DEFENSE OF POCILLOPORID CORALS BY *TRAPEZIA SERENEI* AND *TRAPEZIA BIDENTATA* (MO'OREA, FRENCH POLYNESIA)

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Abstract. Members of the genus *Trapezia* are obligate exosymbionts of pocilloporid corals that defend their hosts from echinoderm attacks. This study investigates the defensive capabilities of two species of trapeziid crab, *Trapezia serenei* and *Trapezia bidentata*, in a series of lab trials in which corals containing each symbiont individually, both symbionts and no symbionts were fed to the echinoderm corallivore, *Culcita novaeguineae*. Treatments were analyzed for differences in feeding scar volume and depth. The presence of either symbiont reduced both scar volume and scar depth, but in both cases this reduction was greater for *T. bidentata* treatments. The co-occurrence of both symbionts further reduced both scar volume and scar depth, suggesting an added benefit to coral hosts containing multiple species of exosymbiont. This may play an important role in the ability of coral colonies to recover from echinoderm attacks. However, the two species did not have a synergistic or even entirely additive effect on defense, and there may be some degree of interference between the two species.

Keywords: corallivory, *Trapezia*, *Trapezia bidentata*, *Trapezia serenei*, *Culcita novaeguineae*, cushion stars, mutualism, Mo'orea, French Polynesia, coral defense, crustacean guards, *Pocillopora*, echinoderm corallivore

INTRODUCTION

Coral reefs form some of the most diverse ecosystems on the planet, and scleractinian corals are the major architects of these ecosystems, providing a framework for a wide variety of organisms. Coral reefs are currently threatened by a multitude of factors. These include rising sea level, changes in seawater temperature, increased sedimentation, increased frequency of storms, overfishing, and disease. Corallivory, or predation on corals, is another biotic factor that may adversely affect coral reefs or accelerate their decline, especially when combined with other stressors (Rotjan & Lewis 2008). There are corallivores in many taxonomic groups, including fish, annelids, mollusks, echinoderms, and crustaceans (Rotjan and Lewis 2008). Echinoderms leave the largest scars of the corallivores, from which corals show the slowest recovery (Rotjan & Lewis 2008).

Two echinoderm corallivores are present in Moorea. The crown-of-thorns starfish, *Acanthaster planci* (Linnaeus, 1758), is a corallivore notorious for its capacity to decimate coral reefs. Normally a benign member of the coral reef ecosystem, *A. planci* is known to undergo periodic population booms in which coral communities are all but destroyed (Birkeland & Lucas 1990). The cushion star, *Culcita novaeguinea* Muller & Troschell, 1842, is another less-voracious corallivore common throughout the Indo-Pacific (Glynn & Krupp 1986). While an individual cushion star causes only one-fifth the coral mortality of *Acanthaster* per year, *C.*

novaeguineae can be more abundant on coral reefs than *A. planci* during non-outbreak periods (Glynn & Krupp 1986). Both *A. planci* and *C. novaeguineae* feed selectively on certain species of coral, and may be important in determining the structure of coral communities (Glynn 1976, Glynn& Krupp 1986).

Once thought to be defenseless from echinoderm attacks, pocilloporid corals have been shown to host obligate symbiont crustaceans that defend their hosts from echinoderm attacks by snapping and pinching (Glynn 1976, 1983). Despite the small size of these crustaceans, their ability to fend off seastars can be very effective: *C. novaeguineae* feed more frequently on corals lacking crustacean guards (Glynn& Krupp 1986) and the presence of symbionts can actually produce changes in feeding preferences of *A. planci* (Pratchett 2001). In addition to defense, symbionts serve their coral hosts by clearing away sediment (Stewart 2006). In exchange, the corals provide the crustaceans not only with shelter, but also with nutrition in the form of lipids produced by the coral (Stimson 1990). The association between trapeziid crabs and cnidarians is a long-lasting one; trapeziid crabs appear in the fossil record in the mid-Eocene and there is evidence for the co-evolution of these groups (Schweitzer 2005).

While mutualism between pocilloporid corals and their crustacean symbionts has been well-defined, little attention has been given to the interactions among multiple species of crustacean symbionts within the same host. This is largely due to the traditional view that mutualisms are pair-wise relationships, rather than interactions between groups of organisms. However, the presence of two exosymbionts of pocilloporid corals, *Alpheus lottini* and *Trapezia serenei,* reduce the amount of coral eaten by the cushion star, *Culcita novaeguineae* to a greater degree than would be expected from greater numbers of symbionts alone, suggesting a synergistic

defensive relationship between the two species (McKeon et al., unpublished data). Given these findings, their frequency of co-occurrence, and the evidence for communication amongst exosymbionts of the genus *Pocillopora* (Lassig 1977), it is reasonable that other exosymbiont species may have similar synergistic effects on coral defense. This study examines the defensive capabilities of two species of trapeziid crab, *Trapezia serenei* Odinetz, 1984 and *Trapezia bidentata (*Forskål, 1775), that are commonly found living together on *Pocillopora* colonies and investigates the presence of a possible synergistic relationship between these two crabs on coral defense. Experiments are designed to address the hypothesis that the co-occurrence of both decapod species reduces coral consumption by cushion stars.

MATERIALS AND METHODS

Study organisms

The organisms used in this study were: the coral host, *Pocillopora* spp., the echinoderm corallivore, *Culcita novaeguineae,* and the coral symbionts, *Trapezia serenei* and *Trapezia bidentata.*

There are roughly 20 species of *Trapezia* found worldwide, fourteen of which are present in French Polynesia (Poupin 2006). They are all obligate exosymbionts of live pocilloporid corals. Adult crabs often associate as male-female pairs, and only coexist with other conspecifics if they are of much smaller size. On the other hand, adult pairs of multiple species commonly coexist on the same colony. The species of *Trapezia* are very similar morphologically except for their distinct coloration (Patton 1974). *Trapezia serenei* (Figure 1), is distinguishable by its pink coloration and green eyes, and *Trapezia bidentata* (Figure 2), is distinguishable by its orange coloration and black eyes. Both are conspicuous members of the *Pocillopora* system, and commonly coexist on *Pocillopora* colonies.

Figure 1: *Trapezia serenei*

Figure 2: *Trapezia bidentata*

Both species have been shown to defend against echinoderm attacks by pinching at the tube feet and spines of the echinoderm.

Two species of *Pocillopora*, *P. meandrina* Dana, 1846 and *P. verrucosa (Ellis & Solander, 1786)*, were chosen for use as the coral prey of the echinoderms because of their relative abundance on the reef. Due to the similarities in morphology and associated organisms between *Pocillopora meandrina* and *Pocillopora verrucosa,* these two species were treated as a functional group.

Culcita novaeguineae was chosen as the experimental predator because it is the less voracious of the two echinoderm corallivores found in French Polynesia, the other being the crown-of-thorns starfish, *Acanthaster planci*. This meant that relatively small coral colonies were needed to show differences in consumption between treatments.

Collection and care of organisms:

Coral colonies were collected from shallow water habitats East of Avaroa Pass (approximately 17°28'55.16"S, 149°48'16.84"W) at the mouth of Cook's Bay. Colonies of *Pocillopora meandrina* or *Pocillopora verrucosa* of moderate size (60-80 cm. maximum circumference) and roughly hemispherical shape were removed from the substrate at their base. Corals were handled as little as possible before the start of the trials, only being removed from the water for a short period of time to remove unnecessary symbionts. Symbionts that were not required in any given trial were removed using a small stick. They were not injured in this process and were returned to the coral after the trials ended. Trials were conducted in tanks with sufficient depth and flow to maintain coral health. Corals were fed to the cushion stars on the night of collection and the then partially consumed corals were returned to the collection site the following day. While this allowed for no acclimation period for the corals and crabs, it reduced the overall disturbance to the system and the environment.

The trapeziid crabs used in the trials were those naturally occurring on that particular coral colony. I chose not to transfer crabs from one colony to another to avoid injuring the crabs and potentially altering their defensive abilities. This also prevented the transfer of crabs to colonies that were not producing sufficient fat bodies to support them and ensured that the heterosexual pairs used in each trial were naturally occurring. Similarly, sex/ species verification of crabs were completed after the trial to avoid injury. Crabs were between 0.7-1.4 cm, measured from lateral spine to lateral spine. Crabs were returned to the coral colonies they were found on and returned to the lagoon after the completion of the trial.

Cushion stars, ranging from 11-14 cm. in diameter, were collected from the fringing reef near Gump Station. They were held in a flow-through circular tank and starved for a period of 24 hours before being used in a

trial. Individuals were chosen haphazardly for each trial from a pool of individuals. The experimental pool was replaced once during the trial period to ensure that all individuals were healthy. No individual was used in consecutive trials.

Coral consumption experiments

In order to characterize the effects of two species of crab exosymbiont on the volume of coral eaten by cushion stars, coral colonies hosting different crab assemblages were fed to *C. novaeguineaea* individuals and the volume eaten was compared. The crab assemblages were: *T. serenei* alone (one heterosexual pair), *T. bidentata* alone (one heterosexual pair), *T.serenei* (one heterosexual pair) + *T. bidentata* (one heterosexual pair), and no crabs.

In the evening, between 5-6 pm, the coral treatments were placed in a circular tank (diameter= 1.3m, depth=0.6m) with a cushion star. The coral and cushion star were placed approximately one foot apart. The following afternoon (2-3pm), the corals were measured (orthogonal circumference, length, width, height, length of longest branch) as were the feeding scars left behind by the cushion star (circumference, length, width, and depth). Coral and scar volume were estimated using the formula for the volume of an ellipsoid. Volume of coral consumed for each treatment was tested for statistical significance by conducting a student's t-test against the control (no crabs). To test for an interaction between species, a two-way ANOVA was performed on log-transformed data, consistent with the multiplicative model proposed by Soluk and Collins for testing for emergent multiple predator effects (1988), and utilized by McKeon (in review) in testing for "multiple defender effects".

RESULTS

Coral consumption experiments

Volume consumed

All experimental treatments showed a reduction in volume of coral tissue consumed (Figure 3) compared to those lacking exosymbionts, but only the combination of both exosymbionts significantly reduced the volume consumed by the echinoderm relative to the control (p=.0360). However, the results of a 2-way ANOVA on log-transformed data show no significant interaction between the two species (p=.7907). In addition, the reduction in scar volume is less for the treatment with both exosymbionts than would be expected due to a greater number of symbionts (expected=52.3%, actual= 41.9% reduction in volume consumed compared to control).

Between the two exosymbiont species, *T. bidentata* appears to provide greater defense to the coral than *T. serenei*. Corals containing *T. bidentata* had an average scar volume of 275 cm^3 and corals with *T. serenei* had an average scar volume of 358 cm^3, but this difference was not statistically significant(p=0.2281).

There was no relationship between coral size and volume consumed (R^2=.005) or *C. novaeguineae* size and volume consumed (R^2=.0003).

Depth of scar

In addition to reducing the amount of coral consumed by *C. novaeguineae*, exosymbionts reduced the depth of scars left by the corallivore (Figure 4). Scar depths were significantly reduced relative to the control in treatments containing *T. bidentata* (p= .0233) and treatments containing both
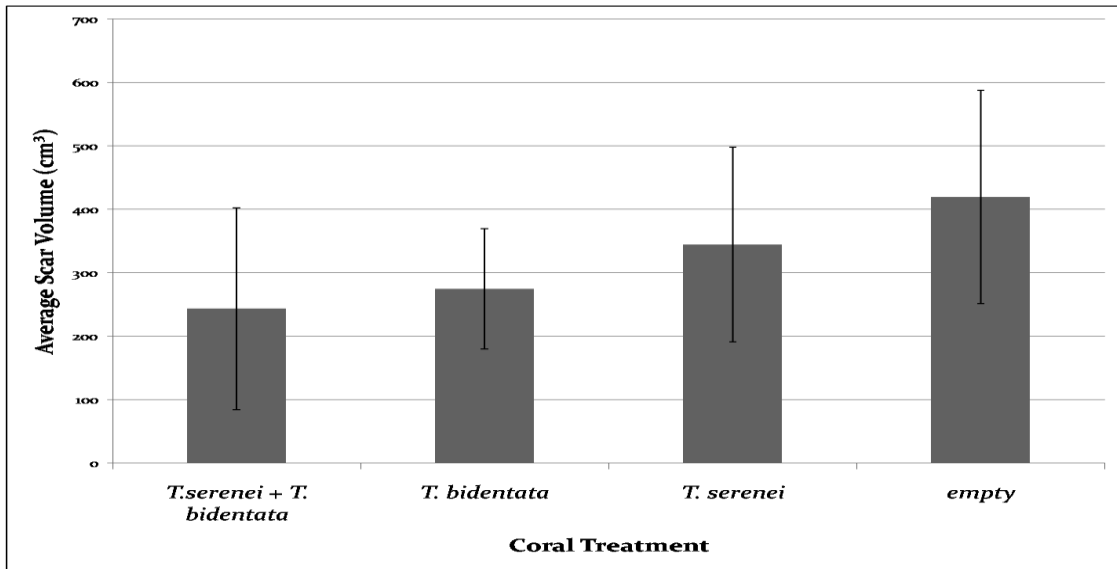
Figure 3: Average size (volume) of scars left by cushion stars feeding on corals containing no crabs (empty), *Trapezia serenei* (one heterosexual pair), *Trapezia bidentata* (one heterosexual pair), and both species together (one heterosexual pair of each)
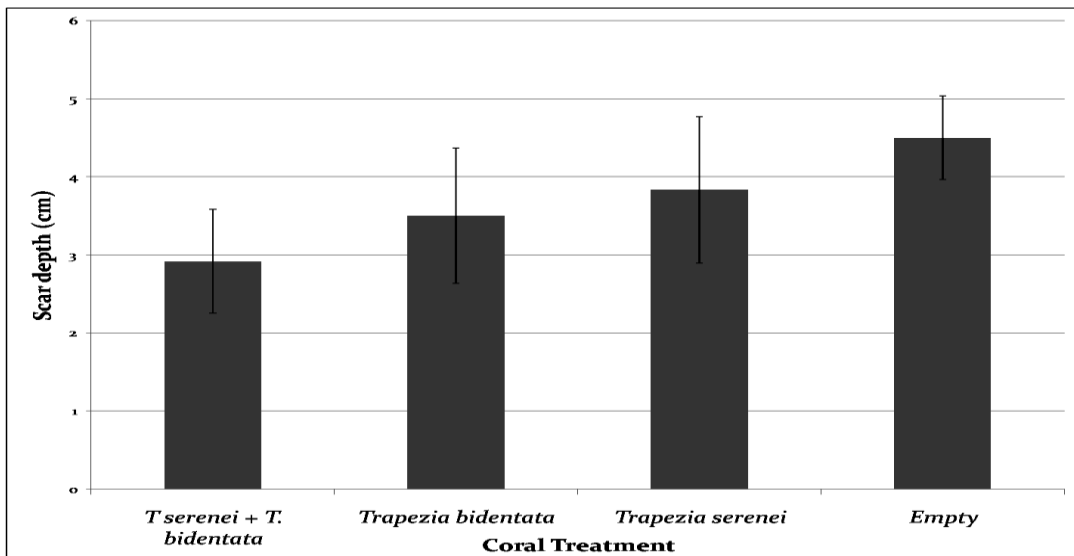

Figure 4: Average depth of *C. novaeguineae* feeding scars on corals containing no crabs (empty), *Trapezia serenei* (one heterosexual pair), *Trapezia bidentata* (one heterosexual pair), and both species together (one heterosexual pair of each)

exosymbionts (p= .0010). Treatments containing both exosymbionts also had significantly smaller scar depth when compared to treatments containing *T. serenei* alone (p= .0257).

As with scar volume, a two-way ANOVA on log-transformed data showed no significant interaction between the two species (p=.8855), and the reduction in scar volume was less than additive (expected=37.0%, actual=35.2% reduction in scar depth relative to control).

There was no relationship between coral size and scar depth (R^2=.002) or cushion star size and scar depth (R^2=.02).

DISCUSSION

The results of this study are in agreement with previous studies that demonstrate the defensive capabilities of Trapeziid crabs. The presence of both *Trapezia bidentata* and *Trapezia serenei* reduce the amount of coral tissue consumed by the echinoderm and the maximum depth into the coral to which echinoderms feed, and both are clearly useful to their host independently.

However, while the presence of either symbiont showed a reduction in scar volume, only the co-occurrence of both symbionts significantly reduced the volume of coral consumed relative to the control. This implies that the presence of multiple exosymbionts may be necessary for effective defense against echinoderms. There does not, however, appear to be a synergistic effect on defense by these two species. In fact, the reduction in volume of coral consumed by the cushion stars was less than would be expected simply due to the presence of a greater number of individuals. In other words, the defensive capabilities of these two species are not entirely additive. One explanation for this is that the species somehow alter the defensive capabilities of the other species and reduce their

effectiveness, suggesting some sort of interference between the two species. Another explanation is that one or both of the species are able to reduce their defensive actions, and thereby reduce their energy expenditure, while still providing equal or greater defense to the coral overall.

A similar trend was observed for the depth of scars left by echinoderms. As with scar volume, the presence of both crabs reduced scar depth further than either species individually, but this reduction was not synergistic or even completely additive. Interestingly, in this case, corals inhabited by *T. bidentata* as well as corals inhabited by both symbionts significantly reduced scar depth relative to the control. Therefore, the effect on scar depth appears to be primarily driven by the presence of *T. bidentata*. This indicates a possible mechanistic difference in defense by the two species. It is possible that *T. bidentata* positions itself further up on the branches than *T. serenei* during an attack, allowing *T.serenei* to reduce its energy expenditure.

The results of this study may be far-reaching. Since corals may not recover fully from large amounts of tissue damage (reviewed by Rotjan & Lewis 2008), the volume of coral tissue consumed and the depth into the coral to which predation occurs may play an important role in the regeneration of a colony after an echinoderm attack, and therefore the ability of a reef to recover from a crown-of-thorns outbreak. Even if regeneration does occur, it usually does so at the expense of growth and reproduction (Rotjan & Lewis 2008). Coral growth may even be suppressed after regeneration stops (Meesters et al. 1994). In addition, if further studies support the idea that multiple species of *Trapezia* provide greater defense to corals, our idea of what is a "healthy" coral colony may have to be altered. For instance, corals may contain one or more species of symbiont and still be more vulnerable to crown-of-thorn

outbreaks than those containing their entire suite of exosymbionts.

The results of the study conducted by McKeon et al. on synergistic defense by two other crustacean guards (in review) and the results of this study show that the presence of multiple exosymbionts is beneficial to the corals, but further studies are needed to clarify why this is the case. McKeon suggests that since *Alpheus lottini* and *Trapezia serenei* display different defensive behaviors, they may provide different, yet complimentary services to their host. Different species of trapeziid crabs most likely use similar defense mechanisms (pinching), but could still provide different services to their host. As previously mentioned, crabs could inhabit different locations on the coral colony, dividing up the defensive "responsibility" spatially and allowing for a greater proportion of the coral to be defended. Crabs could also divide up the defensive "responsibility" temporally. Echinoderms often feed for several hours, and symbionts could "take turns" defending the coral, although this would most likely result in an additive effect on defense. More likely, all symbiont species are able to conserve energy and defend at a lower level for longer periods of time. Or, in a completely alternative scenario, one or more species may serve as the primary defender, with additional species providing other non-defensive services, such as cleaning, that enhance the health of or defensive capabilities of the primary defender(s).

Lastly, further research should be done to determine why trapeziid crabs tolerate individuals of other species but not conspecifics. Resource partitioning is one possible explanation. It is generally accepted that trapeziid crabs feed on coral mucus and to a lesser degree, coral tissue (Knudsen 1967, Patton 1974). While studies on the feeding biology of individual species are lacking and may reveal subtle differences in diet that can explain the co-

occurrence of multiple species of *Trapezia*, it is likely that there is at least some degree of overlap in dietary requirements among different species. Preston (1973) proposed that species of *Trapezia* in Hawaii were segregated according to host colony size, but more recent studies do not support this hypothesis (Huber & Coles 1986, Gotelli & Abele 1983). Hence, trapeziid crabs require similar dietary and microhabitat requirements and are potential competitors. So why is interspecific agonism lower than intraspecific agonism? Since intraspecific aggression is generally sex-specific and interspecific aggression is not, reproductive factors may play a larger role in intraspecific territoriality than resource acquisition (Huber 1987). Vannini (1985) suggested that trapeziid crabs tolerate the presence of alpheid shrimp, which have almost complete niche overlap with *Trapezia* species, because the shrimp alerts the crab of an approaching predator with its loud snapping noise. In this scenario, the benefits of multiple symbionts to the coral host in terms of defense, and the subsequent increase in resources available to its symbionts, outweigh the costs of having competing species present. It remains to be seen why trapeziid crabs tolerate the presence of other crabs and what role colony defense plays in this relationship.

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