

Territorial damselfishes facilitate survival of corals by providing an associational defense against predators

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ABSTRACT: Territorial defense by the herbivorous damselfishes, *Stegastes nigricans* and *S. lividus*, benefits the hermatypic corals growing inside their territories. Coral diversity was significantly higher inside damselfish territories at 2 sites in Moorea, French Polynesia, and at 1 site in Guam, Mariana Islands. In Guam, this pattern was stable for at least 10 yr. Certain coral species, including *Pocillopora damicornis*, were found only inside damselfish territories at these sites. All fishes, including coral-feeding butterflyfishes, approaching territories of *Stegastes* spp. were vigorously chased. Colonies of *P. damicornis* inside territories were not preyed upon by any potential intruders. When transplanted outside of territories, colonies of *P. damicornis* were preyed upon rapidly by several species of butterflyfishes. Feeding rates of individual butterflyfishes on transplanted *P. damicornis* colonies were initially very high and decreased significantly over 30 min as accessible coral tissue was removed. In contrast, transplanted *Porites rus*, a major component of the reef outside of territories in Guam, attracted no predators. This study suggests that territorial damselfishes provide an associational defense for certain coral species that live inside their territories, whereas these species settling outside territories experience heavy predation, resulting in suppressed growth and negligible survival. This demonstrates the potential importance of this type of positive indirect interaction between species in structuring coral reef communities, that protection from predation by coral-feeding fishes is a mechanism by which damselfishes can enhance coral diversity on reefs, and that this association can remain stable for many years.

KEY WORDS: Territoriality · Damselfishes · *Stegastes* · *Pocillopora* · Butterflyfishes · Corallivory · Associational defense · Facilitation

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INTRODUCTION

The complex structures of coral reef communities result from a combination of direct and indirect positive and negative abiotic and biotic interactions that facilitate the existence of certain species while limiting the distribution of others. Studies on community structure have largely focused on direct interactions between organisms as the major biotic structuring forces, with predation and interference competition being the most widely cited mechanisms (Connell 1983). More recently, direct and indirect effects of anthropogenic disturbances have played major roles in structuring coral reef communities, and widespread changes in species composition and

distribution have resulted from overharvesting, pollution, bleaching, disease and climate change (Knowlton & Jackson 2008). Despite recent anthropogenic disturbances on coral reefs, predation remains a major structuring force, and factors that affect predation rates are important for the survival of both predator and prey. Sessile organisms, including corals, have evolved a diversity of morphological, behavioral and chemical defenses to protect them against predation (McClintock & Baker 2001, Gochfeld 2004).

Other important forms of defense include indirect interactions, such as 'associational defenses', in which certain organisms modify a local environment in such a way that is beneficial to the survival of other organisms

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(Hay 1986, Stachowicz 2001, Bruno et al. 2003). In the marine environment, for example, certain palatable seaweeds are subjected to significantly reduced herbivory when they grow in association with unpalatable competitors (Hay 1986, Littler et al. 1986, 1987, Levenbach 2008). Associations between non-competitors are found among small mobile herbivores, such as crabs or amphipods, which may reduce their susceptibility to predation by associating with chemically defended plants (Hay et al. 1989, Duffy & Hay 1994, Stachowicz & Hay 1999) or invertebrates (McClintock & Janssen 1990). Associations among organisms do not require chemical defenses to be successful. For example, morphological aspects of the associate may inhibit access by herbivores or predators (Kerr & Paul 1995, Gagnon et al. 2003). Positive interactions of this sort are a form of facilitation (Hacker & Gaines 1997, Bruno et al. 2003), in which one species benefits from an encounter with another species, and provide a mechanism for maintaining species richness in communities dominated by one or a few major species (Hay 1986, Pennings 1997).

Many herbivorous damselfishes on coral reefs defend territories in which they culture algal 'lawns' of increased algal abundance, diversity and productivity relative to reef areas outside territories (Klumpp et al. 1987, Hixon & Brostoff 1996, Hata et al. 2002, Gobler et al. 2006). Territory occupants are presumed to feed primarily on the algal lawn within their territory. Some herbivorous damselfishes defend their territories only from food competitors, such as other herbivorous fishes (Klumpp & Polunin 1989) or urchins (Williams 1980, Eakin 1987), while others also exclude non-herbivorous fishes (Harrington & Losey 1990) and sea stars (Glynn & Colgan 1988). Territorial defense by damselfishes may also affect the survival and growth of non-prey organisms within their territories, including sessile invertebrates such as corals. Territory holders may have direct or indirect negative effects on the growth or establishment of corals in their territories, either by facilitating overgrowth of corals by algae or by reducing substratum suitable for settlement as a result of the establishment of the algal lawn (Hixon 1997). However, positive effects of damselfish territoriality on the growth of some corals also occur. Although few studies have addressed mechanisms that might explain this phenomenon, competitive exclusion of coral predators may be an important factor (Wellington 1982, Glynn & Colgan 1988, Done et al. 1991). These potential effects of territorial damselfishes on local community structure of other organisms have led to their being labeled 'keystone' species (Williams 1980, Hixon & Brostoff 1983, 1996).

Increased coral diversity or cover inside damselfish territories has been described from reefs in several

Indo-Pacific locations (Sammarco & Carleton 1981, Glynn & Colgan 1988, Done et al. 1991, Jones et al. 2006). Although most of these studies have been descriptive, Gleason (1996) and Glynn & Colgan (1988) proposed potential mechanisms by which this increased diversity could occur. Gleason (1996) identified increased rates of coral recruitment inside damselfish territories, whereas Glynn & Colgan (1988) suggested that by removing crown-of-thorns starfish *Acanthaster planci* from their territories, damselfishes permitted coral survival inside territories during population outbreaks of these coral predators. Although *A. planci* are clearly a threat to corals during episodic outbreaks, coral-feeding fishes represent a more chronic source of predation risk, particularly to highly preferred coral species. The goal of the present study was to evaluate the effect of damselfishes on coral diversity and test the hypothesis that the aggressive territorial behavior of certain damselfishes provides an associational defense for corals against coral-feeding fishes, a chronic source of predation on Indo-Pacific reefs.

MATERIALS AND METHODS

Study sites. Territories of *Stegastes nigricans* (Lacepède) were studied at Moorea, Society Islands, French Polynesia. The primary study site was a fringing reef slope at Maharepa on the north coast of Moorea (17° 28' 50" S, 149° 48' 6" W). The reef slope began 50 m from shore and ranged in depth from 1 to 7 m. *Stegastes nigricans* territories occupied much of the hard substratum at 1 to 3 m depth. Territories consisted predominantly of algal-covered rock and rubble, with a few small coral colonies. At 2 to 7 m depth, all hard substrata outside of territories consisted of extensive colonies of the coral *Montipora* sp. A lagoonal back reef area also was surveyed to examine the effect of damselfish territories on coral diversity and species composition. This site was 1 to 3 m deep at Temae Beach, on Moorea's northeastern shore (17° 30' 3" S, 149° 45' 46" W). The lagoon consisted predominantly of intact dead table acroporids on a sand and rubble bottom, interspersed with a few live massive *Porites* sp. colonies. Territories of *S. nigricans* were also abundant. This portion of the study was conducted in August 1990.

A second study location was the inner reef slope of a large sinkhole surrounded by reef flat at the Piti Bomb Holes Marine Preserve, Guam, Mariana Islands (13° 28' 20" N, 144° 42' 12" E). The survey area was approximately 3 m deep along the west side of the sinkhole. Territories of *Stegastes lividus* (Forster) were contiguous, forming colonies of up to 117 territories

and occupying significant areas of reef slope. The adjacent reef slope consisted predominantly of *Porites cylindrica* (Dana) and *P. rus* (Forskål), whereas the reef flat was composed largely of soft corals in the genus *Sinularia* and bare pavement (Slattery et al. 2008). This portion of the study was conducted in July 1992 and May 2002, and the site was revisited annually from 2003 to 2008.

Effect of damselfishes on coral diversity. Coral diversity and species composition were determined inside and outside damselfish territories at the 3 study sites. In Guam, surveys were performed both in 1992 and again in 2002 to assess whether patterns were stable over time. Percent cover of substrata was determined using a point–intercept method (Hill & Wilkinson 2004). A 60 m transect line was placed along the reef and random number tables were used to select locations inside and outside territories at which a 0.25 m² quadrat was placed. Boundaries of damselfish territories are easily distinguished by the presence of an algal lawn and defensive behavior of the resident fish. Within each quadrat, substratum type was recorded under each of 100 points in a grid pattern.

At both sites in Moorea, the transect line was placed along the reef slope at 2 m depth and quadrats inside and outside damselfish territories were sampled ($n = 26$ of each at the fringing reef site, $n = 10$ of each at the lagoon site). *Stegastes nigricans* territories were dispersed along the entire length of the transect line at both sites. At Piti Bomb Holes in Guam, the transect line was placed along the reef slope at 3 m depth, and quadrats were sampled inside and outside damselfish territories ($n = 15$ of each in 1992, $n = 20$ of each in 2002). In 2002, 500 m² of reef flat (1 to 3 m depth) adjacent to the sinkhole were also surveyed to quantify colonies of *Pocillopora damicornis*.

Percent cover of each substratum type, number of coral species, and Shannon-Wiener diversity indices (H') were compared for the 2 habitats (inside and outside territories) at each site, and between years in Guam, using Mann-Whitney U -tests. Since each data set in Guam was used for 2 comparisons (inside versus outside and 1992 versus 2002), the level of significance was adjusted using the Bonferroni method from 0.05 to 0.025. Nonparametric statistical methods were used due to non-normal distributions of the data. For rare corals (<10% cover), 2×2 contingency tests were used to test for differences in the presence and absence of corals from quadrats inside and outside territories. Variation around mean values throughout the paper refers to 1 SE.

Effect of damselfishes on protection of corals from predation. Coral transplant experiments were performed to determine whether predation by coral-feeding fishes reduces coral survival in the absence of

protection by damselfishes. These experiments were conducted at the fringing reef site in Moorea and on the reef slope in Guam; at the lagoon site in Moorea, strong currents prevented experimentation.

The transplant procedure was similar at both sites. An individual *Pocillopora damicornis* colony inside a damselfish territory was observed initially for 15 min, noting species of fish feeding on the colony and number of bites taken. The colony was then removed from the territory and placed among nearby corals where butterflyfishes were previously observed feeding, or carried around briefly and returned to its original location within the territory (back-transplants). Latency (time from placement on the reef until arrival of individual fish at the transplanted colony) was noted. Feeding rate (no. bites per 5 min period) was determined for the first individual of a focal butterflyfish species to arrive for the first, third and fifth 5 min intervals after its arrival. Individual variation in color pattern and markings facilitated recognition of the focal fish (Reese 1973). Following the feeding observations, each colony was replaced in its original position inside the damselfish territory and responses of the resident damselfish were observed for 15 min.

At the fringing reef site in Moorea, *Pocillopora damicornis* colonies (13.8 ± 0.8 cm diameter, $n = 9$) were transplanted among nearby *Montipora* sp., and the focal butterflyfish species was *Chaetodon lunulatus* (Quoy & Gaimard). Additional colonies were back-transplanted to their original locations inside the territories ($n = 4$). In Guam, *P. damicornis* colonies (12.2 ± 1.1 cm diameter, $n = 8$) were transplanted to sites of high *Porites* spp. cover. Back-transplants were also performed ($n = 5$). In Guam, the focal butterflyfish species was *C. bennetti* (Cuvier), which behaves similarly to *C. lunulatus* and was more common at this site (pers. obs.). As a measure of natural feeding rates of this species at this site we observed feeding of 8 *C. bennetti* on undisturbed *Porites rus* outside territories. Density of butterflyfishes was assessed by visual counts along a 100×2 m transect at the fringing reef site in Moorea ($n = 5$) and in Guam ($n = 9$).

In Guam, several additional control experiments were performed. To determine whether butterflyfish predation on the transplanted colony was due solely to the transplantation procedure or to its novelty as a new object on the reef, *Pocillopora damicornis* colonies were transplanted from inside damselfish territories (12.6 ± 1.7 cm diameter, $n = 5$) to outside territories after dark (19:00 h). The aim was to conceal the transplantation from the butterflyfishes while they were inactive. The site was revisited the following morning (09:00 h). Since extensive predation had already occurred, arrival times and feeding rates of a focal fish were not recorded. Instead, a visual examination of

each coral to estimate percent tissue loss (bare white skeleton) was made at 14, 22, 45, 69 and 88 h after transplant. This enabled an assessment of the fate of *P. damicornis* colonies if left exposed on the reef outside damselfish territories. In addition, *P. damicornis* colonies from the reef flat, at least 10 m from the reef slope, were used in transplants both during day and night (6.8 ± 2.3 cm diameter, $n = 5$ each), to determine whether colonies from outside territories differed from those inside territories. Lastly, *Porites rus* colonies from inside (11.4 ± 0.8 cm diameter, $n = 8$) and outside territories on the reef slope (13.5 ± 1.7 cm diameter, $n = 8$) were transplanted to the same sites outside of territories. *P. rus* was used as a control because it was the dominant species both inside and outside damselfish territories in this habitat, and therefore, it is the predominant food source for butterflyfishes (unpubl. data). For each control experiment, corals were transplanted to all or a subset of the same 8 sites in random order to control for differences in sites that might affect fish behavior on the transplanted colony. In 1992, the first corallivorous butterflyfish to arrive at a transplanted colony was typically *Chaetodon bennetti*; however, in 2002, *C. reticulatus* (Cuvier) was usually the first to arrive and was therefore used as the focal species. *C. bennetti* and *C. reticulatus* exhibited similar feeding behaviors (unpubl. data).

Comparisons were made between the number of bites in the 15 min observation period before transplantation and the pooled number of bites by the focal fish in three 5 min periods after arrival (Wilcoxon signed-rank tests). A univariate repeated measures ANOVA was used to test for within-subject effects (time effect) on number of bites in the first, third and

fifth 5 min feeding periods. Nonorthogonal comparisons of feeding rates between first and third and between third and fifth 5 min periods were used to test the hypothesis that feeding rates decreased over time, possibly due to the removal of accessible tissue from the transplanted colony. For the nocturnal transplants, percent tissue loss was arcsine transformed and changes over time were analyzed by repeated measures ANOVA.

RESULTS

Effect of damselfishes on coral diversity

At all 3 sites, coral diversity (both number of coral species and Shannon-Wiener diversity index) was significantly greater inside damselfish territories than outside territories (Tables 1 & 2). Overall percent coral cover was significantly lower inside territories at the fringing reef site in Moorea and in Guam (Tables 1 & 2). The high percent cover outside of territories was due to a virtual monoculture of *Montipora* sp. at the fringing reef site in Moorea and to large expanses of *Porites* spp. in Guam. At the lagoon site in Moorea, overall percent cover of corals did not differ inside and outside territories; however, with the exception of several massive *Porites* sp. colonies, virtually all live corals at this site occurred inside damselfish territories.

Despite their low overall percent coral cover, several coral species were only found inside damselfish territories. *Pocillopora damicornis* was found only inside territories at the lagoon site in Moorea and on the reef

Table 1. Comparison of substrate cover and number of coral genera inside and outside of damselfish *Stegastes nigricans* territories at fringing reef and lagoon study sites in Moorea, p-values refer to Mann-Whitney *U*-test, except those indicated in the footnote (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS: not significant). Data are means ± 1 SE; ranges are in parentheses; NA: not applicable

Substrate type	Fringing reef territories			Lagoon territories		
	Inside n = 26	Outside n = 26	p	Inside n = 10	Outside n = 10	p
Percent cover						
All corals	16.9 \pm 2.5 (0–45)	91.8 \pm 2.6 (34–100)	***	44.1 \pm 6.0 (23–80)	31.1 \pm 8.3 (0–81)	NS
<i>Montipora</i> sp.	9.4 \pm 2.6 (0–42)	91.0 \pm 2.6 (34–100)	***	3.3 \pm 1.6 (0–13)	0	* ^a
<i>Porites</i> sp.	0	0	NA	12.6 \pm 4.0 (0–33)	31.1 \pm 8.3 (0–81)	**
<i>Pocillopora damicornis</i>	5.3 \pm 0.95 (0–16)	0.038 \pm 0.038 (0–1)	***	20.0 \pm 8.6 (0–80)	0	**
<i>Acropora</i> sp.	0.46 \pm 0.46 (0–12)	0	NS ^a	7.8 \pm 5.8 (0–59)	0	NS ^a
<i>Pavona</i> sp.	0.73 \pm 0.34 (0–6)	0	** ^a	0.4 \pm 0.4 (0–4)	0	NS ^a
<i>Fungia</i> sp.	1.1 \pm 0.64 (0–13)	0.73 \pm 0.37 (0–8)	NS ^a	0	0	NA
Algae	82.0 \pm 2.8 (47–100)	4.0 \pm 1.1 (0–20)	***	48.5 \pm 4.5 (20–69)	1.6 \pm 1.2 (0–11)	***
Rubble/sand	1.0 \pm 0.55 (0–11)	4.2 \pm 2.3 (0–56)	NS ^a	7.4 \pm 3.7 (0.27)	67.3 \pm 9.1 (0–91)	***
Number of coral species	1.92 \pm 0.16 (0–3)	1.23 \pm 0.08 (1–2)	***	2.3 \pm 0.26 (1–3)	0.8 \pm 0.13 (0–1)	***
Coral diversity (<i>H'</i>)	0.44 \pm 0.07 (0–1.08)	0.03 \pm 0.01 (0–0.27)	***	0.51 \pm 0.11 (0–1.03)	0	**

^aSubstrate types for which many quadrats contained zeros were analyzed by 2 \times 2 contingency tests using the proportion of quadrats containing that substrate type inside versus outside of territories; p-values refer to chi-square values

Table 2. Substrate cover types and number of coral genera at Guam study site in 1992 and 2002. Inside versus outside damselfish *Stegastes lividus* territory comparisons performed with Mann-Whitney *U*-test, except for those indicated in the footnote (* $p < 0.025$, ** $p < 0.01$, *** $p < 0.001$; NS: not significant). Data are mean \pm SE (range)

Substrate type	1992 territories			2002 territories		
	Inside n = 15	Outside n = 15	p	Inside n = 20	Outside n = 20	p
Percent cover						
All corals	28.5 \pm 4.1 (4–52)	97.6 \pm 1.7 (80–100)	***	32.2 \pm 3.9 (8–67)	84.9 \pm 4.4 (28–100)	***
<i>Porites rus</i>	5.3 \pm 1.1 (0–16)	50.1 \pm 1.1 (40–60)	***	8.5 \pm 3.1 (0–44)	43.1 \pm 10.0 (0–100)	*
<i>Porites cylindrica</i>	0.53 \pm 0.31 (0–4)	47.5 \pm 1.1 (40–56)	***	0.28 \pm 0.28 (0–6)	38.61 \pm 9.1 (0–100)	***
<i>Pocillopora damicornis</i>	18.4 \pm 3.7 (0–44)	0	***	19.2 \pm 3.1 (0–61)	0	***
<i>Acropora</i> sp.	2.9 \pm 1.4 (0–16)	0	* ^a	1.8 \pm 1.7 (0–33)	0	NS ^a
<i>Pavona cactus</i>	1.3 \pm 0.64 (0–8)	0	* ^a	2.6 \pm 1.1 (0–17)	0	** ^a
Algae	71.5 \pm 4.1 (48–96)	0	***	61.7 \pm 3.9 (31–92)	2.5 \pm 1.0 (0–14)	***
Rubble/sand	0	2.4 \pm 1.7 (0–20)	NS ^a	6.3 \pm 1.7 (0–22)	5.0 \pm 2.9 (0–56)	NS ^a
Number of coral species	2.07 \pm 0.18 (1–4)	1.27 \pm 0.12 (1–2)	***	2.05 \pm 0.17 (1–4)	1.3 \pm 0.11 (1–2)	***
Coral diversity (<i>H'</i>)	0.55 \pm 0.09 (0–1.24)	0.1 \pm 0.05 (0–0.59)	***	0.52 \pm 0.08 (0–1.28)	0.14 \pm 0.06 (0–0.66)	***

^aSubstrate types for which many quadrats contained zeros were analyzed by 2 \times 2 contingency tests using the proportion of quadrats containing that substrate type inside versus outside of territories; p-values refer to chi-square values

slope in Guam, and percent cover of this species was significantly greater inside damselfish territories at all 3 sites (Tables 1 & 2). Corals in the genera *Acropora*, *Pavona* and *Fungia* were relatively rare at these sites. In Moorea, *Acropora* sp. and *Pavona* sp. were only found inside damselfish territories, but percent cover was significantly greater inside territories only for *Pavona* sp. at the fringing reef site (Table 1). In Guam, *Acropora* sp. and *Pavona cactus* were only found inside damselfish territories (Table 2).

Percent algal cover was significantly greater inside damselfish territories at all 3 sites (Tables 1 & 2). Abiotic substratum (sand or coral rubble) was rare at the fringing reef site in Moorea and in Guam, but was a major component of the substratum outside of damselfish territories at the lagoon site in Moorea (Table 1).

Coral community structure on the reef slope at Piti Bomb Holes in Guam remained relatively stable for at least 10 yr. When resurveyed in 2002, coral diversity remained significantly higher inside damselfish territories, and percent coral cover was significantly greater outside territories (Table 2). Percent cover of *Pocillopora damicornis* and *Pavona cactus* were still significantly greater inside territories (Table 2). Percent algal cover also remained higher inside territories. The only significant changes between 1992 and 2002 consisted of a decline in cover of *Porites* spp., which resulted in a decline in overall coral cover outside damselfish territories (from 97.6 \pm 1.7% in 1992 to 84.9 \pm 4.4% in 2002; Mann-Whitney *U*-test: $n_1 = 15$, $n_2 = 20$, $p = 0.006$) and significant increases in area of abiotic substratum both inside (6.3%, $p = 0.0008$) and outside territories (2.6%, $p = 0.02$). Qualitative surveys performed from 1994 to 2001 (M. Slattery pers. comm.)

and from 2003 to 2008 (pers. obs.) were consistent with the quantitative surveys performed in 2002.

In 2002, a few small colonies of *Pocillopora damicornis* were observed on the reef flat in Guam at least 10 m from the reef slope. These corals occurred in very low density (32 in 500 m²) compared with those inside damselfish territories (237 in 60 m²) and were significantly smaller than those inside territories (reef flat: 4.7 \pm 4.8 cm, $n = 32$; inside territories: 12.5 \pm 10.9 cm, $n = 237$; unpaired *t*-test: $t = 4.02$, $df = 267$, $p < 0.0001$). No colonies of *Pocillopora* spp. were found on the reef slope outside damselfish territories.

Effect of damselfishes on protection of corals from predation

During ten 15 min observation periods, *Stegastes nigricans* chased 15 fish species from territories at the fringing reef site in Moorea, including 6 species of butterflyfish. All fish observed near damselfish territories were chased, and none successfully entered territories. *S. nigricans* was never observed feeding on coral, so initial feeding rates on corals inside damselfish territories were zero. Back-transplantation of *Pocillopora damicornis* to their original territories resulted in repeated attempts by the resident damselfish to lift or push the colony. In 3 of 4 cases, the colony was successfully dislodged. In 2 cases, the colony was toppled out of the territory, and butterflyfishes began to feed on it in 3.4 to 4.6 min.

After *Pocillopora damicornis* colonies were transplanted to undefended parts of the reef, butterflyfishes arrived very rapidly (1.7 \pm 0.58 min, $n = 9$). The number

of fish at a transplanted colony during 30 min observation periods ranged from 4 to 23, with up to 8 species present at any given time, including as many as 6 species of butterflyfish (Fig. 1). Overall, 8 species of butterflyfish (*Chaetodon auriga*, *C. citrinellus*, *C. lunula*, *C. ornatissimus*, *C. pelewensis*, *C. reticulatus*, *C. lunulatus* and *C. vagabundus*) fed on the transplanted corals during the 30 min observation periods. Other species that fed on transplanted colonies included the triggerfish *Balistapus undulatus*, the wrasse *Pseudocheilinus hexataenia*, and the predominantly herbivorous angelfish *Centropyge flavissimus*. Butterflyfish density along the reef slope at this site was 41.2 ± 7.3 individuals (ind.) 100 m^{-2} , representing 7.5 ± 2.3 species ($n = 5$ surveys).

Feeding rates were significantly greater on *P. damicornis* colonies transplanted outside of damselfish territories than on those same colonies inside territories in Moorea (Wilcoxon signed-rank test: $n = 9$, $p = 0.009$). Feeding rate before transplantation was zero, and during the first 5 min after its arrival, mean feeding rate of the focal *Chaetodon lunulatus* was 156 ± 12 bites per 5 min period ($n = 9$). Feeding rate of focal individuals decreased significantly over time (Repeated measures ANOVA: $p = 0.0001$; Fig. 2a). Feeding rates between the first and third and between the third and fifth 5 min

periods differed significantly (nonorthogonal comparisons: $p < 0.01$ and $p < 0.05$, respectively). At the end of the 30 min period, bare white skeleton was exposed on several centimeters of the outer tips and branches of all transplanted colonies. Feeding rates of *C. lunulatus* on undisturbed *Montipora*, the predominant coral food source at this site, were 57 ± 3.4 bites per 5 min period ($n = 10$), which was significantly lower than feeding rates on the transplanted *P. damicornis* colonies (Mann-Whitney *U*-test: $n_1 = 10$, $n_2 = 19$, $p = 0.003$).

Stegastes lividus chased 9 species, including 2 species of butterflyfish, from their territories during eight 15 min observation periods in Guam. All fish approaching territories were chased, except for large schools of juvenile rabbitfishes *Siganus* spp. Initial feeding rates on coral colonies inside damselfish territories were zero. Back-transplanted corals were treated similarly to those in Moorea, and 4 out of 5 colonies were successfully dislodged. These landed within territories of other *S. lividus*, which behaved in a similarly agitated manner.

When *Pocillopora damicornis* colonies were transplanted outside of territories in Guam, butterflyfishes arrived in 2 to 30 min (9.6 ± 3.1 min, $n = 8$). A range of 7 to 47 fish arrived at the transplanted colonies during 30 min observation periods, with up to 15 species pre-



Fig. 1. *Pocillopora damicornis*. Colony transplanted onto *Montipora* reef at fringing reef site in Moorea. Four species (11 individuals) of coral-feeding butterflyfishes are shown feeding on the transplanted colony (*Chaetodon lunulatus*, *C. ornatissimus*, *C. reticulatus*, *C. citrinellus*)

sent at once, including up to 8 species of butterflyfish. Overall, 10 species of butterflyfish (*Chaetodon auriga*, *C. bennetti*, *C. ephippium*, *C. lunula*, *C. ornatissimus*, *C. punctatofasciatus*, *C. reticulatus*, *C. ulietensis*, *C. unimaculatus* and *Forcipiger* sp.) fed on the transplanted corals during the 30 min observation periods. Butterflyfish density along the reef slope at this site was 62.6 ± 4.5 ind. 100 m^{-2} , representing 10.9 ± 0.6 species ($n = 9$ surveys).

Mean feeding rates of focal *Chaetodon bennetti* on transplanted *Pocillopora damicornis* were significantly greater than feeding rates on those same colonies inside damselfish territories (121 ± 6.6 bites versus 0 bites per 5 min period; Wilcoxon signed-rank test: $n = 8$, $p = 0.014$). Feeding rates of the focal individual decreased significantly over time (repeated measures ANOVA: $p = 0.0001$, Fig. 2b). Feeding rates between first and third and between third and fifth 5 min periods differed significantly (nonorthogonal comparisons: $p < 0.0001$ and $p < 0.001$, respectively). Tissue condition of transplanted colonies after the 30 min feeding period was similar to that described for colonies in Moorea.

Despite the smaller colony size, *Pocillopora damicornis* colonies transplanted from outside territories (i.e. the reef flat) also attracted corallivores. Butterflyfishes arrived within 1 to 10 min (4.0 ± 2.0 min, $n = 5$). The number of fishes arriving at a transplanted colony during 30 min observation periods ranged from 5 to 10 individuals, whereas up to 14 additional fishes were observed in the vicinity of the transplanted colony but continued swimming without stopping to investigate. Overall, 7 species of butterflyfish (*Chaetodon auriga*, *C. citrinellus*, *C. melannotus*, *C. reticulatus*, *C. ulietensis*, *Forcipiger* sp. and *Heniochus singularis*) fed on the reef flat transplants during 30 min observation periods. Although these colonies appeared browsed before transplantation (e.g. polyps withdrawn, short stubby branches), butterflyfishes were not seen feeding on them during the 30 min before transplantation. Thus, mean feeding rate before transplantation was zero and increased significantly during the first 5 min after arrival of the focal *C. reticulatus* to 148.6 ± 28.4 bites per 5 min period (Wilcoxon signed rank test: $n = 5$, $p = 0.043$). Feeding rates of the focal individual decreased significantly over time (repeated measures ANOVA: $p < 0.0001$, Fig. 2c), and feeding rates differed significantly between the 3 post-transplant periods (non-orthogonal comparisons: $p < 0.01$).

Nocturnal transplantation of *Pocillopora damicornis* from both inside territories and the reef flat did not inhibit butterflyfish predation the following morning. By 09:00 h (14 h post-transplant), up to 50% tissue loss had already occurred (Fig. 3). A repeated measures ANOVA indicated a significant effect of both treat-

ment ($p = 0.0008$) and time ($p < 0.0001$) on tissue loss. Transplanted corals from inside territories lost significantly more tissue than those transplanted from outside territories, and tissue loss in both types of transplants increased over time, with the greatest rate of tissue loss occurring during the first 22 h (Fig. 3).

Porites rus colonies transplanted from either inside or outside of damselfish territories attracted fewer visitors than did *Pocillopora damicornis* transplants. During 60 min observations, only 3 of the 16 transplanted *P. rus* colonies attracted any visitors. These

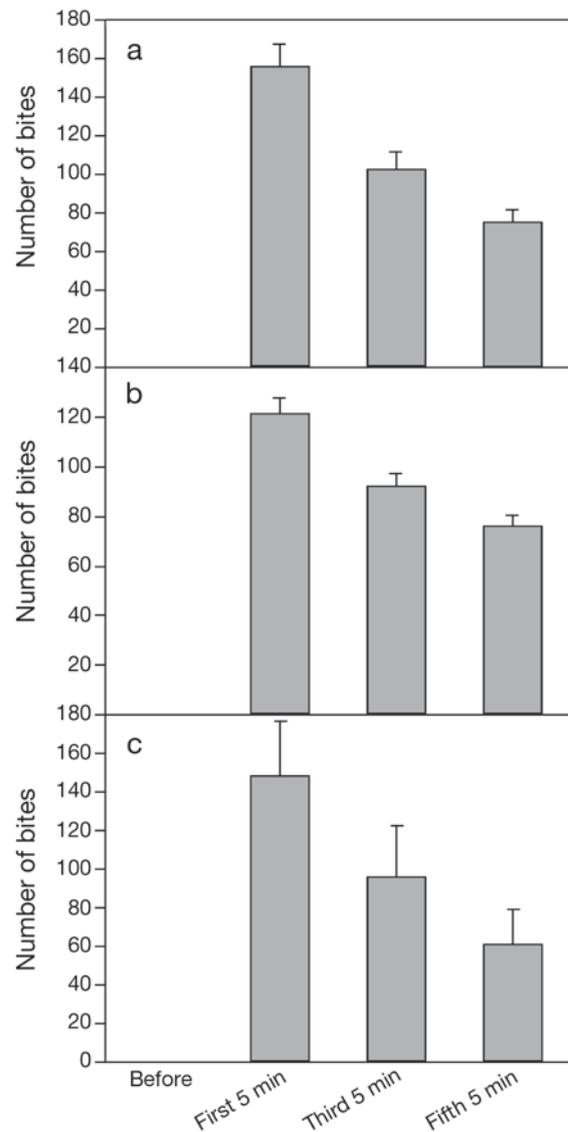


Fig. 2. *Pocillopora damicornis*. Feeding rates on transplants from (a,b) inside and (c) outside territories. Number of fish bites (mean \pm SE) per 5 min for first, third and fifth 5 min periods following transplantation. (a) *Chaetodon lunulatus* in Moorea ($n = 8$). (b) *C. bennetti* in Guam ($n = 8$). (c) *C. reticulatus* in Guam ($n = 5$).

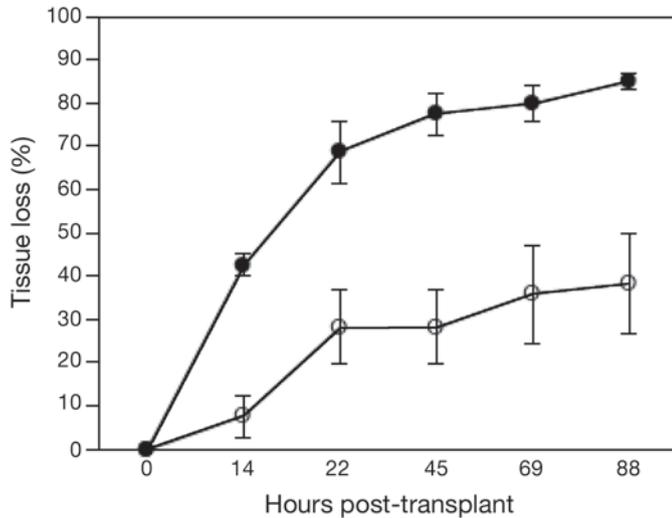


Fig. 3. *Pocillopora damicornis*. Tissue loss (% mean \pm SE) over time on colonies transplanted at night from inside (●) and outside (○) damselfish territories in Guam ($n = 5$ each). Note varying time intervals

consisted of 2 to 12 individuals of up to 8 species, including 4 species of butterflyfish (*Chaetodon bennetti*, *C. lunulatus*, *C. punctatofasciatus* and *C. ulietensis*). Arrival times of butterflyfishes at *P. rus* (n_1) transplants were significantly longer than arrival times at *P. damicornis* (n_2) transplants (Mann-Whitney *U*-test: $n_1 = 16$, $n_2 = 8$, $p = 0.0036$), and although these fishes approached the transplanted *P. rus* colony, none actually fed on the coral tissue. Mean feeding rate of *C. bennetti* on undisturbed *P. rus* outside damselfish territories was 34 ± 3.2 bites per 5 min period ($n = 8$). Since none of the transplanted *P. rus* colonies were preyed upon, transplantation resulted in a significant decrease in feeding rate on *P. rus* from outside territories (Wilcoxon signed-rank: $n = 8$, $p = 0.014$), but no change in feeding rate on *P. rus* transplanted from inside territories.

DISCUSSION

Effect of damselfishes on coral diversity

Corals are often considered characteristic of particular zones on reefs due to physical factors such as light and water motion, or biological factors such as competition and predation. Positive species interactions, including associational defenses, also play an important role in shaping coral reef communities. Territorial grazing damselfishes have been implicated as keystone species for their role in increasing algal community diversity by limiting herbivory within their territories and thereby maintaining their territories in early

successional stages (Williams 1980, Hixon & Brostoff 1983, 1996, Hata & Kato 2002). The intermediate disturbance hypothesis (Connell 1978) has been invoked as a cause of this elevated patch diversity (Hixon & Brostoff 1983, 1996), and is further relevant to the coral communities inside damselfish territories, as modified by Hacker & Gaines (1997) to include positive indirect interactions. The results of the present study demonstrate that some damselfishes also act as keystone species for coral communities on some reefs. By reducing local predation pressure, damselfishes facilitate the coexistence of several coral species and increase overall coral diversity. In the absence of territorial damselfishes, intense predation contributes to the local exclusion of certain coral species.

Fishes can affect community structure on coral reefs by eliminating certain coral species from habitats where corallivorous fishes are abundant (Neudecker 1979, Cox 1986, Littler et al. 1989). Studies in which corals have been transplanted to parts of the reef where they are not normally found suggest that fish predation excludes them from these habitats (Neudecker 1977) or reduces their ability to compete with other corals (Cox 1986). Selective predation on certain coral species (e.g. *Pocillopora damicornis*) reduces prey diversity and creates a community inhabited by a few dominant prey species. If these highly preferred coral species are protected from predation inside damselfish territories, then these territories represent microhabitat refuges from exclusion due to consumers, and this facilitates increased coexistence and enhances diversity of the reef as a whole. Coral diversity was indeed higher inside damselfish territories than outside territories on reefs in both Moorea and Guam, due to the survival of certain corals, such as *Pocillopora* spp., *Acropora* spp. and *Pavona* spp., which are excluded from the reef outside of territories. This pattern has been previously observed in territories of *Stegastes nigricans*. In a survey of reef recovery following storm damage, Done et al. (1991) reported a greater number of coral genera inside *S. nigricans* territories on reefs in Moorea, and similar patterns have been noted for *S. nigricans* territories in Tahiti (Glynn & Colgan 1988) and in Papua New Guinea (Jones et al. 2006). However, this pattern appears to be more widespread, with similar phenomena observed in *Hemiglyphidodon plagiometopon* territories on the Great Barrier Reef (Sammarco & Carleton 1981), in *S. lividus* territories in Guam (present study), and in *Stegastes* spp. territories elsewhere in the Indo-Pacific (pers. obs.). In addition, the relative stability of this system over 10 yr at Piti Bomb Holes in Guam indicates that damselfish territories represent a major structuring force for coral communities in certain habitats.

Effect of damselfishes on protection of corals from predation

Considerable experimental and descriptive data have demonstrated that corallivores exhibit preferences among coral prey species. For example, several species of Indo-Paciﬁc coral-feeding butterflyfishes exhibit strong preferences for corals in the genera *Pocillopora*, *Acropora*, and *Pavona* over *Montipora* and *Porites* (Reese 1977, Hourigan et al. 1988, Zekeria 2003, Pratchett 2007). Coral species that are preferred by corallivores are more susceptible to predation as a factor controlling their distribution. The virtual absence of any *Pocillopora* spp., *Acropora* spp. or *Pavona* spp. outside damselfish territories in this study suggests that predation may preclude survival in these habitats, and only when growing in association with damselfish territories are these preferred coral species protected from predation. Other studies support these findings. Glynn & Colgan (1988) found that *Acropora* spp., the preferred prey of the crown-of-thorns starfish, was more abundant inside damselfish territories than outside territories in Tahiti. They proposed that corals growing inside damselfish territories have a high likelihood of survival during a crown-of-thorns starfish outbreak, thereby providing a potential seed population for reef recovery. Wellington (1982) reported that pocilloporid corals have high mortality in deep reef areas due to increased fish grazing in the absence of territorial damselfishes. Done et al. (1991) also suggested that *Pocillopora damicornis* colonies inside *Stegastes nigricans* territories in Moorea were protected from butterflyfish predation by the resident damselfish. However, the association between *P. damicornis* and *Stegastes* spp. territories appears to be facultative rather than obligate, as *P. damicornis* survives in other reef habitats that experience lower levels of predation (e.g. reef flats in Hawaii and Guam, and cyclone- and *Acanthaster*-damaged outer reef slopes in Moorea, pers. obs.).

When transplanted outside of damselfish territories, colonies of *Pocillopora damicornis* were exposed to extremely high rates of predation. Corallivorous butterflyfishes arrived and fed rapidly. The transplanted colonies had large patches of exposed white skeleton after the 30 min transplant period, which probably accounted for the reduced feeding rates of individual butterflyfishes over time, although it is also possible that reduced feeding rate could be a function of satiation. If these colonies had been left on the reef outside territories for longer, it is likely that all tissue would eventually have been removed. In fact, 2 colonies of *P. damicornis* were observed outside damselfish territories at the fringing reef site in Moorea. Both colonies were broken apart and the skeleton was stripped bare

of tissue and overgrown with turf algae. Nonetheless, butterflyfishes were occasionally observed investigating these colonies. While *P. damicornis* colonies can regenerate from lower intensities of tissue removal (Hall 1997), the rapid and extensive predation observed during these brief experiments may preclude regeneration.

The novelty of the transplanted *Pocillopora damicornis* colonies on reef areas outside damselfish territories, and any damage to tissue that might have been caused during the transplant procedure, could attract a greater number of corallivorous fishes than would a naturally settled juvenile *P. damicornis* colony. However, experiments using *Porites rus* in Guam demonstrated that novel colonies of less preferred coral species transplanted in a similar manner to the same locations on the reef did not attract the same feeding intensity as the transplanted *P. damicornis* colonies, suggesting that the latter were highly favored food items not otherwise available. Even when transplanted at night, *P. damicornis* was already consumed as soon as it became light, suggesting that an inherent quality of *P. damicornis*, rather than handling or location, is what makes it so attractive to corallivores. Thus, *P. damicornis* colonies that do settle on the reef outside damselfish territories are probably subjected to high predation pressure, which would decrease the likelihood that they would survive and grow to adult size. In fact, the few *P. damicornis* colonies found outside of damselfish territories in Guam were significantly smaller than those inside territories, and they occurred on the reef flat where butterflyfishes are scarce (pers. obs.). However, even these exhibited signs of predation, with a more compact morphology and retraction of polyps during the day. In addition, there is evidence of higher coral recruitment rates and lower rates of juvenile coral mortality inside damselfish territories. Gleason (1996) found higher rates of coral recruitment on artificial substrata placed inside *Stegastes nigricans* territories in Moorea than on those placed outside territories. This may result from reduced predation, or from reduced sedimentation within damselfish territories, which may benefit the settlement of benthic invertebrates including corals (Ceccarelli et al. 2005). Sammarco & Carleton (1981) reported that coral recruitment rates inside damselfish territories were 5 times higher than rates outside territories on the Great Barrier Reef, and Wellington (1982) found that damselfish territories provided a refuge against juvenile mortality for pocilloporids that settled within the defended area on reefs in Panama.

Why do herbivorous damselfishes defend their territories against coral-feeding fishes? Damselfishes are able to recognize intruders based on body shape and behavior (Losey 1982). However, even if the resident

fish can identify intruders as non-competitors, allowing certain individuals to enter their territory may attract other intruders. The energetic cost of chasing each individual intruder may be less than the cost of attempting to chase a school of intruders. *Stegastes* spp., while certainly highly aggressive, are nonetheless ineffective against schools of intruding parrotfishes, wrasses, rabbitfishes or surgeonfishes (Robertson et al. 1976, author's pers. obs.). On the other hand, since damselfish territories typically occur in large colonies, cooperative defense against predators may increase efficiency (Stachowicz 2001) while reducing the cost of defense to any individual (Getty 1987). Damselfishes might defend the corals inside their territories because they provide shelter and potential nesting sites (Robertson et al. 1981, Glynn & Colgan 1988). Some damselfishes kill portions of the corals growing inside their territories to free substratum for nesting or on which to enlarge their algal mats (Wellington 1982, Knowlton et al. 1988), although there was no evidence of this in the present study. The possibility that damselfishes gain some benefit in terms of shelter from the corals inside their territories cannot be eliminated. However, when the transplanted and back-transplanted corals were replaced in their original positions inside the territories, the resident damselfishes consistently attempted to dislodge them, occasionally toppling them out of their territories. This observation suggests that the damselfishes were not defending the corals themselves. Eakin (1987) also found little evidence for a benefit to the damselfish from their association with corals, although others have suggested that the association of non-territorial damselfishes with corals may represent a mutualism, with the corals providing shelter and the fish providing fertilizer that increases coral fitness (Lieberman et al. 1995, Holbrook et al. 2008).

Any benefit that corals receive from territorial defense by the resident damselfish is apparently incidental. The corals appear to be potentially parasitic, benefiting from territorial defense by the resident damselfish, while taking up space that could otherwise be devoted to algal growth. Associational defenses, such as that described here, may incur costs. For example, palatable plants growing with competitors in the absence of herbivory grew significantly less than those growing alone (Hay 1986, Pfister & Hay 1988, Levine 2000). However, the cost of competition with an unpalatable species was less than the cost of increased consumption in the absence of the competitor (Hay 1986). In the present study, the potential cost to the coral from growing in association with algal competitors appears to be less than the cost of increased predation in the absence of the algae since, at least on the reefs studied, coral growing in the absence of these

algae appears to lead to local exclusion. The fact that damselfishes repeatedly tried to displace the transplanted and back-transplanted control corals when they were returned to their territories suggests that damselfishes may perceive a cost to having corals within their territories. This cost could result from potential competition for space with the algal lawn, or from an increased energetic expense of territory defense if intruders attempted to enter territories with corals present more often. In addition, costs and benefits of species associations may vary over a gradient of predation pressure (Levenbach 2009). Territorial damselfishes worldwide exhibit a range of interactions with corals, from obligate consumption for nutritional purposes, to facultative consumption to clear space for algal growth, to active or passive defense of corals in their territories (Ceccarelli 2007). Therefore, the costs and benefits of associating with corals may be actively weighed by the damselfish and provide varying levels of protection for corals in different habitats.

During the 1980s, Moorea's reefs were subjected to numerous stressors that affected the coral reef community, including cyclones, bleaching events, changes in sea level and outbreaks of *Acanthaster planci* (Done et al. 1991, Gleason 1993, Hoegh-Guldberg & Salvat 1995). Damselfishes may be among the more rapid colonizers of exposed substrate as a result of these events (Letourneur et al. 1993), and it has been suggested that damselfish territories might serve as a refuge for corals during *A. planci* outbreaks (Glynn & Colgan 1988). Likewise, the Piti Bomb Holes site in Guam has also been exposed to numerous large-scale stressors in recent decades. In addition to typhoons and bleaching events (Porter et al. 2005), a massive construction project was undertaken to build an underwater observatory at this site in 1995. Among other effects, this project caused increased sedimentation (Slattery et al. 2008), which may be associated with the shift in composition of the butterflyfish assemblage at this site. Survey results from Piti Bomb Holes in 2002 indicated an overall decline in coral cover and an increase in bare substratum, but only outside of damselfish territories, possibly due to reduced sediment accumulation inside of territories (Ceccarelli et al. 2005). Overall community structure, particularly inside damselfish territories, remained stable over the course of 10 yr. Although *Acanthaster planci* is present in low numbers on the reef at Piti Bomb Holes, there has not been an outbreak of this species there since the 1970s (Porter et al. 2005). This study therefore demonstrates that the association of corals with damselfishes is also important during non-outbreak periods, when other stressors, including chronic predation by resident fish coralivores, may be sufficient to limit survival of certain coral species outside territories. Palatable corals can

survive in the refuge of damselfish territories, thereby increasing patch diversity and providing a potential seed population for reef recovery during periods of mass coral mortality. Territorial damselfishes are abundant components of shallow tropical coral reefs worldwide, and their territorial behavior represents a major structuring force, particularly on Indo-Pacific reefs. While also abundant in the Caribbean Sea, the reduced and less specialized corallivorous fish fauna on Caribbean reefs may reduce their effect to some extent. Clearly, positive interactions of this type play an important role in structuring reef communities where a high density and diversity of predators have the potential to influence the distribution of their preferred prey.

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