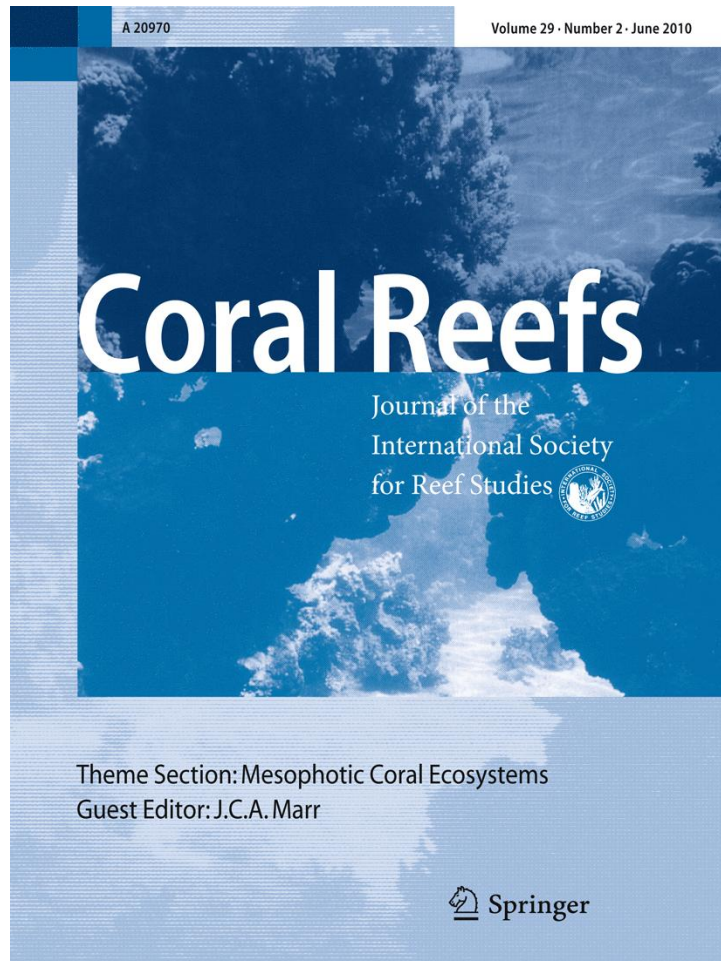


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NOTE

Predators reduce abundance and species richness of coral reef fish recruits via non-selective predation

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Abstract Predators have important effects on coral reef fish populations, but their effects on community structure have only recently been investigated and are not yet well understood. Here, the effect of predation on the diversity and abundance of young coral reef fishes was experimentally examined in Moorea, French Polynesia. Effects of predators were quantified by monitoring recruitment of fishes onto standardized patch reefs in predator-exclosure cages or uncaged reefs. At the end of the 54-day experiment, recruits were 74% less abundant on reefs exposed to predators than on caged ones, and species richness was 42% lower on reefs exposed to predators. Effects of predators varied somewhat among families, however, rarefaction analysis indicated that predators foraged non-selectively among species. These results indicate that predation can alter diversity of reef fish communities by indiscriminately reducing the abundance of fishes soon after settlement, thereby reducing the number of species present on reefs.

Keywords Coral reef fish · Moorea · Predation · Recruitment · Species diversity

Introduction

Spatiotemporal variation in patterns of recruitment in benthic marine fish communities are driven by a diverse suite of factors including oceanographic currents that drive larval supply and post-settlement processes such as competition and predation (Jones 1991; Steele 1997; Schmitt et al. 1999; Shima 1999; Hixon and Jones 2005). A number of studies have documented high rates of predation in reef fishes immediately following settlement (reviewed in Almany and Webster 2006). Most studies on predation in coral reef fishes have focused on how predation affects recruitment rates or population dynamics of one or a few species and have revealed that predation often regulates prey populations by causing density-dependent mortality (reviewed in Hixon and Webster 2002).

Fewer studies have focused on how entire prey assemblages are structured by predation. Predators can reduce species diversity without affecting the relative abundance of prey species by indiscriminant foraging (e.g., Hixon and Beets 1993). Greater reductions in diversity coupled with changes in relative abundance occur when predators feed selectively on rare species (i.e., an oddity effect: Almany and Webster 2004; Almany et al. 2007); whereas, smaller reductions in diversity coupled with changes in relative abundance occur when predators target abundant prey species (e.g., Webster and Almany 2002).

To date, the majority of studies exploring the effects of predators on diversity of reef fishes have manipulated the abundance of only a subset of predator species, namely relatively sedentary “resident” predators, without

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manipulating the abundance of more mobile “transient” predators. The current study examined the influence of both resident and transient predators on the composition, abundance, and diversity of juvenile reef fishes in Moorea, French Polynesia by monitoring natural recruitment to small patch reefs exposed to or protected from predators.

Materials and methods

This study was conducted in the backreef of Cook's Bay, Moorea, French Polynesia (17°3'S, 149°50'W). Moorea is encircled by a barrier reef that forms a system of shallow lagoons (mean depth ~6 m) characterized by small patch reefs interspersed with sand (Galzin and Pontier 1985), which provides a relatively uniform habitat with generally high settlement of coral reef fishes (Planes et al. 1993).

A matrix of reefs (3 rows \times 7 reefs) was placed parallel to shore on a sandflat (3.5 m deep). Each reef was separated from one another and natural reefs by at least 15 m of open sand. Reefs were constructed of live *Pocillopora cf. verrucosa* coral heads (30 ± 1.3 cm diameter, 20 ± 5.3 cm high; mean \pm SE) placed on concrete blocks using Z-Spar marine epoxy. Each of the 21 reefs was randomly assigned to one of three treatments: full cage (– predators), no cage (+ predators), or partial cage (cage control) ($n = 7$ per treatment). Coral size did not differ between treatments ($F_{1,19} = 0.11$, $P = 0.89$).

Predator-exclosure cages were constructed of 1-cm² mesh galvanized steel wire. Cages were placed over the reefs and attached to two pieces of rebar (1 cm diameter) driven 0.5 m into the sand on opposite sides of the reef. Full cages (75 cm tall \times 70 cm diameter) completely enclosed the reef, effectively excluding most piscivorous fishes, but allowed settling fishes to pass through. Partial cages (70 cm diameter \times 50 cm tall and elevated ~20 cm above the sand) were open at the top and bottom to allow access to all piscivore guilds (resident or transient), while partially controlling for the presence of the cage (Steele 1996; Connell 1998).

Recruitment was measured over a 54-day period during the 2008 austral summer (14 February to 8 April), a period of relatively high recruitment in Moorea. Surveys were conducted every 3–7 days during the first 25 days of the experiment, but after that only a single final survey was conducted at 54 days, due to logistical constraints. During each survey, SCUBA divers identified and counted coral reef fish recruits on each reef. To characterize the relative abundance of predatory species during the duration of the study, the number of piscivorous fishes were counted within 1 m of each reef and also along three 100 \times 1 m band transects extending along each row of the reef array. Predator surveys were conducted during all but the final

recruit survey. Fishes were categorized as predators based on Holbrook and Schmitt (2002), who used diver observations and videotape to identify the main predators of small reef fishes in Moorea. All cages were scrubbed of fouling organisms 2 days prior to each survey so as not to disturb fishes during the surveys, although no significant algal growth was noted within the cages during the experiment.

The effect of predators on total recruit abundance (i.e., all species pooled) was modeled using a generalized linear model with a log link function. Because the data were counts, they approximated a Poisson error distribution. However, data exhibited overdispersion (residual deviance = 53.09, residual $df = 18$), therefore a quasi-Poisson error distribution was assumed. A one-way analysis of deviance (ANODEV) with orthogonal contrasts tested the effects of predators on total recruit abundance. ANODEV is analogous to ANOVA, but examines differences in deviance rather than variance using likelihood ratio tests to compare two nested models, allowing flexibility in the assumed underlying error distribution. Two orthogonal contrasts tested the effect of cage treatments on recruit abundance: the first tested for cage artifacts (cage control versus no cage) and the second tested the effects of predators (cage versus no cage and cage control) in the absence of cage artifacts. Due to a predominance of zeros in the data, two sample permutation tests were subsequently used to test for both family-specific effects of predators on recruitment and cage artifacts at the family level. Predator-exposed treatments (no cage and cage control reefs) were pooled for all analyses since cage artifacts were not detected for recruit abundance ($t_{1,18} = 0.47$, $P = 0.64$; Figs. 1, 2), species richness ($t_{1,18} = 0.301$, $P = 0.76$, Fig. 3a), rarefied richness (Fig. 3b), nor abundance at the family level ($P > 0.87$, Fig. 2). All statistical analyses were conducted on data collected from the final survey (day 54) using R statistical software (R Development Core Team 2009).

Effects of predators on recruit diversity were examined for both species richness and rarefied species richness, to explore possible mechanisms of predator effects on diversity. The effect of predators on non-rarefied richness was modeled similarly to effects on abundance, using a generalized linear model with a log link and a Poisson distribution (overdispersion parameter assumed = 1, residual deviance = 19.01, residual $df = 18$). A one-way ANODEV with orthogonal contrasts tested the effects of caging on non-rarefied species richness (cage artifact: cage control versus no cage; predator effect: cage versus no cage and cage control). Rarefaction analysis was used to standardize species richness to a comparable number of individuals (Gotelli and Colwell 2001). Rarefaction curves were generated using community analysis software EstimateS

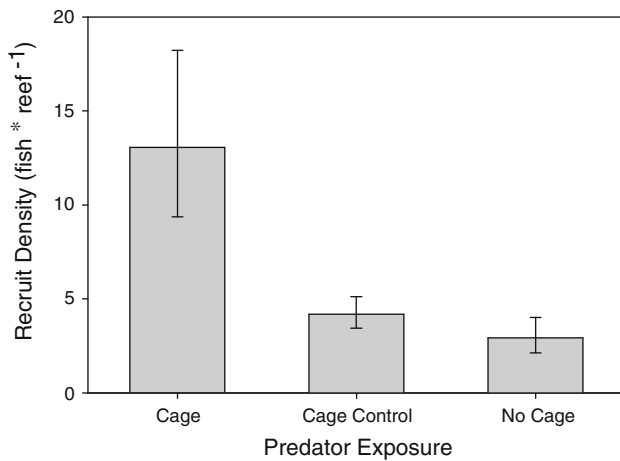


Fig. 1 Mean recruit density on reefs in predator-exclosure cages, cage controls, or no cages at the end of the 54-day experiment. Error bars represent 95% confidence intervals

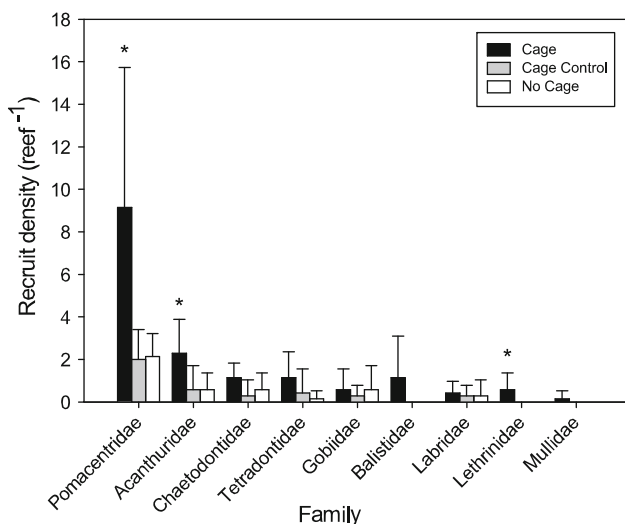


Fig. 2 Mean density of recruits in each family on reefs in three predator-exposure treatments. Error bars represent 1 SD. Statistically significant differences ($P < 0.05$) are denoted by asterisk

(Colwell 2006). Comparison of the curves revealed whether predator effects on diversity were driven by simply reducing abundance or by selective foraging behavior of predators (Almany and Webster 2004).

Results and discussion

Predators had strong, negative effects on prey fish recruitment. At the end of the experiment (day 54), a total of 172 recruits were observed across all treatments from 20 species and nine families (Table 1). The presence of predators reduced recruit abundance by 74% compared to reefs where predators were absent ($t_{1,18} = 5.09$,

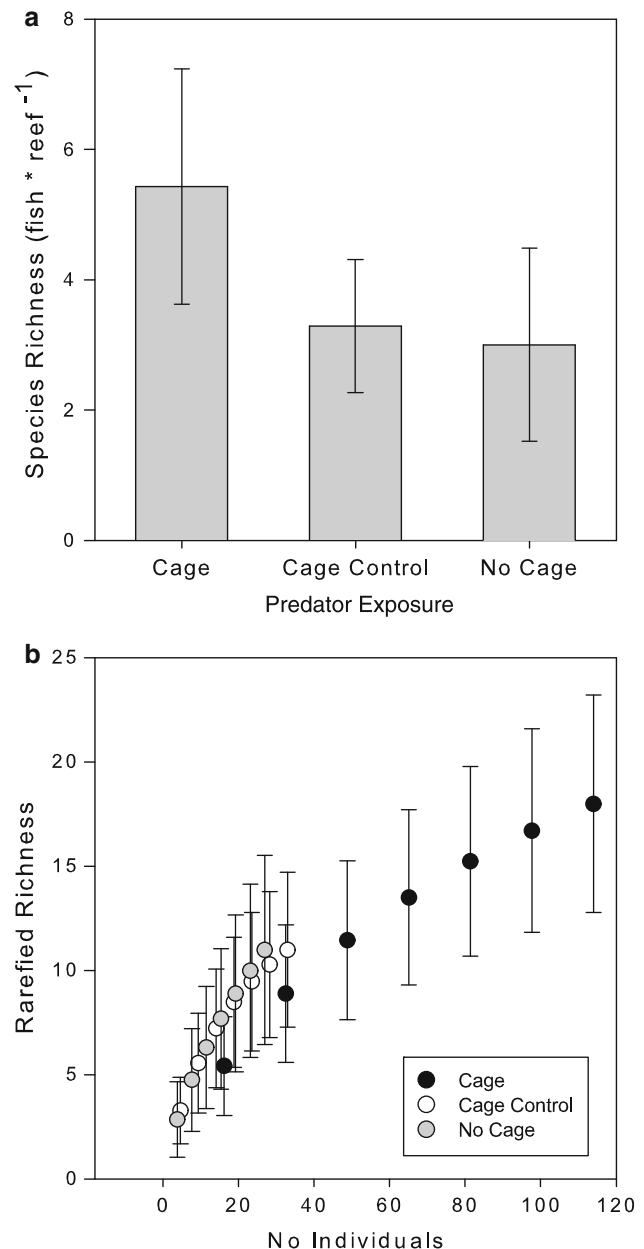


Fig. 3 Effect of predators on prey species diversity. Species richness (a) and rarefied richness (b) of coral reef fish recruits on reefs in three predator-exposure treatments. Means \pm 95% confidence intervals are shown

$P < 0.001$; Fig. 1; Table 1). Each of the nine recruit families had lower densities on reefs exposed to predators than on reefs protected from them, with the magnitude of reduction differing somewhat among families (Fig. 2). Reductions were statistically significant for only Acanthuridae ($P = 0.008$), Lethrinidae ($P = 0.026$), and Pomacentridae ($P = 0.007$), probably due to low sample sizes for the other families. Balistidae, Lethrinidae, and Mullidae experienced the highest proportional reductions (94, 100, and 100%, respectively) in the presence of

Table 1 Fish recruitment by species: total abundance of recruits at the end of the experiment (day 54) in each treatment (cage, cage control, and no cage; $n = 7$ for each)

Family	Species	Cage	No cage	Cage control	Total	% Reduction (+P versus -P)
Acanthuridae		16	4	4	24	75.0
	<i>Acanthurus nigrofuscus</i>	1	0	0	1	
	<i>Acanthurus olivaceus</i>	2	0	4	6	
	<i>Acanthurus triostegus</i>	4	0	0	4	
	<i>Ctenochaetus flavicauda</i>	9	4	0	13	
Balistidae		8	0	1	9	93.8
	<i>Rhinecanthus aculeatus</i>	8	0	1	9	
Chaetodontidae		8	2	4	14	62.5
	<i>Chaetodon citrinellus</i>	7	2	3	12	
	<i>Chaetodon unimaculatus</i>	1	0	0	1	
	<i>Chaetodon vagabundus</i>	0	0	1	1	
Gobiidae		4	2	4	10	25.0
	<i>Gnatholepis anjerensis</i>	4	2	4	10	
Labridae		3	2	2	7	33.3
	<i>Halichoeres trimaculatus</i>	1	1	2	4	
	<i>Pseudocheilinus hexataenia</i>	0	1	0	1	
	<i>Stethojulius bandanensis</i>	2	0	0	2	
Lethrinidae		2	0	0	2	100.0
	<i>Monotaxis grandoculis</i>	2	0	0	2	
Mullidae		1	0	0	1	100.0
	<i>Parupeneus barberinus</i>	1	0	0	1	
Pomacentridae		64	14	15	93	77.3
	<i>Chromis viridis</i>	2	1	0	3	
	<i>Dascyllus aruanus</i>	5	3	4	12	
	<i>Dascyllus flavicaudus</i>	47	9	8	64	
	<i>Pomacentrus pavo</i>	10	1	3	14	
Tetraodontidae		8	3	1	12	75.0
	<i>Canthigaster bennetti</i>	3	1	0	4	
	<i>Canthigaster solandri</i>	5	2	1	8	
Total		114	27	31	172	

Percent reduction in density of recruits attributable to effects of predators (cage versus no cage and cage control) is presented for each family

predators, but recruitment of Lethrinidae ($n = 2$) and Mullidae ($n = 1$) was low. Pomacentridae, Acanthuridae, and Tetradontidae also suffered large reductions ($\sim 75\%$), whereas the smallest reductions were in the families Gobiidae and Labridae ($\sim 30\%$) (Fig. 2; Table 1).

Predators also significantly reduced the number of prey species per reef by 42% ($t_{1,18} = 2.47$, $P = 0.014$; Fig. 3a). Rarefied species richness, however, was very similar between predator absent and predator present reefs (Fig. 3b), indicating that reduced species richness on reefs exposed to predators was caused by fewer individuals on these reefs compared to caged reefs and not due to selective predation. Similar to other studies on predation in reef fishes (e.g., Webster 2002), this study provides some evidence that predators affect different families to different

extents. Acanthurids and Pomacentrids were much less abundant on reefs exposed to predators than on reefs protected from them, whereas the effects of predators on other families (i.e., Gobiids and Labrids) were smaller. Despite this evidence for variable effects of predators on the abundance of recruits in different families, rarefaction analysis revealed that fewer prey species were found on reefs exposed to predators because predators had indiscriminately reduced the abundance of recruits (Figs. 2, 3b).

Predator surveys documented 12 species from ten families in the vicinity of the reefs, with five taxa (*Halichoeres trimaculatus*, *H. hortulanus*, *Rhinecanthus aculeatus*, *Lethrinus olivaceus*, *Synodus* spp.) composing 80.6% of the observed predators (Table 2). Resident predators were rare, accounting for only 1.4% of all observed predators.

Table 2 Predator abundance: abundance of piscivores for each survey date at the experimental site in Moorea, French Polynesia

Family	Species	Survey day					Mean	% Total
		7	14	18	21	25		
Balistidae	<i>Balistapus undulatus</i>	0	1	0	0	4	1.0	3.6
	<i>Rhinecanthus aculeatus</i>	8	3	5	2	6	4.8	17.1
Bothidae	<i>Bothus</i> spp.	0	1	0	0	1	0.4	1.4
Carangidae	<i>Caranx melampygus</i>	6	2	1	0	0	1.8	6.4
Cirrhitidae	<i>Neocirrhites armatus</i> *	0	0	0	1	0	0.2	0.7
Labridae	<i>Halichoeres hortulanus</i>	6	14	0	0	0	4.0	14.3
	<i>Halichoeres trimaculatus</i>	0	0	3	20	15	7.6	27.1
Lethrinidae	<i>Lethrinus olivaceus</i>	9	7	3	1	1	4.2	15.0
Penguipedidae	<i>Parapercis</i> spp.	1	2	2	0	2	1.4	5.0
Scorpaenidae	<i>Pterois radiata</i> *	0	0	0	0	1	0.2	0.7
Serranidae	<i>Epinephelus merra</i>	1	0	0	0	1	0.4	1.4
Synodontidae	<i>Synodus</i> spp.	0	0	2	3	5	2.0	7.1
Total		31	30	16	27	36	28.0	100

Fishes were categorized as predators according to Holbrook and Schmitt (2002). Values represent total observed predators for each species found within 1 m of experimental reefs and along three 100 × 1 m band transects. Surveys were only conducted for the first 25 days of the study

* Denotes species that were resident predators on experimental reefs. All other species were transient predators at the scale of the reefs used in this study

Recruitment was likely reduced directly by post-settlement predation rather than prey species avoiding reefs exposed to predators. Avoidance of reefs exposed to predators during settlement is unlikely because resident predators were too scarce to provide avoidance cues to settling fishes; and even on reefs with resident predators, Almany (2003) found that reductions in recruitment were caused by predation rather than larval avoidance of reefs with predators. Successful post-settlement emigration away from reefs exposed to predators is also unlikely, because the small juvenile coral reef fishes studied here seldom move across bare sand greater than about 5 m (Frederick 1997). Despite a different assemblage of predator and prey fishes, these general findings mirror those of similar studies in other regions, including the Bahamas (Carr and Hixon 1995; Steele and Forrester 2002; Almany 2004; Almany and Webster 2004; Stallings 2008), the Caribbean (Hixon and Beets 1993; Beets 1997), and the Great Barrier Reef (Caley 1993; Connell 1998, 2000; Webster 2002; Almany 2004).

The results of this study suggest that the predator guild studied in Moorea foraged non-selectively on recently settled fishes, thereby lowering species richness. This finding is in accord with work by Hixon and Beets (1993), which indicated that predators in the Caribbean were non-selective, consuming prey in proportion to their abundance. These results, however, contrast with those of recent studies on the Great Barrier Reef and in the Bahamas (Almany and Webster 2004; Almany et al. 2007), which revealed that predators in these systems tended to selectively prey on rare species, thus decreasing species richness

to a greater extent than would non-selective predation. This difference could be attributed to two things. First, prey fishes in the current study were primarily exposed to transient predators, whereas previous work showing selective predation focused on the effects of resident predators, which may use different foraging tactics. Second, predators in Moorea differ in species composition and may exhibit different foraging strategies from those in the Bahamas and on the Great Barrier Reef.

This study reaffirms the importance of post-settlement predation in structuring prey fish assemblages by documenting strong negative effects of a group of predators on the abundance and composition of juvenile reef fish communities. The proposed mechanism of these effects, non-selective predation, differs from the mechanism documented in previous studies conducted in other regions. It is plausible that the difference among studies is caused by differences in foraging tactics of the predatory species manipulated in the various studies (e.g., resident versus transient predators). The extent to which differences in the effects of predators on the structure of coral reef fish assemblages are related to idiosyncrasies among studies such as the portion of the predator guild manipulated or differences in habitat patch size, versus inherent differences among regions in the predator and prey fauna and their ecological characteristics remains to be resolved by future studies.

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