mean coral tissue loss was 22% of TCVP in undefended corals and 2% of TCVP in defended corals (Binomial Proportions Test, p < 0.005; ESM 1B). Thirty-four corals from which *T. flavopunctata* were removed still possessed a complement of other *Trapezia* species and other symbiotic taxa. We compared attack frequency between *P. eydouxi* with *T. flavopunctata* and smaller *Trapezia* species present (10 attacks/33 corals), to corals from which *T. flavopunctata* had been removed, but with other symbionts left alone (24 attacks/34 corals). Corals with *T. flavopunctata* removed suffered attack by *Acanthaster* more frequently (Binomial Proportions Test, p < 0.005).

Associational Defense

Only live *P. eydouxi* colonies sheltered living corals of other species under and near the colony canopy (Fig. 3). Twelve species of corals were found sheltered around 64% of the live *P. eydouxi* surveyed (ESM 2). Living colonies of these species were otherwise absent from the study area, although they were commonly encountered on the reef far from *P. eydouxi* prior to the *Acanthaster* outbreak. None of the 90 dead *P. eydouxi* sheltered live coral colonies (Binomial Proportions Test, p < 0.005).

Discussion

Efficacy of defense against corallivores differed among *Trapezia* species as well as among size classes. Small (CW = 4-6 mm) *T. punctimanus* and *T. serenei* were comparably effective in defending against *Drupella*, while larger (CW = 9-10 mm) *T. serenei* were

ineffective. However, large (CW = 9-11 mm) *T. serenei* were effective in defending against

Culcita, while small *T. serenei* (CW = 4 - 6 mm) were not. Furthermore, large (CW = 9-11 mm)

T. serenei were significantly more effective host defenders than comparably sized *T. bidentata*

against *Culcita* predation, suggesting that specific identity, as well as size plays a role in the level

of protective service provided to the coral host. Finally, during the *Acanthaster* outbreak only

corals hosting the largest *Trapezia* species, i.e., *T. flavopunctata* or *T. rufopunctata*, survived.

Smaller *Trapezia* species were unable to protect their hosts against the largest of the three

predators, and the corals were quickly attacked when *T. flavopunctata* were removed.

These results suggest ecological complementarity, as well as a hierarchy of defensive

effectiveness among different species and sizes of *Trapezia*. Small crabs effectively defend their

hosts against the small predator *Drupella*, but fail against larger predators such as *Culcita*: small

Pocillopora were always consumed entirely by *Culcita*, regardless of the presence or absence of

small *Trapezia*. The crabs flee the coral, or are consumed along with the host.

Medium sized crabs are effective against *Culcita*, with effectiveness varying among

species, but they do not defend against *Drupella* or *Acanthaster*. The largest crabs actively

defend against *Acanthaster*, but their efficacy against the other coral predators remains untested.

Thus, barring the untested possibility of negative interactions, a coral harboring all of these

symbionts may be defended against all three corallivores, while a coral with a lesser complement

of *Trapezia* species may remain vulnerable to some predators. An additional aspect of this

within guild complementarity, or 'species stacking', is that several species may create additional

synergistic defensive effects even against the same coral predator (McKeon et al. 2012).

These results also suggest that the characteristics of the mutualism between *Trapezia* and

Pocillopora may shift as the resident crabs and coral hosts increase in size. Because the feeding

scars of the corals without symbionts in the small *T. serenei* and *T. punctimanus* experiments were nearly the same size as the feeding scars in both groups of the large *T. serenei* experiments, it may be possible that the threat to smaller crabs and their correspondingly smaller hosts by *Drupella* predation is proportionally greater. This proportional response may explain why larger crabs did not respond as effectively as the smaller crabs to *Drupella*. Glynn (1980) suggested that another small species of *Trapezia, T. formosa* may not play a role in defending their host corals against *Acanthaster*. However, we have shown that smaller species of *Trapezia* previously thought to be ineffective guards, because they were only tested against *Acanthaster,* can play important defensive roles against other corallivores.

The efficacy of protection provided by two species of *Trapezia* (*T. serenei* and *T. bidentata*) against *Culcita* differed under controlled conditions. Both significantly reduced the frequency of attack and volume of tissue consumed by *Culcita*, but *T. serenei* was more effective. This may be because *T. serenei* is more common in the back reef habitat where *Culcita* populations are most dense, while *T. bidentata* is more common in fore reef environments where *Culcita* is less frequently encountered in Mo'orea.

Both attack rate and the amount of coral tissue consumed by *Acanthaster* were significantly reduced by the presence of the largest species in the system, *Trapezia flavopunctata*. *Acanthaster* preyed upon *P. eydouxi* when *Trapezia flavopunctata* were removed. Species of *Pocillopora* that do not host *T. flavopunctata* were completely consumed by *Acanthaster* in the reef area studied, despite the frequency of occupancy of other *Trapezia* spp. exceeding 90% (Stewart et al. 2006; McKeon et al. 2012).

The protective impact of *T. flavopunctata* appeared to extend beyond the host coral, providing protection for a microcommunity of reef corals in the vicinity of their host. Sixty-one

colonies of thirteen other reef coral species, eliminated from the reef in all other areas by *Acanthaster*, were found sheltering in the vicinity of 90 *P. eydouxi*-symbiont communities surveyed. Indirect, associational defense has previously been documented among reef corals in the same location (Kayal et al. 2010). The protection provided by the presence of the largest species of *Trapezia* is another mechanism for the survival of reef corals in *Acanthaster* outbreaks.

The results of these experiments raise many questions about the *Trapezia – Pocillopora* mutualism. Glynn (1980) demonstrated that *Trapezia* respond aggressively to chemical signals produced by *Acanthaster*, but whether *Trapezia* are able to detect and respond to chemical signals produced by other corallivores such as *Drupella* remains unknown.

During an analysis of coral population dynamics in Australia, Hughes and Connell (1987) found that 39% of *Pocillopora damicornis* measuring less than 10 cm² died over the course of one year, while only 8% of *P. damicornis* measuring between 10 and 50 cm² suffered the same fate. While differential mortality is expected with changes in colony size, impacts of mutualists on different sizes of corals should be examined. The frequency of occurrence of *Trapezia* in medium-sized *Pocillopora* colonies is well documented (Huber and Coles 1985; Sin and Lee 2000; Stewart et al. 2006) but our understanding of the occurrence of *Trapezia* in very small corals is limited. Further investigation into the role of small crabs of the genus *Trapezia* in the survival of very young *Pocillopora* colonies is needed.

While the largest crab species provide the greatest defensive efficacy against *Acanthaster,* the energy expenditure of the host coral to maintain the symbiosis may also be costly. As the frequency of *Acanthaster* outbreaks on Mo'orea has been on an approximately 30-year cycle (Faurea 1989) attacks by seastars may be relatively rare events in the life of a coral.

Removal of sediment and deterrence of smaller corallivores, such as *Drupella*, may be more common needs for coral, even if the size of their impact on a colony may not be as severe as that resulting from *Acanthaster* attack. The beneficial role of different symbiont species and size classes to this spectrum of impact may be sufficient to increase the fitness of corals that maintain the nutritive benefits that are provided to the crabs (Stimson 1990).

The experiments we conducted suggest that functional diversity exists in the *Pocillopora-Trapezia* mutualism at a species level. But we must acknowledge the limitations of our study: we were unable to use all species of *Trapezia* present in the system, in a single size and species of *Pocillopora*. Variation within the mutualism was demonstrated to impact coral host survival across the size ranges of host and symbiont. Interactions between the species and size classes are likely an integral part of the mechanisms that promote the existence of the *Pocillopora-Trapezia* mutualism, but have yet to be explored in depth. Variation in the services provided by mutualists has been recorded in a wide variety of systems (Addicott 1986; Bronstein and Hossaert-McKey 1996; Del-Claro and Oliveira 2000). Therefore, the assumptions underlying construction of functional groups are weaker than generally noted in the literature, and functional groups are of questionable utility in understanding diverse mutualist systems.

Our studies suggest that measuring a diversity of response variables is important in assessing the level of functional diversity present in a system. Our results demonstrate the importance of the *Trapezia-Pocillopora* mutualism in response to corallivory, including an outbreak of *Acanthaster*. A diverse commensal fauna may provide individual corals with greater protection from a suite of predators. Moreover, these benefits cascade beyond the individual coral colony and may have far-reaching impacts on the reef, by altering the demography of small

corals, structuring the surviving communities of corals and offering associational defenses and

refuge to nearby corals during catastrophic predator outbreaks.

Acknowledgements

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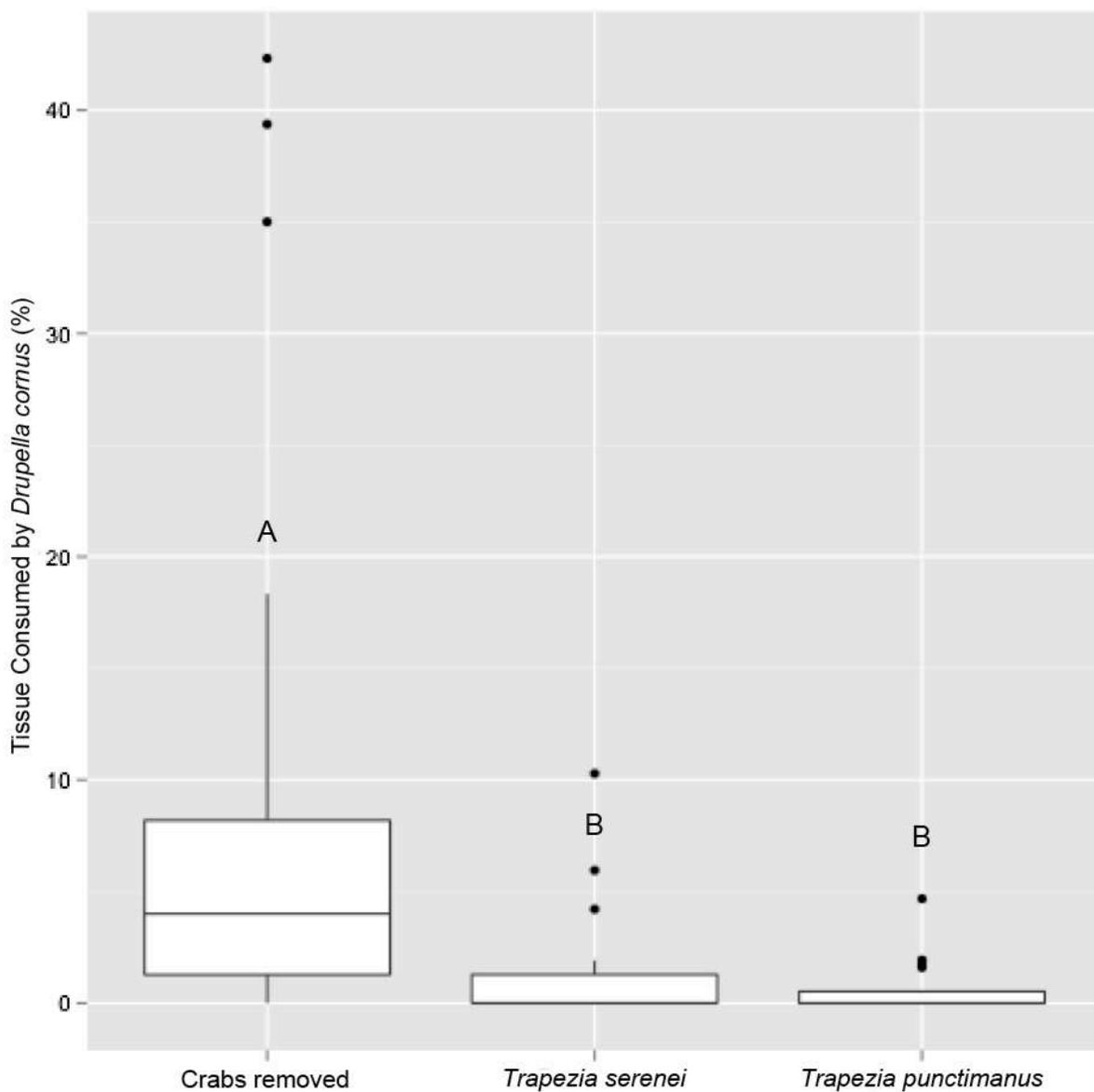Four species of crown-of-thorns starfish. Biol Lett 4:696-699

Figure 1

Percentage of coral tissue volume proxy consumed by *Drupella cornus* in corals hosting the

small size-class of *Trapezia serenei* and *Trapezia punctimanus*. Letters indicate post-hoc

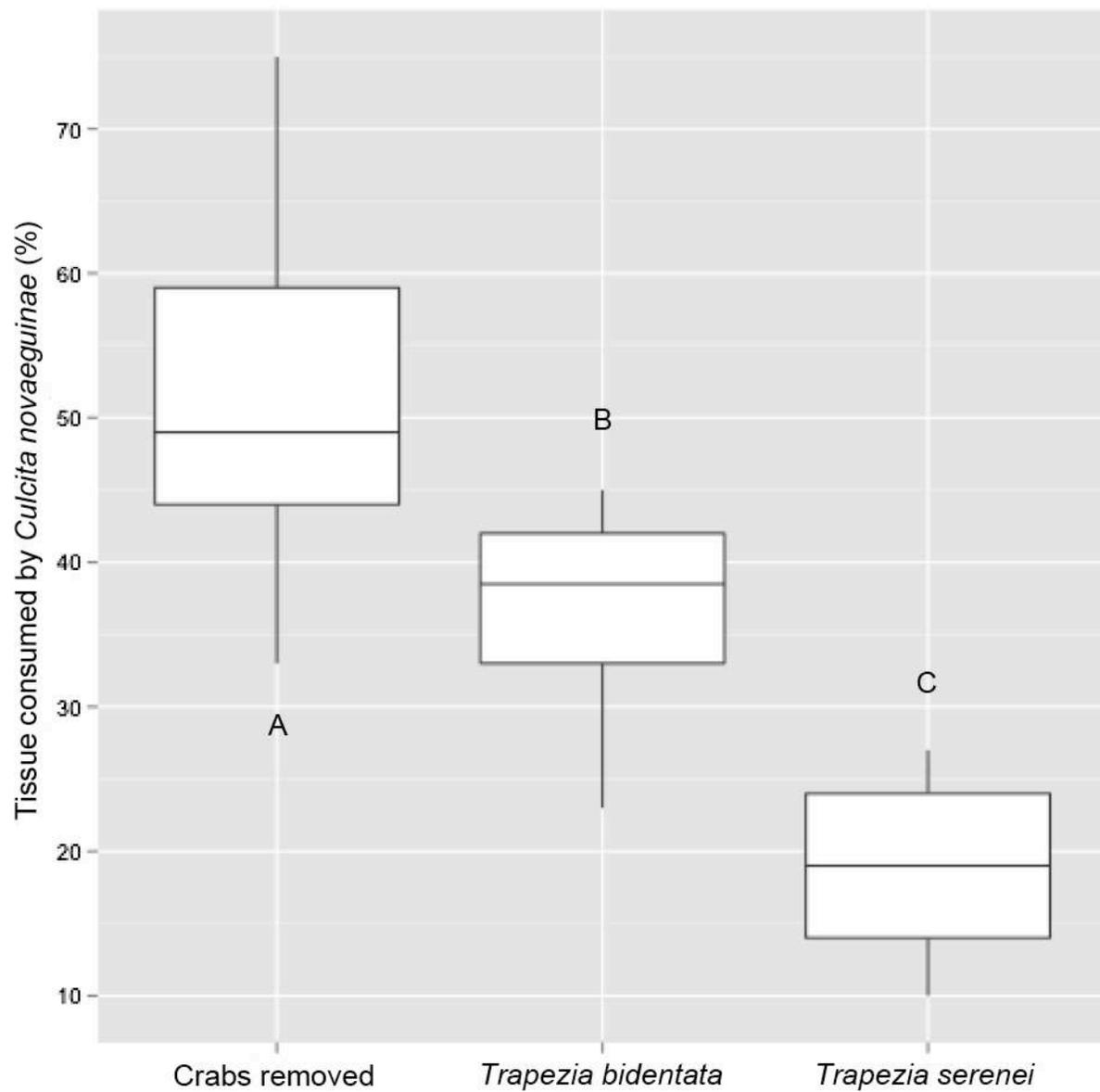statistically significant differences between groups.

Figure 2

Percentage of coral tissue volume proxy consumed by *Culcita novaeguineae* in corals hosting the large size-class of *Trapezia bidentata* and *Trapezia serenei*. Letters indicate post-hoc statistically significant differences between groups.
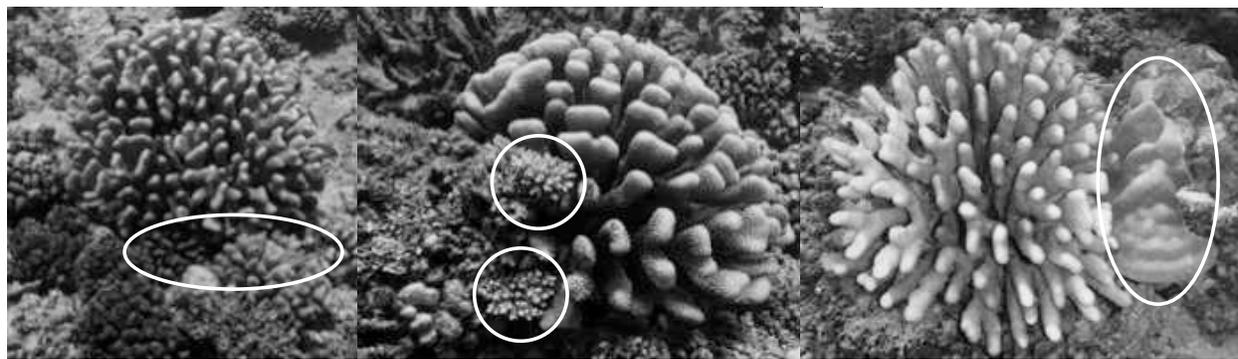
Figure 3

Examples of corals sheltered by living *Pocillopora eydouxi* and *Trapezia flavopunctata*.