EFFECTS OF DIFFERENTIAL GRAZING ON THE IMPORTANCE OF DAMSELFISH TERRITORIES AS ALGAL REFUGES

JON S. BEADELL, JAMES W. HOURDEQUIN, ANITA L. MANNAN, AND E. HANK TALIAFERRO

Abstract. Damselfish territories may contribute to high algal diversity on the Discovery Bay reef by providing certain species with a refuge from herbivores that would otherwise forage on these species to their exclusion. Results are consistent with this hypothesis. In areas of high extraterritorial herbivory, damselfish territories supported a total of 34 species of algae while unprotected substrate supported only 20 species. In addition, of the 20 species occurring outside the territory only 4 were not found inside territories. In regions of low extraterritorial herbivory, species richness inside and outside of territories differed by only 3, but approximately 15 algal species were unique to each region. This suggests that while damselfish appear to increase algae richness in regions of high grazing pressure by providing refuges, these fish may also increase richness in areas of low grazing pressure by deflecting the successional trajectory from that taken by ungrazed algae communities. Damselfish species were not equally successful in maintaining refuges. *Stegastes planifrons* and *Stegastes dorsopunicans* each protected an average of approximately 5 species in addition to those found outside territories while *Microspathodon chrysurus* protected, on average, only 1 more species than the number existing outside territories. Although threespot damselfish were observed removing *Amphiroa* sp. from their plots, given that intraterritorial algae communities varied widely across the area studied, there is no evidence that damselfish actively direct the succession of the algal garden towards a unique preferred community.

Key Words: damselfish, macroalgae, species richness, territoriality

INTRODUCTION

Following the mass mortality of *Diadema antillarum*, a major algal grazer, in 1983, the macroalgae community has become a conspicuous and highly diverse component of the reef at Discovery Bay, Jamaica. In the absence of *D. antillarum*, parrotfish (Scaridae), surgeonfish (Acanthuridae), and damselfish (Pomacentridae) represent the most abundant grazers of algae, and these likely have a significant impact on algal distribution, abundance and diversity (Lewis 1986). Parrotfish and surgeonfish forage in schools and may consume between 50 and 100% of algal productivity on shallow forereefs (Hay 1991). In areas of high abundance, these fish may eliminate highly palatable algal species. In Discovery Bay, however, where extensive fishing has severely reduced herbivore populations, the effects of these fish appears to be reduced and more patchily distributed.

Damselfish, ubiquitous members of the reef community, feed on and defend algae growing within small territories that may cover over 50% of shallow reef tracts (Hixon and Brostoff 1996). The three most common species at Discovery Bay demonstrate three levels of aggressiveness against intruding grazers (pers. obs.): *Stegastes planifrons* (threespot) aggressively defends its territory, Microspathodon chrysurus (yellowtail) defends only loosely defined territories and *Stegastes dorsopunicans* (dusky) demonstrates an intermediate level of aggressiveness. Damselfish may maintain increased algal diversity within their territories by preserving algae communities at intermediate levels of succession (Hixon and Brostoff 1996). Alternatively, damselfish may increase diversity within their territories by providing a refuge for those algal species that would otherwise be eliminated by foraging parrotfish and surgeonfish (Lewis 1986).

Variability in grazing regimes may explain in part high algal diversity on the Discovery Bay reef. We hypothesized that heterogeneity in grazing outside of damselfish territories affects the extent to which damselfish territories serve as refuges by maintaining high species richness inside with respect to surrounding substrate. Specifically, we predicted that damselfish territories will be more important as refuges from herbivory where grazing pressure outside territories is highest. Furthermore, we predicted that the extent to which these territories serve as refuges will vary with the aggressiveness of the resident damselfish species. In addition to testing these predictions, we investigated the degree to which algal communities occurring in damselfish territories over a wide range of substrates are similar with respect to species richness and species composition. This comparison was used along with observations of feeding behavior to determine the extent to which damselfish actively "cultivate" their algal gardens.

METHODS

This study was conducted between February 29 and March 8, 1996, in Discovery Bay, Jamaica. Background herbivory levels were assessed at two sites by placing five groups of six *Thalassia testudinum* leaves in areas outside of damselfish territories for six hours (Hay 1981). Site one was an area of moderate coral cover 1 - 2 m deep in the back reef approximately 20 m from the reef crest. Site 2 was an area of fairly extensive coral cover approximately 13 m deep at the mooring one dive site. In order to test whether background herbivory levels affect the extent to which damselfish territories provide a refuge for algal species, paired algal samples were collected from within 5 dusky damselfish and 5 threespot damselfish territories and adjacent areas on similar substrates. A circular petri dish of 6" diameter was haphazardly placed at three points approximately 10" apart forming a triangle within the sampling area, and all algal species under the petri dish were removed and brought to Discovery Bay Marine Laboratory for identification. An ANOVA was used to asses the effects of damselfish territoriality on algal species richness, and the effects of high and low background herbivory levels on the differences in algal species richness inside and outside of damselfish territories. The number of species in common between paired areas inside and outside of damselfish territories was calculated and Jacard's similarity index [# of species in common / # of species in J * # of species in K] was used to assess the similarities in the algal community between the two locations. The effects of territoriality and damselfish species on Jacard's similarity index were assessed using an ANOVA.

To determine how differences in aggressiveness affected algal community composition within damselfish territories, five paired samples were collected from inside and outside of yellowtail damselfish territories at the 40' depth site and compared with the paired samples collected from dusky and threespot territories at the same location. An ANOVA was used to assess the effects of damselfish species and territoriality on algal species richness within territories. The number of species in common beaten paired samples was calculated and an ANOVA was used to determine the effects of damselfish species on Jacard's index of similarity.

To determine the effects of different site locations on algal species composition within damselfish territories, samples from within dusky and threespot territories were collected from a third site patchily covered with algae in a mangrove area 1-2 m deep in Discovery Bay. An ANOVA was used to compare species richness between the three sites and a Jacard's index of similarity was used to asses similarity within territories between the three sites.

Damselfish preferences for algal species were determined by observing 3 dusky, 3 threespot and 3 yellowtail damselfish for five minutes at the 40' site and recording how many bites the fish took of different algal species.

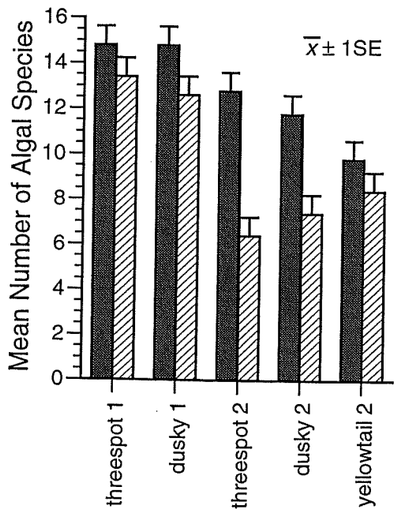
RESULTS

Background Herbivory: *Thalassia* blades placed in the forereef at 12 m were completely consumed (100% herbivory) during the six-hour herbivory trial, while blades in the 2 m deep back reef remained intact (10 - 25% herbivory) following the six hour trial. These tests were used to characterize the back reef as a low herbivory location and the forereef as a high herbivory location.

Effects of Background Herbivory: In all treatments, algal diversity was higher inside territories than outside territories (Fig. 1). However, there was little difference in algal species richness from inside to outside territories in the back reef where herbivory was low; whereas, there was a large difference in species richness in the high herbivory forereef (Table 1; territory and territory * location interaction). Species richness patterns inside and outside territories were similar for dusky and threespot damselfish in both high and low herbivory locations (Fig. 1). To better determine the effects of location on refuge importance, we compared the similarity of algal species inside and outside of damselfish territories. Jacard's coefficient of community indicated that inside and outside algal communities were more similar in the backreef (low herbivory) than in the forereef (high herbivory; Table 2).

Effects of Damselfish Species: In the forereef, threespot and dusky damselfish territories had higher species richness than yellowtail territories (Fig 1; Table 3). The difference in species richness from

inside to outside territories was greater for threespot and dusky damselfish than for yellowtail damselfish (Table 4; damselfish * territory interaction). Additionally, inside and outside algal communities were less similar in threespot and dusky territory pairs than in yellowtail territory pairs (Table 3).



Damselfish Species and Location

Fig. 1. Mean number of algal species inside and outside of threespot, dusky, and yellowtail damselfish territories (n = 5) in the fore reef and back reef of Discovery Bay, Jamaica, West Indies (1's indicate fish on the back reef and 2's indicate fish on the fore reef). Solid bars are species richness inside territories; hatched bars are species richness outside territories.

Effects of Location: There was a strong effect of location on species richness within damselfish territories. Species richness was greatest in the back reef, intermediate in the fore reef, and lowest in the mangrove reef (Fig. 2; F = 41.5, df = 14, P < 0.0001). Algal communities in the three locations were dissimilar with the mangrove and the fore reef being the least similar (Table 5).

Damselfish Feeding Observations: In the fore reef, both dusky and threespot damselfish each fed on ten different species, and yellowtail damselfish fed on five. Yellowtail damselfish spent much of the observation time hidden in coral formations, and it was difficult to assess their diets. All three damselfish species fed on four species in common: *Amphiroa* species 3, *Halimeda incrassata*, *Lobophora variegata*, and *Sargassum fluitans*. Several instances were also observed in which threespot damselfish actively removed *Amphiroa* species 1.

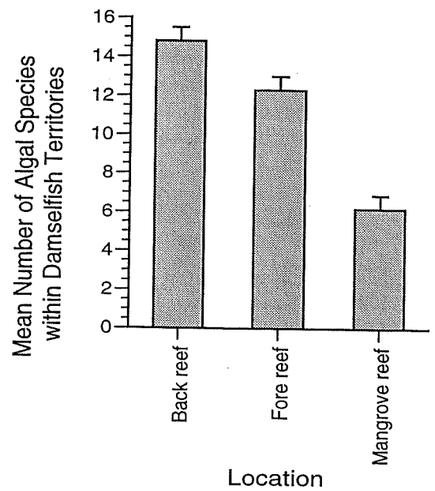


Fig. 2. Mean number of algal species inside threespot and dusky damselfish territories on the back reef, fore reef, and mangrove reef at Discovery Bay, Jamaica, West Indies.

Table 1. Effects of damselfish sp., position inside or outside of territory, and location on algal species richness.

Source	df	F Ratio	Prob > F
damselfish	1	0.055	0.816
in/out	1	17.88	0.0002*
location	1	25.50	0.0001*
damselfish * in / out	1	0.124	0.727
damselfish * location	1	0.0552	0.816
in / out * location	1	4.4690	0.042*
damselfish * location * in / out	1	0.676	0.417

* = P < 0.05

Discussion

Results suggest that damselfish provide important refuges for macro-algae, and that these refuges are most important where there are high levels of background herbivory. In the high-herbivory fore reef, species richness was higher inside territories than outside; whereas, inside and outside richnesses were similar in the back reef. A number of species were found only inside territories in the fore reef, possibly because damselfish territories provide a refuge to the algal species that are most susceptible to herbivory. Species that are highly palatable to herbivores and have limited chemical and structural defenses (Hay 1991) would likely be limited to damselfish territories and locations where herbivory is low. We found that Padina sanctae-crucis, a leafy algal species known to be preferred by parrotfish, only occurred inside territories in all locations.

Table 2. Algal species distribution on the fore reef and back reef and the similarities in communities.

Location	Sp. Inside	Sp. Outside	# of Sp. in Common	Jacard's coefficient	Prob. > F
Fore reef	34	20	16	0.296	0.1023
Back reef	45	42	30	0.345	N/A

Table 3. Algal species distribution in threespot, dusky, and yellowtail damselfish territories and the similarities in communities.

Damselfish sp.	Sp. Inside	Sp. Outside	# of species in common	Jacard's coefficient	Prob. > F
threespot	12.8	6.4	4.8	0.26	N/A
dusky	11.8	7.4	5	0.26	0.0006
yellow-tail	9.8	8.4	7.4	0.41	N/A

Damselfish territoriality may also affect the successional status of algal communities. It is difficult to generalize about the diversity and successional composition of our samples, because we did not measure relative species abundance. However, higher inside territory diversity could be maintained if damselfish support intermediate stages of succession in which early successional colonizers and competitive dominants are excluded (*intermediate disturbance hypothesis*, Connell 1978). Intense grazing outside of territories in the forereef would support colonization by early successional species. By excluding the herbivores, damselfish may allow algal communities to progress towards intermediate stages of succession in which species richness is thought to be highest (Connell 1978).

Table 4. Effects of damselfish sp. and position inside or outside of territory on algal species richness.

Source	df	F Ratio	Prob > F
damselfish	2	0.244	0.786
in/out	1	36.302	0.0001
damselfish * in/out	2	4.634	0.020

Table 5. Similarities in algal communities in the fore reef, back reef, and mangrove reef as seen by Jacard's Coefficient of Community.

	Fore Reef	Back Reef
Back Reef	0.236	N/A
Mangrove Reef	0.167	0.195

Damselfish may also prevent succession from progressing towards low diversity stages of competitive dominance. This could occur if damselfish actively removed competitive dominants, or if they promoted the growth of intermediate or early successional stage species that would otherwise be outcompeted. Hay (1991) suggested that damselfish feeding increased the growth rate of some algal species through repeated cropping. If this were occurring, there would likely be differences in algal composition even in places where background herbivory was low. The similarity between inside and outside algal communities in the back reef suggests that damselfish were not affecting competitive interactions between intermediate successional and dominant species.

Our observations of damselfish removing *Amphiroa* species, an abundant species inside and outside territories in all locations, suggests that active removal may be a factor in the maintenance of high inside-territory species diversity. The extent to which damselfish "actively select" their territories and how this affects algal composition would be an interesting area

for future study.

It did not appear that the presence of multiple species of damselfish contributed to algal diversity in high herbivory locations on the reef. Inside territory species composition was similar between three spot and dusky damselfish, and all of the species that occurred in yellowtail territories also occurred in three spot and dusky territories. There was considerable overlap in the algal species consumed by all three damselfish three species, and this suggests that the extent of territoriality is the most important difference between species.

The considerable differences in algal richness and composition between mangrove, back reef, and fore reef locations many biotic and abiotic factors affect algal distribution. The low algal diversity in the mangrove site could be due to high nutrient levels or low salinity favoring a few competitively dominant algal species. Alternatively, algal composition in the mangrove reef may have been most affected by intense parrotfish grazing around territories.

Our study did not measure algal abundance inside and outside territories and was consequently limited to assessments of species richness and similarity. Future studies might better understand the effects of territoriality by looking at diversity. Studies could also expand upon our feeding observations by placing different algae species inside territories and watching for feeding preference and by looking at damselfish gut contents.

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