

Predators alter community organization of coral reef cryptoфаuna and reduce abundance of coral mutualists

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Abstract Coral reefs are the most diverse marine systems in the world, yet our understanding of the processes that maintain such extraordinary diversity remains limited and taxonomically biased toward the most conspicuous species. Cryptoфаuna that live deeply embedded within the interstitial spaces of coral reefs make up the majority of reef diversity, and many of these species provide important protective services to their coral hosts. However, we know very little about the processes governing the diversity and

composition of these less conspicuous but functionally important species. Here, we experimentally quantify the role of predation in driving the community organization of small fishes and decapods that live embedded within *Pocillopora eydouxi*, a structurally complex, reef-building coral found widely across the Indo-Pacific. We use surveys to describe the natural distribution of predators, and then, factorially manipulate two focal predator species to quantify the independent and combined effects of predator density and identity on *P. eydouxi*-dwelling cryptoфаuna. Predators reduced abundance (34 %), species richness (20 %), and modified species composition. Rarefaction revealed that observed reductions in species richness were primarily driven by changes in abundance. Additionally, the two predator species uniquely affected the beta diversity and composition of the prey assemblage. Predators reduced the abundance and modified the composition of a number of mutualist fishes and decapods, whose benefit to the coral is known to be both diversity- and density-dependent. We predict that the density and identity of predators present within *P. eydouxi* may substantially alter coral performance in the face of an increased frequency and intensity of natural and anthropogenic stressors.

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Introduction

An extraordinary diversity and biomass of invertebrates live inconspicuously embedded within the matrix of coral reefs (Grassle 1973; Brock and Brock 1977; Klumpp et al. 1988; Stella et al. 2011; Enochs and Manzello 2012). For

example, a single coral colony of *Pocillopora damicornis* can house more than 5000 crustaceans per square meter (Grassle 1973). Yet, we know relatively little about the ecological processes that contribute to the diversity, dynamics, and persistence of these more cryptic reef communities. Studies in temperate systems point to predation as a key processes promoting marine community dynamics (i.e., Keystone Predation, Paine 1966), and some evidence suggests an increase in the strength of predation at lower latitudes may contribute to high tropical diversity (Pianka 1966; Schemske et al. 2009; Freestone et al. 2010). However, empirical evidence supporting the positive effects of predators on tropical diversity is mixed. For example, predators can reduce coral and fish diversity by disproportionately consuming rare prey (Chesher 1969; Glynn 1976; Almany and Webster 2004). In contrast, predation can also increase diversity. For example, Stier et al. (2013b) showed that predatory fish can increase prey fish diversity by promoting priority effects (Stier et al. 2013b). Additionally, Marhaver et al. (2012) showed that species-specific microbes promote coral diversity through negative frequency-dependent predation on coral recruits (i.e., a Janzen-Connell effect Janzen 1970; Connell 1971). However, studies examining the effects of predation on tropical marine diversity have been taxonomically biased toward conspicuous and economically valuable corals and fishes. These groups make up only a fraction of tropical marine biodiversity, which is heavily dominated by more cryptic invertebrate species (Stella et al. 2011). Indeed, a survey quantifying the taxonomic breadth of species studied in kelp forests, mangroves, seagrasses, and coral reefs found that species studied in coral reefs have the lowest taxonomic breadth across these four systems (Fisher et al. 2011). Such poor taxonomic coverage in studies of coral reefs restricts our understanding of a major component of tropical biodiversity and may therefore limit our appreciation of the drivers of ecosystem function. In this study, we focus on decapod crustaceans and small-bodied fish that live within corals of the South Pacific. Decapod remains litter the reef and are commonly found in fish stomach dissections (Kulbicki et al. 2005; Enochs and Manzello 2012; Kramer et al. 2012; Leray et al. 2012a, b, 2013), suggesting that crustaceans are major nodes in a vibrant web of tropical marine trophic interactions and that predation may be a key process driving decapod dynamics.

In addition to being a diverse yet underrepresented group in the ecological literature on tropical marine biodiversity, tropical decapods are also relevant, because a subset of decapod species play a crucial role in the resilience of their coral host. Certain species of *Trapezia* and *Alpheus* promote coral growth and survival by alleviating stressors such as seastar predation (Glynn 1983; Pratchett 2001), sedimentation (Stewart et al. 2006), and mucus-

producing snails (Stier et al. 2010). Furthermore, these decapods often co-occur with damselfishes that indirectly promote coral growth through oxygenation (Goldshmid et al. 2004) and nutrient subsidy (Meyer and Schultz 1985; Liberman et al. 1995; Holbrook et al. 2008, 2011). The beneficial effects of mutualists on their host are often dependent on mutualist density and identity (Holland et al. 2002); previous studies show increased coral performance with increased density of and diversity of decapods (McKeon et al. 2012; Stier et al. 2012) and increased density of damselfish (Holbrook et al. 2008). The benefits each mutualist species provides are also highly dependent upon the fish and decapod identity (Holbrook et al. 2011; McKeon et al. 2012; Stier et al. 2012). Therefore, if predation affects the density, diversity, and composition of coral mutualists or if different predator species differentially affect certain mutualist species, then, the performance and resilience of the coral host may be fundamentally altered by predator presence, density, or identity (Knight et al. 2006; Romero et al. 2011).

Here, we quantify the effect of predation in driving the abundance, diversity, and composition of decapods and fishes that live cryptically embedded between the branches of *P. eydouxi*, a dominant, structurally complex, reef-building coral distributed widely across the South Pacific. Our study combines (1) a survey to explore the spatial distribution of our two focal predators: the coral croucher (Scorpaenidae; *Caracanthus maculatus*) and the flame hawkfish (Cirrhitidae; *Neocirrhitus armatus*) and (2) a recruitment experiment to examine the independent and combined effects of each predator species on *P. eydouxi*-associated communities. We show that both flame hawkfish and coral crouchers substantially alter fish and crustacean community organization, and we discuss the implications of shifts in community structure for coral growth and resilience.

Materials and methods

Study site and species

We conducted our study in the lagoon of Opunohu bay on the North shore of Moorea, French Polynesia (17°30'S, 149°50'W). Coral reefs are highly diverse ecosystems, and tens to hundreds of species can co-occur on a single coral colony (Grassle 1973; Lassig 1977; Castro 1988; Leray et al. 2012b). One such coral host is the coral genus *Pocillopora*, which is an important reef-building coral distributed widely across the Indo-Pacific. Multiple trophic levels of fishes and invertebrates live among the branches of *Pocillopora*, which provides structural habitat for several co-occurring carnivorous fishes and a wide diversity of

potential invertebrate prey (~80 % decapods, Odinetz 1983). We focused on the two most common predatory fishes that are strictly associated with pocilloporid corals and co-occur in coral heads at shallow depths: the flame hawkfish (*Neocirrhitus armatus*) and the coral croucher (*Caracanthus maculatus*) (Randall 2005). Both coral crouchers and flame hawkfish are ambush predators that restrict their movement to the inside of the coral host. Thus, both predators and prey share structural refuge from larger predators (a common phenomena in many predator–prey systems, Gotelli and Ellison 2006), causing predators to live in close proximity with a diversity of coral-associated decapod prey species. The two focal predators exhibit slight differences in microhabitat use; coral crouchers remain deep among the coral branches, while the flame hawkfish are more mobile. These two predators primarily comprised of crustaceans and also includes gastropods and fishes (morphological observations in gut contents; Randall 2005; Bacchet et al. 2006), DNA barcoding (Leray et al. 2013), and DNA metabarcoding of prey tissue remains (Leray M, pers comm).

Predator surveys

To describe natural variation in predator density, identity, and co-occurrence, we conducted a visual census of fish predators living among the branches of 93 haphazardly selected live *Pocillopora eydouxi* colonies on the fore reef between 6 and 10 m depth. Since adult predators occur on larger *P. eydouxi*, we focused on corals with a maximum diameter (l) and perpendicular diameter (w) ranging from 20 to 40 cm and height (h) ranging from 15 to 30 cm.

Experimental design

We executed a field experiment to quantify the response of the prey community to shifts in the density, identity, and co-occurrence of coral crouchers and flame hawkfish. We collected 60 dome-shaped *P. eydouxi* (size range, l × w × h: 25 × 25 × 15 to 35 × 35 × 20) from the fore reef and removed all decapod and fish species using a low concentration of anesthetic to minimize coral stress (0.02 % clove oil; Leray et al. 2012b). After invertebrate removal, we transplanted corals to a 6 × 10 array of cinder blocks spaced 8 m apart in a nearby sand flat within Opunohu lagoon. Immediately following coral deployment, we collected 20 solitary fish and 10 male–female pairs of each of the focal predator species from *P. eydouxi* colonies in a nearby lagoonal site using hand nets and anesthetic clove oil (10 %). After tagging each individual fish with a unique color combination of elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, USA) above and below the caudal peduncle, we measured and

randomly assigned fishes to six predator treatments ($n = 10$) (see Electronic Supplemental Material, ESM A for pictures of experimental set-up and predators). We used a combination of an additive and substitutive design: Control (no predator), 1 coral croucher, 2 coral crouchers, 1 flame hawkfish, 2 flame hawkfish, and 1 coral croucher + 1 flame hawkfish. For treatments with two predators of the same species, we retained the original pairing from collection because each of these species is often found in male–female pairs, and the placement of two males on a colony is impossible due to intense aggressive interactions. Predators were deployed from April to August for 126 days, and predator treatments were pressed to maintain initial predator densities. Over the course of the experiment, seven flame hawkfish and five coral crouchers migrated. We returned these fish to their original coral head. Five flame hawkfish and eight coral crouchers died or emigrated from the array and were replaced immediately following their noted disappearance during predator censuses conducted three times per week. At the end of the experiment, all macro-invertebrates were collected using clove oil, identified to the lowest possible taxonomic level, and counted.

Statistical analysis

To test the hypothesis that co-occurrence of coral crouchers and flame hawkfish in *P. eydouxi* is random, we generated 10,000 null distributions of the surveyed data by randomly assigning each of the observed 224 fish predators to 93 corals. We, then compared observed distributions of predator density and co-occurrence (presence/absence) to permuted distributions.

We quantified the abundance and diversity of fishes and decapods to measure the effect of the different predator treatments. For abundance, we pooled the total number of fishes and decapods together for a single analysis. For diversity, we partitioned effects of predators into within and between reef diversity (alpha and beta diversity, respectively). We examined two metrics for within-reef diversity. First, we assessed effects of predators on the mean number of species per individual *P. eydouxi* colony (hereafter species richness). Second, because predator treatments differed substantially in total prey abundance and shifts in abundance can cause corresponding shifts in diversity through sampling effects, we quantified rarefied within-reef diversity using individual-based rarefaction (i.e., alpha diversity adjusted for differences among reefs in number of individuals) (Gotelli and Colwell 2001). Although less studied, predators can affect beta diversity (i.e., the amount that prey diversity varies from reef to reef) by modifying community size, preferential prey consumption, or changing the strength of priority effects (Chase et al. 2009; Stier et al.

2013a). To assess how predator treatments affected beta diversity and composition, we calculated community distance matrices for the 60 coral heads. Differences in beta diversity can occur through shifts in species incidence (i.e., presence-absence) or through differences in species relative abundance. Additionally, differences in alpha diversity can also confound beta diversity estimates (Chase et al. 2011). We therefore examined communities using three distance metrics that emphasize shifts in species incidence (Jaccard index), shifts in species incidence adjusted for differences in alpha diversity (Raup-Crick index), and relative abundance (Manhattan index) (Anderson et al. 2011; Chase et al. 2011).

For each response variable, we conducted four planned orthogonal contrasts to assess the effects of coral couchers (CC) and flame hawkfish (FL) on the prey community: (1) the effect of predators: [Control] vs. [1 CC, 2 CC, 1 FL, 2 FL, 1 CC + 1 FL]; (2) the main effect of predator density: [1CC, 1FL] vs. [2CC, 2FL]; (3) the main effect of predator identity: [1 CC, 2 CC] vs. [1 FL, 2 FL]; and (4) the interaction between predator density and identity: [1 CC, 2 FL] vs. [2 CC, 1 FL]. One additional (non-orthogonal) contrast was made to determine whether mixed versus monospecific assemblages of predators had differential effects on prey abundance, diversity, and composition. We used a *t* test to compare monospecific and mixed treatments, which were contrasted at the same density: [2 CC, 2FL] vs. [1CC + 1FL].

We modeled abundance, richness, and rarefied richness using a general linear model with a Gaussian error distribution. We tested for differences in beta diversity and mean community composition using nonparametric multivariate permutation analogs of univariate Leven's test and ANOVA: PERMADISP (beta diversity: Anderson et al. 2006) and PERMANOVA (composition: Anderson 2001), respectively.

We examined beta diversity using the 10 most abundant species in the dataset (which accounted for 86 % of the total abundance) because rare species increase “stress” in distance calculations (Legendre and Legendre 1998). Note that results for beta diversity and community composition reported below were qualitatively identical whether or not rare species were included. We used the statistical programming environment R 3.0.0 for the computation of all statistics (R Development Core Team 2013) and the “Vegan” package (Oksanen et al. 2013) for community analysis and graphics.

Results

Our surveys showed that predatory fishes frequently co-occurred and were abundant on natural reefs. We found

coral couchers and flame hawkfish in 65 and 81 % of the 93 surveyed corals, respectively. Observed patterns of occurrence and co-occurrence (i.e., presence-absence) of the two predator species among the branches of *P. eydouxi* are no different than expected by chance (Fig. 1b). However, observed density distributions of predatory fishes differed from the expected density distribution estimated from randomizations. Coral croucher densities naturally varied from a single individual to a triplet, with a higher frequency of pairs and a lower frequency of singlets than expected by chance (Fig. 1a). Flame hawkfish, however, exhibited a greater range (1–5) of intra-specific density, and solitary individuals occurred more frequently than expected by chance (Fig. 1c). Both hawkfish and coral couchers have sophisticated mating systems. Facultative monogamy has been documented in studies of flame hawkfish (Donaldson 1989) and in studies of *Caracanthus unipinna*, a closely related congener of the focal coral croucher in this study (*Caracanthus maculatus*) (Wong et al. 2005). Such flexible mating systems likely contribute to the substantial variation in density of the two predators.

In our recruitment experiment, four reefs were consumed by the corallivorous seastar *Acanthaster planci* and were removed from all subsequent analyses, reducing the sample sizes for the 2CC treatment to 8 and the 1Fl and 1CC1Fl treatments to 9. A total of 5921 individuals from 73 species (54 decapods and 19 fishes) were sampled across the 56 experimental reefs after 18 weeks (ESM B). For decapods, 80.4 % of all individuals came from 4 families (Palaemonidae: 50.2 %, Trapeziidae: 10.9 %, Alpheidae: 10.5 %, Galatheidae: 8.8 %), and for fishes, 86 % of individuals were damselfish. Because of the large number of statistical tests present in the analysis, the main text focuses on statistically significant effects (i.e., $p < 0.05$), and ESM C provides the test statistics and p -values for all contrasts. Notably, at a density of two predators per coral, there was no difference in abundance, diversity, or composition between mixed and monospecific predator assemblages (ESM C); therefore we focus on the effects of the other contrasts below.

Predators reduced total abundance

The aggregate effect of predation on prey abundance was a 34 % reduction in abundance ($t_{54} = 2.98$, $p = 0.003$, Fig. 2a). However, doubling predator densities had opposing effects for each focal predator, which produced an interaction between predator density and identity ($t_{54} = 2.64$, $p = 0.008$). Two flame hawkfish decreased prey abundance by an additional 76 % relative to one flame hawkfish, while a doubling in coral croucher density led to a 19 % increase in prey abundance (Fig. 2a).

Fig. 1 Natural variation in density of **a** coral crouchers (CC) and **c** flame hawkfish (FL) from surveys of 93 naturally occurring *Pocillopora eydouxi*. Patterns of co-occurrence are also presented (**b**). Colored bars (CC: blue, FL: red, CC + FL: green) represent 95 % quantiles from 10,000 randomizations of observed distribution of predator co-occurrence

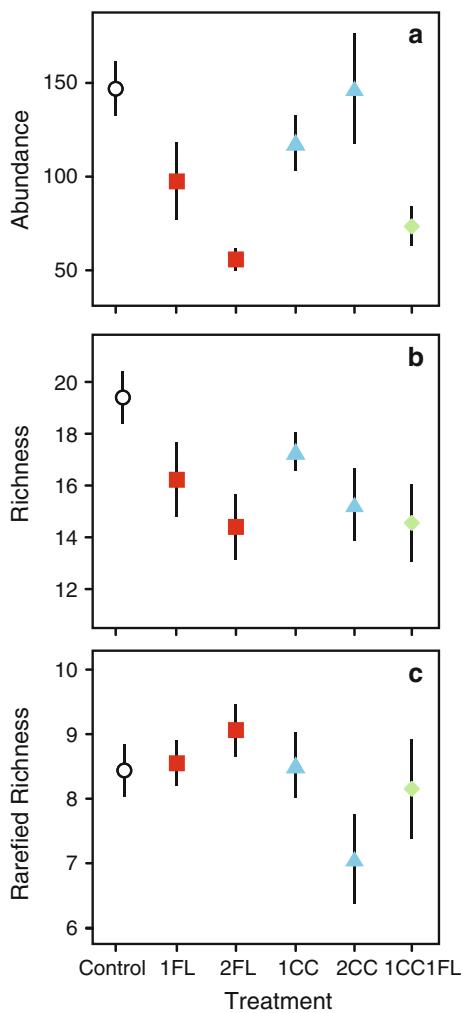
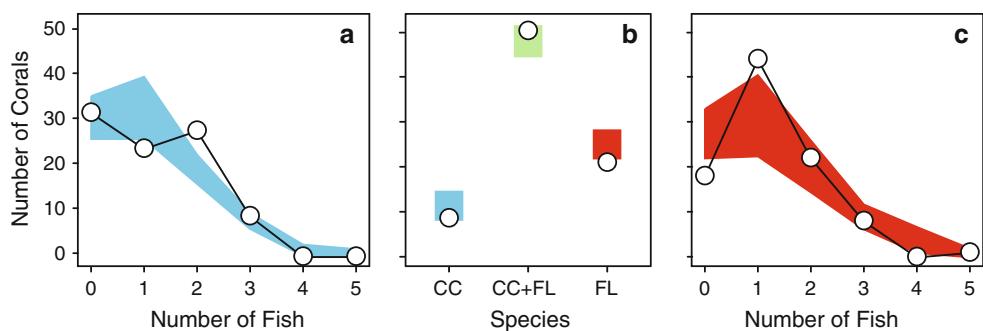


Fig. 2 Effect of predator treatments on total abundance **(a)** richness **(b)**, and rarefied richness (mean \pm 1 SE). Symbols and colors represent predator type (FL: Flame Hawkfish—red; CC: Coral Croucher—blue, mixed assemblage (1FL1CC)—green) and density (one predator—square, 2 predators, triangle, mixed assemblage—diamond)

Predators reduced species richness

On average, predators reduced species richness by 20 % (Fig. 2b) ($t_{54} = 2.95$, $p = 0.005$); however, there was no effect of predators when richness estimates were adjusted

for differences in abundance using rarefaction (Fig. 2c) ($t_{54} = 0.30$, $p = 0.77$), suggesting reduction in prey diversity in the presence of predators was driven by reductions in prey abundance (i.e., a “sampling” effect). There was no significant interaction or main effects of predator density and identity for richness or rarefied richness (ESM C).

Experimental effect of predators on beta diversity

Predator density and identity each significantly affected the beta diversity based on species incidence (identity: Fig. 3, $F^{\pi} = 11.97$; $p = 0.003$; density $F^{\pi} = 4.12$; $p = 0.01$). Reefs with flame hawkfish had 70 % higher beta diversity than those with coral crouchers, and reefs with two predators had 43 % greater beta diversity than those with one predator (Fig. 3b). These effects of predator density and identity can be attributed to the interdependence of alpha and beta diversity when using the Jaccard index. Controlling for differences in species richness using the Raup-Crick metric, we found no effect of predator identity ($F^{\pi} = 1.18$; $p = 0.28$) or density ($F^{\pi} = 0.07$; $p = 0.81$). There was no significant effect of predators or interaction between predator density and identity for beta diversity based on species incidence or relative abundance, and there were no main effects of predator density or identity based on species relative abundance (ESM C).

Predator species produced unique decapod communities

Predators shifted community composition based on prey species relative abundance ($F^{\pi} = 4.41$; $p = 0.002$). Additionally, there was a significant main effect of predator density on composition based on both species incidence ($F^{\pi} = 1.84$; $p = 0.05$, Fig. 3d) and relative abundance ($F^{\pi}_{1,54} = 3.25$; $p = 0.008$, Fig. 3c). Relative to corals with a single predator, corals with two predators had a lower relative abundance of *Chromis viridis* and *Galathea mauritiana*, and a higher relative abundance of *Harpilopis spinigera* (Fig. 3c). Furthermore, the presence of two predators reduced the incidence (i.e., number of reefs

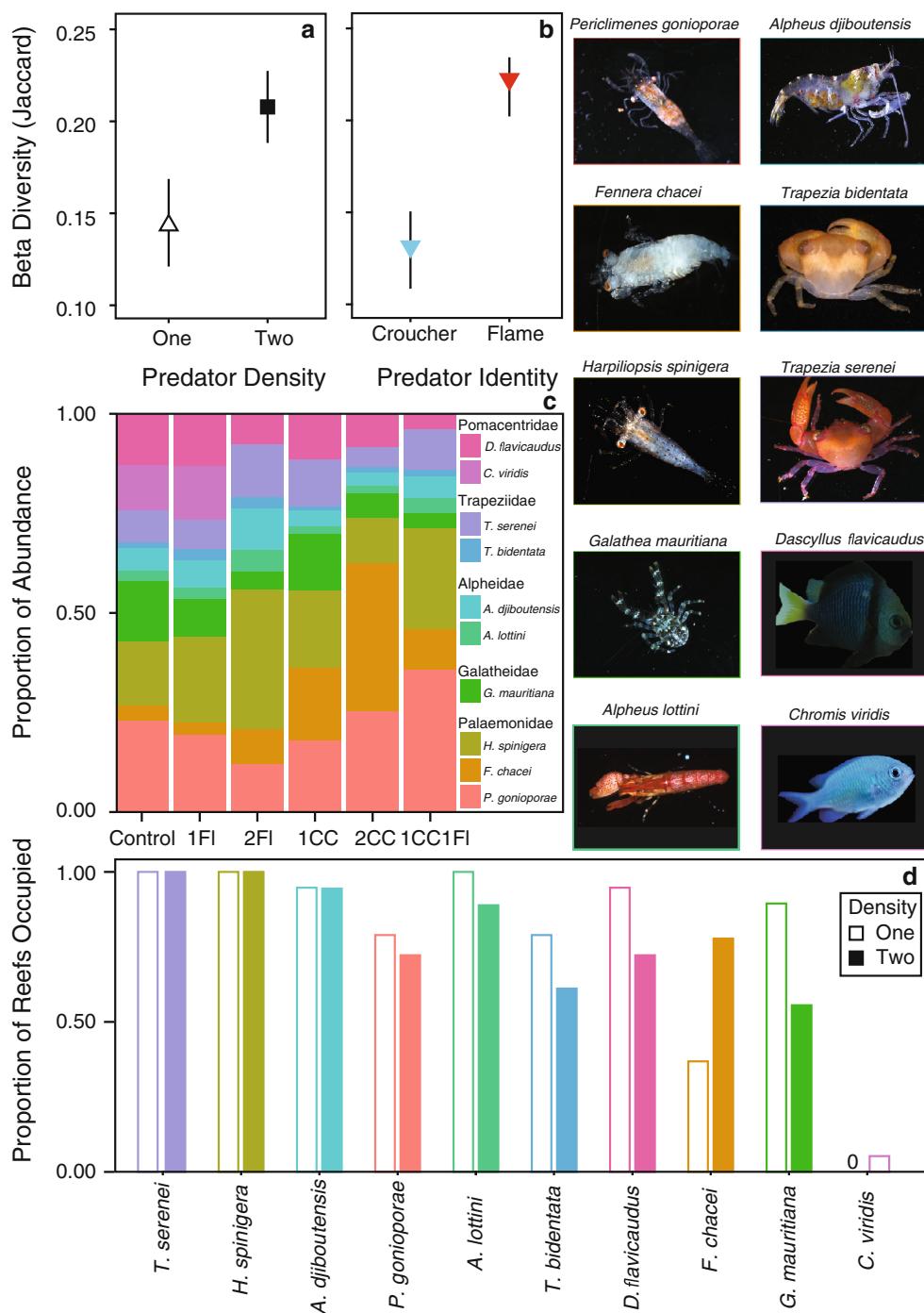


Fig. 3 The effect of predator treatments on beta diversity and species composition of fish and decapod communities: predator density (a) and identity (b) on beta diversity based on species incidence (a, b). In a and b, symbols correspond to predator contrasts (see Fig. 2

occupied) by the majority of common prey species (e.g., *Alpheus lottini*, *Trapezia bidentata*, *Dascyllus flavicaudus*, and *Galathea mauritiana*), but increased the incidence of *Fennera chacei* (Fig. 3d). The two predators differed significantly in how they affected species composition based on species relative abundance ($F^2 = 3.44$; $p = 0.005$,

legend for more detail). Also, shown are pictures of ten most common species and their composition based on relative abundance (c) and incidence (d). Colors in c and d correspond to colors on borders of species photos

Fig. 3c). Relative to coral crouchers, flame hawkfish treatments had a greater relative abundance of *T. bidentata*, *Athanas djiboutensis*, and *H. spinigera*, but had fewer *F. chacei*. There was, however, no aggregate effect of predators on composition based on species incidence, interaction between predator density and identity based on

species incidence or relative abundance, or main effect of predator identity on composition based on species incidence (ESM C).

Predation reduces coral mutualist abundance

Both predator species negatively affected the abundance of the majority of known mutualists species present in our study. Predators reduced the abundance of damselfish by 60 %, with strongest effects observed with two flame hawkfish and the mixed predator treatments (Fig. 4a). All predator treatments had similar effects on *Alpheus lottini*, reducing abundance by an average of 30 % (Fig. 4b). The effects of predators on *Trapezia* were more context dependent. On average, predators reduced small *Trapezia* species (*T. tigrina*, *T. speciosa*, *T. bella*, *T. serenei*, *T. guttata*, *T. bidentata*, and *T. areolata*) by 25 %. These effects were relatively consistent with the exception of the 1 coral croucher treatment, which showed no difference from the control treatment. There was, however, no apparent effect of predators on the abundance of large *Trapezia* spp. (*T. flavopunctata* and *T. rufopunctata*), a group known to have strong defensive benefits during outbreaks of the crown of thorns seastar (*Acanthaster planci*) (Glynn 1983; Pratchett 2001; McKeon 2010).

Discussion

Our study explored the independent and combined effects of two predatory fish species on a diverse decapod prey assemblage. We showed novel effects of predatory fishes on the abundance, diversity, and composition of coral-dwelling fishes and decapods. Predators negatively affected the abundance of nearly all prey species in our experiment, with strong effects on a number of species that are known coral mutualists. Furthermore, predators also negatively affected two common groups from the families Palaemonidae and Galatheidae, but the ecological role of these organisms are not well known and require further study.

The strong negative effect of predators on decapod and fish abundance is likely a product of both consumptive and non-consumptive effects. In addition to eating prey, predators may have changed prey abundance and composition by affecting prey activity (Stankowich and Blumstein 2005), behavior (Preisser et al. 2005), or the strength of interactions among indirectly interacting prey (Orrock et al. 2008). While reefs with predators had fewer species present (i.e., lower richness, Fig. 2b), rarefied diversity was equivalent across treatments (Fig. 2c), suggesting that lower richness on predator treatments was driven by a sampling effect. The two focal predators differed in their effect on total prey and had unique effects on community

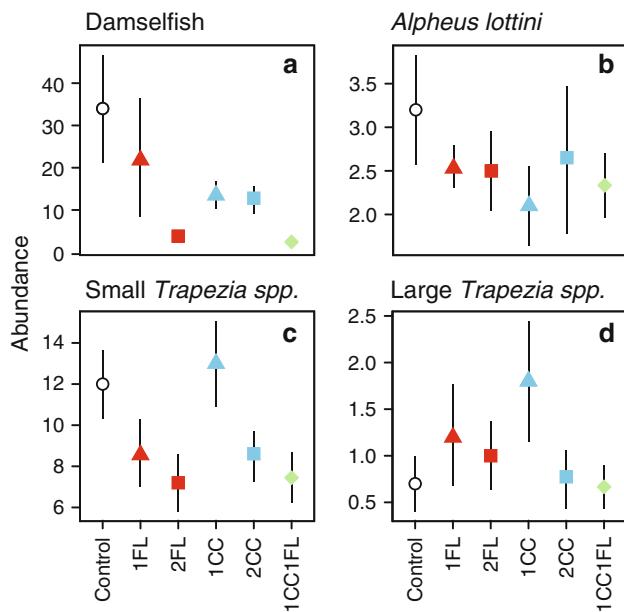


Fig. 4 Effect of six predator treatments on the four major groups of mutualists found in *Pocillopora eydouxi*: damselfish (a), *Alpheus lottini* (b), small-bodied *Trapezia* sp. (c), and large-bodied *Trapezia* sp. (d). We distinguish between small and large *Trapezia* groups (see Results for species identities), because size class is related to characteristic differences in functional roles. Large *Trapezia* are thought to be more critical for anti-predator defense against large seastars, whereas smaller *Trapezia* are better known for defending against smaller gastropods and removing sediment. Symbol shapes and colors are identical to Fig. 2

composition. The stronger negative effects of flame hawkfish on abundance may be attributable to their larger metabolic demand due to higher activity and larger body size. Lastly, we speculate that the differences in prey community composition between the two predator species is a product of predator microhabitat preference (spatial niche partitioning, Munday et al. 2001) with coral crouchers living and hunting deeper among the coral branches than the flame hawkfish (pers. obs.).

Effects of predator density, identity, and diversity

Previous studies examining the effects of predator diversity in modifying prey communities have concluded that both antagonism and cooperation among predators can modify prey community structure and ecosystem function (e.g., Byrnes et al. 2006; Cardinale et al. 2006). However, distinguishing the effects of predator density from diversity and quantifying whether predators are antagonizing or cooperating requires explicitly incorporating the nonlinearities of the predator functional response and the rate of prey depletion throughout an experiment (McCoy et al. 2012). Although uncommon, the functional response and level of prey depletion in the presence of each focal

predator species can be readily estimated, and then, multiple predator species functional response curves can be integrated to generate expected proportions of prey killed under the assumption that predator effects combined independently. However, due to the destructive nature of our sampling in our system in the present study, we were unable to calculate each predator's functional response or the level of prey depletion, because the final prey density was measured after recolonization rather than an instantaneous per capita survival of prey. This same concern applies to testing whether predators antagonize or cooperate as intraspecific predator density changes (sensu Skalski and Gilliam 2001). Our inference about the mechanism(s) underlying the changes in community structure under different predator assemblages (e.g., density-identity interactions, main effects of density, or monospecific versus mixed contrast) is therefore analytically constrained. For example, flame hawkfish had stronger negative effects on abundance with two predators relative to one predator, whereas the effects of coral crouchers decreased with a doubling in intraspecific density. The increased abundance of prey in the presence of high coral croucher density may be evidence for intraspecific antagonism, or alternatively, a single predator may indirectly affect the foraging ability of another predator in the absence of antagonism by simply depleting the prey base and increasing the amount of time another predator spends searching for prey (McCoy et al. 2012). The increased negative effect of high-density predators on species richness is similarly difficult to interpret. We can, however, say that monospecific and mixed predator treatments exhibited statistically identical species richness, a finding that concurs with the only other study that has examined community-level response to predator diversity in demographically open marine systems (O'Connor and Bruno 2009).

The consequences of predation on mutualists

Mutualist diversity often increases host production. For example, trees increase their productivity when the diversity of root microbes increase (Van der Heijden et al. 1998), and in ant-plant mutualisms, acacia tree fitness is maximized when a diversity of ant mutualists are present throughout the tree's ontogeny (Palmer et al. 2010). It is becoming clear that predation can fundamentally alter mutualisms by modifying mutualist density, behavior, or composition (Anderson and Midgley 2002; Knight et al. 2006; Romero et al. 2011). In this system, mutualist services by decapods and fishes are known to increase with mutualist density and diversity (Holbrook et al. 2008; McKeon et al. 2012; Stier et al. 2012); therefore, we hypothesize that the negative effects of each of our focal predators on mutualist abundance and diversity are likely

to have negative indirect effects on coral growth and survival. One caveat to this hypothesis is that one of the large *Trapezia* species (*T. rufopunctata*) is known to increase the mortality of newly settled damselfishes (Schmitt et al. 2009); however, larger *Trapezia* were seemingly unaffected by the presence of our two focal predators (Fig. 4d).

The effects of the predators differed somewhat depending on the predator treatment and mutualist group. For example, the two flame hawkfish reefs and the mixed-species predator treatment nearly eliminated damselfish from the community, whereas the other predator treatments maintained somewhat larger populations. The effects of predators on abundance of *Alpheus lottini* and small-bodied *Trapezia spp.* were more uniform, with the exception that a single coral croucher had no obvious effect on small-bodied *Trapezia*. At the scale of the array, the decreased incidence of certain mutualists (e.g., *Alpheus lottini*, *Trapezia bidentata*, *Dascyllus flavicaudus*) in treatments with two predators relative to one predator will likely add to the reduced level of mutualist services. Our findings complement a recent study that focused the role of a third additional predator found in this system, the arc-eye hawkfish (*Paracirrhites arcatus*), affecting the density of mutualistic damselfish. Arc-eye hawkfish reduced damselfish density, which has cascading negative indirect effects on coral growth (Holbrook et al. 2011).

Antagonistic and synergistic interactions among mutualists can be common in systems where a diverse set of mutualists co-occur. The presence of predators may either disrupt or magnify these mutualist-mutualist interactions (e.g., due to changes in mutualist density, behavior, or composition), thereby altering host performance. In this system, the decreased density and incidence of *A. lottini* in the presence of predators may compound the negative indirect effect of predators on the host, because *T. serenei* and *A. lottini* are known to synergize while defending corals from predatory seastars (McKeon et al. 2012). Although untested, synergies within or among other decapod or fish species may be similarly modified by the presence of predators.

Predation on mutualists may also alleviate the host from the energetic costs of symbiosis, which, depending on environmental conditions, may be so costly as to have a net negative effect on host performance. In this system, the hypothesized negative indirect effects of coral crouchers and flame hawkfish on corals may be mitigated by the fact that corals provide lipid bodies to their decapod mutualists in exchange for the decapod's protective services (Stimson 1990). These lipid bodies are a marine analog to extrafloral nectaries produced by the plants in ant-plant mutualisms where plants often subsidize ants with nectar in exchange for ant protective services against herbivores. Additionally, nitrogenous waste excretion by the predators may

positively affect the coral by acting as a nutrient subsidy. In contrast to the decapod mutualists, the fish-coral mutualism is unknown to cost the host coral energy. Given the suite of direct, indirect, and higher-order interactions present in *P. eydouxi* communities, it is difficult to translate the consequences of the short-term interactions measured here and in other studies for the lifetime reproductive success of host corals. Future studies should focus on disentangling the effects of trophic and mutualistic interactions across the coral ontogeny to measure the relative contribution of certain interactions to host fitness (Palmer et al. 2010).

In conclusion, our findings add to a growing body of literature that suggests that predators, despite their strong effects, do not act as stabilizing agents for diverse tropical marine systems. Although predation in this system does not stabilize prey diversity (e.g., through frequency-dependent or keystone predation), the unique compositional differences produced by each predator treatment provides novel insight into the processes governing spatio-temporal variation in the size and structure of key coral mutualist communities. Indeed, the mutualist fishes and decapods studied here *do* act as stabilizing forces by facilitating the growth and survival of the coral in the presence of a suite of anthropogenic and natural stressors, and this allows *P. eydouxi* to persist and provide structure for a number of other non-mutualist species that hide within the branches of the coral. Furthermore, our study expands upon the limited taxonomic breadth in studies of reef ecosystems (Fisher et al. 2011) by examining the ecological drivers of a diverse, but poorly studied group of fishes and decapods that are a major component of the diet for commercially important fisheries species (e.g., snappers and groupers) (Kulbicki et al. 2005). Developing a mechanistic understanding of the processes governing the structure and dynamics of small but critically important cryptofauna communities is a key to understanding the dynamics and stability of diverse coral reef ecosystems.

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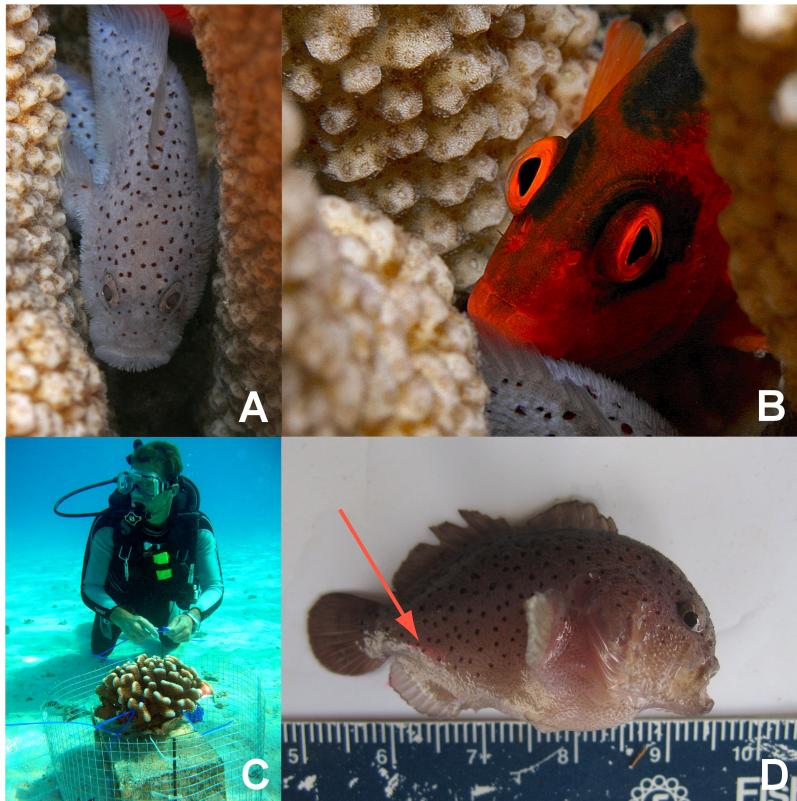
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ESM - A: Focal predator species and experimental manipulations

Two predatory fishes: A) the coral croucher (*Caracanthus maculatus*) and B) the flame hawkfish (*Neocirrhitus armatus*) inside of *Pocillopora sp.* coral heads. Photo credits: Thomas Vignaud. Experimental coral zip-tied to a cinder block (C) in the lagoon of Moorea. Coral croucher tagged with a unique color combination of elastomer just above the anal fin (see arrow in D).



ESM - B: Effect of predators on 10 most abundant decapod

Response of the ten most common species to each predator treatment (control – black, flame hawkfish: FL – red, coral croucher: CC – blue, and mixed species assemblage - green).

Figure B1

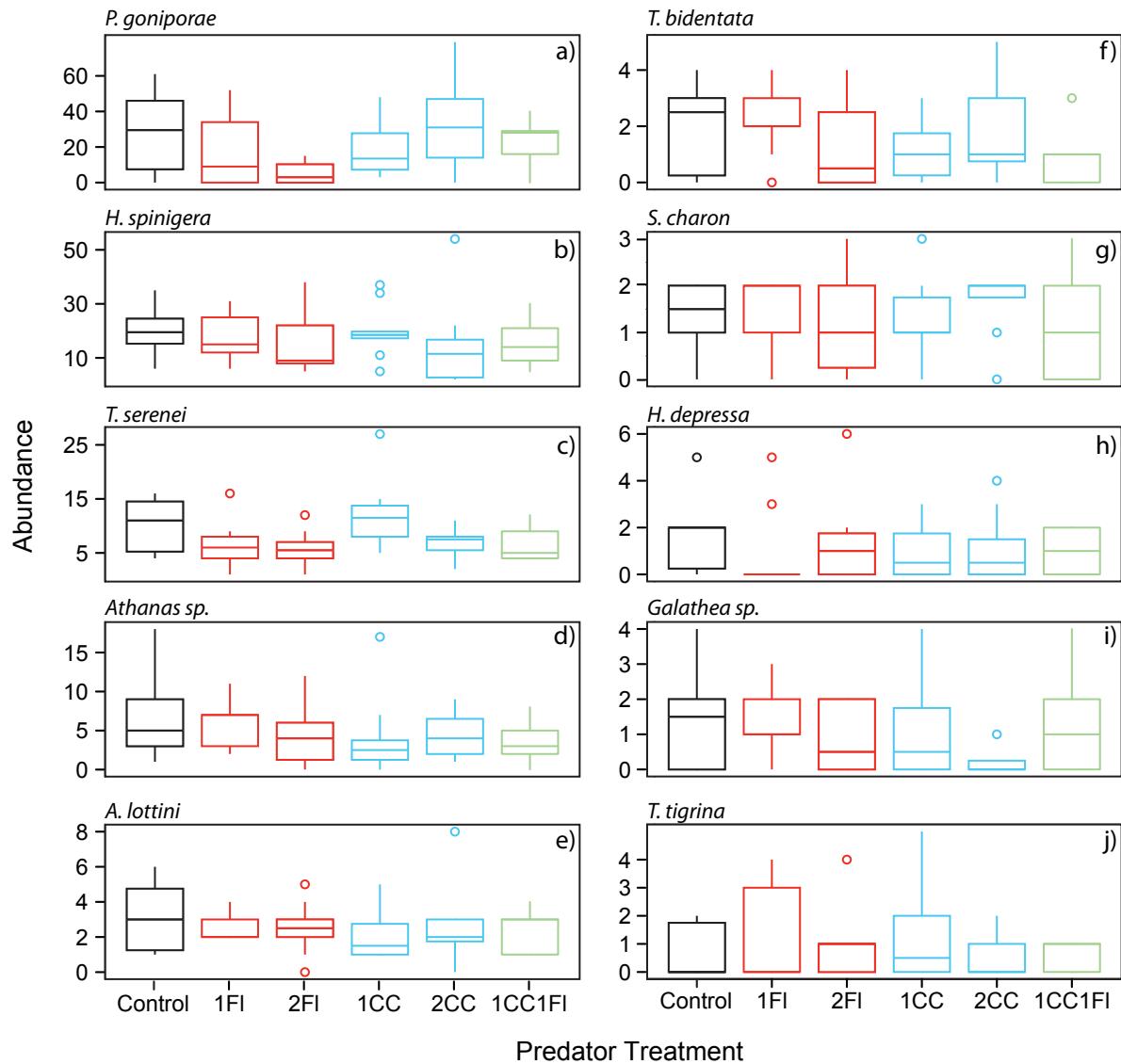


Plate B1b Photographs of decapod species that recruited on experimental reefs.

A: *Alpheus dolorus* (Alpheidae); B: *Alpheus pachychirus* (Alpheidae); C: *Alpheus cf. sizou* (Alpheidae); D: *Alpheus diadema* (Alpheidae); E: *Alpheus columbianus* (Alpheidae); F: *Synalpheus cf. gracilirostris* (Alpheidae); G: *Arete cf. indicus* (Alpheidae); H: *Cuapetes cf. ensifrons* (Palaemonidae); I: *Periclimenes gonioporae* (Palaemonidae); J: *Harpiliopsis depressa* (Palaemonidae); K: *Fennera chacei* (Palaemonidae); L: *Chlorocurtis jactans* (Pandalidae); M: *Thor amboinensis* (Hippolytidae); N: *Saron marmoratus* (Hippolytidae); O: *Thinora maldivensis* (Hippolytidae); P: *Calaxius sp.* (Axiidae); Q: *Trapezia bidentata* (Trapeziidae); R: *Trapezia serenei* (Trapeziidae); S: *Trapezia tigrina* (Trapeziidae); T: *Trapezia flavopunctata* (Trapeziidae); U: *Trapezia areolata* (Trapeziidae); V: *Liomera monticulosa* (Xanthidae); W: *Galathea mauritiana* (Galatheidae); X: *Perinia tumida* (Majidae)



Table B1 Mean (\pm 1SD) abundance of all fishes and decapods inside *P. eydouxi* at the end of the recruitment study. Empty cells represent 0. CC: *Caracanthus maculatus*; FL: *Neocirrhites armatus*.

Family	Species	Control		1CC		2CC		1FL		2FL		1CC1FL	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Palaemonidae	<i>P. gonioporae</i>	29.30	23.20	18.30	14.36	33.63	25.61	16.22	19.66	5.40	6.15	22.33	14.57
Palaemonidae	<i>H. spinigera</i>	20.70	8.96	19.80	9.48	15.13	17.24	18.00	9.15	15.70	11.77	15.89	8.88
Palaemonidae	<i>F. chacei</i>	4.60	13.51	18.80	40.79	49.25	84.73	2.67	5.98	3.90	4.12	6.44	17.85
Galatheidae	<i>G. mauritiana</i>	19.30	17.68	14.50	8.06	8.00	14.17	7.89	7.25	2.00	3.74	2.33	2.74
Trapeziidae	<i>T. serenei</i>	1	4.85	11.90	6.30	6.75	2.76	6.33	4.56	5.90	3.07	6.44	3.05
Alpheidae	<i>A. djiboutensis</i>	7.10	5.90	4.00	4.97	4.50	2.98	5.56	3.17	4.60	4.01	3.44	2.83
Alpheidae	<i>A. lottini</i>	3.20	1.99	2.10	1.45	2.63	2.39	2.56	0.73	2.50	1.43	2.33	1.12
Trapeziidae	<i>T. bidentata</i>	2.00	1.63	1.10	0.99	1.75	1.75	2.33	1.32	1.30	1.70	1.00	1.22
Alpheidae	<i>S. charon</i>	1.40	0.70	1.20	0.92	1.63	0.74	1.44	0.88	1.20	1.03	1.22	1.09
Palaemonidae	<i>H. depressa</i>	1.60	1.51	0.90	1.10	1.13	1.55	0.89	1.83	1.30	1.83	0.89	0.93
Alpheidae	<i>A. pachychirus</i>	1.30	1.34	1.10	1.45	0.25	0.46	1.22	0.97	0.90	0.99	1.33	1.32
Portunidae	<i>T. admete</i>	1.00	0.94	1.20	1.23	0.63	0.74	0.78	0.97	0.90	0.88	0.67	0.87
Trapeziidae	<i>T. tigrina</i>	0.70	0.95	1.30	1.70	0.50	0.76	1.22	1.64	0.90	1.20	0.56	0.53
Hyppolitidae	<i>T. paschalidis</i>	1.10	2.47	0.70	2.21	2.50	7.07	0.11	0.33	0.60	0.84	0.33	0.71
Alpheidae	<i>A. diadema</i>	0.50	0.53	0.80	0.92	0.38	0.74	1.11	1.05	0.20	0.42	0.44	1.01
Xanthidae	<i>D. hispida</i>	1.10	1.29	0.30	0.67	0.50	0.93	0.78	0.83	0.20	0.42	0.33	0.50
Trapeziidae	<i>T. guttata</i>	0.40	0.70	0.40	0.70	0.25	0.71	0.56	1.33	0.40	0.97	0.67	1.41
Palaemonidae	<i>C. cf. ensifrons</i>	0.20	0.63	0.20	0.63	0.63	1.19	0.56	0.88	0.50	0.53	0.44	1.01
Trapeziidae	<i>T. areolata</i>	0.50	0.85	0.50	0.71	0.13	0.35	0.33	0.50	0.10	0.32	0.22	0.44
Epialtidae	<i>M. monoceros</i>	0.30	0.67	0.10	0.32	0.25	0.71	0.44	0.88			0.22	0.44
Alpheidae	<i>S. gracilirostris</i>	0.20	0.63	0.10	0.32	0.13	0.35	0.22	0.67	0.30	0.67		
Hyppolitidae	<i>T. amboinensis</i>	0.30	0.67	0.40	0.52			0.11	0.33				
Palaemonidae	<i>C. jactans</i>	0.10	0.32					0.11	0.33	0.60	1.90		
Alpheidae	<i>A. columbianus</i>	0.50	1.58			0.25	0.71						
Alpheidae	<i>A. equalis</i>	0.20	0.42							0.30	0.48	0.22	0.44
Trapeziidae	<i>T. speciosa</i>			0.50	1.58	0.25	0.71						
Trapeziidae	<i>T. rufopunctata</i>			0.40	0.70	0.25	0.71			0.10	0.32		
Alpheidae	<i>A. dolerus</i>	0.40	0.70					0.22	0.44				
Pilumnidae	<i>P. tahitensis</i>	0.30	0.95							0.30	0.48		
Galatheidae	<i>Phylladiorhynchus sp</i>							0.11	0.33			0.44	1.33
Xanthidae	<i>P. speciosa</i>			0.10	0.32							0.44	0.88

Alpheidae	<i>A. parvirostris</i>	0.20	0.63			0.11	0.33		0.11	0.33			
Trapeziidae	<i>T. bella</i>	0.10	0.32		0.13	0.35			0.22	0.67			
Xanthidae	<i>C. laevissima</i>	0.10	0.32		0.13	0.35	0.11	0.33	0.10	0.32			
Xanthidae	<i>X. lamarcki</i>	0.10	0.32		0.25	0.46			0.11	0.33			
Alpheidae	<i>Alpheus sp.</i>		0.20	0.63	0.13	0.35							
Xanthidae	<i>Cymo sp.</i>	0.10	0.32	0.20	0.63								
Xanthidae	<i>C. quadrilobatus</i>	0.20	0.63				0.11	0.33					
Epioltidae	<i>P. tumida</i>	0.10	0.32					0.10	0.32				
Epioltidae	<i>M. orientalis</i>	0.10	0.32	0.10	0.32								
Porcellanidae	<i>Petrolisthes sp.</i>							0.20	0.42				
Trapeziidae	<i>T. flavopunctata</i>			0.10	0.32				0.11	0.33			
Xanthidae	<i>P. paumotensis</i>	0.20	0.42										
Xanthidae	<i>L. monticulosa</i>	0.10	0.32	0.10	0.32								
Alpheidae	<i>A. indicus</i>						0.11	0.33					
Alpheidae	<i>S. tumidomanus</i>					0.11	0.33						
Alpheidae	<i>A. sizou</i>							0.11	0.33				
Axiidae	<i>Calaxius sp.</i>	0.10	0.32										
Hypapolitidae	<i>S. marmoratus</i>					0.11	0.33						
Palaemonidae	<i>Onycocaris sp.</i>	0.10	0.32										
Portunidae	<i>T. coeruleipes</i>	0.10	0.32										
Xanthidae	<i>M. nudipes</i>			0.10	0.32								
Xanthidae	<i>P. pugil</i>	0.10	0.32										
Xanthidae	<i>P. semigranosa</i>				0.13	0.35							
Pomacentridae	<i>D. flavicaudus</i>	16.20	6.61	11.70	9.62	10.88	8.08	11.00	12.09	3.40	4.58	2.33	2.69
Pomacentridae	<i>C. viridis</i>	14.70	35.82					11.11	33.33				
Pomacentridae	<i>D. aruanus</i>	3.10	2.60	1.80	1.55	1.38	1.69	0.22	0.67	0.40	0.70	0.11	0.33
Pomacentridae	<i>P. modestus</i>	1.20	1.55	0.70	0.82	0.25	0.71	0.89	1.27	0.30	0.67	0.33	0.50
Scorpaenidae	<i>S. fowleri</i>	0.40	0.70			0.75	1.16	0.56	0.88				
Pomacentridae	<i>P. pavo</i>	0.30	0.48	0.50	0.71					0.40	0.97	0.11	0.33
Labridae	<i>T. hardwicke</i>	0.20	0.42	0.30	0.48	0.25	0.46	0.22	0.44	0.10	0.32	0.22	0.44
Scorpaenidae	<i>A. coccineus</i>			0.40	0.84	0.38	0.52	0.22	0.44			0.11	0.33
Gobiidae	<i>Eviota sp.</i>			0.60	0.84					0.10	0.32		
Acanthuridae	<i>Acanthurus sp</i>	0.20	0.42			0.13	0.35			0.10	0.32		
Scorpaenidae	<i>S. tinkhami</i>	0.20	0.63					0.11	0.33			0.11	0.33
Chaetodontidae	<i>C. citrinellus</i>	0.10	0.32	0.20	0.63								
Apogonidae	<i>A. semipunctata</i>	0.10	0.32			0.13	0.35	0.11	0.33				

Holocentridae	<i>S. microstoma</i>			0.13	0.35	0.22	0.67		
Cirrhitidae	<i>P. arcatus</i>			0.13	0.35			0.11	0.33
Pomacentridae	<i>S. bandanensis</i>		0.10	0.32				0.11	0.33
Apogonidae	<i>O. angustatus</i>	0.10	0.32						
Balistidae	<i>P. flavimarginatus</i>		0.10	0.32					
Scorpaenidae	<i>P. antennata</i>					0.10	0.32		

ESM - C: Community response to five contrasts among six predator treatments.

We do not report main effects of predator density and identity (ID) when there is a significant interaction between density and identity (Density*ID). Degrees of freedom are not available for beta diversity or composition tests because they are perumetation based. Bolded values are significant (i.e. $p < 0.05$)

	Predation		Density*ID		Density		ID		Diversity	
Response	test statistic	p value	test statistic	p value						
abundance	$t = 2.98$, df = 54	0.003	$t = 2.64$, df = 54	0.008	NA	NA	NA	NA	$t = 0.90$, df = 54	0.376
richness	$t = 2.98$, df = 54	0.008	$t = 0.13$, df = 54	0.901	$t = 1.58$, df = 54	0.121	$t = 0.77$, df = 54	0.446	$t = 0.13$, df = 54	0.895
rarefied richness	$t = 0.30$, df = 54	0.77	1.86, df = 54	0.068	$t = 0.88$, df = 54	0.379	$t = 1.91$, df = 54	0.061	$t = 0.03$, df = 54	0.98
Beta (Jaccard)	$F^{\pi} = 2.47$	0.137	$F^{\pi} = 1.06$	0.371	$F^{\pi} = 11.97$	0.003	$F^{\pi} = 4.12$	0.01	$F^{\pi} = 0.02$	0.898
Composition (Jaccard)	$F^{\pi} = 2.45$	0.085	$F^{\pi} = 1.91$	0.171	$F^{\pi} = 4.12$	0.049	$F^{\pi} = 11.97$	0.001	$F^{\pi} = 1.23$	0.243
Beta (Manhattan)	$F^{\pi} = 2.47$	0.104	$F^{\pi} = 1.92$	0.189	$F^{\pi} = 0.34$	0.573	$F^{\pi} = 0.91$	0.362	$F^{\pi} = 0.01$	0.918
Composition (Manhattan)	$F^{\pi} = 4.41$	0.004	$F^{\pi} = 0.83$	0.551	$F^{\pi} = 3.25$	0.006	$F^{\pi} = 3.44$	0.009	$F^{\pi} = 0.58$	0.659
Beta (Raup-Crick)	$F^{\pi} = 3.81$	0.069	$F^{\pi} = 0.15$	0.148	$F^{\pi} = 0.07$	0.807	$F^{\pi} = 1.18$	0.282	$F^{\pi} = 0.18$	0.788