Epifaunal invertebrate assemblages associated with branching Pocilloporids in Moorea, French Polynesia

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ABSTRACT

Reef-building corals can harbour high abundances of diverse invertebrate epifauna. Coral characteristics and environmental conditions are important drivers of community structure of coral-associated invertebrates; however, our current understanding of drivers of epifaunal distributions is still unclear. This study tests the relative importance of the physical environment (current flow speed) and host quality (e.g., colony height, surface area, distance between branches, penetration depth among branches, and background partial mortality) in structuring epifaunal communities living within branching Pocillopora colonies on a back reef in Moorea, French Polynesia. A total of 470 individuals belonging to four phyla, 16 families and 39 genera were extracted from 36 Pocillopora spp. colonies. Decapods were the most abundant epifaunal organisms (accounting for 84% of individuals) found living in Pocillopora spp. While coral host characteristics and flow regime are very important, these parameters were not correlated with epifaunal assemblages at the time of the study. Epifaunal assemblages associated with Pocillopora spp. were consistent and minimally affected by differences in host characteristics and flow regime. The consistency in abundance and taxon richness among colonies (regardless of habitat characteristics) highlighted the importance of total habitat availability. With escalating effects of climate change and other localized disturbances, it is critical to preserve branching corals to support epifaunal communities.
The complex architecture of branching corals provide shelter as well as food in the form of coral tissue, mucus, and associated detritus to the taxa that live within them (Castro, 1988). In turn, many branching corals are reliant upon invertebrates that live among their branches for protection from predators (Pratchett, 2001; McKeon et al., 2012; McKeon & Moore, 2014) and cleaning of sediment deposits (Stewart et al., 2006), thus forming mutually beneficial associations (Glynn, 1980, 1987; Leray et al., 2012). Coral crabs of the genus Trapezia, for instance, protect branching corals from corallivorous crown-of-thorns sea stars and can reduce the negative effects vermetid snails may have on coral growth and overall survival (Shima, Osenberg & Stier, 2010; Stier et al., 2010). Although some symbionts could be harmful (i.e., corallivorous snails), many are beneficial and these are the most abundant (McClanahan, 1994).

Approximately 870 species of invertebrates associate with corals (Stella et al., 2011), but the true diversity may be much higher (Carvalho et al., 2019) and vary in relation to reef habitat diversity and the topographic complexity provided by scleractinian corals (Sale, 1991; Wilson, Graham & Polunin, 2007; Graham & Nash, 2013). Light attenuation and availability can vary greatly within a colony, thus providing a variety of light microenvironments for exosymbionts (Kaniewska et al., 2011). Invertebrates most reliant upon branching corals are vulnerable to severe impacts if declines in coral cover and abundance occur (Stella, Munday & Jones, 2011; Enochs, 2012). Coral mortality can lead to a reduction in the abundance of epifaunal taxa, but it also depresses individual fitness of invertebrates with consequences for their recruitment and population persistence (Pratchett et al., 2004; Stella, Munday & Jones, 2011; Stella et al., 2014).

The characteristics of coral colonies and environmental conditions are important drivers of community structure of reef-associated invertebrates (Klumpp, McKinnon & Mundy, 1988; Kaandorp, 1999; Vytopil & Willis, 2001; Kane et al., 2009; López-Pérez et al., 2017; Counsell et al., 2018) and of reef fish communities (Jones et al., 2004; Feary et al., 2007). Habitat selection and availability determine spatial distribution and abundance of epifaunal assemblages on coral reefs. Invertebrates may prefer complex habitat structures that prioritize refuge from predation (Stella et al., 2011). The density and richness of organisms harbored in coral colonies with variable and complex branch growth forms, exemplified by many Pocilloporids, are often high (Vytopil & Willis, 2001; Kane et al., 2009; Stella, Jones & Pratchett, 2010; Stella et al., 2011). Similarly, high water flow may enhance richness and diversity of epifaunal invertebrates by increasing nutrient supply and particulate matter relied upon as food by coral-dwellers (Kaandorp, 1999).

Since flow regime varies greatly both at the scale of a single coral colony and entire reef, epifaunal assemblages can exhibit a range of responses to different flow conditions, depending on their tolerance to hydrodynamic processes (Kaandorp, 1999; Hench & Rosman, 2013). For instance, the reef crest is a shallow wave-exposed habitat often exposed to high flow regime, which may strongly favor organisms that are mechanically and physiologically adapted (Madin et al., 2013; Pisapia, Anderson & Pratchett, 2014). There is evidence that wave energy may play a significant role in structuring cryptic coral reef fish communities with calmer sites showing higher diversity and abundance of small cryptic fishes (Depczynski & Bellwood, 2005). The morphology of coral colonies can also vary...
greatly with different flow regimes (Madin & Connolly, 2006; Madin et al., 2014), thereby affecting the abundance and taxon richness of epifaunal communities associated with these colonies (Kaandorp, 1999; Kane et al., 2009). Importantly, flow is intricately involved in dictating settlement processes affecting dispersal and supply of larvae (Willis & Oliver, 1990). Larval concentration and delivery rates are strongly affected by current flow speed (Cowen & Castro, 1994). These pre-settlement factors strongly influence how epifaunal communities aggregate to corals.

Colony size is another important factor in driving distribution and persistence of epifaunal assemblages. It is expected that with increasing colony area the amount of habitat available increases and as a result the number of species present increase (Simberloff, 1972). For instance, both the number and size of crabs associated with branching Pocilloporid colonies on shallow reefs are positively related to colony size (Castro, 1978). Some invertebrates such as Trapezia crabs move to a larger host colony when the rate at which they ingest coral mucus becomes detrimental to the colony (Castro, 1978). Trapezia spp. are territorial and only one breeding pair typically occupies a single host colony regardless of colony size (Preston, 1973; Stier et al., 2012). Some invertebrates such as decapod crustaceans have an asymptotic relationship with colony size at about 6,000 cm$^3$ so new species are not added with increasing colony area (Abele & Patton, 1976). Many studies have investigated the relationship between invertebrates assemblages and their coral host (Stella, Jones & Pratchett, 2010; Holbrook, Schmitt & Brooks, 2011; Leray et al., 2012; Head et al., 2015; Britayev et al., 2017; Counsell et al., 2018), and, in particular, many studies documented that colony size is a key driver in invertebrates community metrics (Abele & Patton, 1976; Julian Caley, Buckley & Jones, 2001; Leray et al., 2012). However, how epifaunal assemblages scale with the coral host remains partially unclear. For example, the abundance and size of invertebrates such as Tetralia crabs are independent of live coral surface area (Vytopil & Willis, 2001), indicating that the relationship between colony size and epifaunal assemblages may vary. Understanding under what contexts invertebrate abundance and taxon richness scale with colony size is critical, as loss of larger colonies may greatly enhance the risk of extirpation or extinction of coral-dwellers.

Previous studies have documented the importance of partial mortality (e.g., loss of live polyps) in driving epifaunal assemblages (Stella, Jones & Pratchett, 2010; Leray et al., 2012). Dead coral colonies and colonies with high partial mortality may harbor higher diversity of invertebrates, especially obligate coral dwelling organisms (Stella, Jones & Pratchett, 2010; Enochs, 2012; Leray et al., 2012; Head et al., 2015). With declining live tissue cover, new microhabitats within the colony are formed allowing for other species to utilize new available resources (Stella, Jones & Pratchett, 2010). Partial mortality and colonization of the dead skeleton by algae may thus favor a mixed community composed of both coral obligate and non-obligate species and an increase in species diversity. Leray et al. (2012) documented significant changes in decapod communities with partial mortality, observing an increase in species diversity with increasing tissue loss. However, the increase in partial mortality also resulted in a shift from coral obligate to
non-obligate decapods species. This study aimed to refine previous findings and improve understanding of the role of partial mortality in structuring epifaunal assemblages.

In recent years, unprecedented degradation of coral reefs habitats due to global warming has occurred throughout the tropics (Heron et al., 2017; Hughes et al., 2017). Habitat degradation has not been uniform on reefs, but rather it correlated with patterns of thermal stress which varied according to reef position and depth (Hughes et al., 2017, 2018, 2019). Flow regime can dramatically influence the outcome for the same species of corals located on different parts of the reef (West & Salm, 2003). Since flow may contribute to patchiness in habitat degradation, it is expected that the outcome of coral-associated invertebrates could also vary with flow. Here, we investigated how current flow speed and host characteristics such as colony height (which may be the most likely feature to interact with differential flow) and partial mortality relate to density and taxon richness of epifaunal assemblages associated with Pocillogorids on a reef flat in Moorea, French Polynesia. This study could aid in a better understanding of consequences of habitat degradation and loss of biodiversity on coral reefs.

MATERIALS AND METHODS

We investigated epifaunal invertebrate assemblages associated with colonies of the branching Pocillopora spp., in Moorea, French Polynesia in January 2018. Twelve colonies of Pocillopora spp. were haphazardly collected between the reef crest and shore along three reef transects (~400 m) in ~2 m depth (n = 36 adult colonies), where flow regime has been extensively described through time series analyses of the Moorea Coral Reef Long Term Ecological Research program (MCR-LTER; http://mcr.lternet.edu; Hench, Leichter & Monismith, 2008; Hench & Rosman, 2013). Flow across the reef flat on the north shore of Moorea is unidirectional from the crest towards back reef and it has been shown to be relatively uniform across the whole flat (Hench, Leichter & Monismith, 2008; Hench & Rosman, 2013). To ensure that differences in epifaunal assemblages were representative of assemblages on the north shore of Moorea, three back reef sites were haphazardly chosen to collect coral colonies (Fig. 1). The presence of a boating channel running through the study sites may have influenced some of the variables measured, either by disrupting natural flow patterns or influencing animal behavior, particularly that of predatory fishes near the channel which may influence epifaunal communities. Consequently, the colonies collected directly adjacent to the channel were examined for any persistent differences from the rest of the dataset using an ANOVA. However, no differences were found.

Pocillopora spp. are some of the most common branching corals in the back reef community of Moorea (Edmunds, Leichter & Adjeroud, 2010). Since morphological features are unreliable indicators of species (Edmunds et al., 2016; Johnston et al., 2017), colonies were identified at genus level based on genera specific morphological features (Veron, 2000; Edmunds et al., 2016; Johnston et al., 2017).

We tested the hypotheses that flow speed, colony characteristics, and partial mortality affected the community structure of the epifaunal assemblage associated with Pocillopora spp. by haphazardly selecting different colonies across a flow speed and wave exposure gradient (sampling from reef crest to the shore). The north shore back reef, where the
study was conducted, is characterized by wave-driven circulation (Hench, Leichter & Monismith, 2008). Waves drive flow over the reef crest, through the lagoon, and back out through a pass (Hench, Leichter & Monismith, 2008). Flow was measured near the crest and near the shore at the MCR-LTER site during the study for six consecutive days. Three-dimensional water velocity was measured using a Nortek (Boston, MA) Aquadopp acoustic doppler profilers (ADP) deployed upstream near the reef crest and another deployed downstream (ca 500 m from the reef crest). Flow speed was measured in 10-cm bins from 20 cm above the benthos to the water surface at 1-min intervals (accuracy ±1% of measured value ±0.5 cm/s). Because flow was measured at one upstream and downstream site, it was not possible to investigate whether there was a relationship between actual flow velocity and invertebrate community composition. Conversely, this study investigated whether the position of colonies upstream versus downstream (Fig. 1) may correlate to epifaunal abundance and diversity. The colonies ranged from 67 m to 458 m away from the crest.

To characterize the mobile epifaunal invertebrates, each colony was immediately placed in a plastic bag and transported in an individual shaded bucket to the Richard B. Gump South Pacific Research station. Colonies were processed to investigate epifaunal assemblages and host characteristics immediately after collection following Stella, Jones & Pratchett (2010). Epifaunal invertebrates larger than ~5 cm (e.g., some trapeziids, ophiuroids, and Alpheus lottini) were removed with forceps, and smaller invertebrates were removed using a brief rinse (≤60 s) in fresh water without damaging the coral skeleton. Submergence of the corals in fresh water caused epifaunal invertebrates to fall out of the coral branches (e.g., small palaeomonid shrimp). While the validity of this approach
has been previously supported (Stella, Jones & Pratchett, 2010), it is possible that some smaller invertebrates may have not been sampled. Invertebrates that escaped from the colonies in the buckets used for transportation were collected by filtering the seawater through a 1 x 1 mm mesh net. The corals were then carefully inspected to ensure collection of all epifaunal invertebrates, including small cryptic macrofauna. Once collected, invertebrates were placed on ice, photographed, fixed in 95% ethanol, and later transported to California State University, Northridge (CA) for identification (and enumeration) (Fig. 1). Following Stella, Jones & Pratchett (2010), each specimen was identified to the lowest possible taxon based on all current literature (e.g., Zootaxa; Castro, Ng & Ahyong, 2004; McKeon & Moore, 2014; Rouzé et al., 2017) and with the assistance of taxonomic consultations. More specifically, 62% of individuals were identified at species level, 18% at genus level and 16% at family or class level. It is possible that ethanol preservation skewed the ability to identify taxa to a finer taxonomic resolution, particularly the palaemonid shrimp.

Several coral colony measurements were taken following Stella, Jones & Pratchett (2010) to test how morphological features including size of coral host affect abundance and diversity of epifaunal invertebrates. For each colony, maximum planar diameter, colony height, space between branches (n = 5 random points per colony), penetration depth between branches (n = 3 random points per colony) and percentage of partial mortality (to the nearest 5%) were measured (Stella et al., 2014; Counsell et al., 2018). Partial mortality was visually estimated following Pisapia, Anderson & Pratchett (2016). Dead tissue was overgrown by algal turf in all colonies. However, it was not possible to determine time and/or specific cause of injury from these observations. The average of the maximum planar diameter (D) (cm) and the perpendicular diameter (d) (cm) of each colony was used to estimate their two-dimensional projected surface following Linares, Pratchett & Coker (2011). The area was calculated based on the assumption that the colony was an ellipse (A = π D d/2). Living area (e.g., colony surface area (cm²)) was then calculated by multiplying the two-dimensional surface area by 1—proportion of dead tissue for each colony. All remaining measurements were taken with a measuring tape and recorded to the nearest mm. Coral colonies were sacrificed at the end of the study. Research was completed under permits issued by the Haut-commissariat de la Republique en Polynésie Française (DRRT) (Protocole d’Accueil 2017–2018).

Data analyses
Since short-term measurements of flow were not expected to drive instantaneous shifts in resident invertebrate communities, flow was treated as a categorical variable (i.e., colonies were categorically grouped as “upstream or downstream”) in all analyses. Individual generalized linear mixed effects (GLMM) were used to test whether there was a relationship between flow (upstream versus downstream) with each of the five colony characteristics (2D projected surface area, colony height, space between branches, penetration depth between branches and partial mortality). Colony characteristics were the dependent variables and transect was a random variable. Individual GLMMs were then used to test the relationship between colony metrics (colony morphology, colony size and
partially host mortality) and flow (upstream versus downstream) on species diversity or abundance. Univariate analyses were chosen to deal with co-linearity between variables and avoid over-parameterized models with insufficient data to estimate coefficients robustly. All assumptions such as goodness of fit, dispersion, and collinearity among the predictors were tested and met. To address potential non-independence issues, the random variable ‘transect’ was included to account for the grouping of coral colonies along the three transects. A Laplacian approximation GLMM with negative binomial distribution was used for the abundance of epifauna model due to over-dispersion of data, while a Poisson distribution was used for the taxon richness model.

We used a PERMANOVA (999 permutations) to investigate potential differences in community structure in decapods (as the dominant functional group; Table 1) associated with varying degrees of partial mortality because live coral tissue is a food source for some decapod species. One colony with 15% of partial mortality was overly influential on statistical analyses because of the lack of data in this category and was excluded from all analyses.

Because taxon richness levels are highly dependent on sample size, we used rarefaction curves to assess any potential underestimation of taxon richness due to a low sample size (Fig. S1). More specifically, using the R package vegan and the rarefy function, we tested whether the appropriate sample size to measure the community was reached. Rarefaction was performed using counts of individual taxa. Rarefaction curves estimated the expected number of species in a small sample of individuals drawn randomly from a larger sample (Gotelli & Abele, 1983). All analyses were performed using R 3.4.1 packages lme4, vegan, stats and Mass (Oksanen et al., 2013; Team et al., 2015).

RESULTS
A total of 470 individuals belonging to 4 phyla, 16 families, 39 genera, and 18 species were identified (Table 1) from 36 Pocillopora spp. colonies. Epifaunal invertebrate densities ranged from 0 to 90 individuals per colony, while taxon richness per colony varied from 2 to 14 (Table 1). Decapod crustaceans comprised the highest proportion (85%) of total epifauna for Pocillopora spp. (Table 1). Decapoda mainly belonged to the Trapeziidae, Alpheidae and Palaemonidae (Table 1). Among Trapezia crabs, T. lutea were the most abundant species living in Pocillopora spp. accounting for 25% of all Decapoda (Table 1).

Coral colony areas ranged from 136 to 511 cm² (Table 2). The maximum diameter of coral colonies varied from 11 cm to 24 cm with overall average of 16.9 ± 0.5 cm. Partial mortality was <5% in 19 colonies, 10% in 5 colonies, and 15% in one colony (Table 2). In the absence of any major disturbances, these levels of partial mortality could be considered natural (Wakeford, Done & Johnson, 2008; Pisapia, Anderson & Pratchett, 2016).

Flow speed at the upstream mooring averaged 0.23 ± 0.004 m/s during the study and was consistently higher than flow at the downstream mooring (0.18 ± 0.004) (Fig. 2). The difference between the upstream and downstream flow velocity was consistent during the six days of sampling (Fig. 2). Flow (i.e., upstream versus downstream) did not have any significant effect on colony characteristics, epifaunal abundance, or richness (Table 3).
Table 1  Total taxon abundances found in *Pocillopora* spp. in the back-reef of Moorea. The unknown Palaemonids were included in abundance but not diversity estimates. Decapoda was the dominant functional group, hence life histories traits are reported based on *Huber & Coles (1986)*, *Vytopil & Willis (2001)*, *Stella, Jones & Pratchett (2010)* and *Stella et al. (2011)*.

| Phylum         | Class        | Order  | Family  | Genus and Species   | Total Number of individuals | Life-history |
|----------------|--------------|--------|---------|---------------------|-----------------------------|--------------|
| Arthropoda     | Malacostraca | Decapoda| Trapeziidae | *Trapezia areolata* | 4                           | Specialist   |
|                |              |        |         | *Trapezia globosa*  | 3                           | Specialist   |
|                |              |        |         | *Trapezia formosa*  | 4                           | Specialist   |
|                |              |        |         | *Trapezia lutea*    | 100                         | Specialist   |
|                |              |        |         | *Trapezia punctimanus* | 2                         | Specialist   |
|                |              |        |         | *Trapezia septata*  | 1                           | Specialist   |
|                |              |        |         | *Trapezia serenei*  | 43                          | Specialist   |
|                |              |        |         | *Trapezia tigrina*  | 8                           | Specialist   |
|                |              |        | Alpheidae| *Alpheus lottini*   | 66                          | Specialist   |
|                |              |        |         | *Alpheus sp. White* | 10                          | Specialist   |
|                |              |        |         | *Acanthanas sp.*    | 3                           | Specialist   |
|                |              |        |         | *Synalpheus sp.*    | 2                           | Specialist   |
|                |              |        | Xanthidae| *Chlorodiella nigra* | 16                         | Generalist   |
|                |              |        |         | *Chlorodiella sp.*  | 1                           | Generalist   |
|                |              |        |         | *Psaumis cavipes*   | 1                           | Generalist   |
|                |              |        |         | *Luniella pugil*    | 24                          | Generalist   |
|                |              |        |         | *Pilodus sp.*       | 3                           | Generalist   |
|                |              |        |         | *Liomera cinctimanus* | 1                   | Generalist   |
|                |              |        | Palaeomonidae| *Coralliocaris* | 7                           | Generalist   |
|                |              |        |         | *Harpiliopsis sp.* | 7                           | Generalist   |
|                |              |        |         | *Unknown*           | 62                          | Generalist   |
|                |              |        |         | *Jocaste sp.*       | 5                           | Generalist   |
|                |              |        | Paguridae| *Paguris sp.*       | 1                           | Generalist   |
|                |              |        |         | *Unknown*           | 1                           | Generalist   |
|                |              |        | Majiidae| *Menathius sp.*     | 2                           | Generalist   |
|                |              |        | Epialtidae| *Tiarinia sp.*      | 4                           | Generalist   |
|                |              |        | Diogenidae| *Calcinus sp.*      | 9                           | Generalist   |
|                |              |        | Domeciidae| *Domecia hispida*   | 12                          | Generalist   |
|                |              |        |         | *Domecia*           | 2                           | Generalist   |
| Tanaidacea     |              |        |         | Unknown             | 1                           | Generalist   |
| Amphipoda      |              |        |         | *Amphipoda*         | 3                           | Generalist   |
| Echinodermata  |              |        |         | *Ophiuroids*        | 15                          | Generalist   |
|                | Echinoida    |        |         | *Ophiocoma erinaceus* | 5                   | Generalist   |
|                | Bivalvia     |        |         | *Ophiocoma sp.*     | 3                           | Generalist   |
|                | Mollusca     |        |         | *Ophiactis sp.*     | 5                           | Generalist   |
|                | Camarodonta  |        |         | *Echinometra sp.*   | 1                           | Generalist   |
|                | Pectinida    |        |         | *Chlamys sp.*       | 1                           | Generalist   |
|                | Conidae      |        |         | *Conus sp.*         | 1                           | Generalist   |
|                | Neogastropoda|        |         | Unknown             | 2                           | Generalist   |
|                | Buccinidae   |        |         |                    |                             |              |
None of the host characteristics were a good predictor of epifaunal taxon richness and abundance (Table 3). There was also no clear relationship between epifaunal communities and colony size (Fig. S1).

There was a significant shift in community composition of epifaunal assemblages with different degrees of background partial mortality (PERMANOVA 999 permutations, $F_{1/33} = 21.9, p = 0.001$; Fig. 3). While obligate live-coral associated taxa, such as *Trapezia* and *Alpheus* (*Huber & Coles, 1986; Vytopil & Willis, 2001; Stella, Jones & Pratchett, 2010; Stella et al., 2011*) and more generalist Decapoda taxa (*Vytopil & Willis, 2001; Stella, Jones & Pratchett, 2010; Stella et al., 2011*) were all more abundant in colonies with no partial mortality (Fig. S2), there was not a statistically significant relationship (Fig. S2).

The rarefaction curves indicated a possible underestimation of taxon richness (e.g., the species accumulation curves using corals as samples did not saturate to the regional richness) (Fig. S3). Consequently, an increase in the sample size (e.g., number of coral colonies sampled) may result in an increase in taxon richness (*Sgarbi & Melo, 2018*).
DISCUSSION

This study documented a highly diverse and abundant invertebrate community associated with *Pocillopora* spp. commonly found in the back reef of Moorea. Several microhabitat characteristics and one external environmental factor were tested for their influence on invertebrate diversity and abundance. However, epifaunal assemblages associated with *Pocillopora* spp. were consistent and minimally affected by differences in host characteristics and flow regime. These findings highlighted the importance of total habitat availability (e.g., availability of live coral colonies). Abundance and local distribution of invertebrates have been shown to positively correlate with habitat availability in the Great Barrier Reef (*Stella et al.*, 2011). The complex relationships between coral-dwellers and corals will ultimately determine consequences of habitat loss on invertebrate persistence (*Enochs*, 2012; *Enochs & Manzello*, 2012).

The most abundant taxa were the decapod crustaceans (and specifically *Trapezia* crabs), which is consistent with other studies (*Vytopil & Willis*, 2001; *Stewart et al.*, 2006; *Pisapia et al.*, 2020).

![Figure 2](https://doi.org/10.7717/peerj.9364/fig-2) Hourly values of flow speed (m/s) at the upstream mooring (blue line) and the downstream mooring (red line) from the 11th to the 17th of January 2018.

Full-size [DOI: 10.7717/peerj.9364/fig-2](https://doi.org/10.7717/peerj.9364/fig-2)
Stella, Jones & Pratchett, 2010; Stella et al., 2011; Head et al., 2015). Stewart et al. (2006) reported that 95% of individuals in Pocillopora colonies were from the genus Trapezia. These crabs are also beneficial to the host coral, providing defense from predators such as crown-of-thorns starfish (Glynn, 1980; Pratchett, 2001).

The levels of background partial mortality observed here were well within the range of Pacific reefs in absence of major disturbances, such as the Indian Ocean and Australia’s Great Barrier Reef (Pisapia et al., 2015; Pisapia, Anderson & Pratchett, 2016). Previous findings indicated that partial mortality sustain a diverse range of epifaunal assemblages (Enochs & Hockensmith, 2008; Enoch, 2012; Enoch & Manzello, 2012). However, the percentage of tissue loss in the colonies sampled in this study only ranged between 0% and 15% (Table 2), compared 0–100% reported in Leray et al. (2012). This limited range in tissue loss may explain the lack of effect of tissue loss on epifaunal assemblages.

Different levels of partial mortality corresponded to higher abundance of obligate decapods such as Trapezia crabs. However, there was not a statistically significant relationship between abundance of obligate and mutualist Decapoda taxa and partial mortality. Previous studies documented a higher abundance specifically of more obligate taxa such as alpheids and trapeziids in colonies with no partial mortality (Stella, Munday & Jones, 2011; Stella et al., 2011; Leray et al., 2012). Alpheids and trapeziids strongly rely on live corals, have highly specific patterns of coral use (Vytopil & Willis, 2001; Stella, Jones & Pratchett, 2010) and as specialized taxa, they strongly depend on live tissue and are less able to cope with fluctuations in resource availability (Townsend, Begon & Harper, 2003). Xanthids and other generalist decapods were also abundant in colonies with no partial mortality; however, they opportunistically inhabit live coral colonies, and may

| Table 3 Summary output of the Generalized Linear Mixed Models (GLMM) for epifaunal abundance and taxon richness. Transect was a random variable. Due to the low replicate number, variation explained by the random effect and the standard deviation equaled to zero or was very low in some models. The dfs were 31. One colony was removed from all analyses. |
|--------------------------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Epifaunal abundance                              | Estimate        | Standard error  | z-Value         | Pr              | Standard deviation (random effect) |
| Surface area                                     | 0.003           | 0.001           | 1.05            | 0.29            | 1.88 e−06        |
| Partial mortality                                | 0.01            | 0.03            | 0.40            | 0.68            | 0.06             |
| Colony height                                    | 0.02            | 0.32            | 0.43            | 0.65            | 0                |
| Space between branches                           | 0.03            | 0.42            | 0.07            | 0.93            | 0.07             |
| Penetration depth                                | 0.02            | 0.07            | 0.30            | 0.75            | 0.07             |
| Flow                                             | 0.02            | 0.22            | 0.12            | 0.89            | 0.07             |
| Taxon richness                                   | Estimate        | Standard error  | z-Value         | Pr              | Standard deviation (random effect) |
| Surface area                                     | −0.0003         | <0.001          | −0.41           | 0.67            | 0.12             |
| Partial mortality                                | 0.03            | 0.02            | 1.70            | 0.08            | 0.16             |
| Colony height                                    | 0.01            | 0.01            | 0.89            | 0.37            | 0.11             |
| Space between branches                           | −0.008          | 0.24            | −0.03           | 0.91            | 0.16             |
| Penetration depth                                | 0.05            | 0.05            | 0.99            | 0.32            | 0.16             |
| Flow                                             | −0.10           | 0.14            | −0.71           | 0.47            | 0.16             |

Stella, Jones & Pratchett, 2010; Stella et al., 2011; Head et al., 2015). Stewart et al. (2006) reported that 95% of individuals in Pocillopora colonies were from the genus Trapezia. These crabs are also beneficial to the host coral, providing defense from predators such as crown-of-thorns starfish (Glynn, 1980; Pratchett, 2001).

The levels of background partial mortality observed here were well within the range of Pacific reefs in absence of major disturbances, such as the Indian Ocean and Australia’s Great Barrier Reef (Pisapia et al., 2015; Pisapia, Anderson & Pratchett, 2016). Previous findings indicated that partial mortality sustain a diverse range of epifaunal assemblages (Enochs & Hockensmith, 2008; Enoch, 2012; Enoch & Manzello, 2012). However, the percentage of tissue loss in the colonies sampled in this study only ranged between 0% and 15% (Table 2), compared 0–100% reported in Leray et al. (2012). This limited range in tissue loss may explain the lack of effect of tissue loss on epifaunal assemblages.

Different levels of partial mortality corresponded to higher abundance of obligate decapods such as Trapezia crabs. However, there was not a statistically significant relationship between abundance of obligate and mutualist Decapoda taxa and partial mortality. Previous studies documented a higher abundance specifically of more obligate taxa such as alpheids and trapeziids in colonies with no partial mortality (Stella, Munday & Jones, 2011; Stella et al., 2011; Leray et al., 2012). Alpheids and trapeziids strongly rely on live corals, have highly specific patterns of coral use (Vytopil & Willis, 2001; Stella, Jones & Pratchett, 2010) and as specialized taxa, they strongly depend on live tissue and are less able to cope with fluctuations in resource availability (Townsend, Begon & Harper, 2003). Xanthids and other generalist decapods were also abundant in colonies with no partial mortality; however, they opportunistically inhabit live coral colonies, and may
not be fundamentally dependent upon abundant live coral for their local persistence (Stella, Jones & Pratchett, 2010; Stella et al., 2011). Since obligate coral-dwellers have also been observed in dead colonies (Stella et al., 2011; Head et al., 2015), it is possible that they temporarily move between live and dead colonies, particularly as juveniles, in search of optimal habitat. Importantly, even though dead branches offered sub-optimal habitats, survivorship of obligate coral-dwelling invertebrates will ultimately depend upon availability of live coral tissue (Stella, Jones & Pratchett, 2010; Stella et al., 2011).

Flow at upstream and downstream was not good predictors of abundance and composition of epifaunal invertebrate assemblages on Moorea back reefs. It is possible that at the time of the study differences in flow regime from shore to the reef crest were minimal relative to other times of the year due to high wave-driven swells at the time of the

**Figure 3** nMDS visually representing PERMANOVA output. PERMANOVA investigated shifts in community composition of Decapoda with varying levels of background partial morality. The nMDS was based on a distance matrix using the counts of each Decapoda taxa in each coral colony. Size of the dots refers to varying percentages of background partial morality.
study. During the austral summer, flow on the reef flat is generated by long periods of swell breaking on the reef crest (Hench, Leichter & Monismith, 2008). Even though most of the energy is dissipated when the waves break on the crest, flow speed may still be high across the back reef as observed here (Hench, Leichter & Monismith, 2008; Hench & Rosman, 2013). Previous studies have quantified the importance of physical drivers such as flow, water movement and wave height in driving abundance and diversity of coral assemblages (Gove et al., 2015) and associated epifaunal communities (Counsell et al., 2018).

Small and large coral colonies of Pocilloporids are functionally dissimilar (Edmunds & Burgess, 2016) and this may reflect on diversity and persistence of invertebrate assemblages. While colony size is an important driver of abundance and diversity of coral-dwelling invertebrates (Head et al., 2015; Counsell et al., 2018), findings from the present study indicate that colony size was not related to abundance and taxon richness of these invertebrates. It is possible that the range of host sizes found in this study was relatively small compared to other studies thus explaining a lack of relationships between colony size and epifaunal abundance and taxon richness. Colony size sampled here ranged from 136 to 510.7 cm², the average colony was 16.9 ± 0.5 cm versus 21.1 ± 9.2 cm sampled by Counsell et al. (2018). Within-colony heterogeneity may vary with different colony sizes, for example, larger colonies may have a great variety of light microenvironments across their surface which may or may not be favorable for epifaunal assemblages (Kaniewska et al., 2011; Edmunds & Burgess, 2016). The reduced heterogeneity associated with the small range of host size measured here may explain why there was a weak or no effect of colony size on abundance and taxon richness of epifaunal invertebrates. The correlation between epifaunal abundance and size of dead colonies is also relatively low suggesting that these invertebrates may also not scale proportionally with size of dead colonies (Head et al., 2015).

CONCLUSIONS
This study investigated whether flow regime and host characteristics may affect density and taxon richness of epifaunal assemblages associated with Pocilloporids on a Moorea reef flat. We showed that, for Moorea back reef, epifaunal assemblages associated with Pocillopora spp. were consistent and minimally affected by differences in host characteristics and flow regime. The consistency in abundance and taxon richness among colonies (regardless of habitat characteristics) highlighted the importance of total habitat availability. On Moorea back reefs, it is critical to ensure presence of branching corals to support abundance and taxon richness of epifaunal communities.

ACKNOWLEDGEMENTS
Thank you to S. Doo, S. Ginther for assistance in the field, to P.J. Edmunds for comments on the manuscript and to Richard B. Gump South Pacific Research for logistic help. Thank you to the two anonymous reviewers who greatly improved the manuscript. Thank you also to Hong Kong Branch of Southern Marine Science and Engineering.
This is contribution number 308 of the CSUN Marine Biology Program and a contribution from the MCR-LTER.

**ADDITIONAL INFORMATION AND DECLARATIONS**

**Funding**
This study was funded by the Moorea Coral Reef (MCR) Long Term Ecological Research. Funding was provided by a grant from the National Science Foundation (OCE 14-15268). This research was funded in part by the National Science Foundation Award #1924281 to NJS. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Grant Disclosures**
The following grant information was disclosed by the authors:
Moorea Coral Reef (MCR) Long Term Ecological Research.
National Science Foundation: OCE 14-15268 and OCE 19-24281.

**Competing Interests**
The authors declare that they have no competing interests. Robert Carpenter funded the project but has no competing interests.

**Author Contributions**
- Chiara Pisapia conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Jessica Stella performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Nyssa J. Silbiger performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Robert Carpenter performed the experiments, authored or reviewed drafts of the paper, funded the project, and approved the final draft.

**Field Study Permissions**
The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):
Research was completed under permits issued by the Haut-commissariat de la Republique en Polynesie Francaise (DRRT) (Protocole d’Accueil, 2018).

**Data Availability**
The following information was supplied regarding data availability:
The raw data and code used in the analyses are available in the [Supplemental Files](http://dx.doi.org/10.7717/peerj.9364#supplemental-information).

**Supplemental Information**
Supplemental information for this article can be found online at [http://dx.doi.org/10.7717/peerj.9364#supplemental-information](http://dx.doi.org/10.7717/peerj.9364#supplemental-information).
REFERENCES
Abele LG, Patton WK. 1976. The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography* 3(1):35–47 DOI 10.2307/3038097.

Britayev TA, Spiridonov VA, Deart YV, El-Sherbiny M. 2017. Biodiversity of the community associated with Pocillopora verrucosa (Scleractinia: Pocillogoporidae) in the Red Sea. *Marine Biodiversity* 47(4):1093–1109 DOI 10.1007/s12526-017-0759-3.

Carvalho S, Aylagas E, Villalobos R, Kattan Y, Berumen M, Pearman JK. 2019. Beyond the visual: using metabarcoding to characterize the hidden reef cryptobiome. *Proceedings of the Royal Society B: Biological Sciences* 286(1896):20182697 DOI 10.1098/rspb.2018.2697.

Castro P. 1978. Movements between coral colonies in Trapezia ferruginea (Crustacea: Brachyura), an obligate symbiont of scleractinian corals. *Marine Biology* 46(3):237–245 DOI 10.1007/BF00390685.

Castro P. 1988. Animal symbioses in coral reef communities: a review. *Symbiosis* 5:161–184.

Castro P, Ng PK, Ahyong ST. 2004. Phylogeny and systematics of the Trapeziidae Miers, 1886 (Crustacea: Brachyura), with the description of a new family. *Zootaxa* 643(1):1–70 DOI 10.11646/zootaxa.643.1.1.

Counsell CW, Donahue MJ, Edwards KF, Franklin EC, Hixon MA. 2018. Variation in coral-associated cryptofaunal communities across spatial scales and environmental gradients. *Coral Reefs* 37:827–840.

Cowen RK, Castro LR. 1994. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. *Bulletin of Marine Science* 54(1):228–244.

Depczynski M, Bellwood DR. 2005. Wave energy and spatial variability in community structure of small cryptic coral reef fishes. *Marine Ecology Progress Series* 303:283–293 DOI 10.3354/meps03283.

Edmunds PJ, Burgess SC. 2016. Size-dependent physiological responses of the branching coral *Pocillopora verrucosa* to elevated temperature and PCO2. *Journal of Experimental Biology* 219(24):3896–3906 DOI 10.1242/jeb.146381.

Edmunds PJ, Leichter JJ, Adjeroud M. 2010. Landscape-scale variation in coral recruitment in Moorea, French Polynesia. *Marine Ecology Progress Series* 414:75–89 DOI 10.3354/meps08728.

Edmunds PJ, Leichter JJ, Johnston EC, Tong EJ, Toonen RJ. 2016. Ecological and genetic variation in reef-building corals on four Society Islands. *Limnology and Oceanography* 61(2):543–557 DOI 10.1002/lno.10231.

Enochs IC. 2012. Motile cryptofauna associated with live and dead coral substrates: implications for coral mortality and framework erosion. *Marine Biology* 159(4):709–722 DOI 10.1007/s00227-011-1848-7.

Enochs IC, Hockensmith G. 2008. Effects of coral mortality on the community composition of cryptic metazoans associated with *Pocillopora damicornis*. In: *Proceedings of the 11th International Coral Reef Symposium*, Ft. Lauderdale, FL. Vol. 26. 1368–1372.

Enochs IC, Manzello DP. 2012. Responses of cryptofaunal species richness and trophic potential to coral reef habitat degradation. *Diversity* 4(1):94–104 DOI 10.3390/d4010094.

Feary DA, Almany GR, Jones GP, McCormick MI. 2007. Coral degradation and the structure of tropical reef fish communities. *Marine Ecology Progress Series* 333:243–248 DOI 10.3354/meps333243.

Glynn PW. 1980. Defense by symbiotic crustacea of host corals elicited by chemical cues from predator. *Oecologia* 47(3):287–290 DOI 10.1007/BF00398518.
Glynn PW. 1983. Increased survivorship on corals harbouring crustacean symbionts. *Marine Biology Letters* 4:105–111.

Glynn PW. 1987. Some ecological consequences of coral-crustacean guard mutualisms in the Indian and Pacific Oceans. *Symbiosis* 4:301–323.

Glynn PW, Enochs IC. 2011. *Invertebrates and their roles in coral reef ecosystems, coral reefs: an ecosystem in transition*. Berlin: Springer, 273–325.

Gotelli NJ, Abele LG. 1983. Community patterns of coral-associated decapods. *Marine Ecology Progress Series* 13:131–139 DOI 10.3354/meps013131.

Gove JM, Williams GJ, McManus MA, Clark SJ, Ehses JS, Wedding LM. 2015. Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. *Marine Ecology Progress Series* 522:33–48 DOI 10.3354/meps11118.

Graham NAJ, Nash KL. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32(2):315–326 DOI 10.1007/s00338-012-0984-y.

Head CE, Bonsall MB, Koldewey H, Pratchett MS, Speight M, Rogers AD. 2015. High prevalence of obligate coral-dwelling decapods on dead corals in the Chagos Archipelago, central Indian Ocean. *Coral Reefs* 34(3):905–915 DOI 10.1007/s00338-015-1307-x.

Hench JL, Leichter JJ, Monismith SG. 2008. Episodic circulation and exchange in a wave-driven coral reef and lagoon system. *Limnology and Oceanography* 53(6):2681–2694 DOI 10.4319/lo.2008.53.6.2681.

Hench JL, Rosman JH. 2013. Observations of spatial flow patterns at the coral colony scale on a shallow reef flat. *Journal of Geophysical Research: Oceans* 118(3):1142–1156 DOI 10.1002/jgrc.20105.

Heron SF, Eakin CM, Douville F, Anderson KL, Day JC, Geiger E, Hoegh-Guldberg O, Van Hooidonk R, Hughes T, Marshall P. 2017. Impacts of climate change on World Heritage coral reefs: a first global scientific assessment, Report. UNESCO World Heritage Centre, Paris.

Holbrook SJ, Schmitt RJ, Brooks AJ. 2011. Indirect effects of species interactions on habitat provisioning. *Oecologia* 166(3):739–749 DOI 10.1007/s00442-011-1912-5.

Huber ME, Coles SL. 1986. Resource utilization and competition among the five Hawaiian species of Trapezia (Crustacea, Brachyura). *Marine Ecology Progress Series* 30(1):21–31.

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-Y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK. 2017. Global warming and recurrent mass bleaching of corals. *Nature* 543(7645):373–377 DOI 10.1038/nature21707.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G. 2018. Global warming transforms coral reef assemblages. *Nature* 1(7702):492–496 DOI 10.1038/s41586-018-0041-2.

Hughes TP, Kerry JT, Connolly SR, Baird AH, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Jacobson M, Liu G, Pratchett MS, Skirving W, Torda G. 2019. Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change* 9(1):40–43 DOI 10.1038/s41558-018-0351-2.
Johnston EC, Forsman ZH, Flot J-F, Schmidt-Roach S, Pinzón JH, Knapp IS, Toonen RJ. 2017. A genomic glance through the fog of plasticity and diversification in Pocillopora. Scientific Reports 7(1):5991 DOI 10.1038/s41598-017-06085-3.

Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101(21):8251–8253 DOI 10.1073/pnas.0401277101.

Julian Caley M, Buckley KA, Jones GP. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. Ecology 82(12):3435–3448 DOI 10.1890/0012-9658(2001)082[3435:SEEOHF]2.0.CO;2.

Kaandorp JA. 1999. Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. Marine Biology 134(2):295–306 DOI 10.1007/s002270050547.

Kane CN, Brooks AJ, Holbrook SJ, Schmitt RJ. 2009. The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. Environmental Biology of Fishes 84(1):1–10 DOI 10.1007/s10641-008-9577-z.

Kaniewska P, Magnusson SH, Anthony KR, Reef R, Kühl M, Hoegh-Guldberg O. 2011. Importance of macro-versus microstructure in modulating light levels inside coral colonies 1. Journal of Phycology 47(4):846–860 DOI 10.1111/j.1529-8817.2011.01021.x.

Klumpp DW, McKinnon AD, Mundy CN. 2017. Mechanical vulnerability explains size-dependent mortality of reef corals. Ecology Letters 17(8):1008–1015 DOI 10.1111/ele.12306.

Leray M, Béraud M, Anker A, Chancerelle Y, Mills SC. 2012. Acanthaster planci outbreak: decline in coral health, coral size structure modification and consequences for obligate decapod assemblages. PLOS ONE 7(4):e35456 DOI 10.1371/journal.pone.0035456.

Linares C, Pratchett MS, Coker DJ. 2011. Recolonisation of Acropora hyacinthus following climate-induced coral bleaching on the Great Barrier Reef. Marine Ecology Progress Series 438:97–104 DOI 10.3354/meps09272.

López-Pérez A, Granja-Fernández R, Benítez-Villalobos F, Jiménez-Antonio O. 2017. Pocillopora damicornis-associated echinoderm fauna: richness and community structure across the southern Mexican Pacific. Marine Biodiversity 47(2):481–490 DOI 10.1007/s12526-016-0489-y.

Madin JS, Baird AH, Dornelas M, Connolly SR. 2014. Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444(7118):477–480 DOI 10.1038/nature05328.

Madin JS, Dell AI, Madin EMP, Nash MC. 2013. Spatial variation in mechanical properties of coral reef substrate and implications for coral colony integrity. Coral Reefs 32(1):173–179 DOI 10.1007/s00338-012-0958-0.

McClanahan TR. 1994. Coral-eating snail Drupella cornus population increases in Kenyan coral reef lagoons. Marine Ecology Progress Series 115:131–137.

McKeon CS, Moore JM. 2014. Species and size diversity in protective services offered by coral guard-crabs. PeerJ 2(3):e574 DOI 10.7717/peerj.574.

McKeon CS, Stier AC, McIlroy SE, Bolker BM. 2012. Multiple defender effects: synergistic coral defense by mutualist crustaceans. Oecologia 169(4):1095–1103 DOI 10.1007/s00442-012-2275-2.
Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2013. Package Vegan: Community Ecology Package Version 2. Available at http://CRAN.Rproject.org/package=vegan.

Pisapia C, Anderson K, Pratchett MS. 2014. Intraspecific variation in physiological condition of reef-building corals associated with differential levels of chronic disturbance. PLOS ONE 9(3):e91529 DOI 10.1371/journal.pone.0091529.

Pisapia C, Anderson KD, Pratchett MS. 2016. Temporal consistency in background mortality of four dominant coral taxa along Australia’s Great Barrier Reef. Coral Reefs 35(3):839–849 DOI 10.1007/s00338-016-1421-4.

Pisapia C, Sweet M, Sweatman H, Pratchett MS. 2015. Geographically conserved rates of background mortality among common reef-building corals in Lhaviyani Atoll, Maldives, versus northern Great Barrier Reef. Australia Marine Biology 162(8):1579–1586 DOI 10.1007/s00227-015-2694-9.

Pratchett MS. 2001. Influence of coral symbionts on feeding preferences of crown-of-thorns starfish Acanthaster planci in the western Pacific. Marine Ecology Progress Series 214:111–119 DOI 10.3354/meps214111.

Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NA. 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity 3(3):424–452 DOI 10.3390/d3030424.

Pratchett MS, Wilson SK, Berumen ML, McCormick MI. 2004. Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23(3):352–356 DOI 10.1007/s00338-004-0394-x.

Preston EM. 1973. A computer simulation of competition among five sympatric congeneric species of xanthid crabs. Ecology 54(3):469–483 DOI 10.2307/1935333.

Rouzé H, Leray M, Magalon H, Penin L, Gélin P, Knowlton N, Fauvelot C. 2017. Molecular characterization reveals the complexity of previously overlooked coral-exosymbiont interactions and the implications for coral-guild ecology. Scientific Reports 7(1):1–16 DOI 10.1038/s41598-016-0028-x.

Sale PF. 1991. Habitat structure and recruitment in coral reef fishes. In: Bell SS, McCoy ED, Mushinsky HR, eds. Habitat Structure, Population and Community Biology Series. Vol. 8. Dordrecht: Springer, 197–210.

Sgarbi LF, Melo AS. 2018. You don’t belong here: explaining the excess of rare species in terms of habitat, space and time. Oikos 127(4):497–506 DOI 10.1111/oik.04855.

Shima JS, Osenberg CW, Stier AC. 2010. The vermetid gastropod Dendropoma maximum reduces coral growth and survival. Biology Letters 6(6):815–818 DOI 10.1098/rsbl.2010.0291.

Simberloff D. 1972. Properties of the rarefaction diversity measurement. American Naturalist 106(949):414–418 DOI 10.1086/282781.

Stella JS, Jones GP, Pratchett MS. 2010. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. Coral Reefs 29(4):957–973 DOI 10.1007/s00338-010-0648-8.

Stella JS, Munday PL, Jones GP. 2011. Effects of coral bleaching on the obligate coral-dwelling crab Trapezia cymodoce. Coral Reefs 30(3):719–727 DOI 10.1007/s00338-011-0748-0.

Stella JS, Munday PL, Walker SPW, Pratchett MS, Jones GP. 2014. From cooperation to combat: adverse effect of thermal stress in a symbiotic coral-crustacean community. Oecologia 174(4):1187–1195 DOI 10.1007/s00442-013-2858-6.

Stella JS, Pratchett MS, Hutchings PA, Jones GP. 2011. Diversity, importance and vulnerability of coral-associated invertebrates. Oceanography and Marine Biology: An Annual Review 49:43–116.
Stewart HL, Holbrook SJ, Schmitt RJ, Brooks AJ. 2006. Symbiotic crabs maintain coral health by clearing sediments. Coral Reefs 25(4):609–615 DOI 10.1007/s00338-006-0132-7.

Stier AC, Gil MA, McKeon CS, Lemer S, Leray M, Mills SC, Osenberg CW. 2012. Housekeeping mutualisms: do more symbionts facilitate host performance? PLOS ONE 7(4):e32079.

Stier AC, McKeon CS, Osenberg CW, Shima JS. 2010. Guard crabs alleviate deleterious effects of vermetid snails on a branching coral. Coral Reefs 29(4):1019–1022 DOI 10.1007/s00338-010-0663-9.

Stimson J. 1990. Stimulation of fat-body production in the polyps of the coral Pocillopora damicornis by the presence of mutualistic crabs of the genus Trapezia. Marine Biology 106(2):211–218 DOI 10.1007/BF01314802.

Team RC, Pinheiro J, Bates D, DebRoy S, Sarkar D. 2015. nlme: linear and nonlinear mixed effects models. R Package Version 3.1. Available at https://CRAN.R-project.org/package=nlme.

Townsend CR, Begon M, Harper JL. 2003. Essentials of ecology. Hoboken: Blackwell Science.

Veron JEN. 2000. Corals of the World. Townsville MC: Australian Institute of Marine Science.

Vytopil E, Willis B. 2001. Epifaunal community structure in Acropora spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. Coral Reefs 20(3):281–288 DOI 10.1007/s003380100172.

Wakeford M, Done TJ, Johnson CR. 2008. Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27(1):1–13 DOI 10.1007/s00338-007-0284-0.

West JM, Salm RV. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conservation Biology 17(4):956–967 DOI 10.1046/j.1523-1739.2003.02055.x.

Willis BL, Oliver JK. 1990. Direct tracking of coral larvae: implications for dispersal studies of planktonic larvae in topographically complex environments. Ophelia 32(1–2):145–162 DOI 10.1080/00785236.1990.10422029.

Wilson SK, Graham NAJ, Polunin NVC. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151(3):1069–1076 DOI 10.1007/s00227-006-0538-3.