

# Predation and landscape characteristics independently affect reef fish community organization

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**Abstract.** Trophic island biogeography theory predicts that the effects of predators on prey diversity are context dependent in heterogeneous landscapes. Specifically, models predict that the positive effect of habitat area on prey diversity should decline in the presence of predators, and that predators should modify the partitioning of alpha and beta diversity across patchy landscapes. However, experimental tests of the predicted context dependency in top-down control remain limited. Using a factorial field experiment we quantify the effects of a focal predatory fish species (groupers) and habitat characteristics (patch size, fragmentation) on the partitioning of diversity and assembly of coral reef fish communities. We found independent effects of groupers and patch characteristics on prey communities. Groupers reduced prey abundance by 50% and gamma diversity by 45%, with a disproportionate removal of rare species relative to common species (64% and 36% reduction, respectively; an oddity effect). Further, there was a 77% reduction in beta diversity. Null model analysis demonstrated that groupers increased the importance of stochastic community assembly relative to patches without groupers. With regard to patch size, larger patches contained more fishes, but a doubling of patch size led to a modest (36%) increase in prey abundance. Patch size had no effect on prey diversity; however, fragmented patches had 50% higher species richness and modified species composition relative to unfragmented patches. Our findings suggest two different pathways (i.e., habitat or predator shifts) by which natural and/or anthropogenic processes can drive variation in fish biodiversity and community assembly.

**Key words:** *Cephalopholis argus*; coral reef fish; diversity partitioning; fragmentation; oddity effect; predation; single large or several small; species–area relationship; species diversity.

## INTRODUCTION

Recent theoretical studies have merged concepts from food web ecology and biogeography to gain insight into how the trophic composition of communities and the strength of species interactions shift across heterogeneous landscapes. These efforts have yielded several predictions. First, characteristic differences between trophic levels in factors such as resource requirements (Holt et al. 1999), trophic generalization (Gravel et al. 2011), dispersal ability (Chase et al. 2010), or sensitivity to demographic stochasticity (Holt 2010) can cause predators and prey to respond differently to shifts in patch size and isolation (Holt 2010, Gravel et al. 2011). Second, models and observational studies (Ryberg and Chase 2007, Holt 2010, Ryberg et al. 2012) suggest that

the capacity of predators to increase prey extinction can mitigate the positive effects of habitat area on species diversity (i.e., the species–area relationship). This can produce different species–area relationships in the presence and absence of predators and modify the partitioning of alpha and beta diversity in patchy landscapes. Here we focus on this latter issue and explore whether the top-down effect of predators on prey communities varies with patch size and modifies the partitioning of prey diversity.

Ignoring trophic interactions, three main processes underlie positive correlations between habitat area and biodiversity: (1) sampling effects (i.e., larger areas require more sampling effort which leads to more species collected [Connor and McCoy 1979]); (2) environmental heterogeneity (i.e., larger areas support more habitat types and thus support more species); and (3) demographic effects (i.e., habitat area influences colonization, extinction, and dispersal [reviewed in Rosenzweig 1995, Drakare et al. 2006]). With respect to demographic effects, trophic biogeography theory focuses solely on the role of predators in affecting prey

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extinction rates, a well-documented effect of predators (Sih et al. 1985). For example, an extension of the Equilibrium Theory of Island Biogeography by Ryberg and Chase (2007) and a generalization by Holt (2010) predict that predators affect the slope of the species–area relationship ( $Z$ ) for prey.

Whether predators increase or decrease the slope of the prey species–area relationship is dependent upon the foraging strategy of a predator and whether this behavior varies consistently with habitat area. If the effect of predation is dependent upon habitat area, then, depending on whether predators increase or decrease prey diversity, the additive extinction will either magnify or attenuate the reduced extinctions with increasing habitat area. If predators increase diversity by disproportionately consuming dominant competitors (i.e., keystone predation [Power et al. 1996]), frequency-dependent predation (i.e., Janzen–Connell effects [Janzen 1970, Connell 1971]), or prey switching (Murdoch 1969, Abrams and Matsuda 1996), then patches with predators should have higher  $Z$  values (i.e., species–area relationships with steeper slopes) because predators are decreasing prey extinction rates. Alternatively, if predators reduce diversity by either making species susceptible to demographic stochasticity (Sih et al. 1985), disproportionately consuming rare prey (Spiller and Schoener 1998), or reducing abundances of all species (Almany and Webster 2004), then patches with predators should have higher extinction rates, thereby producing lower  $Z$  values (i.e., shallower species–area relationships) relative to patches with no predators (Holt 2010).

In addition to predicting  $Z$  values, trophic biogeography theory also predicts the effect of predators on diversity partitioning within and among patches. Historically, researchers have focused on the effect of predators on alpha diversity, but recent theory makes explicit predictions about the role of predators in diversity partitioning. Specifically, assuming an additive diversity partitioning ( $\alpha + \beta = \gamma$ ), Ryberg et al. (2012) showed that generalist predators can increase prey extinction rates, which can lead to a decrease in alpha diversity ( $\alpha$ ) and a corresponding increase in beta diversity ( $\beta$ ). Furthermore, their model demonstrates that when predators reduce gamma diversity ( $\gamma$ ) by acting as environmental filters and homogenizing diversity across patches (e.g., through eliminating prey that are poorly morphologically or chemically defended), reduced alpha and beta diversity can result in reduced gamma diversity. Additionally, predators often reduce community size, and metacommunity theory predicts that reductions in community size should increase beta diversity (Orrock and Fletcher 2005, Orrock and Watling 2010). Specifically, Orrock and Watling (2010) used a competition–colonization model to show that reductions in community size can increase the probability that superior competitors are lost from a given patch due to ecological drift. Therefore, when

communities are small, landscapes will likely exhibit high beta diversity driven by stochastic colonization by different species, relative to a landscape with larger communities where a single competitively dominant species will homogenize the landscape by competitively excluding inferior species. Empirical studies support the hypothesis that predators can affect partitioning of alpha and beta diversity through acting as environmental filters and homogenizing diversity across patches (Chase et al. 2009), and by modifying the strength of priority effects (Chase et al. 2009, Stier et al. 2013b).

Trophic biogeography captures only a subset of the possible ways in which predators can interact with habitat characteristics and drive the partitioning of diversity across patchy landscapes. For example, larger habitats often contain greater environmental heterogeneity (i.e., niche availability), a factor known to mediate predation–competition interactions (Werner et al. 1983). Trophic biogeography additionally ignores other habitat characteristics known to mediate predator–prey dynamics (e.g., spatial habitat heterogeneity [Huffaker 1958, Crowley 1978], refuge availability [Diehl 1993], habitat complexity [reviewed in Jeffries and Lawton 1984], and fragmentation [reviewed in Ryall and Fahrig 2006]) that often covary with habitat area. Advances in trophic biogeography theory will require tests of existing theoretical predictions focused on predation–habitat area effects, as well as theoretical and empirical extension of the theory to include interactions between predation and habitat characteristics such as spatial heterogeneity, refuge availability, and fragmentation.

Here, we quantify the independent and combined effects of predation and two habitat characteristics, patch size and patch fragmentation, on community organization of coral reef fish communities. We begin by using field surveys to examine the natural distributions of fishes and explore whether predators affect changes in fish abundance and diversity with habitat availability. These surveys find prey respond similarly to shifts in habitat as predator abundance increases. However, our surveys sum the total availability of habitat in large transects to encompass the full fish community, including fishes with larger ranges. This summation includes patches of different size, spatial configuration, and quality, each of which can modify predator–prey dynamics in different ways. Furthermore, the interaction between predation and habitat area proposed in trophic biogeography theory is a demographic effect that may be obscured by increases in environmental heterogeneity in larger patches that might interact with predators. Additionally, if predators and prey share habitat, the effects of predators may mask top-down control (e.g., Shima et al. 2008). Therefore we coupled our surveys with a factorial field experiment where we manipulated habitat size (controlling for environmental heterogeneity) and the presence of a focal piscivorous predator (*Cephalopholis argus*; hereafter grouper) to test the trophic biogeography prediction that predators modify

the positive effects of habitat area on species diversity through demographic effects (i.e., modifying local prey extinction rates). Additionally, we test Ryberg et al.'s (2012) hypothesis that predators can alter partitioning of alpha and beta diversity in patchy landscapes. As natural and anthropogenic activities modify reef habitats, changes in habitat size are often accompanied by increased habitat fragmentation, though community-level interactions between habitat fragmentation and predation have been understudied. Therefore, we also test the hypothesis that habitat fragmentation (controlling for changes in habitat area) modifies the effects of groupers on prey abundance and species diversity.

## MATERIALS AND METHODS

### *Study system*

The island of Moorea (French Polynesia: 17°30' S, 149°50' W) is surrounded by a barrier reef with a shallow lagoon that ranges from 0.8 to 1.3 km wide (Galzin and Pointer 1985). The lagoon is interspersed with patch reefs within a matrix of sand, fine coral rubble, and coral pavement, with individual patch reefs separated by distances ranging from less than a meter to tens of meters.

### *Field survey to assess effect of predators on the prey species-area relationship*

We surveyed the abundance and diversity of fishes and coral habitat availability (quantified as total coral volume) in 19 plots, each 50 × 10 m, separated by a minimum of 200 m and distributed along a 7-km portion of the lagoon on the north shore of Moorea. Plots (5–7 m depth) were chosen to represent the range in cover of live coral present in mid-lagoon habitats (1–50%), and there was no systematic relationship between similarity in cover of live coral and proximity of sites to one another. Scuba divers identified and counted all reef-associated fishes and quantified the volume of corals on each survey plot over a three-month period during the austral winter. The same two observers did all fish counts. For abundance, we used the larger number observed by the two divers for any species with up to 25 individuals, after which the average of the two counts was taken. For each plot, all corals with a diameter >15 cm were identified and measured (mean = 99 corals per plot, range = 6–301 corals per plot; most abundant coral taxa were *Pocillopora* spp., *Porites rus*, massive *Porites* spp., *Montipora* spp., *Acropora* spp. [Holbrook et al. 2008]).

Species were categorized into two separate trophic levels using the database from Fishbase.org (Froese and Pauly 2013). Species with Fishbase trophic level ≥3.5 were assigned as predators, and species with trophic level <3.5 were defined as prey (Tremblay-Boyer et al. 2011, Tolimieri et al. 2013; see Appendix A for trophic level assignments). We conducted two separate analyses on the survey data. First, using ANCOVA we tested whether habitat volume differentially affected abun-

dance and richness of predators and prey. Hereafter we refer to “predator(s)” when referring to the diverse assemblage of predator species found in our observational study and “grouper(s)” when referring to the focal predator in our experiment (see *Field experiment to separate effects of habitat and groupers on abundance and diversity*). Abundance, richness, and total coral volume were all log<sub>10</sub> transformed to improve normality and heterogeneity of variance. Second, we used multiple regression analysis to quantify the effects of habitat availability (the sum of the total coral volume in each plot) and variation in predator abundance that is unexplained by habitat volume (i.e., the residuals of the correlation between habitat volume and predator abundance) on the abundance and diversity of the prey fish community. Because predators and prey often share habitat, positive correlations often exist between the abundance of predators and abundance of prey despite negative effects of predators on prey through predation (e.g., Gotelli and Ellison 2006). Our residuals approach removes the positive covariance between predators and prey driven by shared habitat to isolate the expected negative effects of predators on prey due to consumption.

### *Field experiment to separate effects of habitat and groupers on abundance and diversity*

Previous studies of coral reef fish communities have documented the influence of predators on the composition of prey communities (Almany and Webster 2004, Almany et al. 2007, Stallings 2008, Heinlein et al. 2010). At both the population and community level, habitat attributes can modify the effects of predation on prey abundance, diversity, and composition (e.g., Beukers and Jones 1997). We conducted a field experiment to separate the effects of habitat and predation in driving patterns of prey abundance and diversity by orthogonally manipulating patch size and the presence of groupers. Our experiment was conducted on 18 experimental patch reefs (hereafter patch) that were spaced 15 m apart on a sand flat in the Maharepa lagoon on the north shore of Moorea. Reefs of two sizes (small reefs consisted of four adjacent cinder blocks, each 0.5 × 0.25 × 0.25 m; large reefs consisted of eight cinder blocks in a 4 × 2 array) were constructed at 20 m depth. Each reef surface was covered in live *Porites rus* coral (0.25 m in diameter), which was collected from a nearby reef and affixed to cinder blocks using marine epoxy (see Appendix B for a diagram depicting experimental reefs). Experimental reef sizes were representative of the most common patch sizes in field surveys. Surveyed coral colonies varied substantially in size (range, 0.002–66.0 m<sup>3</sup>), but the majority of colonies (77%) were small (<1 m<sup>3</sup>; median, 0.21 m<sup>3</sup>) and the majority of the colonies <1 m<sup>3</sup> were ≤0.25 m<sup>3</sup> (68%; Appendix C). We focused on variation in habitat size within this range and chose our experimental reef sizes accordingly: small (0.25 m<sup>3</sup>) and large (0.5 m<sup>3</sup>). All patch reefs were isolated from the

nearest natural reefs by a minimum of 50 m to discourage immigration of juvenile and adult fishes between experimental and natural reefs. Additionally, because we were interested in distinguishing the effects of habitat area from the effects of patch number (*sensu* Ryall and Fahrig 2006), we maintained a constant total reef area among treatments differing in reef size (i.e., the sum of reef area across the 6 large patches was equal to the sum of the area across all 12 smaller units, with  $n=6$  large reefs and  $n=12$  small reefs). Following construction, a cylindrical cage (diameter, 1.5 m; height, 1 m) composed of galvanized hardware cloth (wire mesh) with a mesh size of 1 cm<sup>2</sup> was placed over each experimental reef. The cages were necessary to retain groupers and restrict immigration by transient species that cross large areas of sand; the large mesh size allowed larval fishes to readily settle through the cages onto the experimental reefs (e.g., Doherty and Sale 1986). Previous studies at a nearby site suggested no effects of caging on settlement (Heinlein et al. 2010). The combination of the reef sizes used in our experiment and the cages allowed us to narrow the species pool to small-bodied and site-attached fishes, e.g., individuals that were potential prey for the groupers.

Twelve peacock groupers (*Cephalopholis argus*, our focal predator with a wide diet breadth [Randall and Brock 1960]) were collected using hand nets and the anesthetic eugenol and added to half of the reefs selected at random (grouper size [mean  $\pm$  SD] = 20.6  $\pm$  1.7 cm total length). A small number of settlers had colonized the reefs following their construction; therefore immediately prior to adding the groupers we removed all recent settlers from both grouper and nongrouper treatments using hand nets and eugenol. We added one grouper to small reefs and two groupers to large reefs to create a similar density of groupers per coral habitat area across reef treatments (Appendix B). After groupers were added, natural colonization of other fishes occurred for three months (March–May 2009), after which time divers visually censused the experimental reefs to characterize the abundance and diversity of the fish communities. Cages were 100% effective at retaining the groupers throughout the duration of the experiment.

#### Data analysis

Predation and patch characteristics can modify community structure and affect a suite of characteristics including within-patch (alpha) diversity (hereafter species richness), among-patch (beta) diversity, and species composition. The importance of a sampling effect as an underlying mechanism of species–area relationships is not relevant to the equilibrium-based model of trophic biogeography. However, at the local scale, predators can fundamentally alter the number of prey and therefore influence the possible number of prey sampled within a community. Because we expected that reefs with more fish might also have a greater diversity of fish species

(Almany and Webster 2004), we used individual-based rarefaction (Gotelli and Colwell 2001) to distinguish between effects of groupers and habitat driven by reductions in abundance from those arising from compositional shifts (e.g., due to frequency dependence; see Appendix D for more detail on inferring predator foraging behavior using rarefaction).

Studies examining the role of predators in driving biodiversity and coexistence have primarily focused on changes in species richness through mechanisms such as frequency dependence, modification of competition, or prey preference (reviewed in Chesson 2000). Less studied, however, are the effects of predators on beta diversity. We compared alpha diversity, beta diversity, and compositional patterns across each of the four experimental treatments using both incidence and abundance-based metrics. In total, we examined eight different response variables: (1) total abundance of all species (hereafter abundance), (2) species richness (the number of species within a patch uncorrected for differences in abundance), (3) rarefied species richness (the number of species within a patch corrected for abundance), (4) beta diversity based on species incidence (the Jaccard index [ $\beta_{Jac}$ ], a metric focused on the gain or loss of a species), (5) beta diversity based on species incidence but adjusted for the interdependence of alpha and beta diversity [the Raup-Crick index,  $\beta_{RC}$ ; Chase et al. 2011]), (6) beta diversity based on species relative abundance (the Manhattan index [ $\beta_{Man}$ ], focused on changes in relative number of individuals per species), (7) community composition based on species incidence, and (8) community composition based on species relative abundance. (For details on methods used for response variables 4–7 see Anderson et al. 2006, 2011.) The Raup-Crick metric ranges from  $-1$  to  $1$ , and is interpreted differently from Jaccard's dissimilarity. Values close to zero are representative of communities that are assembled at random, values greater than 0 are estimated as more dissimilar than expected by chance, and values less than zero are estimated as less dissimilar than expected by chance (Chase et al. 2011). We applied a square-root transformation to abundance and richness to improve normality and homogeneity of variance. In addition, we applied a square-root transformation to the species matrix prior to calculations of distance matrices associated with the Manhattan index ( $\beta_{Man}$ ) to adjust for shifts in variability that might be driven by concurrent shifts in mean abundance.

To test the effects of patch size and groupers we used a two-factor ANOVA (grouper presence or absence crossed with small or large patch size) to analyze each of the univariate response variables (i.e., abundance, richness, and rarefied richness), and multivariate permutation tests (PERMADISP and PERMANOVA; Anderson et al. 2006, 2011) to examine the effects of patch size and grouper presence on beta diversity and mean community composition. We used the statistical programming environment R 2.12.2 (R Development



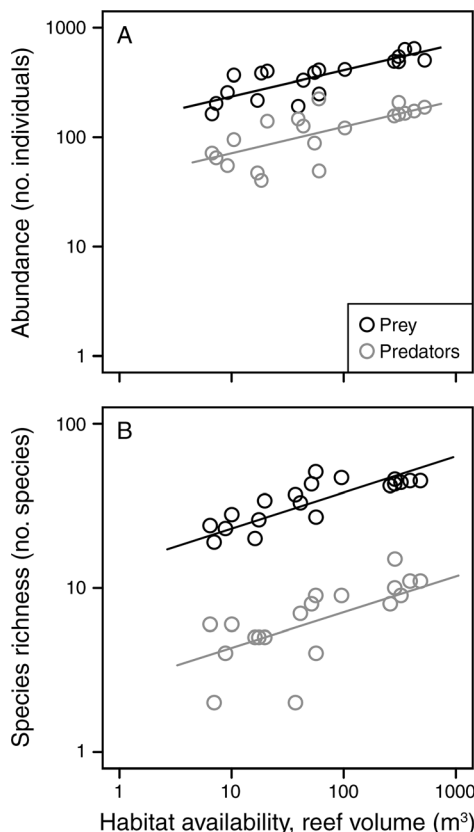


FIG. 1. Relationship between habitat availability, measured as total coral volume (i.e., live coral volume + dead coral volume), and (A) the abundance and (B) species richness of predators (gray symbols) and prey (black symbols) from 19, 15  $\times$  10 m plots across the northern shore of Moorea. Regression lines in panels (A) and (B) share the same slope because there was no detectable difference between the slopes of the abundance–area or species–area relationships for predators relative to prey. Note that data in each panel are plotted on  $\log_{10}$ – $\log_{10}$  scale.

Core Team 2013); the “vegan” package was used for multivariate community analysis and graphics.

To test the effects of patch fragmentation and groupers we compared whether the effect of groupers on prey communities on large reefs (1 m<sup>3</sup>) differed from the effect of groupers on pairs of small reefs (i.e., two small 0.5-m<sup>3</sup> reefs considered as one large but fragmented reef area). In the analysis of habitat fragmentation, we examined all possible combinations of the 12 small experimental reefs as pairs equivalent to 6 large reefs by sampling three pairs of small reefs from each of the grouper ( $n = 6$ ) and no-grouper ( $n = 6$ ) small-patch treatments with replacement for 10 000 iterations and replacement conducted between iterations. During each iteration, the two-factor ANOVA approach (or its multivariate analogue) was applied on each of the eight measured response variables. We used a randomization test to compare the observed  $F$  statistics to those from

the 10 000 iterations to obtain a  $P$  value. Note that our approach to examining the interactive effects of groupers and fragmentation assumes the absence of grouper–grouper interactions such as interference or cooperation. While the overall density of groupers is identical on two pooled small reefs and one large reef (2 groupers per 1-m<sup>3</sup> reef), interactions between the two groupers on large reefs could confound the interpretation of the interaction between groupers and fragmentation effects. Although cooperative and antagonistic interactions between predator species have been documented on reefs (Hixon and Carr 1997, Bshary et al. 2006, Stallings 2008), potential intraspecific predator–predator interactions that cause predation rates to deviate from independent effects have been relatively poorly studied in reef fish. We know of only one species (the arc-eye hawkfish, *Paracirrhites arcatus*) where intraspecific predator–predator interactions have been studied in reef fish systems, and studies at the population (Stier et al. 2013a) and community (Stier et al. 2013) level both found that predators foraged identically when they were alone or with conspecifics. Interactions between peacock groupers are very conspicuous, where the side of their body turns a white color and their “tiger” stripes are easily visible. In periodic dives to examine the integrity of the cages we observed no evidence of aggressive coloration, or any cooperative or antagonistic interactions in treatments where two groupers were present in the same cage; however, we do not know precisely whether groupers changed their foraging behavior in the presence of a second conspecific. We therefore limit our interpretation of the predation–fragmentation interaction to the assumption of independent grouper effects.

## RESULTS

### *Survey to assess effect of predators on the prey species–area relationship*

Analysis of the survey data revealed a strong positive correlation between habitat availability and both prey abundance and predator abundance, and the effect of habitat availability on abundance was equivalent for both trophic levels (Fig. 1A; ANCOVA, habitat  $\times$  trophic level,  $F = 0.566$ ,  $P = 0.58$ , common slope = 1.75 [1.39, 2.13]). Survey data also revealed a strong positive correlation between habitat availability and species richness of both predators and prey, with no differences between trophic levels in the rate at which richness increased with habitat availability (Fig. 1B; ANCOVA, habitat  $\times$  trophic level,  $F = 0.53$ ,  $P = 0.60$ ; common slope = 1.56 [1.30, 1.83]). There was no interaction between habitat availability and residual predator abundance on either prey abundance ( $F_{1,15} = 0.509$ ,  $P = 0.62$ ) or prey richness ( $F_{1,15} = 0.12$ ,  $P = 0.91$ ). There was no evidence for an independent top-down effect of predator abundance (residual) on either prey abundance ( $F_{1,15} = 0.63$ ,  $P = 0.54$ ) or prey species richness ( $F_{1,15} = 0.14$ ,  $P = 0.89$ ).

*Field experiment to separate effects of habitat and groupers on abundance and diversity*

In surveys conducted three months after the establishment of the 18 experimental reefs, we counted a total of 366 fishes from 11 different families and 42 species (Appendix E). Five families made up 81% of the total fish abundance: 32% damselfishes (Pomacentridae), 16% gobies (Gobiidae), 15% snappers (Lutjanidae), 10% pufferfishes (Tetraodontidae), and 8% surgeonfishes (Acanthuridae). The effects of groupers and patch characteristics (size, fragmentation) on each of the eight response variables were independent ( $P > 0.20$  for interaction term in all analyses); therefore we summarize each of the three main effects (groupers, patch size, patch fragmentation) individually in the following sections.

*Patch size effects*

Collectively, the total reef area provided by the 12 small experimental reefs was equivalent to the total reef area provided by the 6 large experimental reefs. The average abundance of fish on large experimental reefs was greater than the average abundance of fish on small experimental reefs ( $F_{1,14} = 7.10$ ,  $P = 0.02$ ). Prey abundance increased by 36% with the doubling in patch size between small and large experimental reefs (Fig. 2A). Despite having equivalent reef area and greater average fish abundance, larger reefs collectively had 30% lower total diversity (i.e., gamma diversity, the total number of species per treatment) than did pooled small reefs (Appendix E). There was no main effect of patch size for the other response variables (richness,  $F_{1,14} = 0.01$ ,  $P = 0.95$ , Fig. 2B; rarefied richness,  $F_{1,14} = 2.90$ ,  $P = 0.11$ , Fig. 2C;  $\beta_{\text{Jac}}$ ,  $F_{1,14}^{\pi} = 0.042$ ,  $P = 0.84$ ;  $\beta_{\text{RC}}$ ,  $F_{1,14}^{\pi} = 1.44$ ,  $P = 0.269$ ;  $\beta_{\text{Man}}$ ,  $F_{1,14}^{\pi} = 0.59$ ,  $P = 0.44$ ; composition (Jaccard),  $F_{1,14}^{\pi} = 1.30$ ,  $P = 0.18$ ; composition (Manhattan),  $F_{1,14}^{\pi} = 0.99$ ,  $P = 0.36$ ). ( $F^{\pi}$  is the pseudo  $F$  ratio [Chase 2007]). While we first analyzed our data with habitat coded as categorical variables (i.e., small and large), in a second analysis we estimated the slope of the relationship between log species richness and log habitat size and found no difference in  $Z$  values for each of the grouper treatments or difference from zero ( $Z_{\text{Pred}} = 0.18 \pm 0.59$ ;  $Z_{\text{No Pred}} = -0.05 \pm 0.22$ ).

*Fragmentation effects*

There was no significant effect of fragmentation on prey abundance ( $P = 0.25$ , Fig. 2A). Fragmented patches (i.e., paired, small experimental reefs) had significantly higher species richness ( $P = 0.05$ , Fig. 2B) than unfragmented patches (i.e., large experimental reefs), but this effect was nonsignificant when abundance was controlled for using rarefaction (rarefied richness,  $P = 0.11$ , Fig. 2C). Beta diversity ( $\beta_{\text{Jac}}$ ,  $P = 0.18$ ;  $\beta_{\text{Man}}$ ,  $P = 0.27$ ) was unaffected by fragmentation. There were, however, main effects of fragmentation on mean community composition based on species incidence ( $P = 0.049$ , Fig. 3A, C) and marginally significant effects on

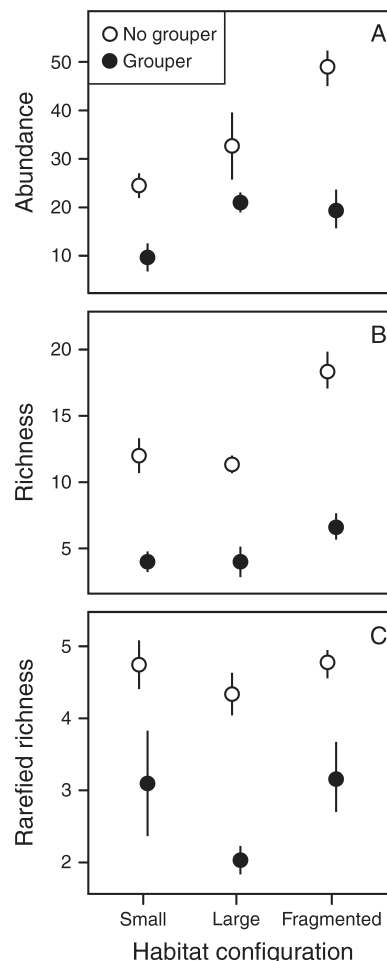


FIG. 2. Effect of habitat configuration and groupers on (A) prey total abundance, (B) species richness, and (C) rarefied species richness (the number of species within a patch corrected for abundance; see *Methods: Data analysis*) of fishes (mean  $\pm$  SE). Effects were determined after three months of colonization to small, large, and fragmented patches in the presence (solid circles) and absence (open circles) of groupers.

mean community composition based on species relative abundance ( $P = 0.075$ , Fig. 3B). Specifically, relative to fragmented reefs (i.e., pairs of small reefs) of the same area, whole reefs (i.e., large experimental reefs) had a greater relative abundance of breams (Lethrinidae, 65% more), butterflyfishes (Chaetodontidae, 16% more), gobies (Gobiidae, 21% more), and damselfishes (Pomacentridae, 4% more), but fewer soldierfishes (Holocentridae, 46% fewer), surgeonfishes (Acanthuridae, 16% fewer), and pufferfishes (Tetraodontidae, 35% fewer).

*Grouper effects*

Groupers reduced gamma diversity (i.e., the total number of species across all reefs) by 45% (Appendix E) and prey abundance by 50% ( $F_{1,14} = 15.88$ ,  $P = 0.001$ , Fig. 2A). Across both small and large experimental reefs, groupers reduced species richness by 66% ( $F_{1,14} =$

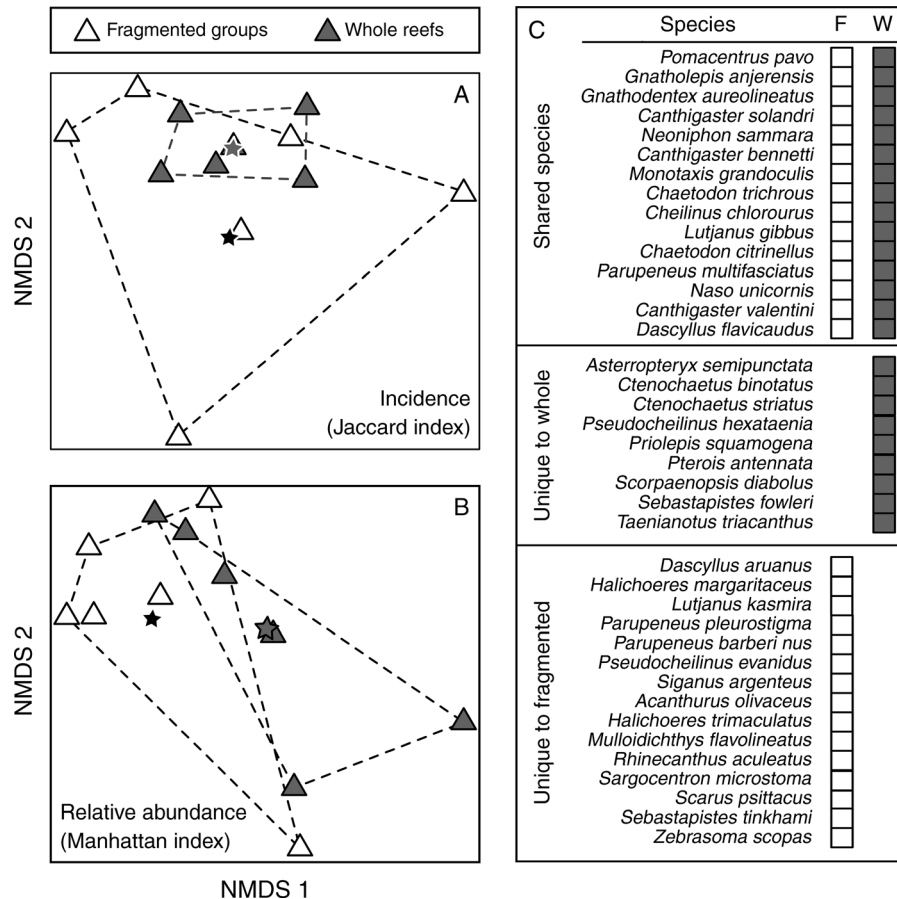


FIG. 3. Main effects of fragmentation on prey community composition based on (A) species incidence and (B) species relative abundance after three months of colonization. Data for the fragmented groups are white; data for whole reefs are gray. Stars signify a two-dimensional representation of the multivariate mean, and the areas of convex hulls are representative of relative beta diversity between treatments. Increased overlap in hulls indicates that reefs (points) in different groups were similar in composition. Also shown is a tile plot (C) that shows the shared and unique species to the fragmented “F” and whole “W” treatments, which are responsible for significant differences in mean community composition based on species incidence in panel A. Note that significant differences in mean community composition based on species incidence were tested using randomization (see *Methods*); therefore data shown here represent nonmetric multidimensional scaling (NMDS) conducted on a species matrix that was the average of all 10 000 randomizations.

50.43,  $P = 0.001$ , Fig. 2B) and decreased rarefied richness (i.e., adjusting for differences in abundance between grouper and no-grouper treatments) by 36% ( $F_{1,14} = 11.52$ ,  $P = 0.007$ , Fig. 2C). The persistent negative effect of groupers on species richness beyond sampling effects (i.e., groupers reduced rarefied richness) suggests that groupers disproportionately affected rare species more than common species; across large and small patches groupers removed 36% of common species (the upper 25% quartile of rank abundance), but reduced rare species (the lower 25%) by 64%.

The presence of groupers significantly affected beta diversity based on both species incidence and species relative abundance. Reefs with groupers had 10% greater variation in species incidence ( $\beta_{Jac}$ ,  $F_{1,14}^{\pi} = 3.74$ ,  $P = 0.05$ , Fig. 4A); however, the increase in  $\beta_{Jac}$  on grouper reefs was caused by a decrease in alpha diversity. When beta diversity was corrected for the

effects of groupers on alpha diversity, reefs without groupers had 77% lower beta diversity than reefs with groupers ( $\beta_{RC}$ ,  $F_{1,14}^{\pi} = 10.67$ ,  $P = 0.004$ , Fig. 4B). Groupers homogenized the relative abundance of species, reducing  $\beta_{Man}$  by 66% ( $\beta_{Man}$ ,  $F_{1,14}^{\pi} = 42.53$ ,  $P = 0.001$ , Fig. 4C). However, effects of groupers on beta diversity were not detected in the fragmentation analysis ( $\beta_{Jac}$ ,  $P = 0.483$ ;  $\beta_{RC}$ ,  $P = 0.24$ ;  $\beta_{Man}$ ,  $P = 0.195$ ), suggesting that pairing small reefs eliminated the effects of groupers on beta diversity observed in the patch size analysis. Groupers also affected mean community composition based on incidence (grouper effect in the patch size analysis,  $F_{1,14}^{\pi} = 5.72$ ,  $P = 0.001$ , Fig. 4D; fragmentation analysis,  $P = 0.003$ ) and relative abundance (patch size analysis,  $F_{1,14}^{\pi} = 5.72$ ,  $P = 0.001$ , Figs. 4E and 5; fragmentation analysis,  $P = 0.002$ ) in similar ways. Of the 42 species of fish observed, 8 species were unique to the experimental reefs with groupers and 24

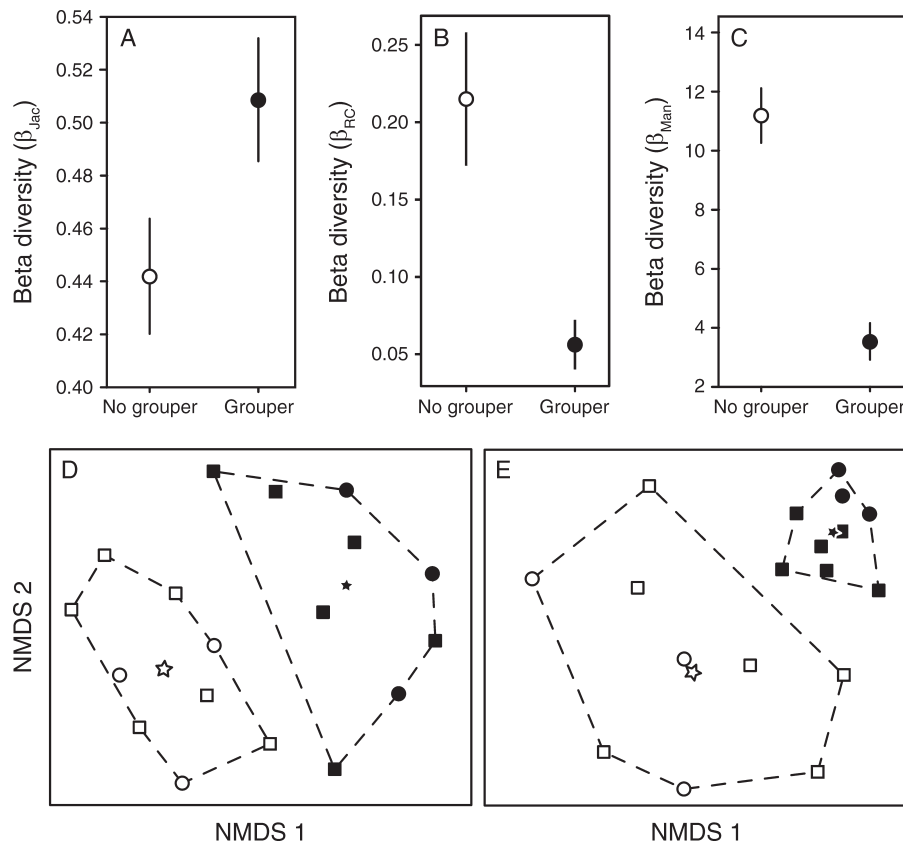


FIG. 4. Composition and beta diversity of fish communities for two metrics (mean  $\pm$  SE) based on species incidence (A, B, D) and species relative abundance (C, E) of communities in the presence (solid symbols) and absence (open symbols) of groupers after three months of colonization. Beta diversity is based on species incidence ( $\beta_{Jac}$ ,  $\beta_{RC}$ ) and relative abundance ( $\beta_{Man}$ ) at three months. Stars signify a two-dimensional representation of the multivariate mean, and the area of convex hulls are representative of relative beta diversity between treatments. Increased overlap in hulls indicates that reefs (a point) in different groups were similar in composition. NMDS represents nonmetric multidimensional scaling.

species were unique to reefs without groupers (Fig. 5C). The remaining species were shared across grouper and no-grouper treatments, but differed in their average abundance ( $F_{1,14} = 9.73$ ,  $P = 0.001$ , Fig. 5B). Compared to no-grouper reefs, grouper reefs had a greater relative abundance of damselfishes (Pomacentridae, 67% more), but fewer gobies (Gobiidae, 30% fewer), brems (Lethrinidae, 5% fewer), butterflyfishes (Chaetodontidae, 7% fewer), soldierfishes (Holocentridae, 6% fewer), surgeonfishes (Acanthuridae, 11% fewer), and pufferfishes (Tetraodontidae, 3% fewer) (Fig. 5A). These shifts in composition are represented at the species level for the eight most abundant species (Fig. 5B).

#### DISCUSSION

Historically, theoretical and empirical studies quantifying interactions between predation and other forces affecting biodiversity have focused on predation–competition interactions (Chase et al. 2002). More recently, theoretical studies have begun to explore additional interactions between predation and factors such as disease (Holt and Roy 2007), abiotic disturbance (Gallet

et al. 2007), and patch size (Ryberg and Chase 2007). However, complementary field experiments exploring these interactions remain limited.

Past research suggests that, in aggregate, predators on prey fish communities in Moorea act as generalists (Heinlein et al. 2010). With a generalist predator, theory predicts that prey fish should have different  $Z$  values in the presence of predators (Ryberg and Chase 2007, Holt 2010). Our experiment suggests that groupers disproportionately affected rare species, which should further magnify the negative effects of groupers on the slope of the species–area relationship by further increasing extinction prey rates. Despite these predictions and knowledge of predator foraging behavior, our experiment demonstrated that, at small spatial scales, predation, patch size, and fragmentation independently affect certain aspects of the reef fish community. The Theory of Island Biogeography and its food web derivative are equilibrium models and may therefore not always apply to experiments or surveys at local spatial scales. Studies documenting a negative effect of predators on  $Z$  values have been conducted at relatively small spatial scales



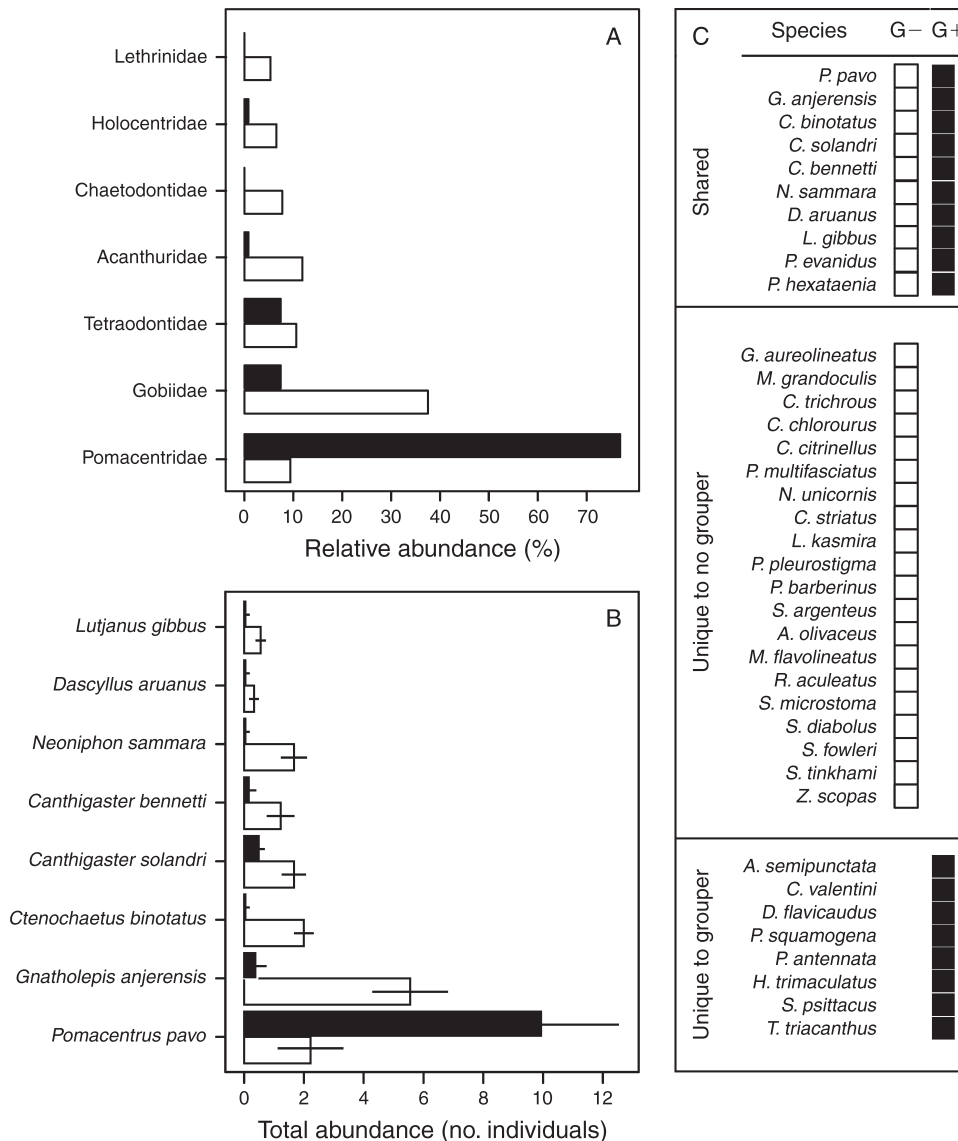


FIG. 5. Effects of predation on the (A) relative abundance (%) of the prey community pooled across all reefs, (B) the mean abundance ( $\pm$ SE) of eight shared species (two shared species were excluded because only one individual was present in each treatment), and (C) the species incidence of all species between grouper and no-grouper treatments. The seven most abundant families of reef fish in panel A comprise  $\sim$ 90% of the total community. Fragmentation data are the mean from resampling pairs of fragmented reefs. In panels A and B, groupers (black) are contrasted to no groupers (white). Tile plot (C) shows the shared and unique species present in the No grouper (G-) and Grouper (G+) treatments (see Fig. 3 for full species names).

such as those in Ryberg and Chase (2007); however, other studies have found that Z values are higher in areas with predators. For example, Östman et al. (2007) found that habitat area was only correlated with prey diversity in the absence of predators in Ozark glades, and for some groups of insects (Homoptera) negative Z values were estimated in the absence of predators, a pattern similar to that observed in our study.

#### Habitat effects

In our experiment a greater abundance of fishes recruited to larger patches relative to smaller patches.

Positive effects of habitat on abundance may occur if larger reefs are larger "targets" for settling fish. Thus larger reefs may have sampled a greater number of larvae (i.e., the "target area" hypothesis [Gilpin and Diamond 1976, Schmitt and Holbrook 2000]). Depending on the extent of the "target area" effect, larger patches also may support greater abundance due to demographic effects. Specifically, larger patches can support larger population sizes if resources are more readily available, and could have lower probabilities of local extinction due to demographic stochasticity. A previous experiment that manipulated habitat and

estimated recruitment in sites of low and high habitat availability found that a combination of target effects and limited crowding is likely responsible for greater abundance. Specifically, a sixfold increase in habitat availability only led to a 1.3-fold increase in settlement, which reduced competition for predator-free space and increased estimates of recruitment for two species also present in our data set (*Dascyllus flavicaudus* and *Halichoeres trimaculatus* [Stier and Osenberg 2010]).

The lack of a discernible increase in species richness between small and large patches in our experiment (i.e., a species–area relationship) was somewhat surprising given the substantial increase in prey abundance and the well-known correlation between reef size and species richness at local (Chittaro 2002) and regional spatial scales (e.g., Tittensor et al. 2007). However, by constructing reefs standardized in coral composition to isolate the demographic effects predicted by trophic biogeography theory, we limited other mechanisms that are thought to contribute to species–area relationships on reefs, such as environmental heterogeneity (Chittaro 2002). For example, as reefs get larger, they often have higher coral diversity, which can attract new species of fish that are associated with only certain species of coral (Holbrook et al. 2008, Messmer et al. 2011). While classic theory of fragmentation suggests negative effects of fragmentation on species diversity when controlled for changes in habitat area, fragmentation can have either positive or negative effects due to increased immigration (Grez et al. 2004), decreases in predator abundance (Hovel and Lipcius 2001), or reduced resource competition (Collins and Barrett 1997, Wolff et al. 1997, Caley et al. 2001). Indeed, on coral reefs, positive effects of fragmentation may be the norm rather than the exception. Early observational studies comparing patch and continuous reefs suggested that patchy reef habitats may exhibit higher abundance and species richness (Ault and Johnson 1998), and a recent experiment that quantified the effects of fragmentation on reef fish communities while controlling for reef area documented positive effects of fragmentation on reef fish abundance and biodiversity of fish communities in Papua New Guinea (Bonin et al. 2011). Similarly, in crustacean communities inhabiting the coral *Stylophora pistillata*, Caley et al. (2001) showed positive effects of reef fragmentation on the abundance of *Trapezia cymodoce*. Both of these studies suggested that alleviated competition on fragmented reef habitats was the likely mechanism driving the positive effects of fragmentation. We observed increases in species richness (strongest in the absence of groupers) and substantial changes in species composition for fragmented patches relative to whole reefs. Reduced competition among territorial damselfish may be a contributing factor to the observed positive effects of fragmentation on richness in our study (e.g., as in Caley et al. 2001, Bonin et al. 2011). Additionally, although the mechanism for this phenomenon remains poorly understood, one explanation for

the observed shifts in community composition is that certain species of fishes preferentially live on small rather than large patches. These corroborative effects of fragmentation identified in our study and the studies discussed above highlight the importance of integrating fragmentation into the trophic biogeography theory that currently focuses solely on effects of habitat area.

Overall, changes in reef size affected abundance but not species richness, whereas reef fragmentation increased species richness and altered species composition. Notably, the lack of a species–area relationship and the observed positive effects of fragmentation on fishes that we document here differ somewhat from other studies of reef fragmentation and habitat loss. For example, habitat loss led to substantial declines in diversity of coral reef fishes (Jones et al. 2004), and fragmentation of coral habitat had no effect on species richness of invertebrate commensals of the coral *Stylophora pistillata* (Caley et al. 2001). Thus, while our results largely concur with Bonin et al. (2011), the differences in the responses of reef fishes compared to invertebrates (a group that constitutes much of the biodiversity on coral reefs) may require unique landscape management strategies.

While patch-scale manipulations can be informative to understand the response of ecological communities at the level of landscapes (McGarigal and Cushman 2002), we cautiously interpret the implications of our study at larger spatio-temporal scales and note that the positive effects of fragmentation on diversity may be transient and will depend on spacing of resulting patches relative to the home range of the organisms in question (Bonin et al. 2011). The benefits of reduced competition for resources in fragmented habitats may only occur early in the colonization period immediately following a large disturbance (e.g., a cyclone or seastar outbreak) that has substantially reduced the total fish density of a reef or in a location where there is heavy recruitment limitation. Once a reef has recovered to moderate densities, competition for resources such as predator-free space may become limiting (sensu Bonin et al. 2011). Long-term demographic studies of corals in the Caribbean suggest that the fragmentation of large corals to smaller corals can substantially reduce the survival probability of a focal coral colony (Edmunds and Elahi 2007); therefore, if fragmented corals inevitably die, those dead corals are likely to exhibit lower fish diversity due to a restricted occupancy of fish species that are habitat generalists (i.e., nonobligate coral dwellers).

The observed shifts in abundance and community structure with changes in patch size and fragmentation are relevant to reef restoration approaches. Reef conservation and restoration are often practiced at the meter scale through subsidizing degraded reef with artificial reef (e.g., reef balls) or through coral propagation. Despite the popularity of artificial reefs as a tool to mitigate reef decline and fragmentation, few studies have addressed the importance of patch size and fragmenta-

tion in reefs, making it difficult to generate practical recommendations for optimizing restoration approaches (Osenberg et al. 2002). Restoration organizations might consider the possible benefits of several small patches relative to single large patches, with the caveat that smaller patches also exhibited substantial shifts in species composition.

### *Grouper effects*

At the community level, groupers acted as environmental filters, reducing species richness, increasing beta diversity, and shifting the composition of prey communities by disproportionately affecting rare species. The mechanism underlying the observed differences in community structure in the presence and absence of groupers may have been driven by a combination of consumptive and nonconsumptive effects. Predatory fishes on reefs primarily reduce prey abundance through consumption of newly settled fishes that are either naïve to the location of refuges, or are inferior competitors for predator-free space (Schmitt and Holbrook 1999, Holbrook and Schmitt 2002, Almany and Webster 2006). Evidence for the capacity of prey to preferentially settle to reefs without predators is mixed. Recent work has found settling fishes can avoid predators using olfactory cues (Dixon et al. 2010, Vail and McCormick 2011); however, other, similar studies found no effect of caged predators on settlement rates (Almany 2003). Lastly, the higher abundance of the territorial damselfish *Pomacentrus pavo* on patches with groupers may also have inhibited settlement by other later-arriving species by making newly settled fishes more susceptible to predation, or through direct aggressive interactions (sensu Almany 2004), further contributing to the decrease in prey diversity in the presence of groupers. Therefore, the observed predator-driven shifts in abundance and diversity may have been driven by postsettlement predation, settlement preference of prey species, or indirect negative effects of predators through increasing the abundance of *P. pavo*.

On our experimental reefs, groupers reduced prey diversity and shifted the composition of prey communities by disproportionately affecting rare species. Although less common than generalist predation, higher relative consumption of rare species has previously been described in other systems, including lizard predation on spiders (Spiller and Schoener 1998), and for other predatory fishes on coral reefs in both the Bahamas and Great Barrier Reef (Almany and Webster 2004, Almany et al. 2007). This “oddity effect” may be particularly prevalent when predators are hunting individuals within an aggregation (e.g., shoaling fishes or herding ungulates) where some individuals differ substantially in behavior, morphology, or coloration. Alternatively, it is possible groupers prefer species that are more rare and/or larger in body size. Some of the rarer species in our data set also tend to be larger in body size (e.g., surgeonfishes), and may therefore offer a

greater energetic return (Almany and Webster 2004, Almany et al. 2007).

Extensive analysis of diets of peacock groupers in Hawaii corroborates the findings we present here and points towards prey selectivity rather than size selectivity. Size-specific predation was species dependent, with a preference for smaller species of surgeonfish (Acanthuridae), butterflyfish (Chaetodontidae), and parrotfish (Labridae) (Dierking et al. 2009). In addition, the low preference observed for damselfish as a dietary item may explain the high abundance of *P. pavo* on grouper plots in our experiment relative to the nongrouper plots, where this weak space competitor was likely excluded by larger-bodied, stronger competitors. Furthermore, *P. pavo* may have actively selected reefs with groupers if groupers offer a refuge from competition or other predators (e.g., as has been shown in birds [Uchida 1986, Haemig 1999]).

Reefs with groupers exhibited a small (but significant) increase in incidence-based beta diversity measured as the Jaccard's dissimilarity ( $\beta_{JAC}$ ); therefore, the observed pattern was a higher level of species turnover among reefs with groupers. However, this increase in  $\beta_{JAC}$  was likely driven by the substantial decrease in alpha diversity (Fig. 2B), which can lead to a corresponding increase in beta diversity due to the interdependency of alpha and beta diversity (Chase et al. 2011). When we used the Raup-Crick metric to adjust beta diversity estimates for the lower alpha diversity on reefs with groupers, the qualitative effect of groupers on beta diversity reversed, with strong negative effects of groupers on beta diversity ( $\beta_{RC}$ ). Significantly lower Raup-Crick beta diversity in the presence of groupers suggests that reefs with groupers are more similar to communities assembled at random relative to patches without predators.

Our findings contrast the results of observational and experimental studies that quantified the effects of fish predators on diversity partitioning and community assembly in pond invertebrate communities. Chase et al. (2009) similarly found decreased gamma diversity, Jaccard's beta diversity, and species richness in the presence of fish predators, but in contrast found that predators increased Raup-Crick beta diversity, suggesting pond communities with fish were more deterministically assembled than fishless ponds (Chase et al. 2009). We hypothesize that the near-random assembly of reef fish communities in the presence of groupers is a product of reduced community size. Smaller community size can dampen the role of competitive asymmetry on assembly, thereby increasing the relative importance of stochastic assembly (Orrock and Fletcher 2005, Chase 2010, Orrock and Watling 2010). Thus, our study supports the Trophic Biogeography Theory predictions regarding the effects of predators on diversity partitioning (i.e., affecting  $\alpha$ ,  $\beta$ , and  $\gamma$ ) proposed by Ryberg et al. (2012), and furthermore documents a novel role of predators in promoting stochastic community assembly.

Nearly all grouper species are generalist mesopredators. Recent studies have shown that the abundance of mesopredators on Pacific reefs is positively correlated to increased fishing pressure (e.g., Sandin et al. 2008), and that mesopredators can reduce diversity and alter fish community structure (Stallings 2008). Furthermore, the grouper focused on here (*Cephalopholis argus*) is of particular interest because in 1956 and 1961, 2385 individuals were purposely introduced from Moorea, French Polynesia, into Hawaii (Oahu and Hawaii) as a targeted fisheries species (Randall 1987). This species is now among the most dominant species on the main Hawaiian islands, and has been a disappointment as a fishery, because of concern over bioaccumulation of the neurotoxin ciguatera (Dierking 2007). Recent evaluation of *C. argus* populations on the west coast of Hawaii suggest populations have exploded in the ~50 years since their introduction to an estimated 56 290 individuals (Dierking 2007). To feed such an extraordinary population increase takes an estimated  $\sim 8 \times 10^6$  prey (Dierking 2007). Larger top predators are present but at low densities in Moorea, a phenomenon that likely promotes high *C. argus* density; high densities of *C. argus* are also additionally facilitated by limited fishing pressure due to an estimated 100-fold higher prevalence of ciguatera in Moorea populations relative to Hawaii (Dierking 2007). The functional consequences of shifts in community structure (e.g., changes in abundance or diversity of lower trophic levels) driven by these large populations of selective intermediate predators are poorly understood. We observed grouper-induced shifts in community structure, particularly an increase in damselfishes (planktivores) and decreases in surgeonfishes (herbivores) and gobies (benthic invertivores). These changes in community structure suggest that reefs with an elevated abundance of mesopredators may experience modified ecosystem function (e.g., changes in plankton flux, benthic invertebrate abundance, and primary production). Future work will be required to quantify the functional consequences of such substantial shifts in fish community structure for the larger reef community.

In conclusion, our study reveals that both predation and habitat characteristics have strong, but independent, effects on the abundance, diversity, and composition of reef fishes. This finding indicates that communities at the local scale may deviate from some trophic biogeography predictions, suggesting that additional work is necessary to link biogeography with food web interactions at local scales. We do, however, find support for other aspects of trophic biogeography theory, in particular, the predicted effect of predation in driving the partitioning of diversity and community assembly (Ryberg et al. 2012). Our study is among the first studies in marine systems to simultaneously examine the importance of trophic interactions and landscape heterogeneity in driving marine communities. Understanding the nature of patch characteristics and predator effects at local scales can

provide useful insight into our ability to understand how human-driven shifts in the abundance of predators (either through fishing pressure or species introductions) and size and configuration of patches at large spatial scales may modify the dynamics of organisms in demographically open systems.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Trophic level assignments from surveys ([Ecological Archives E095-111-A1](#)).

### Appendix B

Reef configuration ([Ecological Archives E095-111-A2](#)).

### Appendix C

Coral colony size frequency distribution ([Ecological Archives E095-111-A3](#)).

### Appendix D

Predation and rarefaction ([Ecological Archives E095-111-A4](#)).

### Appendix E

Total prey colonization ([Ecological Archives E095-111-A5](#)).

## APPENDIX A: TROPHIC LEVEL ASSIGNMENTS FROM SURVEYS

Assignment of trophic level for species observed in surveys. Trophic level was assigned from mining the fishbase database (<http://fishbase.org>)

Family	Species	Predator or Prey	Fishbase (TL)
Acanthuridae	<i>Acanthurus lineatus</i>	prey	2
Acanthuridae	<i>Acanthurus nigricans</i>	prey	2
Acanthuridae	<i>Acanthurus nigricauda</i>	prey	3
Acanthuridae	<i>Acanthurus nigrofuscus</i>	prey	2
Acanthuridae	<i>Acanthurus olivaceus</i>	prey	2.2
Acanthuridae	<i>Acanthurus pyroferus</i>	prey	2
Acanthuridae	<i>Acanthurus triostegus</i>	prey	2
Acanthuridae	<i>Ctenochaetus binotatus</i>	prey	2
Acanthuridae	<i>Ctenochaetus flavicauda</i>	prey	2.2
Acanthuridae	<i>Ctenochaetus striatus</i>	prey	2
Acanthuridae	<i>Naso annulatus</i>	prey	2
Acanthuridae	<i>Naso lituratus</i>	prey	2.3
Acanthuridae	<i>Zebrasoma scopas</i>	prey	2
Apogonidae	<i>Pristiapogon exostigma</i>	predator	3.7
Apogonidae	<i>Pristiapogon fraenatus</i>	predator	3.5
Apogonidae	<i>Pristiapogon kallopterus</i>	predator	3.5
Apogonidae	<i>Ostorhinchus nigrofasciatus</i>	predator	3.6
Apogonidae	<i>Ostorhinchus novemfasciatus</i>	predator	4
Apogonidae	<i>Nectamia savayensis</i>	prey	3.3
Apogonidae	<i>Cheilodipterus quinquelineatus</i>	predator	3.8
Aulostomidae	<i>Aulostomus chinensis</i>	predator	4.2
Balistidae	<i>Balistapus undulatus</i>	prey	3.4
Balistidae	<i>Melichthys vidua</i>	prey	3.4
Balistidae	<i>Rhinecanthus aculeatus</i>	prey	3.3
Balistidae	<i>Sufflamen bursa</i>	prey	3.1
Blenniidae	<i>Atrosalarias fuscus</i>	prey	2
Blenniidae	<i>Plagiotremus tapeinosoma</i>	predator	3.8
Bothidae	<i>Bothus pantherinus</i>	predator	3.5
Callionymidae	<i>Callionymus simplicicornis</i>	prey	3.1

Caracanthidae	<i>Caracanthus maculatus</i>	prey	3.2
Carangidae	<i>Caranx melampygus</i>	predator	4.5
Chaetodontidae	<i>Chaetodon citrinellus</i>	prey	3.1
Chaetodontidae	<i>Chaetodon lunula</i>	prey	3.4
Chaetodontidae	<i>Chaetodon lunulatus</i>	prey	3.3
Chaetodontidae	<i>Chaetodon ornatissimus</i>	prey	3.3
Chaetodontidae	<i>Chaetodon quadrimaculatus</i>	prey	3.3
Chaetodontidae	<i>Chaetodon reticulatus</i>	prey	2.6
Chaetodontidae	<i>Chaetodon unimaculatus</i>	prey	3.1
Chaetodontidae	<i>Chaetodon vagabundus</i>	prey	3.3
Chaetodontidae	<i>Forcipiger longirostris</i>	predator	3.5
Chaetodontidae	<i>Heniochus chrysostomus</i>	prey	3.3
Cirrhitidae	<i>Paracirrhites arcatus</i>	predator	3.6
Congridae	<i>Conger cinereus</i>	predator	4.4
Fistulariidae	<i>Fistularia commersonii</i>	predator	4.3
Gobiidae	<i>Coryphopterus neophytus</i>	prey	2.6
Gobiidae	<i>Ctenogobiops feroculus</i>	prey	3.3
Gobiidae	<i>Gnatholepis anjerensis</i>	prey	2.2
Holocentridae	<i>Myripristis berndti</i>	predator	3.7
Holocentridae	<i>Myripristis kuntze</i>	prey	3.3
Holocentridae	<i>Neoniphon argenteus</i>	predator	4
Holocentridae	<i>Neoniphon opercularis</i>	predator	3.6
Holocentridae	<i>Neoniphon sammara</i>	predator	3.6
Holocentridae	<i>Sargocentron caudimaculatum</i>	predator	3.9
Holocentridae	<i>Sargocentron microstoma</i>	predator	3.6
Holocentridae	<i>Sargocentron spiniferum</i>	predator	3.5
Holocentridae	<i>Sargocentron tiere</i>	predator	3.5
Holocentridae	<i>Sargocentron tiereoides</i>	predator	3.6
Labridae	<i>Bodianus axillaris</i>	prey	3.4
Labridae	<i>Cheilinus chlorourus</i>	prey	3.4
Labridae	<i>Cheilinus oxycephalus</i>	prey	3.3
Labridae	<i>Cheilinus trilobatus</i>	predator	3.5
Labridae	<i>Coris aygula</i>	prey	3.4
Labridae	<i>Coris gaimard</i>	predator	3.5
Labridae	<i>Cymolutes praetextatus</i>	predator	3.5

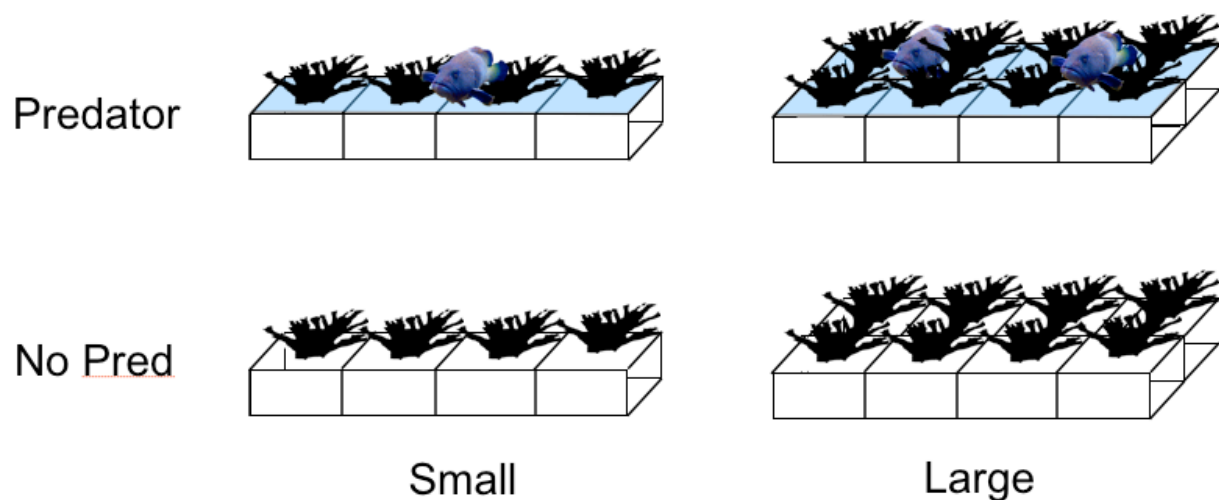


Labridae	<i>Epibulus insidiator</i>	predator	3.8
Labridae	<i>Gomphosus varius</i>	predator	3.6
Labridae	<i>Halichores hortulanus</i>	prey	3.4
Labridae	<i>Halichores marginatus</i>	prey	3.3
Labridae	<i>Halichores trimaculatus</i>	predator	3.5
Labridae	<i>Hologymnosus annulatus</i>	predator	4.2
Labridae	<i>Pseudocheilinus evanidus</i>	predator	3.5
Labridae	<i>Pseudocheilinus hexataenia</i>	prey	3.2
Labridae	<i>Pseudojuloides atavai</i>	prey	3.4
Labridae	<i>Stethojulis bandanensis</i>	prey	3.2
Labridae	<i>Thalassoma amblycephalum</i>	prey	3.1
Labridae	<i>Thalassoma hardwicke</i>	predator	3.6
Labridae	<i>Thalassoma lutescens</i>	prey	3.4
Lethrinidae	<i>Gnathodentex aureolineatus</i>	prey	3.3
Lethrinidae	<i>Monotaxis grandoculis</i>	prey	3.2
Lutjanidae	<i>Lutjanus fulvus</i>	predator	4.1
Microdesmidae	<i>Gunnellichthys monostigma</i>	prey	3.3
Mullidae	<i>Mulloidichthys flavolineatus</i>	prey	3.3
Mullidae	<i>Mulloidichthys vanicolensis</i>	predator	3.6
Mullidae	<i>Parupeneus barberinus</i>	prey	3.2
Mullidae	<i>Parupeneus cyclostomus</i>	predator	4.2
Mullidae	<i>Parupeneus multifasciatus</i>	predator	3.5
Muraenidae	<i>Echidna nebulosa</i>	predator	4
Muraenidae	<i>Gymnothorax javanicus</i>	predator	3.9
Muraenidae	<i>Gymnothorax meleagris</i>	predator	4.5
Muraenidae	<i>Gymnothorax richardsonii</i>	predator	3.8
Muraenidae	<i>Scuticaria tigrina</i>	predator	3.8
Ostraciidae	<i>Ostracion meleagris</i>	prey	2.9
Pinguipedidae	<i>Parapercis millepunctata</i>	predator	3.5
Pomacanthidae	<i>Centropyge bispinosa</i>	prey	2.8
Pomacanthidae	<i>Centropyge flavissima</i>	prey	2.8
Pomacentridae	<i>Chromis iomelas</i>	prey	2.7
Pomacentridae	<i>Chromis margaritifer</i>	prey	3
Pomacentridae	<i>Chromis viridis</i>	prey	2.4

Pomacentridae	<i>Chrysiptera brownriggii</i>	prey	2.7
Pomacentridae	<i>Dascyllus aruanus</i>	prey	2.5
Pomacentridae	<i>Dascyllus flavicaudus</i>	prey	2.8
Pomacentridae	<i>Plectroglyphidodon lacrymatus</i>	prey	2.2
Pomacentridae	<i>Pomacentrus pavo</i>	prey	3
Pomacentridae	<i>Stegastes albifasciatus</i>	prey	2
Pomacentridae	<i>Stegastes fasciolatus</i>	prey	2.2
Pomacentridae	<i>Stegastes nigricans</i>	prey	2.2
Scaridae	<i>Scarus altipinnis</i>	prey	2
Scaridae	<i>Scarus frenatus</i>	prey	2
Scaridae	<i>Scarus psittacus</i>	prey	2
Scaridae	<i>Scarus sordidus</i>	prey	2
Scorpaenidae	<i>Pterois antennata</i>	predator	3.6
Scorpaenidae	<i>Pterois radiata</i>	predator	3.6
Scorpaenidae	<i>Scorpaenodes guamensis</i>	prey	3.4
Scorpaenidae	<i>Sebastapistes cyanostigma</i>	predator	3.8
Scorpaenidae	<i>Synanceia verrucosa</i>	predator	4.2
Serranidae	<i>Cephalopholis argus</i>	predator	4.5
Serranidae	<i>Epinephelus hexagonatus</i>	predator	4.1
Serranidae	<i>Epinephelus merra</i>	predator	3.8
Synodontidae	<i>Saurida gracilis</i>	predator	4.2
Synodontidae	<i>Synodus binotatus</i>	predator	4
Tetraodontidae	<i>Arothron hispidus</i>	prey	3.1
Tetraodontidae	<i>Arothron meleagris</i>	prey	3.4
Tetraodontidae	<i>Canthigaster solandri</i>	prey	3
Zanclidae	<i>Zanclus cornutus</i>	prey	2.9

## APPENDIX B. REEF CONFIGURATION

Individual reefs were constructed of cinder blocks (0.5m x 0.25m x 0.25m). Blocks were placed adjacent to each other with openings facing outward and strapped together with a plastic tie run through the center of the reef. Four or eight blocks formed the small and large reefs, respectively. On the top of each block, a *Porites rus* coral (0.25m diameter) was attached using marine epoxy to provide shelter for reef fishes. All reefs were caged (not shown in the diagram below). We approximated experimental reef volume as a cube (including the 0.25m diameter of the coral) with each block having the dimensions 0.5m x 0.25m x 0.5m (L x W x H), making reefs with 0.5 m<sup>3</sup> and 1.0 m<sup>3</sup>, respectively.



## APPENDIX C: CORAL COLONY SIZE FREQUENCY DISTRIBUTION

Figure C1: Size frequency distribution for all colonies seen in the reef surveys (N = 19 500 m<sup>2</sup> survey plots, 1581 total corals).

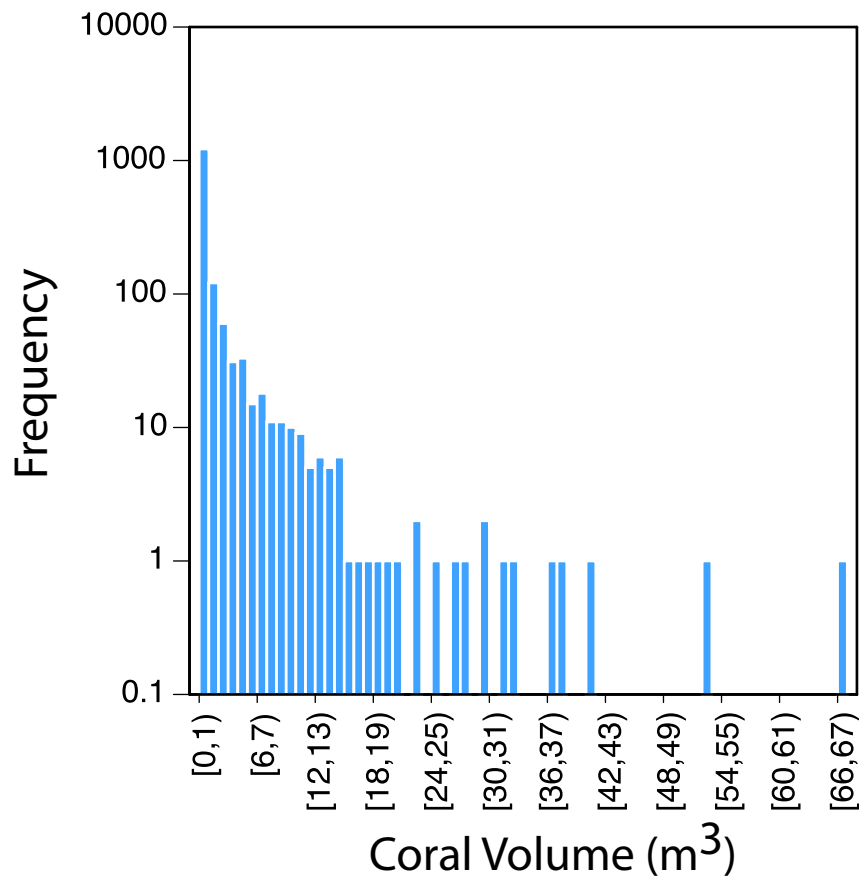
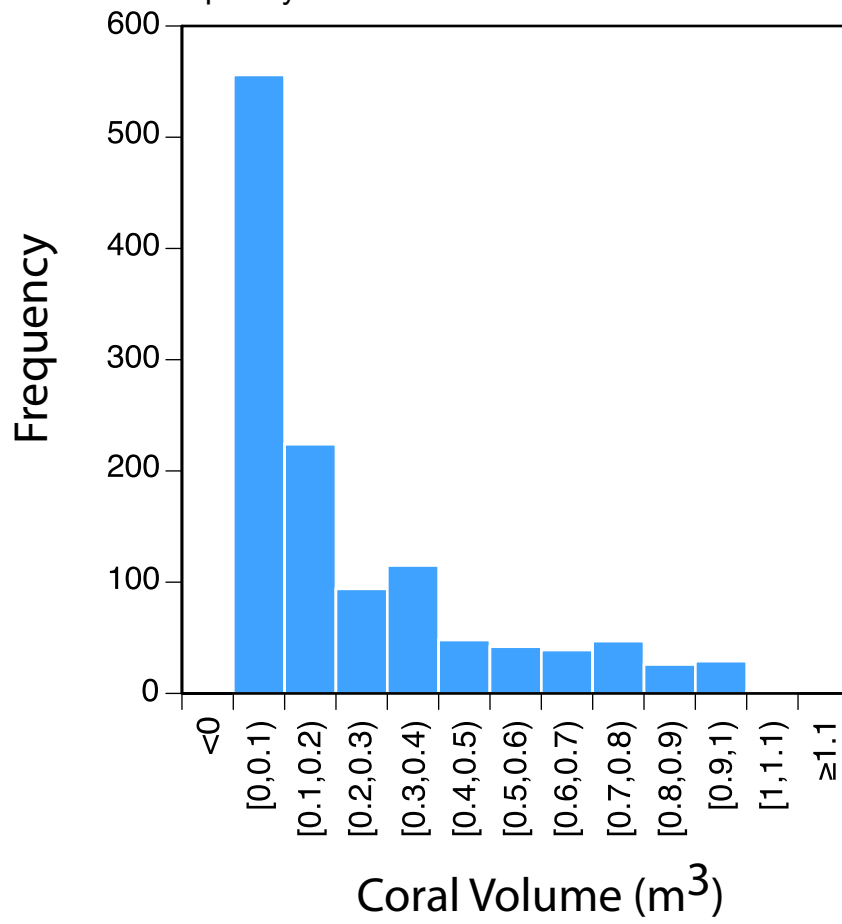




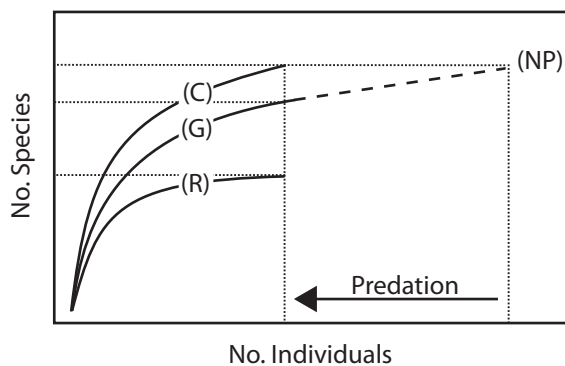
Figure C2: Size frequency distribution of colonies <



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## APPENDIX D: PREDATION AND RAREFACTION

Figure D1: Individual-based rarefaction curves for the three potential ways in which predators can alter prey diversity within a patch (i.e., alpha diversity or species richness). Reproduced from Almany and Webster (2004). A patch that has no predators will have a rarefaction curve labeled NP. On short time scales, predators will nearly always reduce prey abundance (arrow at bottom), but the manner in which this reduced abundance affects species richness depends on whether predators forage as generalists or if they exhibit frequency dependent predation. If predators are generalist they will have rarefaction curve G. If predators disproportionately eat common species they will increase diversity relative to generalist predators (curve C), and if predators disproportionately consume rare species they will produce rarefaction curve R.



Almany, G. R. and M. S. Webster. 2004. Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* **85**:2933-2937.

## APPENDIX E. TOTAL PREY COLONIZATION

Table E1: Colonization of all recorded species of fish summed over 18 reefs for small and large patches in the absence and presence of predators.

Family (common name)	Total Colonization			
	No Predator		Predator	
	Small	Large	Small	Large
<i>Genus species</i>				
Holocentridae (Squirrelfishes)				
<i>Neoniphon sammara</i>	9	6	1	0
<i>Sargocentron microstoma</i>	1	0	0	0
Blenniidae (Blennies)				
<i>Petroscirtes xestus</i>	0	1	0	0
Pomacentridae (Damsel-fishes)				
<i>Dascyllus aruanus</i>	3	0	1	0
<i>Dascyllus flavicaudus</i>	0	0	1	1
<i>Pomacentrus pavo</i>	19	1	39	51
Labridae (Wrasses and Parrotfishes)				
<i>Cheilinus chlorourus</i>	4	2	0	0
<i>Halichoeres margaritaceus</i>	1	0	1	0
<i>Halichoeres trimaculatus</i>	0	0	1	0
<i>Pseudocheilinus evanidus</i>	1	0	1	0
<i>Pseudocheilinus hexataenia</i>	1	0	1	0
<i>Scarus psittacus</i>				
Gobiidae (Gobies)				
<i>Asterropteryx semipunctata</i>	0	0	0	4
<i>Gnatholepis anjerensis</i>	31	19	1	3
<i>Priolepis squamogena</i>	0	1	0	0
Tetraodontidae (Pufferfishes)				
<i>Canthigaster bennetti</i>	5	6	2	0
<i>Canthigaster solandri</i>	10	5	4	1
<i>Canthigaster valentini</i>	0	0	1	1
Acanthuridae (Surgeonfishes)				
<i>Acanthurus olivaceus</i>	0	1	0	0
<i>Ctenochaetus binotatus</i>	13	9	1	0
<i>Ctenochaetus striatus</i>	0	2	0	0

<i>Naso unicornis</i>	2	1	0	0
<i>Zebrasoma scopas</i>	1	0	0	0
Chaetodontidae (Butterflyfishes)				
<i>Chaetodon citrinellus</i>	4	1	0	0
<i>Chaetodon trichrous</i>	2	6	0	0
Lethrinidae (Emperorfishes)				
<i>Gnathodentex aureolineatus</i>	18	24	0	0
<i>Monotaxis grandoculis</i>	4	9	0	0
Siganidae (Rabbitfishes)				
<i>Siganus argenteus</i>	2	0	0	0
<i>Siganus spinus</i>	0	1	0	0
Lutjanidae (Snappers)				
<i>Lutjanus gibbus</i>	3	2	1	0
<i>Lutjanus kasmira</i>	2	0	0	0
Mullidae (Goatfishes)				
<i>Mulloidichthys flavolineatus</i>	1	0	0	0
<i>Parupeneus pleurostigma</i>	2	0	0	0
<i>Parupeneus barberinus</i>	2	0	0	0
<i>Parupeneus multifasciatus</i>	3	1	0	0
Scorpaenidae (Scorpionfishes)				
<i>Scorpaenopsis diabolus</i>	0	1	0	0
<i>Sebastapistes fowleri</i>	0	1	0	0
<i>Sebastapistes tinkhami</i>	1	0	0	0
<i>Taenianotus triacanthus</i>	0	0	0	1
<i>Pterois antennata</i>	0	0	0	1
Ballistidae (Triggerfishes)				
<i>Rhinecanthus aculeatus</i>	1	0	0	0
Total Abundance	146	100	56	62
Gamma Diversity	28	22	14	7

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