

THE ASSOCIATION AND DIVERSIFICATION OF TRAPEZIA CRABS WITH THEIR OBLIGATE *POCILLOPORA* CORAL HOSTS IN MO'OREA, FRENCH POLYNESIA

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Abstract. Natural and anthropogenic disturbances are changing coral reef systems at local and global scales. In Mo'orea, French Polynesia, it is unsure whether a Pocilloporid- and Poritid-dominant reef represents either a transitional, recovering community or a new, stable community (Pratchett 2010). Understanding the species-specific associations between coral-symbionts and their coral hosts will provide a more precise look at how the symbionts contribute to their relationship. To better understand this mutualism, this study combined field surveys with phylogenetic analyses to examine the species-specific association between *Trapezia* crabs and their *Pocillopora* coral hosts and asked more broadly if there is an association between physical variables measured in the field and a constructed phylogeny of species within the genus *Trapezia*. There was a significant association between certain species of *Trapezia* and *Pocillopora* (Likelihood ratio, $\chi^2=84.49$, $df=16$, $p<0.0001^*$), where *T. rufopunctata* was found most frequently with *P. edyouxi* (80.75%) and *T. serenei* on *P. meadrina* (63.4%) and *P. verrucosa* (37.50%). Discriminant analyses support that differences between crab communities can be largely attributed to the morphological features (coral size and branching depth) of coral hosts. Field observations and paired with a morphological phylogeny support a trend where similar sized corals were found to be associated with more closely related crab species.

Key words: *Trapezia*; crabs;; *Pocillopora*; coral; coral morphology; mutualism; back reef; community structure; cyclone; *Acanthastar*; disturbance; habitat availability

INTRODUCTION

Natural and anthropogenic disturbances are changing coral reef systems at local and global scales. Disturbances alter structural (e.g. biodiversity, species composition, habitat availability) and functional (e.g. productivity) components of communities (Holbrook et al. 2008).

In Mo'orea, French Polynesia, multiple disturbances (one cyclone and four bleaching events between 1991 and 2006) have changed total coral cover and composition (Adjeroud 2009). Herbivorous *Acanthastar planci* (Crown of Thorn Starfish) has caused a disproportionate loss of *Acropora* and *Montipora* corals in the past thirty years (Pratchett et al 2010). As a result, coral assemblages are shifting from an Acroporid-dominated state to a Pocilloporid- and Poritid-

dominated state (Lenihan et al. 2011, Pratchett et al. 2010).

Coral reefs embody a system of give and take. Corals provide structure and definition to ecosystems of coral-associates and also benefit from the services that these associates provide (Hay et al. 2004). Reef building corals, like those of the family Pocilloporidae, provide habitat to thousands of species and are highly prone to recurring stresses (Holbrook et al. 2008). Moreover, natural and anthropogenic disturbances are gaining increasing concern as changes to the coral reef communities can have cascading effects on their symbionts (Gibson 2011, Sin 2000).

Mutualisms direct how coral-associates partition space, establish niches, compete, and cooperate (Hardin 1970, Stier 2010). For example, coral-associated invertebrates may exhibit a high degree of preference for one or two coral species (Gibson 2011). In branching

corals, many different organisms utilize the structural complexity, raising the question of how specific can a mutualistic interaction be? Do these relationships change in an oscillating state?

The choice of habitat by coral associates is important in understanding the processes that determine their distribution and abundance (Sin 1999). Xanthid crabs of the genus *Trapezia* ("Guard Crabs") are obligate symbionts on scleractinian corals from the family Pocilloporidae, which they depend on for habitat and food (coral mucus, polyps, and eggs) while providing services to their coral hosts, such as guarding corals from *A. planci*, cleaning off sediment, (Glynn 1983, Knudsen 1967, Stewart 2006), and wiping mucus nets of predatory vermetid snails (Stella 1967, Stier 2010). *Trapezia* species often occur in heterogeneous mixtures with their congeners on the same head of coral (Gotelli 1985, Carlson 2002).

In Mo'orea, there are 13 identified *Trapezia* species (Biocode 2010, Castro 1997). While previous studies on coral communities have favored certain *Trapezia* species (e.g. *T. cymodoce*, *T. serenei*), this study strives to capture the genus *Trapezia* in its localized entirety and the degree to which its interactions can be characterized. To better understand this mutualism, this study combined field surveys with phylogenetic analyses to examine: (1) whether there is a species-specific association between these crabs and their coral hosts and (2) if there is an association between physical variables measured in the field and a constructed phylogeny of species within the genus *Trapezia*.

METHODS

Study organism: Trapezia spp.

Trapezia represents a genus of small, brightly colored, morphologically distinct crabs whose range includes the Indo west Pacific and the tropical eastern Pacific Ocean (Castro 1996). In Mo'orea, French Polynesia there have been 13 *Trapezia* species identified (Biocode 2009, Castro 1996). Each can be distinguished morphologically by color and

size. Trapeziid crabs are coral symbionts, usually associated with *Pocillopora*, *Stylophora*, and *Seriatopora* in which they depend on for habitat, food (coral mucus, polyps, and eggs), combat predators like *A. planci*, and also provide services to their coral hosts, such as cleaning off sediment (Glynn 1983, Knudsen 1967, Sin and Lee 2000, Stewart 2006) and mucus nets of predatory vermetid snails (*Dendopoma maximum*) (Stella 1967, Stier et al. 2010).

Study organism: Pocillopora spp.

The genus *Pocillopora* is a polymorphic genus, with distinguishable wart-like growths called verrucae. There are four species of *Pocillopora* in Mo'orea, each structurally different. *P. edouxyi* is characterized by stout, upright, flattened branches; *P. meadrina* has uniform sprawling branches with small uniform verrucae; *P. verrucosa* is identified by uniform upright branches with clearly distinct verrucae; and *P. damnicornis* has fine and widely separated branches (Veron 1986). Multiple species within the genus are commonly found on the same coral colony (Gotelli 1985).

Study area

This study was conducted from October to November 2012 in Mo'orea (17°30'S, 149°50'W) in the Society Archipelago, French Polynesia. Mo'orea is a volcanic island surrounded by extensive areas of coral reef. The north coast experiences moderate

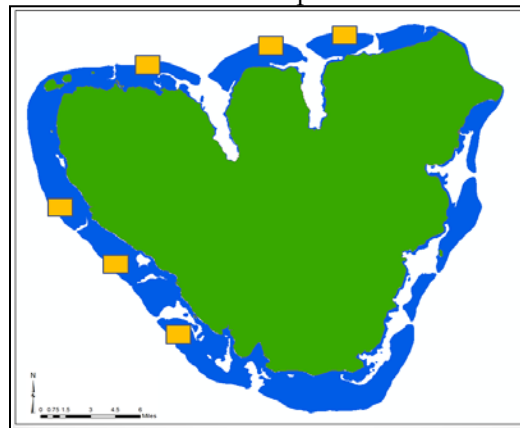


FIGURE 1: A total of six sites on the North and West shore were chosen to capture environmental and habitat variation around the island.

northern swells during the austral summer (Nov-Apr), whereas the south, east, and west coasts are exposed to high amplitude southern swells throughout the remainder of the year (Penin et al. 2009).

Study sites

Surveys were conducted in the back reef at 6 different locations. Three sites were selected to represent the environmental and habitat variation on the North and West side of the island (Fig. 1). Sites were located near major passes to demarcate physical separations between sites, but at least 800m from a pass to avoid confounding variables associated with boat traffic (e.g. changes in water velocity).

Surveys were conducted in the back reef at 6 different locations (Fig. 1). Three sites were selected to represent the environmental and habitat variation on the North (17°29'5.55"S 149°52'13.75"W, 17°28'39.49"S, 149°49'54.16"W, 17°28'25.71"S 149°48'35.87"W) and West side (17°30'39.28"S 149°55'25.87"W, 17°32'7.84"S 149°54'48.03"W, 17°33'41.79"S 149°53'13.20"W) of the island. Sites were located near major passes to demarcate physical separations between sites, but at least 800m from a pass to avoid confounding variables associated with boat traffic (e.g. changes in water velocity).

Field methods

Surveys were conducted in the back reef at each site. The starting point was haphazardly and randomly chosen. Five 30m x 2m band transects were run perpendicular to shore to create a gradient for wave action. Each transect was separated by 10m.

To survey for crabs, I snorkeled along the transect tape towards shore, stopping at each individual *Pocillopora*, to conduct a 3-minute search for *Trapezia* within the coral head. I first looked at the whole head of coral to see if any color caught my eye, then visually scanned each row within the branching coral head for the crabs. Crab identification was aided by a poking the crab to move it to a more visible area and by a laminated photo field guide.

Variables capturing environmental and coral morphology variations were recorded. Macro-habitat data on water depth and velocity were recorded. Three blocks of plaster of Paris, otherwise known as clod card, were made and placed at each site to measure water motion. They were placed preferably heads of *Pocillopora* at each site and often next to in the approximate vicinity of the surveyed site, normally near a pole to assistance in relocating the blocks. Micro-environmental data on coral volume, branching depth, and percent dead coral cover were also recorded. Percent dead cover was estimated by visually examining the percent of the coral that was gray, covered in algae, or knocked off.

Data analyses

To test whether there was a significant different representation of each *Trapezia* species on their host coral, data was pooled across sites and analyzed with a contingency test. Biotic interactions between crab species were analyzed by examining the association between their communities and host corals with discriminant analyses. Discriminant analyses were also used to see if physical variables (water depth, coral diameter, coral branch depth, and percent dead) separated the communities of crabs from one another.

A dichotomous key including 13 species *Trapezia* crabs in French Polynesia was used to construct a morphological phylogeny. To better match the phylogeny with field observations, the seven most abundant *Trapezia* species were extracted to construct a new phylogeny. Mesquite was used to analyze the correlation between physical variables measured and evolutionary relationships within the genus *Trapezia*. All statistical analyses were conducted on JMP (version 10.0)

RESULTS

Seven species *Trapezia* were recorded: *T. areolata*, *T. bidentata*, *T. globosa*, *T. rufopunctata*, *T. serenei*, *T. tigrina*, and *T. flavopunctata*. Three species of *Pocillopora* were recorded: including *P. meandrina*, *P. verrucosa*, and *P. edyouxi*. Pilot studies indicated that *P. damnicornus* mostly

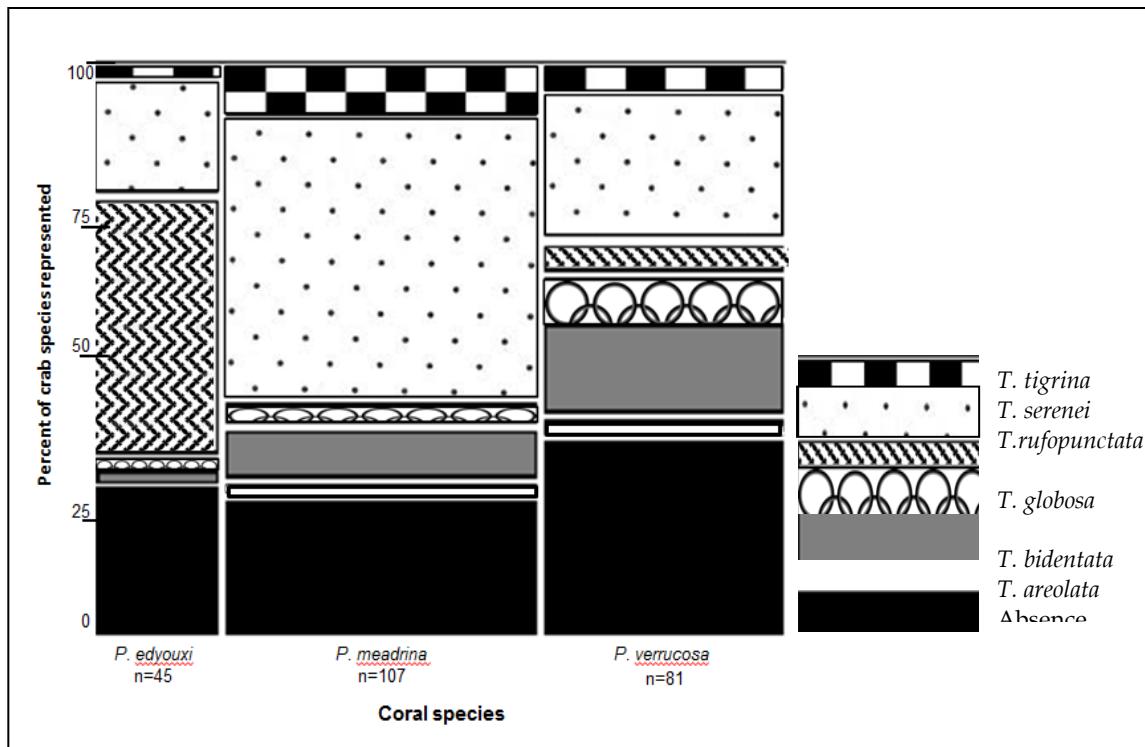


FIGURE 2. Relationships between coral species and associated crab species. *Trapezia* species are not found randomly across their host corals (likelihood ratio, $n = 257$, $DF=16$, $\chi^2 = 84.49$, $p < .0001^*$). *Trapezia* species are indicated by pattern. Length of bars indicate the total abundance of the respective crab species on the coral species. Width of bars indicates the sampled population size.

occurred within the lagoon and was nearly never observed in the back reef, and was hence excluded from the surveys. A total of 233 corals were surveyed, 97 on the north shore and 136 on the west shore

Association between crabs and coral

There was a significant association between certain species of *Trapezia* and *Pocillopora* (Likelihood ratio, $\chi^2=84.49$, $df=16$, $p < .0001^*$) (Fig. 2). While all seven crabs utilized each coral to some extent, several were found predominantly on one species of coral. The majority of the total *T. rufopunctata* were on *P. edyouxi* (80.75%). *T. serenei* was found most frequently on *P. meadrina* (63.4%) and *P. verrucosa* (37.50%). Certain crab species were not seen on coral. *T. bidentata* were found on *P. meadrina* and *P. verrucosa*, but not *P. edyouxi*. *T. areolata* was completely absent on *P. edyouxi*. *T. rufopunctata* was completely absent on *P. meadrina*

Coral structure and crab communities

Crab communities were significantly different on each coral host (Fig. 3). The canonical plot illustrates the crab communities and multivariate means in the two dimensions of a discriminant analysis, showing the differences between the crab groups (JMP manual). The colors represent the coral species and each dot represents the sampled community on the respective coral. The conical graphs represent 95% confidence limits, where non-intersecting circles indicate statistical significance. The crab communities on *P. meadrina* and *P. verrucosa* are more similar (Fig.3). Whereas *P. edyouxi* is more separated, indicating its community of crabs is more distinct.

T. serenei, *T. bidentata*, and *T. rufopunctata*, the three most abundant species, strongly

influence the differences in crab communities. The biplot shows which *Trapezia* species most strongly control the direction of the variables in conical space (Fig. 4). Majority of species are clustered along Canonical 1 (x-axis), explaining most of the variation in the communities between coral. *T. serenei* and *T. bidentata* extend along Canonical 2 (y-axis) in opposite directions, indicating that these two species exert the most sway on the differences observed in those communities

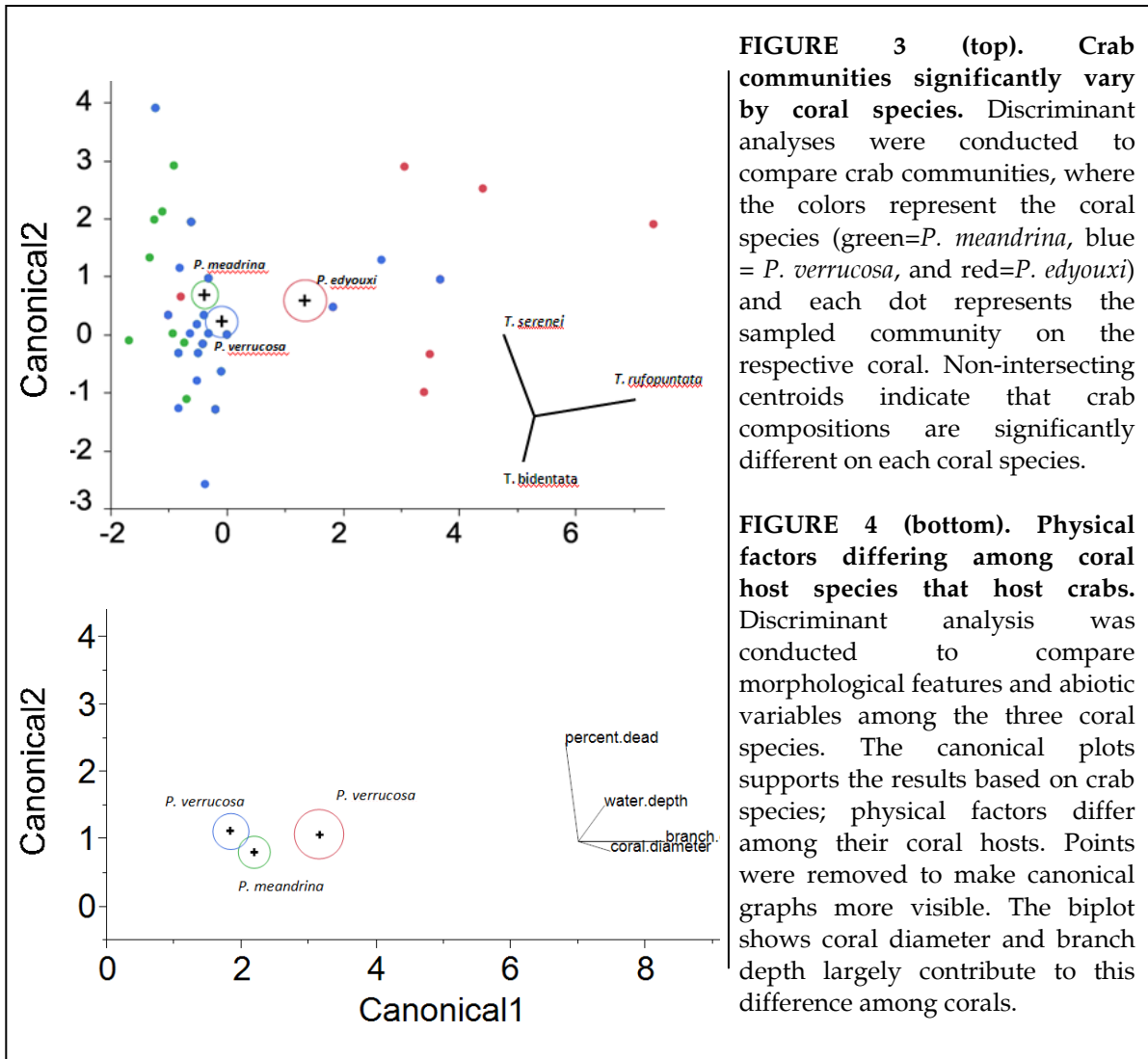
*Crab communities:
physical and environmental factors*

Physical and environmental variables support the differences illustrated by the crab communities. Morphological features of the coral explain most of the differences between crab communities (Fig. 4). The canonical plot supports the hypothesis that *P. meandrina* and

P. verrucosa are structurally more similar than either relates to *P. edyouxi*. Coral diameter and branching depth of the three *Pocillopora* species are significantly different (Fig. 4 biplot). Percent dead coral cover and water depth explain the minor differences in mean of each coral species.

Crab communities: intraspecific competition

There was an overall negative association between pairs of *Trapezia* species (Figure 5). Pair-wise comparisons between the three most abundant *Trapezia* species show that the presence of one species was negatively associated with that of others. Where *T. serenei* was in higher abundance, *T. rufopunctata* was significantly found in less abundance (Fig. 5a, likelihood ratio, $p < .0001$). *T. serenei* was significantly less abundant in the presence of *T. bidentata* (Fig. 5b, likelihood ratio, $p < .0295$)



. *T. bidentata* and *T. rufopunctata* appeared in comparable frequency and was largely outweighed by records where both species were absent (Fig. 4c, likelihood ratio, $p < .0001$).

Phylogeny of *Trapezia*

When coral diameter is mapped onto a phylogeny of *Trapezia* species, similar sized corals were found to be associated with more closely related crab species (Fig. 6). Sister taxa *T. rufopunctata* and *T. flavorpunctata* are associated with larger corals, whereas *T. areolata*, which is less closely related, is associated with smaller sized corals. Independent correlation contrasts showed that this trend was not statistically significant. Coral branch depth, water depth, and the percent dead coral cover did not show clear patterns with respect to *Trapezia* phylogeny and were statistically insignificant.

DISCUSSION

Association between crabs and coral

Field surveys support that a species-specific specialization does exist between the genera of *Trapezia* and *Pocillopora*. Comparing the proportion of coral species utilized and the total coral species available provides evidence that there is a host preference by *T. rufopunctata* and *T. serenei*. For example, *T.*

rufopunctata was nearly exclusively on *P. edyouxi*, whereas *T. serenei* was dominantly on *P. meandrina*. These species-specific interactions may be a consequent of the morphology of the crab, the structure of the coral, or a combination of the two (Sin et al 2003). *T. rufopunctata* is one of the largest *Trapezia* species, with a large spotted carapace. The width and depth of *P. edyouxi* may provide *T. rufopunctata* with the most suitable habitat.

Coral structure and crab communities

The canonical graphs suggest that coral morphology is driving the differences seen in the crab communities (Fig. 4). The low branching structure shared by both *P. meandrina* and *P. verrucosa* corals may offer comparable landscapes for their associated *Trapezia* species. On the contrary, the deep branching *P. edyouxi* may provide habitat for a different community of *Trapezia*, and may set stage for a different suite of interactions. Communities of different *Trapezia* species will likely support different types of competition and cooperation.

In examining crab communities on each coral host, the three most abundant species strongly direct the difference between the communities. The abundance of these three species largely outweighs the other species found, suggesting that the difference in communities (Fig. 3) describes an intraspecific

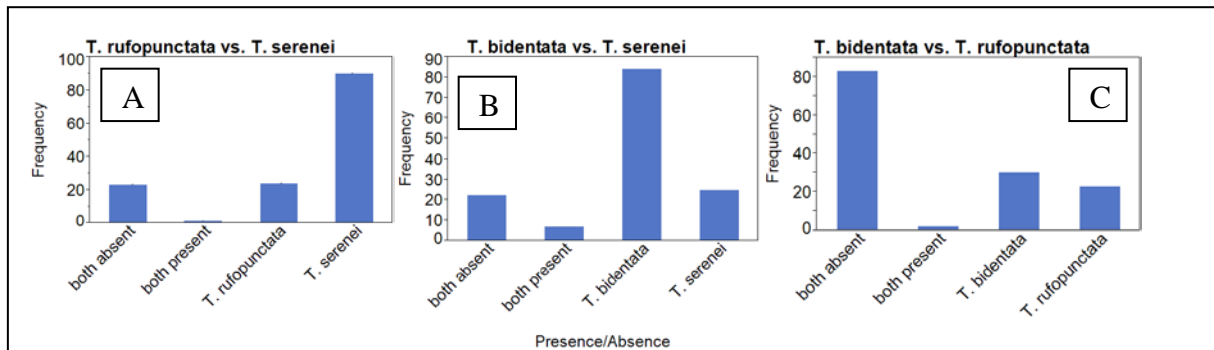


FIGURE 5: Pair-wise comparisons in co-occurrence of the three most abundant *Trapezia* species, *T. serenei*, *T. rufopunctata*, and *T. bidentata*. Overall, there was a negative association between the co-occurrence of two species (a) Higher frequency of *T. serenei* in the presence of *T. rufopunctata* (likelihood ratio, $p < .0001$) (b) Higher frequency of *T. bidentata* in the presence of *T. serenei* (likelihood ratio, $p < .0295$) (c) Neither *T. bidentata* or *T. rufopunctata* exclude on another (likelihood ratio, $p < .0001$)

interaction or reflects the disproportion of crab species on each coral host.

*Crab communities:
physical and environmental factors*

Differences in crab communities may be attributed to the structural differences between the three species of *Pocillopora*. Coral diameter and branching depth are directly associated with coral morphology (Fig. 3). Each species of *Pocillopora* provide distinct habitats for their associates. For example, *P. edyouxi* has characteristically deeper and wider branches than *P. verrucosa* and *P. meadrina*. The micro-landscapes within the coral allow for different sized crabs.

Directional differences in site selection may have also influenced the coral structure. Coral loss and succession has been most studied on the north side of Mo'orea and has provided background on the shifts in coral assemblage (Adjeroud et al 2007, Pratchett et al 2010). However, the north shore and west shore has experienced different magnitudes of changes, both from the hurricane and seasonal variations (personal communication Tangaroa, Penin 2007).

Wave velocity has been shown to influence the coral morphology, where areas of high velocity may experience stunted coral growth to provide more structural stability (Veron 1986). *P. verrucosa*, the most abundant *Pocillopora* species in most back reef systems, has particularly shown responses in growth form with environmental conditions and geographic location (Veron 1986). Seasonal changes in wave velocity coupled with large scale changes caused by hurricanes or *A. planci* may also influence the associations between *Trapezia* species and their host corals, between *Trapezia* communities and their hosts, and interactions within *Trapezia* communities.

Functional features of coral and crab diversity

While *Pocillopora* represents a genus of diverse branching coral, structure and function are intertwined features of all species of coral. The morphological features of the coral provide an inherent example of form, but function can also be less apparent. For

example, the function of mucus is a primary physiological function for coral growth

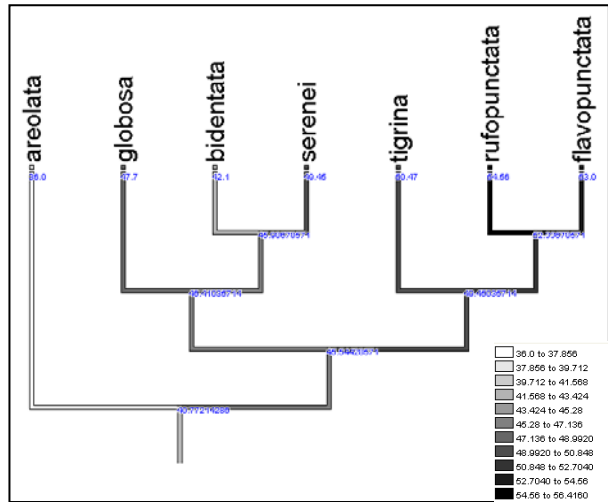


FIGURE 6. Coral size mapped on the morphological phylogeny of the genus *Trapezia*. The gray scale indicates increasing coral size (cm), where darker colors indicate larger corals.

(Meikle 1988). Coral mucus also provides lipids and polysaccharides as a food source for *Trapezia* crabs (Stimson 1990) and has been seen to increase in production in the presence of crustacean symbionts (Glynn 1983). Notably, different coral species produce different types of coral mucus (Meikle 1988, Wild 2004). Discrimination among coral hosts may not only be tied to the physical features of the coral or habitat requirements, but also to the chemical cues. *Trapezia* species may have preference for certain coral mucus, for the most suitable ratio of lipids and polysaccharides for their dietary needs. The combination of coral structure and the compounds within the mucus may be responsible for attracting obligate species of *Trapezia*.

Association between Trapezia evolution and coral characteristics

The association between the genera *Trapezia* and *Pocillopora* can be dated to the Eocene (Schweister 1984). To disentangle the species-specific relationship between *Trapezia* and *Pocillopora*, a phylogeny of *Trapezia* was

paired with field observations. The trend between the phylogeny of *Trapezia* species and coral size suggests that preference for larger corals is associated with the divergence of species within this genus. While this phylogeny is small and limited, it provides a basis and need for construction of a larger phylogeny to better describe the evolutionary relationship between *Trapezia* and *Pocillopora* at the species-level.

Moreover, the summation of field and phylogenetic data strongly suggests that specialists and generalists exist within the genus *Trapezia*. In comparing the most abundant species, two species appear to be example characters: *T. serenei* may be more of a generalist that is found in comparable abundance in *P. meandrina* and *P. verrucosa*, whereas *T. rufopunctata* is highly specialized to *P. edyouxi*.

While other *Trapezia* species found in lower numbers may be extreme habitat specialists (Sin 1999), *T. serenei* and *T. rufopunctata* may be indicators of how *Trapezia* populations may shift under a changing environmental state. Generalists are typically less sensitive to habitat disturbances, having the liberty to colonize a wide range of territories. On the other hand, specialists are much more vulnerable and dependent on a particular habitat. *T. serenei* and *T. rufopunctata* may incur different obstacles in a transitional reef environment

Influence of a disturbed coral reef

Changes in the coral reef assemblage have surely influenced the availability of habitats and consequently the crab-coral interactions that exist at the individual and community level (Sin 2000). Recent natural disasters in Mo'orea provide an opportunity to understand the impact of disturbance on relationships between coral and coral-symbionts. The current shift to Pocilloporid- and Poritid-dominated state and an overall increase in total coral cover on reef slopes pose changes to the existing coral-associate communities (Pratchett et al 2010).

The degree of a species-specialization will influence the population's abundance, ability to find suitable habitat, and adapt to

more changing microhabitats (Sin 2000). Habitat generalists that were found among all the corals, like *T. tigrina*, *T. globosa*, *T. bidentata*, are expected to be more correlated by the total amount of habitat rather than the amount of particular habitats (Sin et al 2000). Current associations between corals and coral-associates may have already shifted, be in transition, or may shift in the near future.

There was a disproportionate representation of *Trapezia* and *Pocillopora* species in the survey. Among *Trapezia*, *T. areolata*, *T. globosa*, *T. tigrina*, and *T. flavopunctata* were notably less abundant. An unequal number of corals surveyed (*n*_{*P. edyouxi*}=44, *n*_{*P. meandrina*}=107, *n*_{*P. verrucosa*}=82). Across all corals censused, there were no crabs were found 25% of time. This may be function of a recovering reef, surveying limitations (e.g. time of day surveyed), or by difficulty to conduct a non-disruptive survey. Efforts to balance the dataset were trifled by the obstacle of finding equal numbers of each coral species at each site, illustrating the spatial changes in micro-habitats along the same side of the island.

Future Directions

To respect the sensitivity of the recovering coral reef, this study did not remove any coral for identification purposes and was limited to in-field identification. The majority of previous *Trapezia* work have acknowledged the tight relationship between the crab and coral and have removed corals to better study and identify the crabs (Stella et al 2010, Stewart et al 2006). Identification of all *Trapezia* species was limited to visual encounters, an arguably more difficult and less precise process than identification would be in a lab setting.

The findings of this study begs to expand the phylogeny of genus *Trapezia*, building from that of Mo'orea or French Polynesia. The genus *Trapezia* consists of 59 species, ranging across the Indo west-Pacific to Tropical east-Pacific (Castro 1996, WoRMS). Moreover, a larger phylogeny would allow for a better understanding of the evolutionary associations between species of this unique crab-coral mutualism.

This study sets stage for studying understanding how the mutualism between these guard crabs and host corals may change as new actors come in play. The branching complexity of *Pocillopora* corals offers habitat and food for a number of conspecifics. Among the diverse number of organisms that coinhabit a space, vermatid snails have attracted recent attention as a threat to coral health (Stier et al 2010). On Mo'orea, vermatids have been traditionally eaten but have recently witnessed a spike in population. As "guard crabs," future studies would what happens when there is another predator or threat is introduced? What type of association exists between *Trapezia* crabs and vermatid snails?

CONCLUSION

The small symbiotic relationships as described between *Trapezia* and *Pocillopora*, where the associate increases the survivorship of their host coral, will prove to be increasingly important in a changing reef environment. While it is unsure whether the shift to a Pocilloporid-and Poritid-dominant reef represents either a transitional, recovering community or a new, stable community (Pratchett 2010), understanding the species-specific associations between coral-symbionts and their coral hosts will provide a more precise look at how the symbionts contribute to their relationship.

Furthermore, examining the degree of species-specific associations allows us to better grasp how coral communities will change with natural and anthropogenic episodic changes and how these are augmented by climate change locally and globally. There is much evidence that *Trapezia* holds mutualistic ties with fish (*Paragobiodon echinocephalus*, *P. lacunicola*) and shrimp (*Alpheus lottini*), who all interact with their host corals. In understanding the associations between *Trapezia* and *Pocillopora*, future studies will be able to grasp intraspecific and interspecific cooperation, competition, and how these relationships function at the individual and ecological level in the face of environmental change.

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