

Predator density and timing of arrival affect reef fish community assembly

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Abstract. Most empirical studies of predation use simple experimental approaches to quantify the effects of predators on prey (e.g., using constant densities of predators, such as ambient vs. zero). However, predator densities vary in time, and these effects may not be well represented by studies that use constant predator densities. Although studies have independently examined the importance of predator density, temporal variability, and timing of arrival (i.e., early or late relative to prey), the relative contribution of these different predator regimes on prey abundance, diversity, and composition remains poorly understood. The hawkfish (*Paracirrhites arcatus*), a carnivorous coral reef fish, exhibits substantial variability in patch occupancy, density, and timing of arrival to natural reefs. Our field experiments demonstrated that effects of hawkfish on prey abundance depended on both hawkfish density and the timing of their arrival, but not on variability in hawkfish density. Relative to treatments without hawkfish, hawkfish presence reduced prey abundance by 50%. This effect increased with a doubling of hawkfish density (an additional 33% reduction), and when hawkfish arrived later during community development (a 34% reduction). Hawkfish did not affect within-patch diversity (species richness), but they increased between-patch diversity (beta) based on species incidence (22%), and caused shifts in species composition. Our results suggest that the timing of predator arrival can be as important as predator density in modifying prey abundance and community composition.

Key words: coral reefs; diversity; Moorea, French Polynesia; *Paracirrhites arcatus*; predation; priority effects; reef fish; variance.

INTRODUCTION

Predator migration, mortality, and recruitment can lead to temporal variability in predator density, creating a habitat landscape consisting of a mosaic of patches with differing patterns of predator occupancy, mean density, and timing of arrival (relative to prey). Such an assortment of predator patch occupancies may substantially alter the strength of predation, creating distinct patterns of prey abundance, diversity, and composition. Of the numerous studies identifying predation as a key process in prey coexistence, relative abundance, and composition (e.g., Sih et al. 1985, Spiller and Schoener 1998), the majority focus on effects of chronic predator exposure at a constant level (i.e., presence-absence or a gradient of predator densities).

Variability in ecological processes has historically been considered noise; however, more recently, empir-

ical studies of predation (Butler 1989, Navarrete 1996), stress (Benedetti-Cecchi et al. 2006), disturbance (Bishop and Kelaher 2007), phenotypic plasticity (Miner and Vonesh 2004), and plant-herbivore interactions (Atalah et al. 2007) have documented the emergent effects of spatial and temporal variability. These effects of variance are usually explained by Jensen's inequality: if $f(x)$ is nonlinear, then the mean of the function is not equal to the function evaluated at the mean ($\bar{f(x)} \neq f(\bar{x})$). Thus, studies that use a mean predator density (i.e., which focus on $f(\bar{x})$) will not describe the effect of predators when there is substantial variation around $f(\bar{x})$ (see Ruel and Ayres 1999, Inouye 2005). Ecologically, there are many reasons to expect effects of predator density on prey to be nonlinear (Skalski and Gilliam 2001). Temporal variability in predator densities can reduce the strength of the effect of predators by shifting the availability of spatial or temporal refuges for prey. For example, Butler (1989) showed that temporally variable sunfish predation can produce unique macroinvertebrate communities in freshwater lakes relative to communities exposed to chronic sunfish predation. In intertidal invertebrate communities, Navarrete (1996) found that variable densities of whelks (the predator)

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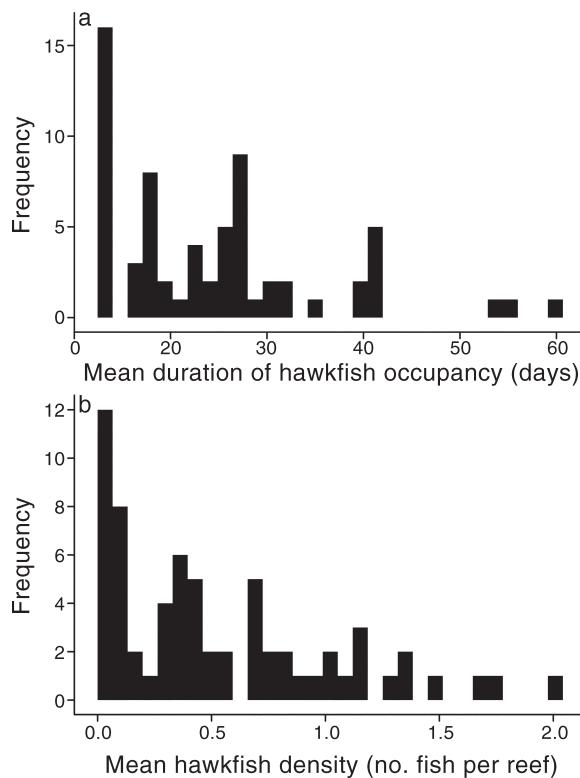


FIG. 1. Summary of surveys of 192 patch reefs on the northern shore of Moorea, Society Islands, from February to June 2005 (approximately two times per week). (a) Frequency distribution of mean (right-censored) duration of hawkfish occupancy events on surveyed reefs. Occupancy events were defined as consecutive survey observations of hawkfish presence on a reef (maximum time between survey observations = 4 days). The duration of each occupancy event is the number of consecutive days of hawkfish presence, assuming that hawkfish were present on days between consecutive sightings. Note that our surveys did not allow us to discern among individual hawkfish; therefore, in some instances individual fish may have been lost and replaced by a new, similar-sized immigrant between census points. The mean duration of occupancy is the average duration of all occupancy events recorded for a given reef. (b) Time-averaged density of hawkfish from surveys of 192 patch reefs in Moorea.

allowed some prey to survive and grow while the whelk was absent and achieve a size refuge when the whelk was later present. This escape from predation modified competitive dynamics and altered the prey community.

In addition to the effects of predator variance in affecting community organization, timing of predator arrival, especially relative to the timing of prey, can also modify the role of predation in community assembly by modifying priority effects (Morin 1984, Louette and De Meester 2007, Hoverman and Relyea 2008), succession (Olito and Fukami 2009), and alternative stable states (Price and Morin 2004). Predators may starve if they arrive in communities before prey, thereby alleviating predation pressure when prey do arrive. Alternatively, when predator and prey arrival times overlap, early predators may have the strongest effects, because prey

will have insufficient time to reach size refugia, develop morphological or chemical defenses, or gain knowledge of predator-free space. Similarly, in size-structured systems, predators and prey may compete early in ontogeny, so early-arriving predators may avoid a competitive bottleneck (Olson et al. 1995).

Reef fish communities are ideal for examining comparative effects of predator density, temporal variability in predation pressure, and timing of predator arrival relative to prey. Piscivores on reefs affect the abundance and diversity of prey (Hixon 1991, Hixon and Beets 1993, Almany and Webster 2006), and exhibit extensive spatio-temporal variability in abundance (Doherty 1991, Connell and Kingsford 1998, Dahlgren and Eggleston 2000). Here, we documented spatial and temporal variation in a predatory reef fish, the hawkfish *Paracirrhites arcatus* (hereafter hawkfish), on natural reefs. Then, we used a field experiment to evaluate the independent and combined effects of predator density, variation in predator density, and timing of predator arrival on abundance and diversity of fish communities.

METHODS

Study system, site, and species

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 0.8–1.3 km wide, and is ~3–7 m deep (Galzin and Pointer 1985). The lagoon is interspersed with patch reefs within a matrix of sand, fine coral rubble, and coral pavement (Galzin and Pointer 1985), with individual patch reefs separated by less than a meter, to tens of meters. Hawkfish are a common, diurnal, sit-and-wait carnivore found perched upon the branches of *Acropora* spp. and *Pocillopora* spp. coral within the lagoon. Their diet includes recently settled fishes, shrimps, and other crustaceans (M. Leray, personal communication).

Quantifying temporal patch occupancy of hawkfish

To quantify natural variability in hawkfish density, we visually censused the abundance of hawkfish on 192 small patch reefs (area = $4.02 \pm 1.67 \text{ m}^2$, mean \pm SD) approximately twice per week from February to June 2005 (126 samples). We found hawkfish on 66 of the 192 surveyed patch reefs; we focus our analysis on 55 of the 66 reefs where hawkfish were observed at least twice. To summarize overall occupancy we calculated the average number of hawkfish per reef. Per reef, hawkfish were observed an average of 13.3 ± 7.7 days of the 126 census days; density ranged from 1 to 5 hawkfish per patch reef (when hawkfish were present: 1.22 ± 0.27 hawkfish, mean \pm 1 SD; Fig. 1b). The 55 reefs were occupied $47\% \pm 27\%$ of the 126 census days with a coefficient of variation of $1.48\% \pm 0.94\%$ (mean \pm 1 SD). To compute patterns of occupancy, we interpolated between observations, assuming that hawkfish were continuously present between observations where they were present, continuously absent between observations where they

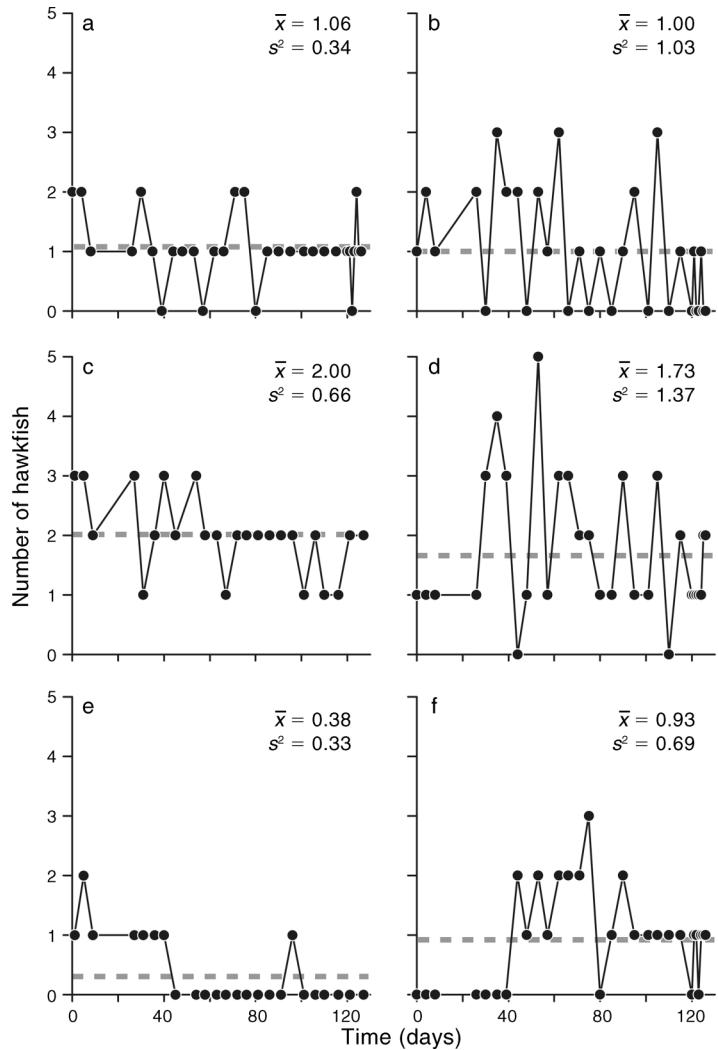


FIG. 2. Examples of six characteristic patterns of patch occupancy by hawkfish from surveys of 192 reefs in the north lagoon of Moorea from February to June 2005. Hawkfish exhibited differences in density: (a, b) low density; (c, d) high density. Hawkfish also exhibited differences in timing of arrival: (e) early; (f) late. Within a given hawkfish density, patches differed in the frequency (i.e., time interval between hawkfish occurrences) at which hawkfish were present, leading to differences in variability: (a) low density, low variability; (b) low density, high variability; (c) high density, low variability; (d) high density, high variability. Not shown (but present) were patches where hawkfish were absent for the entire survey duration. Mean and variance of the number of hawkfish for the survey duration are given in the top right corner of each plot, and the time-averaged mean is plotted as a dashed gray line.

were absent, and arrived or left reefs at a time halfway between successive observations where the occupancy changed. Reefs remained occupied by hawkfish for 23.80 ± 11.02 days (mean ± 1 SD; lower 25% quartile, 16.08 days; upper 25% quartile, 60.67 days; Fig. 1a). On each of the 55 reefs, hawkfish numbers varied through time, idiosyncratically (Fig. 1b). On average, hawkfish were continuously present for 7 ± 16.4 days (lower 25% quartile, 4 days; upper 25% quartile, 15 days) and continuously absent for 5 ± 18.9 days (lower 25% quartile, 4 days; upper 25% quartile, 15 days). We synthesized these observations into six types of natural variation in hawkfish density: (1) low mean predator density associated with low variance (Fig. 2a); (2) low mean predator density associated with high variance (Fig. 2b); (3) high mean predator density associated with low variance (Fig. 2c); (4) high mean predator density associated with high variance (Fig. 2d); (5) early-arriving predators (Fig. 2e); and (6) late-arriving predators (Fig. 2f). Note that the observed variation in the occupancy of hawkfish across the 55 reefs is

primarily a product of hawkfish movement (i.e., immigration and emigration) and to a lesser degree a function of hawkfish recruitment and mortality.

We further explored the prevalence of these different characteristic “early” and “late” hawkfish by examining the survey data for the presence and absence of hawkfish relative to the seven days after the new moons in our data when settling reef fish are most sensitive to predation (Almany and Webster 2006 and citations therein). Hawkfish were continuously present on reefs for the seven days following the new moon (i.e., “early”) for 32% of the periods observed, and continuously present from seven days after the new moon until the next new moon (i.e., “late”) for 22% of the periods observed. They were continuously absent for 35% of the early periods and 24% of the late periods (Fig. 3).

Effects of predator density, temporal variability, and timing of arrival

To quantify the effects of the six types of natural variation in hawkfish density, we constructed an

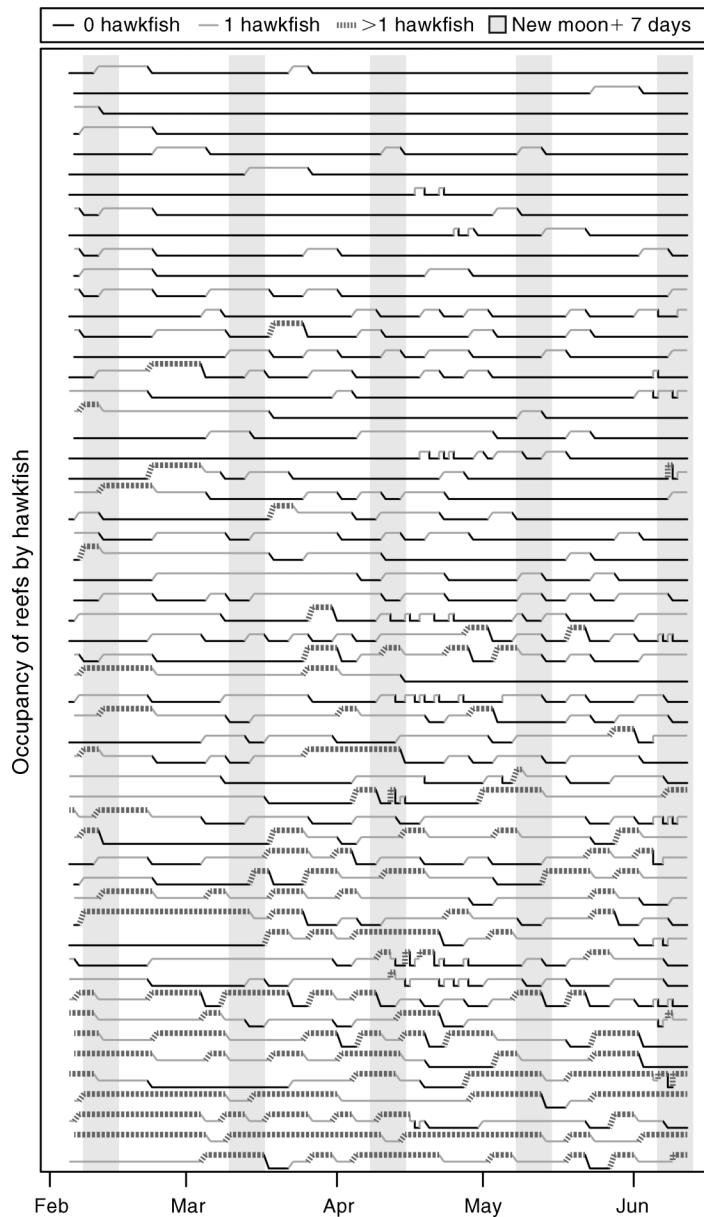


FIG. 3. Temporal trajectories of hawkfish occupancy on 55 reefs relative to the seven days following new moons (shaded gray) from February to June 2005. Each row represents a single reef; line coding represents the hawkfish occupancy category (black line, absent; gray line, 1 hawkfish; heavy dashed line, >1 hawkfish). Reefs are ordered by hawkfish occupancy, with the fewest days occupied by hawkfish at the top and the greatest number of days occupied by hawkfish at the bottom.

experimental array consisting of 35 artificial reefs standardized for size, coral species composition, and complexity. Two rows of reefs were constructed on the northern shore of Moorea in water 3–5 m deep. Rows and artificial reefs within rows were separated from each other by 15 m, and the array was separated from nearby natural reefs by a minimum of 50 m. This separation among reefs provides a distance great enough to ensure independence of replicate reefs and minimize the movement of hawkfish among experimental and natural patch reefs. A study tracking the movement of 24 tagged hawkfish among experimental reefs found no movement among reefs spaced by 15 m (Stier et al. 2012). Each of the 35 reefs consisted of a 1-

m^2 base of six cinder blocks, to which we attached, using marine epoxy, one colony each of: *Pocillopora verrucosa* (15–20 cm diameter), *P. eyduxi* (30–35 cm diameter), massive *Porites* spp. (a complex of *P. lobata* and *P. lutea*; 40–50 cm diameter), *Porites rus* (35–40 cm diameter), and *Montipora* spp. (30–40 cm diameter). We also surrounded each reef with 10 small pieces of coral rubble (~ 20 cm in diameter).

Immediately following reef construction, and prior to colonization by fishes, we implemented a 120-d fish recruitment study consisting of two equal time steps (0–60 days and 60–120 days). Five hawkfish treatments were randomly assigned to each of the 35 patch reefs ($n = 7$ per treatment): (1) Control, zero hawkfish for 120

days; (2) Early Only, two hawkfish from day 0–60 and zero hawkfish from day 60–120; (3) Late Only, zero hawkfish from day 0–60 and two hawkfish from day 60–120; (4) Low Density, one hawkfish for 120 days; and (5) High Density, two hawkfish for 120 days (Fig. 4). This design therefore included three mean hawkfish densities (0, 1, or 2), two temporal variances (0 or nonzero), and two arrival times (early vs. late) (see Appendix A for a diagram).

Hawkfish were collected with hand nets and anesthetic (clove oil) from colonies of wide-branching *Pocillopora* spp. ~800 m from the experimental array. For treatments with two hawkfish (Early Only, Late Only, and High Density), we collected pairs of hawkfish (72.4 ± 4.4 mm SL) occupying the same *Pocillopora* colony. We conducted a press experiment, maintaining each of the five treatments for the entire 120-d duration by monitoring hawkfish treatments every other day (missing hawkfish were replaced within 24–48 h of their disappearance; this happened on nine separate occasions during the 120-d experiment (5 fish after 60 d and 4 fish after 120 d). Divers visually censused the entire fish community at 60 and 120 d. Notably, there was no recruitment of other predator species to our reefs with the exception of one lionfish recruit, which was removed immediately after its settlement.

Defining the prey community

On average, 15% ($SD = 8$) of fish on each reef were adults that were readily distinguishable from newly settled fishes due to their drastic differences in size. The three transient adult species (*Balistapus undulatus*, *Chætodon vagabundus*, and *Centropyge flavissimus*) are commonly seen traversing large sand flats, and occasionally visit patch reefs for shelter. These three transient species made up >95% of the adult fish observed on experimental reefs and did not differ statistically in abundance across hawkfish treatments ($P > 0.3$ for all three species). We believe the observed effects of hawkfish are likely independent of these adult immigrants; therefore, we excluded these individuals from our analyses (to isolate the effect of hawkfish on the early recruitment process), but included all other observed fish. Furthermore, we believe that despite immigration by these three species that the separation of our experimental array from natural reefs by 50 m was adequate to isolate the prey community of interest. Note that seven recruits of each of these species were observed on our reefs (readily distinguishable by their size and coloration from adults) and were therefore included in the analysis. A fraction of the observed prey community was likely either too large (particularly goatfishes [Mullidae] and soldierfishes [Holocentridae]) or too chemically defended (e.g., pufferfishes [Tetraodontidae]) to be consumed by hawkfish. However, we retained these species in our analysis because hawkfish are also capable of indirectly inducing mortality of recently settled fishes by making individuals more susceptible to larger-mouthed transient predators

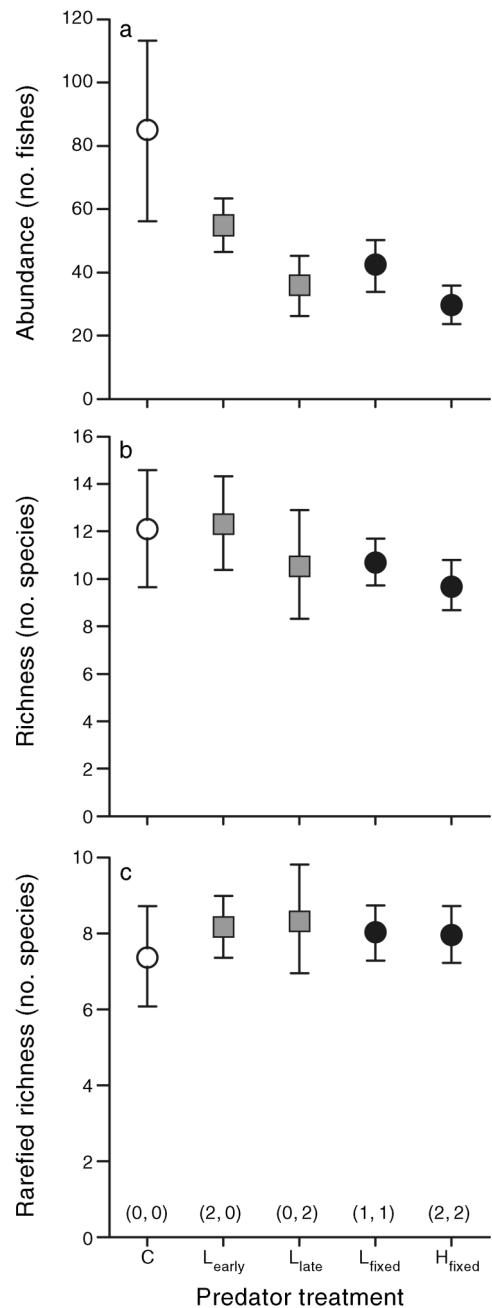


FIG. 4. Mean (± 2 SE) (a) total abundance, (b) species richness, and (c) rarefied species richness of fishes after 120 days in each of five treatments: control (C), early arrival (L_{early}), late arrival (L_{late}), low density (L_{fixed}), and high density (H_{fixed}). Fill shades and symbols represent mean hawkfish densities (0, white; 1, gray; 2, black) and temporal variance in density (circles, fixed; squares, variable), respectively. In panel (c), values in parentheses above each treatment on the x-axis represent the hawkfish density in each treatment at each of the two time steps: 0–60 d and 60–120 d. See the section *Rarefied species richness and beta diversity* for explanation of “rarefaction.”

(Schmitt et al. 2009). Note that these relatively large or highly chemically defended settlers were not particularly abundant in the data set, and the removal of these species does not qualitatively change the effects of hawkfish described below.

Traditionally, investigators have focused on the role of predators in affecting within-patch diversity (species richness) and species composition through mechanisms such as frequency dependence, disturbance, prey preference, or the removal of competitive dominants (reviewed in Chesson 2000). While these mechanisms can cause increases or decreases in species richness, as well as modify the relative abundance or incidence (i.e., presence-absence) of individuals within the average patch, predators can also affect beta diversity (i.e., between-patch diversity). For example, predators can: (1) reduce beta diversity by acting as environmental filters; (2) increase or decrease beta diversity by increasing or decreasing the strength of priority effects; or (3) increase beta diversity by reducing the total number of individuals and thereby increasing the importance of stochastic assembly (Chase et al. 2009 and citations therein). We therefore quantified seven different descriptors of the prey fish community (excluding hawkfish from the sample) within and between patches: (1) total fish abundance, (2) species richness, (3) rarefied species richness (i.e., species richness standardizing the number of individuals across treatments), (4) rarefied beta diversity based on the Jaccard index (β_{Jac}), an index that emphasizes differences in species incidence, (5) rarefied beta diversity based on a metric that emphasizes differences in species relative abundance, the Manhattan index (β_{Man}), (6) community composition based on the Jaccard index, and (7) community composition based on the Manhattan index. Note that tests for differences in community composition are exploring differences among groups in the location of the multivariate mean, whereas tests for differences in beta diversity are comparing variation around the multivariate mean for a given treatment.

We used four planned orthogonal contrasts to examine treatment effects on each of the seven response variables: (1) Hawkfish Contrast, the effect of the presence of hawkfish, [Control] vs. [Early Only, Late Only, Low Density, High Density]; (2) Density Contrast, the effect of hawkfish density, [Early Only, Late Only, Low Density] vs. [High Density]; (3) Variance Contrast, the effect of constant vs. variable hawkfish density, holding means constant, [Low Density] vs. [Early Only, Late Only]; and (4) Timing Contrast, the effect of timing of hawkfish arrival, [Early Only] vs. [Late Only]. Collectively, these contrasts isolate the three characteristics we want to explore: predator density (contrasts 1 and 2), temporal variance (3), and timing of arrival (4). Hereafter we refer to each of these contrasts as the Hawkfish Contrast, Density Contrast, Variance Contrast, and Timing Contrast. Below, we provide more detail on the calculation of each response variable as

well as a description of the associated statistical contrast. In a recent study of hawkfish predation on single prey species, Stier et al. (2012) found no evidence for interference or cooperation among hawkfish as predator densities increased. Therefore, we predict that (1) predation pressure should increase additively with predator density. We also predict that (2) variation in predation pressure will produce unique prey communities by disrupting the establishment of dominant competitors. Finally, we predict that (3) the effects of timing of predator arrival will depend on the characteristics of the prey fish assemblage at the time of hawkfish arrival. Later-arriving predators will have weaker effects than earlier-arriving predators if prey reach a size refuge by colonizing and growing before predators arrive. Alternatively, if reefs are higher in fish density during later time periods, later-arriving predators will have stronger effects than early-arriving predators because reefs with a longer colonization period will have greater competition for predator-free space.

Abundance and species richness

Total fish abundance was calculated by summing the abundance of prey fishes across all prey species on each reef (excluding hawkfish). Similarly, species richness was estimated as the number of species occurring on each reef. Effects of hawkfish contrasts on total abundance were evaluated using a generalized linear model (GLM) with a quasi-Poisson distribution and a log-link (overdispersion parameter estimate, $\theta = 5.48$). Species richness was estimated using linear models.

Rarefied species richness and beta diversity

Estimates of species richness and beta diversity can be sensitive to differences in overall abundances within and among patches. Because predators reduce prey abundance, we expected that hawkfish would reduce species richness, either through frequency dependent foraging (in particular, the preferential consumption of rare species) or simply by reducing overall density (i.e., a sampling effect). If hawkfish were primarily generalist predators, reducing overall density, then among-treatment differences in species richness diversity would disappear after rarefaction (see Almany and Webster 2004). Individual-based rarefaction has classically been used to adjust species richness estimates for differences in abundance of organisms across sites by estimating the mean species richness in repeated subsamples from each site (Gotelli and Colwell 2001). Although the importance of bias in species richness estimates due to differential sample sizes across treatments has been previously recognized, its effect on estimates of beta diversity is less clear. Developing estimates of differences in beta diversity that account for differences in sample size is particularly important in empirical ecology, where manipulating a given ecological process with a focus on changes in species diversity often leads to concurrent shifts in the number of individuals. For example, in this

study, reefs with hawkfish have approximately half as many fish as reefs without hawkfish. Here, we develop and implement a three-step approach to individual-based rarefaction to estimate rarefied species richness (α_{rar}) and beta diversity (β_{Jac} and β_{Man}) that ensures that the number of individuals sampled was comparable across reefs and treatments.

- 1) For each contrast we determined the minimum number of individuals on a reef in *any* treatment, and then randomly subsampled that number of individuals in proportion to their abundance on the focal reef (e.g., for the Timing Contrast we determined the minimum number of individuals across all replicate reefs in both the Early Only and Late Only treatments and then rarefied all reefs to that minimum number of individuals).
- 2) For each treatment (e.g., Early Only), we repeated this subsampling 1000 times. For each replicate, we computed measures of both species richness and beta diversity (the mean bootstrapped distance from each reef to the respective treatment centroid [i.e., distance between each reef's multivariate location and the multivariate location of the mean community composition per treatment]). Because our treatments had unequal sample sizes, we bias corrected the estimated distances to centroid in each of the contrasted groups using a $\text{sqrt}(n/(n-1))$ correction (analogous to the correction applied in the standard estimation procedure for sample standard deviations). This bias correction for beta diversity contrasts based on unequal sample sizes is novel, although the possibility of such bias is mentioned (and dismissed) by Anderson (2001) and this type of bias correction is discussed in more detail (in a different context) by O'Neill and Mathews (2000). An option for applying this bias correction automatically will be available in the *betadisper* function in an upcoming release of the *vegan* package for community analysis (J. Oksanen, *personal communication*).
- 3) Finally, we compared the estimated species richness and beta diversity distributions for each treatment group within a contrast using a two-tailed test.

A reasonable null expectation is that the abundances of individual species follow a Poisson distribution. If so, a reduction in mean abundance of fishes in the presence of hawkfish should be accompanied by a subsequent reduction in the within-reef variance (because the variance of a Poisson distribution is equal to its mean). Reductions in within-reef variance should therefore tend to homogenize the among-reef heterogeneity (i.e., reduce un-rarefied β_{Man}). If the observed decrease in beta diversity is entirely driven by this mean–variance scaling, it should disappear if we remove the mean–variance relationship. We therefore square-root transformed the species matrix prior to the β_{Man} analysis (which should remove the mean–variance scaling for Poisson, or quasi-Poisson, distributed variables).

Species composition

Mean community compositions were compared using PERMANOVA (a nonparametric multivariate permutations ANOVA, Anderson 2001). Similar to MANOVA, PERMANOVA compares dissimilarity variance components within a group vs. between groups; however, rather than using a standard F ratio, a pseudo F ratio (which we call F_{π} , the same as F^{π} in Chase 2007) is calculated through permutations of the dissimilarity matrix.

We used the statistical programming environment R 2.12.2 for the computation of all statistics (R Development Core Team 2011). Specifically, we used the *vegan* package 2.0-2 (Oksanen et al. 2011) for multivariate community analysis and graphics.

RESULTS

Across the 35 experimental reefs, we counted 1709 fishes from 14 different families and 61 species (Appendix B). Out of all the individuals, 81% came from four families: 33% damselfishes (Pomacentridae), 25% gobies (Gobiidae), 12% cardinalfishes (Apogonidae), and 11% wrasses (Labridae). (See Appendix B for a plot of the relative abundance of each species by taxonomic family.) Prey fishes arrived to the reef as settlers, with settlement peaking around the new and full moons. Hawkfish affected abundance, beta diversity, and composition, with no evidence for effects on species richness. We summarize effects on total abundance and diversity below.

Predation intensity: hawkfish contrast and density contrast

Hawkfish density affected abundance, beta diversity, and mean community composition of prey fishes. After 120 d of recruitment, reefs with hawkfish had 50% fewer prey fishes than reefs without hawkfish (Fig. 4a; $t_{32} = 6.18$, $P = 0.01$). Reefs ranged from 6 to 16 species per reef (10 ± 2.5 species, mean \pm SD), but there was no evidence for effects of hawkfish on species richness (Fig. 4b; α , $t_{32} = 1.24$, $P = 0.23$) or rarefied species richness (Fig. 4c; α_{rar} , $t_{32} = -0.64$, $P = 0.53$). Hawkfish did, however, affect beta diversity. Relative to control reefs, reefs with hawkfish had 20.5% higher variation in beta diversity based on species incidence (Fig. 5a, b; β_{Jac} , $F_{\pi, 1,33} = 13.08$, $P = 0.05$) with no effect on beta diversity based on species relative abundance ($P = 0.10$). Additionally, hawkfish led to shifts in mean community composition across treatment reefs based on species relative abundance ($F_{\pi, 1,33} = 7.13$, $P = 0.01$; Appendix B), but not for species incidence ($F_{\pi, 1,33} = 1.13$, $P = 0.31$).

Effects of hawkfish on prey abundance and beta diversity intensified with a doubling in hawkfish density. Reefs with two hawkfish had 33% fewer prey than reefs with one hawkfish (Fig. 4a; $t_{32} = 2.11$, $P = 0.01$). A doubling in hawkfish density also increased beta diversity by 15% based on species incidence (β_{Jac} , $F_{\pi, 1,33} = 2.60$, $P = 0.02$) and reduced spatial variation in species relative

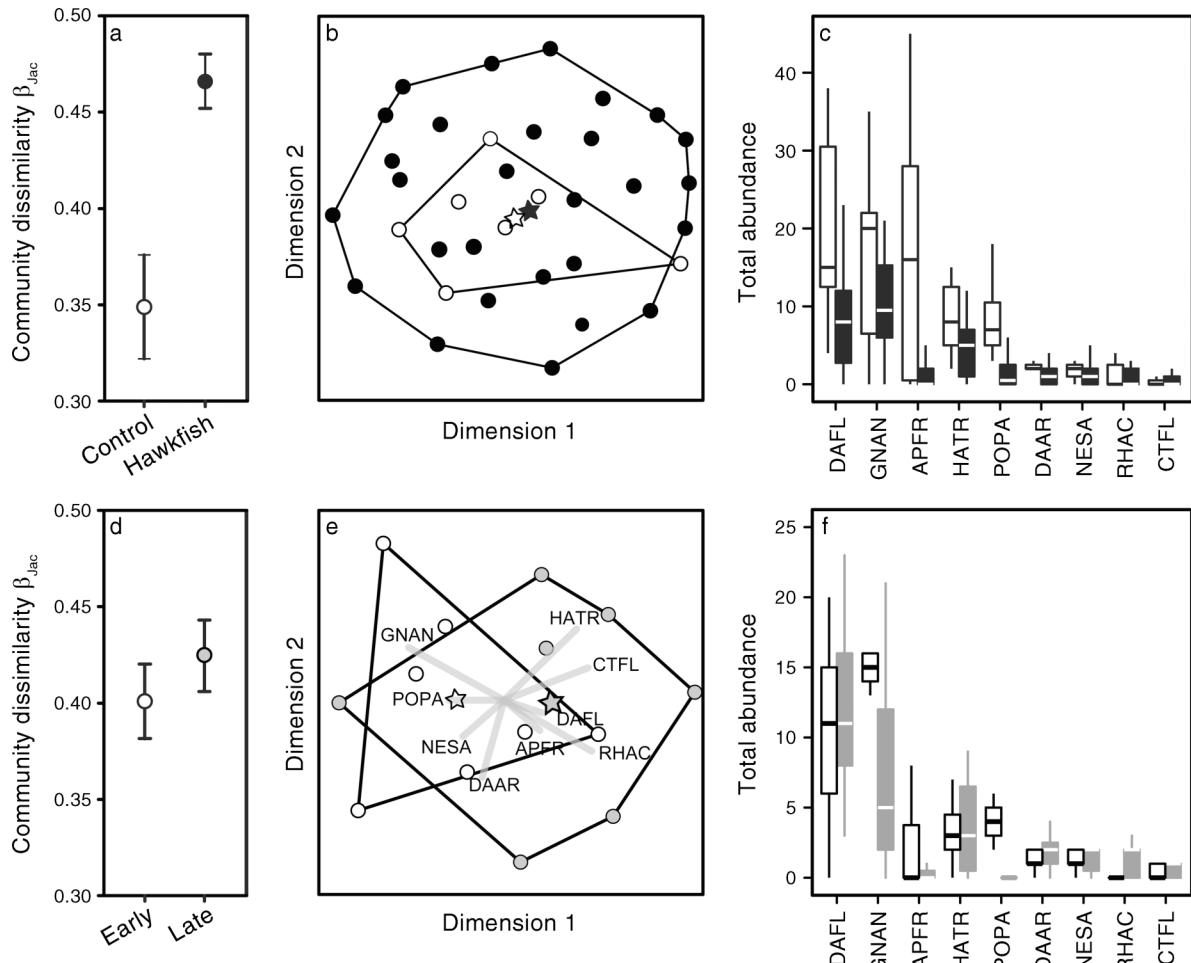


FIG. 5. Beta diversity of species incidence (β_{Jac}) at 120 days. Two contrasts are depicted: Hawkfish Contrast: [Control] vs. [Early Only, Late Only, Low Density, High Density], and the Timing Contrast: [Early Only] vs. [Late Only]. Treatment symbol codes in panels (a)–(c) are control (white) and hawkfish (black), and in panels (d)–(f) are early (white) vs. late (gray). Panels (a) and (d) represent deviation of each reef from treatment mean (mean \pm SE). Panels (b) and (e) are nonmetric multidimensional scaling (NMDS) plots, represented as the average location from 1000 subsamples during rarefaction, with stars at the hull center representing the multivariate mean in two-dimensional space. Increased overlap in hulls indicates that reefs (circles) in different groups were similar in mean community composition; the area of hulls can loosely be interpreted as a measure of beta diversity. In panel (e), vectors and associated species abbreviations (first two letters of genus followed by first two letters of the species) represent the location of the nine most abundant species in multivariate space. These species vectors are representative of species location based on all reefs within a given treatment (i.e., early or late). Boxplots in panels (c) and (f) show differences in total abundance of the top nine species (a visual representation of significant shifts in composition based on species relative abundance). Horizontal lines across the boxes represent the median, the tops and bottoms of the boxes represent the first and third quartile of the data, and the whiskers represent the highest value that is within 1.5 times the interquartile range of the top or bottom. Species shown: *Gnatholepis anjerensis* (GNAN), *Dascyllus flavicinus* (DAFL), *Apogon frenatus* (APFR), *Halichoeres trimaculatus* (HATR), *Pomacentrus pavo* (POPA), *Neoniphon samara* (NES), *Dascyllus aruanus* (DAAR), *Rhinecanthus aculeatus* (RHAC), and *Ctenochaetus flavissimus* (CTFL).

abundance by 10% (β_{Jac} , $P = 0.03$). While the presence of hawkfish affected mean community composition across treatment reefs, this effect was independent of hawkfish density (incidence: $F_{\pi, 1, 26} = 1.01$, $P = 0.44$; relative abundance, $F_{\pi, 1, 26} = 0.94$, $P = 0.49$).

Variance contrast

The abundance, diversity, and composition of fishes on reefs with fixed hawkfish densities [Low Density] were statistically indistinguishable from reefs with

variable hawkfish density [Early Only, Late Only] (abundance, $t_{32} = 0.27$, $P = 0.79$; α , $t_{32} = 1.33$, $P = 0.20$; α_{rar} , $t_{32} = -0.18$, $P = 0.80$; β_{Jac} , $P = 0.39$; β_{Man} , $P = 0.18$; composition [incidence], $F_{\pi, 1, 19} = 1.15$, $P = 0.28$; composition [relative abundance], $F_{\pi, 1, 19} = 1.15$, $P = 0.37$). While reefs with variable hawkfish density [Early Only + Late Only] did not differ from reefs with fixed density [Low Density], considered independently the [Early Only] reefs did have higher average abundance

TABLE 1. Species that were present in both treatments (first column), or unique to Early Only or Late Only treatments.

Shared species	Unique to early treatment	Unique to late treatment
<i>Gnatholepis anjerensis</i>	<i>Rhinecanthus aculeatus</i>	<i>Naso lituratus</i>
<i>Dascyllus flavicaudus</i>	<i>Parupeneus barberinus</i>	<i>Chromis viridis</i>
<i>Apogon fraenatus</i>	<i>Valenciennea strigata</i>	<i>Balistapus undulatus</i>
<i>Halichoeres trimaculatus</i>	<i>Zebrasoma scopas</i>	<i>Thalassoma hardwicki</i>
<i>Pomacentrus pavo</i>	<i>Rhinecanthus rectangularis</i>	<i>Stethojulis bandanensis</i>
<i>Neoniphon sammara</i>	<i>Apogon nigrofasciatus</i>	<i>Scarus psittacus</i>
<i>Dascyllus aruanus</i>	<i>Dascyllus trimaculatus</i>	<i>Ctenochaetus striatus</i>
<i>Chaetodon citrinellus</i>	<i>Ctenochaetus binotatus</i>	<i>Stegastes fasciolatus</i>
<i>Canthigaster bennetti</i>	<i>Naso unicornis</i>	<i>Lutjanus kasmira</i>
<i>Acanthurus olivaceus</i>		<i>Scarus sordidus</i>
<i>Canthigaster solandri</i>		
<i>Acanthurus triostegus</i>		
<i>Pseudocheilinus hexataenia</i>		
<i>Chaetodon trichrous</i>		
<i>Gomphosus varius</i>		

Notes: The differences shown drive the differences in mean community composition based on species incidence. Species in each column are ordered from most common (top) to least common (bottom) for each group.

and species richness than [Late Only] and [Low Density] reefs (Fig. 4a, b).

Timing of predator arrival: timing contrast

Timing of hawkfish arrival (Early vs. Late) significantly affected prey abundance and mean community composition. Late-arriving hawkfish decreased total abundance by 34% relative to early-arriving hawkfish (Fig. 3a; $t_{32} = 2.15$, $P = 0.04$). Mean community composition differed between early- and late-arriving hawkfish when comparing species incidence across treatment reefs ($F_{\pi, 1,12} = 1.73$, $P = 0.05$, Fig. 5e, Table 1) and relative abundance ($F_{\pi, 1,12} = 2.34$, $P = 0.01$; Fig. 5f). Specifically, 15 species were shared in common, but there were 9 unique species to the Early Only treatment and 10 species that were unique to the Late Only treatment. There was, however, no effect of hawkfish timing of arrival on species richness (Fig. 4b, c; α , $t_{32} = 1.32$, $P = 0.20$; α_{rar} , $t_{32} = -0.19$, $P = 0.86$) or beta diversity (Fig. 4c; β_{Jac} , $P = 0.91$; β_{Man} : $F_{\pi, 1,12} = 0.40$, $P = 0.78$).

DISCUSSION

Predators that also compete with their prey for space can affect prey assemblages through three mechanisms. First, predators can directly consume newly settled individuals. Second, predators can act as interference competitors for space with their potential prey. Third, prey may exhibit conflicting antipredator responses by behaviorally avoiding resident predators via shifting away from the habitat and therefore increasing their vulnerability to more transient predators. These three mechanisms likely explain the negative effects of hawkfish presence, and increasing hawkfish densities. Hawkfish are known predators of recently settled fishes with whom they often share habitat. Additionally, competitive dominance of hawkfish over nonprey species is

known to increase susceptibility of subordinate fishes to larger transient predators (e.g., jacks and emperorfishes [Schmitt et al. 2009]). This increased susceptibility of subordinate competitors to larger-mouthed transient predators is the more compelling of a host of possible mechanisms by which individuals in the community that were too large to be consumed directly by hawkfish were affected by the hawkfish treatments (Appendix B).

Diversity response

There was no evidence for effects of hawkfish on species richness or rarefied species richness, suggesting that hawkfish are generalist predators, reducing individuals in proportion to their abundance, but not enough to consistently reduce the number of species per reef. (See Appendix C for a plot showing no correlation between rank abundance and proportion of individuals lost for species shared across hawkfish and no hawkfish treatments.) However, the positive or negative indirect effects that we were unable to quantify may have masked the consumptive effects of hawkfish. Hawkfish did, however, increase beta diversity based on species incidence. We posit shifts in the strength of priority effects as a possible mechanism for the observed shift in beta diversity. In many systems, species gain a competitive advantage over other species by being the first to colonize a patch (i.e., priority effects [Morin 1999]). A combination of priority effects and stochasticity in timing of species arrival may introduce spatial heterogeneity in species composition and affect beta diversity. Priority effects are prevalent in reef fish ecosystems for a number of groups present in our study, including: gobies (Steele 1997, Munday 2004), damselfishes (Sweatman 1985), and wrasses (Geange and Stier 2009). Along with spatial and temporal variability in recruitment, priority effects may contribute to the observed reef-to-reef variation in species incidence. The strength of priority

effects can increase in the presence of predators if predators facilitate the competitive exclusion of late-arriving species (Chase et al. 2002, 2009), a phenomenon that may also be present in coral reef fishes where older established residents are aggressive toward newly settled fishes and exclude them from predator-free space (Almany 2003). Hawkfish may therefore have facilitated an increase in beta diversity through enhancing the strength of priority effects in their dual role as both predators and space competitors with newly settled recruits (Schmitt et al. 2009). Note that differences in species incidence based on mean community composition does not translate to differences in species richness, because two treatments can have the same number of species without having the same species identity. Similarly, differences in mean community composition do not necessarily produce differences in beta diversity. Two communities could have identical species turnover across replicate patches while retaining differences in mean community composition.

Temporal variance

Previous studies that have orthogonally manipulated predation frequency (i.e., whether a predator is present all of the time or intermittently) and predation intensity (i.e., the number of predators) have documented the importance of both frequency and intensity in generating unique compositional assemblages of prey in intertidal (Navarrete 1996) and freshwater (Butler 1989) invertebrate communities. Here, however, we found no demonstrable effects of predator temporal variability (i.e., the Variance Contrast) on patterns of abundance, diversity, or community composition of prey species. This divergence of our results from those of Navarrete (1996) and Butler (1989) may be because pairs of hawkfish had twice the effect of an individual hawkfish (i.e., their effects were independent), a phenomenon consistent with our previous work examining hawkfish foraging behavior on a single prey species at different hawkfish densities (Stier et al. 2012). The absence of interactions between members of a pair of hawkfish discounts any a priori expectation that temporal variability will modify the strength of predation due to Jensen's inequality (i.e., nonlinear effects of predator density that produce clear expectations for how temporal variation in predator density will affect the mean-variance relationship, see *Introduction*). Notably, we manipulated a specific component of variance known as temporally autocorrelated variance. While we did not detect demonstrable effects of this specific type of variance, it is possible that other types of variance (e.g., temporally uncorrelated) will also be important in this system. For example, in a modeling study of competition between rare forbs and grasses in a California grassland system, Levine and Rees (2004) showed that only certain types of temporal variability in the environment proved beneficial to the persistence of rare forbs. Specifically, multiple consecutive favorable

years led to dominance by grass, but when there was high variation or negative temporal autocorrelation in environmental quality, forbs were capable of persisting. Thus both temporally uncorrelated variance and temporally autocorrelated variance can play important roles in driving ecological dynamics. We expect to explore the role of additional types of variance in predation pressure in our future work.

Timing of predator arrival

Timing of predator arrival affected prey abundance and composition. The consequences of timing of species arrival have been broadly studied with respect to competitive dynamics, including amphibians (Lawler and Morin 1993), ants (Palmer et al. 2002), odonates (Morin 1984), and reef fishes (Munday 2004, Geange and Stier 2009), and to a lesser extent, predator-prey dynamics (Morin 1984, Louette and De Meester 2007). We hypothesize that in our study, later-arriving hawkfish had strong negative effects on prey abundance because of greater competition among prey for predator-free space during the second 60 d of the experiment (sensu Carr et al. 2002). Prey fishes recruiting to reefs during the initial period of the experiment (0–60 d) had few competitors for space because patches started empty, whereas prey recruiting to patches after 60 d were exposed to ~40 resident fishes per patch. This greater level of crowding in the second 60 d likely led to an increase in susceptibility of prey to predation by hawkfish (as well as transient predators) via competition for predator-free space. The timing of predator arrival was also relevant to the effects of hawkfish on beta diversity and composition. The effects of two hawkfish for 120 d was equivalent to having two hawkfish for 60 d in the latter half of the 120-d window, suggesting that predator density may be most important during crucial temporal windows during community assembly (i.e., a density by time interaction). Note that in order to isolate the effects of hawkfish timing of arrival in this system, it was necessary to isolate direct hawkfish effects from potential confounding or interactive effects of other predators and competitors that may have either augmented or mitigated how hawkfish affected community organization. Although we recognize that the approach we used here is somewhat artificial because we began with empty reefs (which seldom occurs, with the exception of large disturbance events such as cyclones), this approach was necessary to isolate the effects of timing of hawkfish arrival from other potentially confounding processes that may affect community composition (e.g., priority effects of other competitors or predators in the system).

Recent theoretical work integrating generalist predation into storage effect models suggests generalist predators affect the long-term maintenance of diversity via a reduction of storage effects, whereby a weakening of covariance between environment and competition replaces competition with apparent competition (Kuang

and Chesson 2008, 2009). Our empirical work suggests these theories may need to incorporate additional complexity related to the relative timing of arrival of generalist predators and prey. We present evidence that the relative arrival of a generalist predator and prey increased beta diversity, producing unique prey assemblages that over the long term may promote species coexistence.

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SUPPLEMENTAL MATERIAL

Appendix A

Experimental design diagram and photo of experimental reef ([Ecological Archives E094-094-A1](#)).

Appendix B

Species lists and rank abundance diagrams for 60- and 120-day censuses ([Ecological Archives E094-094-A2](#)).

Appendix C

Predator foraging behavior analysis and figure ([Ecological Archives E094-094-A3](#)).

APPENDIX A: Experimental Design

Schematic of the five experimental predator treatments established to simulate characteristic modes of patch occupancy by hawkfish as observed in field surveys. Table at right shows corresponding mean density (\bar{x}) and temporal variance in density (s^2) for each of the treatments during the 120 d experiment. See *Methods* for a more detailed description of the experiment.

Figure A1 Five experimental predator treatments and their associated mean and variance.

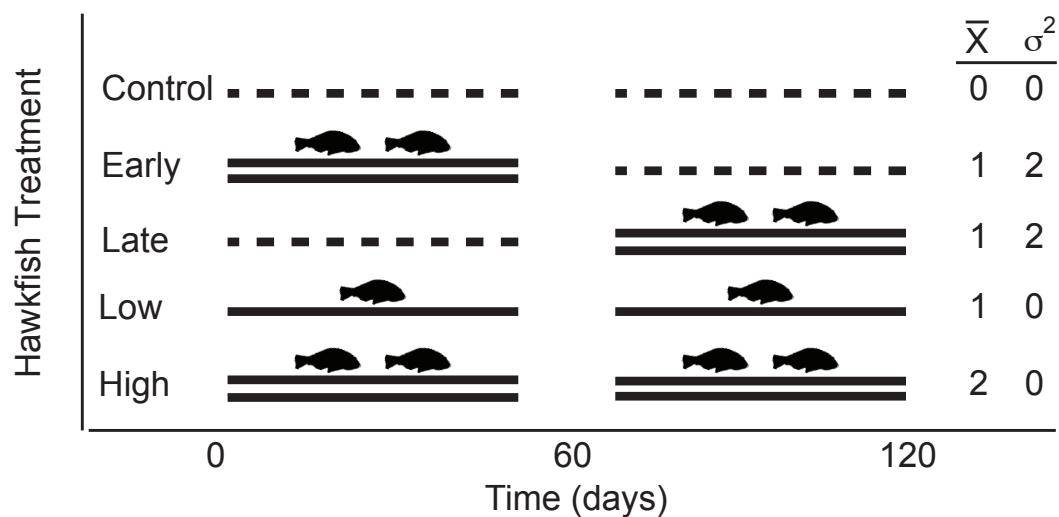


Figure A2 An example experimental reef with corals pasted to cinderblocks: *Porites rus* (left), *Pocillopora spp.* (center), *Montipora sp.* (front right), *Porites sp.* (back right). See *Methods* for additional details on reef construction and dimensions.



Photo Credit: *Adrian Stier*

APPENDIX B: Species Lists

Species lists, size at settlement, and abundance plots by treatment for censuses on 60 d and 120 d. Lists and plots are in order of total rank abundance across all hawkfish treatments. Each dot on a plot (Figs. B1 & B2) represents the total number of individuals in a given treatment. Note \log_{10} scale on both plots

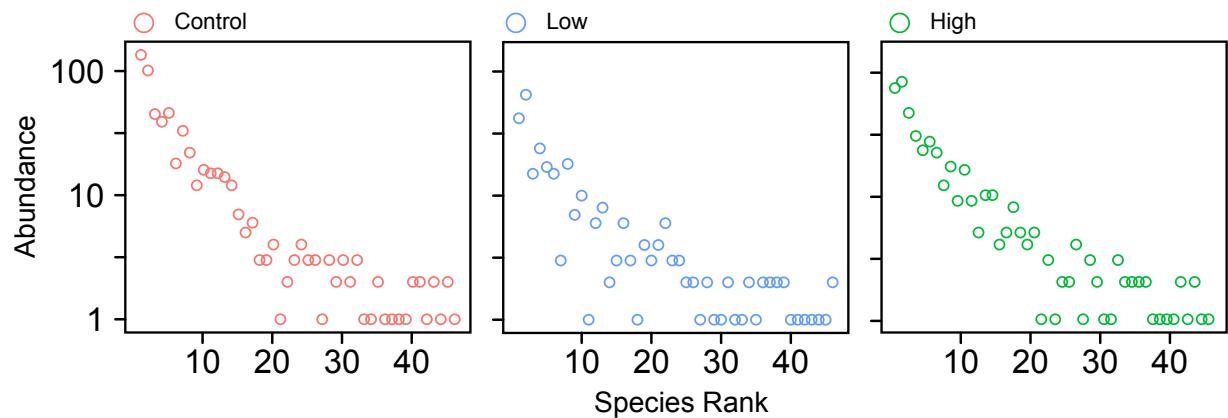
60 Days

Rank	Species	Size	Rank	Species	Size
1	<i>Dascyllus flavicaudus</i> ^I	0.8	31	<i>Pseudocheilinus hexataenia</i> ^I	1.3
2	<i>Halichoeres trimaculatus</i> ^I	0.8	32	<i>Siganus argenteus</i> ^I	6.5
3	<i>Gnatholepis anjerensis</i> ^E	1.0	33	<i>Thalassoma hardwicki</i> ^I	1.5
4	<i>Neoniphon sammara</i> ^I	3.5	34	<i>Heniochus chrysostomus</i> ^I	4.7
5	<i>Rhinecanthus aculeatus</i> ^I	1.2	35	<i>Labroides bicolor</i> ^E	1.0
6	<i>Chaetodon citrinellus</i> ^I	3.5	36	<i>Monotaxis grandoculis</i> ^I	3.0
7	<i>Pomacentrus pavo</i> ^I	2.0	37	<i>Neocirrhitus armatus</i> ^E	2.0
8	<i>Apogon fraenatus</i> ^I	2.2	38	<i>Parupeneus multifasciatus</i> ^I	6.2
9	<i>Canthigaster solandri</i> ^I	1.0	39	<i>Plectroglyphidodon lacrymatus</i> ^E	2.0
10	<i>Parupeneus barberinus</i> ^I	5.0	40	<i>Pseudobalistes flavimarginatus</i> ^I	2.0
11	<i>Dascyllus aruanus</i> ^I	0.7	41	<i>Thalassoma amblycephalum</i> ^I	2.0
12	<i>Balistapus undulatus</i> ^E	2.0			
13	<i>Acanthurus olivaceus</i> ^I	3.3			
14	<i>Sargocentron microstoma</i> ^I	6.7			
15	<i>Zebrasoma scopas</i> ^I	3.3			
16	<i>Scarus psittacus</i> ^E	1.0			
17	<i>Acanthurus nigrofasciatus</i> ^E	3.3			
18	<i>Chromis viridis</i> ^I	0.7			
19	<i>Stethojulis bandanensis</i> ^I	0.7			
20	<i>Canthigaster bennetti</i> ^I	1.5			
21	<i>Parupeneus pleurostigma</i> ^I	6.2			
22	<i>Rhinecanthus rectangulus</i> ^E	2.0			
23	<i>Chaetodon trichrous</i> ^I	3.9			
24	<i>Gomphosus varius</i> ^I	1.0			
25	<i>Naso unicornis</i> ^I	6.4			
26	<i>Chaetodon vagabundus</i> ^I	2.6			
27	<i>Cheilinus chlorourus</i> ^E	3.0			
28	<i>Ctenochaetus striatus</i> ^I	3.0			
29	<i>Naso lituratus</i> ^I	6.8			
30	<i>Centropyge flavissimus</i> ^I	1.3			

¹Maamaatuaiahutapu, M., G. Remoissenet, and R. Galzin. 2006. Guide d'identification des larves de poisson récifaux de Polynésie française. CRISP, Noumea, New Caledonia.

^ESize at settlement estibated visually by an observer on SCUBA to the nearest 0.5 cm Total Length.

Figure B1. Rank-abundance diagrams at 60 days (red: control, blue: low density, and green: high density).



120 d

Rank	Species	Size (cm)	Rank	Species	Size (cm)
1	<i>Gnatholepis anjerensis</i> ^E	1.0	33	<i>Dascyllus trimaculatus</i> ^I	1.0
2	<i>Dascyllus flavicaudus</i> ^I	0.8	34	<i>Monotaxis grandoculis</i> ^I	3.0
3	<i>Apogon fraenatus</i> ^I	2.2	35	<i>Parupeneus barberinus</i> ^I	5.0
4	<i>Halichoeres trimaculatus</i> ^I	0.8	36	<i>Stegastes fasciolatus</i> ^I	1.7
5	<i>Pomacentrus pavo</i> ^I	2.0	37	<i>Coryphopterus neophytus</i> ^E	
6	<i>Neoniphon sammara</i> ^I	3.5	38	<i>Ctenochaetus binotatus</i> ^I	4.7
7	<i>Dascyllus aruanus</i> ^I	0.7	39	<i>Lutjanus kasmira</i> ^I	3.9
8	<i>Chaetodon citrinellus</i> ^I	3.5	40	<i>Naso unicornis</i> ^I	6.4
9	<i>Rhinecanthus aculeatus</i> ^I	1.2	41	<i>Neocirrhitus armatus</i> ^E	
10	<i>Canthigaster bennetti</i> ^I	1.5	42	<i>Parupeneus multifasciatus</i> ^I	6.2
11	<i>Acanthurus olivaceus</i> ^I	3.3	43	<i>Scarus sordidus</i> ^I	
12	<i>Canthigaster solandri</i> ^I	1.0			
13	<i>Acanthurus triostegus</i> ^I	3.3			
14	<i>Zebrasoma scopas</i> ^I	3.3			
15	<i>Chromis viridis</i> ^I	0.7			
16	<i>Stethojulis bandanensis</i> ^I	0.7			
17	<i>Pseudocheilinus hexataenia</i> ^I	1.3			
18	<i>Valenciennea strigata</i> ^I	4.5			
19	<i>Balistapus undulates</i> ^E	2.0			
20	<i>Thalassoma hardwicki</i> ^I	1.5			
21	<i>Rhinecanthus rectangulus</i> ^E	2.0			
22	<i>Scarus psittacus</i> ^E	1.5			
23	<i>Centropyge flavissimus</i> ^I	1.3			
24	<i>Chaetodon trichrous</i> ^I	3.9			
25	<i>Gomphosus varius</i> ^I	1.0			
26	<i>Myripristis kuntee</i> ^I	4.0			
27	<i>Naso lituratus</i> ^I	6.8			
28	<i>Acanthurus achilles</i> ^E				
29	<i>Acanthurus nigrofasciatus</i> ^E				
30	<i>Apogon nigrofasciatus</i> ^E				
31	<i>Chaetodon vagabundus</i> ^I	2.6			
32	<i>Ctenochaetus striatus</i> ^I	3.0			

¹Maamaatuaiahutapu, M., G. Remoissenet, and R. Galzin. 2006. Guide d'identification des larves de poisson récifaux de Polynésie française. CRISP, Noumea, New Caledonia.

^ESize at settlement estibated visually by an observer on SCUBA to the nearest 0.5 cm Total Length.

Figure B2. Rank-abundance diagrams at 120 days (red: control, yellow: early hawkfish, green: late hawkfish, blue: low density, and purple: high density).

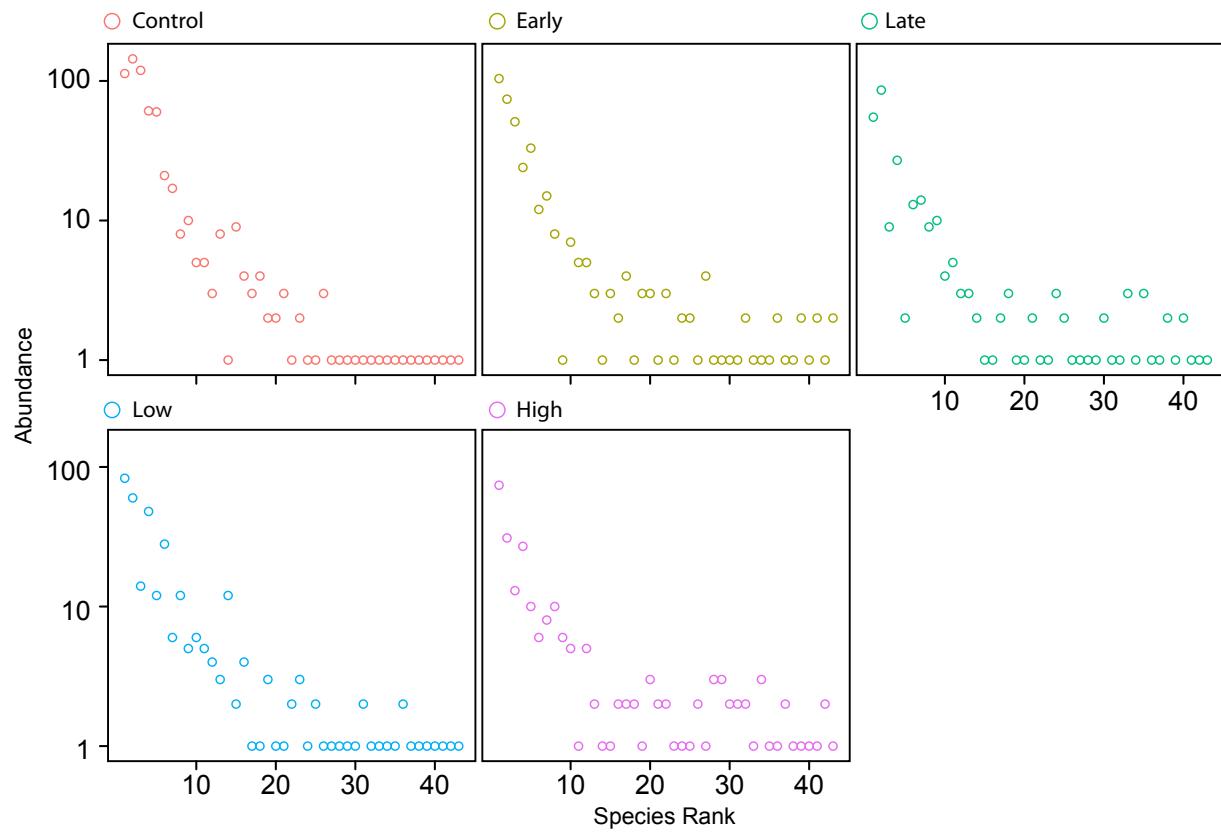
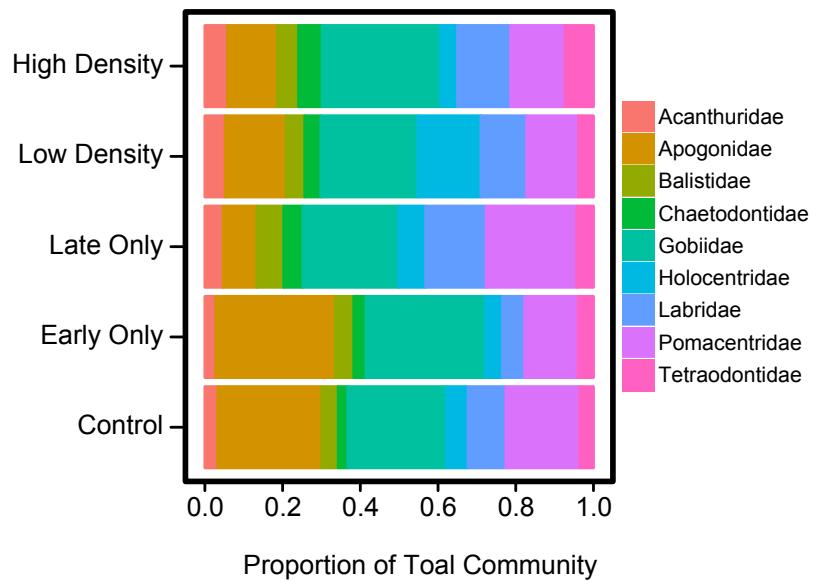


Figure B3. Taxonomic composition measured as the proportion of the total fish community for nine families across each of five hawkfish treatments.



APPENDIX C: Predator Foraging Behavior

Correlation plot of species rank abundance (1 abundant, 25 rare) and the proportional change in abundance of 25 prey species between the control treatment and high density treatment (i.e., $[(\text{Control} - \text{High Density}) / \text{Control}]$) (Fig. C1). Individual-based rarefaction curves did not differ for reefs with versus without hawkfish despite large differences in abundance between these two reef treatments. The absence of a consistent difference in the proportional change in abundance between common and rare species suggests that hawkfish are generalist predators, reducing individuals in proportion to their abundance, but not enough to consistently reduce the number of species per reef.

Figure C1: Correlation of rank abundance and the proportion change in abundance for control and high density treatments (i.e., $[(\text{Control} - \text{High Density}) / \text{Control}]$).

