

Algal Garden Cultivation and Guarding Behavior of Dusky Damselfish on Coral Rubble and Intact Reef in Dry Tortugas National Park

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Abstract

In the past 30 years, cold events and disease have reduced branching coral reefs in Dry Tortugas National Park, USA to rubble fields. Damselfish constituted the main source of herbivory in branching coral habitat, but it is unclear how the equilibrium between territoriality and grazing resources has been affected by habitat change. In this study, the agonistic behavior and algal garden farming of dusky damselfish (*Stegastes adustus*) was compared between coral rubble and patch reef territories. Underwater observations showed no significant difference in mean numbers of antagonistic grazers entering both rubble and patch territories ($p=0.12$); however dusky damselfish showed a more conspicuous aggressive strategy in rubble territories ($p=0.03$). Gardens exhibited a clear higher species diversity ($p=0.0001$) in rubble (species=13) than in patch reef (species=7). It is plausible that dusky damselfish defending flat rubble territory are better able to detect possible intruders than damselfish guarding more complex patch reef. In a highly saturated living space, dusky damselfish successfully colonize live and dead coral areas and, while patch reef may offer a more concealed site, the newly created rubble fields represent bigger territories and the chance to cultivate a greater variety of algae.

Keywords: algal farming, coral reef, territoriality

Introduction

Damselfishes (family Pomacentridae) are important members of the Caribbean reef ichthyofauna and are considered to be 'keystone species' vital to healthy reef ecology (Hixon and Brostoff, 1983). Even though pomacentrids make up less than 5% of the herbivores' biomass (Williams *et al.*, 2001) and, could be considered less efficient algal grazers when compared to scarids and acanthurids, these fishes profoundly shape reef communities through their agonistic guarding behavior and selective algal farming. In fact, many damselfish confine their range to well-defined territories that include algal lawns. Damselfish gardens are characterized by high level of algal biomass (Lobel, 1980; Sammarco, 1983) and are strongly defended against intruders (Brawley and Adey, 1977; Robertson *et al.*, 1981; Foster, 1985; Letourneur, 2000). Their influence on coral reefs is far-reaching, as it impacts growth and survival of corals (Kaufman, 1977; Eakin, 1988), grazing activity by other herbivores (Foster, 1987; Williams *et al.*, 2001), and algal diversity (Hixon and Brostoff, 1982; Hata and Kato, 2003; Zemke-White and Beatson, 2005).

Healthy coral reefs are traditional damselfish habitat; however, many reef systems in the Caribbean and Florida reef track have been in a serious state of decline. Twenty years ago mass mortality of the long spined sea urchin, *Diadema antillarum*, resulted in a reduction in algae grazing on Caribbean reefs by up to 99% (Carpenter, 1990), and dramatically increased algal biomass. Nearly overnight Caribbean reefs were transformed from coral-dominated to algae-dominated system (Williams *et al.*,

2001). In the winter of 1976-77, a destructive cold front along the Florida strip wiped out 96% of branching coral within two meters of the surface (Porter *et al.*, 1982; Bohnsack, 1983). Staghorn coral, *Acropora cervicornis*, was especially hard hit by the cold event and experienced the most far-reaching decline (Davis, 1982; Wallman *et al.*, 2004). Subsequently, surviving staghorn coral was subjected to diseases and algal growth, and collapsed in most of the Caribbean (Aronson and Precht, 1997). Likewise, the once extensive branching coral formations in Dry Tortugas National Park (DTNP) have been reduced to rubble fields (Davis, 1982). Little is known about how damselfish have responded to changes in reef habitat or how the loss of traditional structure has affected algal farming in the group. In addition, it is unclear how changes in reef structure may have affected interaction between damselfish and their major competitors.

The purpose of our study was to compare algal garden attributes and assess agonistic behavior of the dusky damselfish, *Stegastes adustus*, on patch reef and branching coral rubble in DTNP. Specific objectives of our study were to determine 1) territory size, 2) number and diversity of intruder fishes defended against, and 3) algal garden composition, in both reef and rubble habitats. The DTNP was an ideal site for our study because it is a marine protected area relatively isolated from fishing pressure, and has abundant patch reef habitat in close proximity to recently formed rubble fields. A better understanding of defense strategies used by damselfish in disturbed and undisturbed reef habitats could provide useful insight into damselfish ecology, and possible changes in their role as keystone species on Caribbean reef environments.

Methods

Field observations of dusky damselfish were conducted between 0800 and 1700, in shallow water (1-2.5 m) on patch reef and coral rubble on the northwest side of Loggerhead Key, DTNP (Figure 1), in May 2008. Territory size, algal garden composition (algal type), and fish encounters of dusky damselfish not involved in nesting activities were recorded. Data were collected by five teams of two snorkelers. After a dusky damselfish territory was identified, the fish was allowed to become accustomed to the researchers' presence for 10 minutes (Wallman *et al.*, 2004). Following the 10 minutes pre-observation period, defended territories were delineated using eight weighted marker pins that were placed at 45° intervals around the approximate center point of the fish' territory. Pins were adjusted inward or outward of the center point as dictated by fish movement over the following 20 minutes. Territory size was measured (cm) from a selected point near the center of the territory extending out to each of the marker. All territory sizes were reduced to a 1:20 scale and plotted onto constant weight paper. Territories were weighted (g) and grams converted into territory area (m²).

Following territory size determinations, fish entering a territory (*i.e.*, fish encounters) were observed over the subsequent 15-minute period and recorded using a digital Sony Handycam DCR-SR40 in a waterproof housing. A guarding encounter was considered to be an aggressive movement toward an intruder, *i.e.*, non site-bond herbivores (Ceccarelli, 2007), showing lateral display, chasing, or biting (Draud *et al.*, 1990). Fishes entering the damselfish home range that did not elicit a guarding response were also documented. Videos were reviewed later at the University of West Florida where the number of challenged and unchallenged fish was determined and each intruder fish identified to species. A list of intruder species encountered, challenged and unchallenged, was also compiled. At the end of each video period, algae within each garden were randomly scraped from the garden and preserved in 70% ethanol for later identification. Samples of algae were examined under a dissecting microscope and identified to at least genus (Taylor, 1960). One-way ANOVA was used to compare territory size, algal diversity and number of fish encountered (challenged, unchallenged and pooled), on rubble and patch habitat. Non-normal data were transformed prior to analysis. All statistical comparisons were based on $\alpha=0.05$.

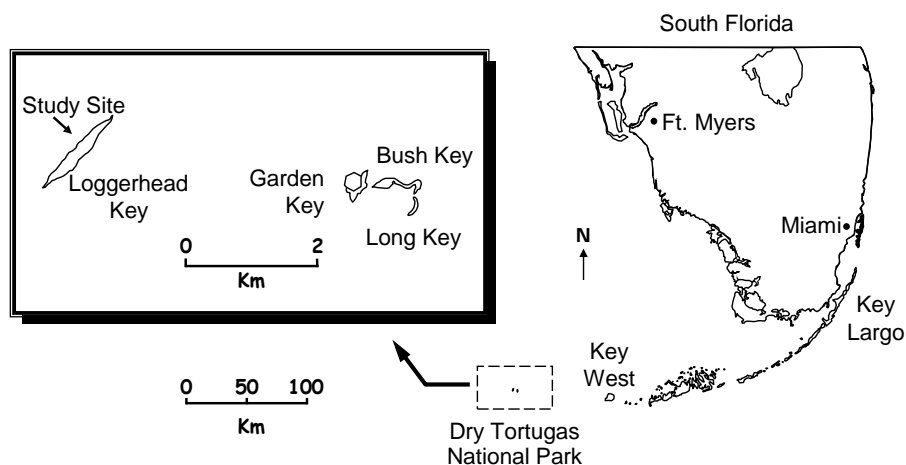


Figure 1. Patch and rubble study site off Loggerhead Key, Dry Tortugas National Park, Florida, USA.

Results

Dusky damselfish were abundant throughout the reef on the northwest side of Loggerhead Key, DTNP. A total of 50 h of underwater observations were made across 37 territories. Territory size was significantly larger for damselfish living on rubble versus patch reef (one way ANOVA $F=1.66$, $p<0.01$, $\alpha=0.05$; Table 1). Underwater observations revealed that dusky damselfish defended feeding areas against solitary herbivorous fishes, but virtually ignored long spine sea urchins found in dusky's territories. Grazing herbivorous and egg-eating fishes attempted to enter both rubble and patch territories with equal frequency (one-way ANOVA on transformed data $F=1.68$, $p=0.12$, $\alpha=0.05$). Yellowtail damselfish, *Microspathodon crysurus*, and redlip blenny, *Ophioblennius macclurei*, were tolerated in the territories by dusky damselfish, regardless of site type. Although antagonistic pressure of herbivorous and egg-eating fish was similar for the two types of reef, dusky damselfish in rubble territories chased out statistically more invader fish than than duskys on patch reef (one-way ANOVA on transformed data $F=2.04$, $p=0.03$, $\alpha=0.05$). Gardens exhibited significant differences in algae diversity between habitat types as well (one-way ANOVA $F=2.04$, $p=0.0001$, $\alpha=0.05$) with rubble gardens displaying nearly twice the diversity seen in patch territories (Tables 1 and 2).

Table 1. Mean territory size along with standard error. Number of intruders and number of challenges are presented as min¹, median², max³. Algae diversity is represented as number of species.

Site type	n	Territory size (m ²)	Number of intruders	Number of challenges	Algae diversity
Patch	16	2.34±0.096	7 ¹ , 14.5 ² , 37 ³	0 ¹ , 2 ² , 6 ³	7
Rubble	21	2.75±0.109	5 ¹ , 21 ² , 68 ³	0 ¹ , 4 ² , 14 ³	13

Table 2. Algal species composition within *Stegastes adustus* territories in DTNP.

Algae species	Patch territory	Rubble territory
<i>Anothricum</i> spp	x	x
<i>Ceramium</i> spp	x	x
<i>Cystoseira myrica</i>	x	x
<i>Dictyopteris delicatula</i>		x
<i>Dictyota bartayrensis</i>		x
<i>Dictyota dichotoma</i>	x	x
<i>Dictyota linearis</i>		x
<i>Halimeda</i> spp	x	x
<i>Lobophora variegata</i>		x
<i>Rhipilia tomentosa</i>		x
<i>Rosenvingea intricate</i>	x	x
<i>Rosenvingea sanctae-crucis</i>		x
<i>Wrangelia</i> spp	x	x

Discussion

Staghorn coral — which constituted more than fifty percent of total coral coverage in DTNP until 30 years ago — has been remarkably slow to recover and has most likely affected damselfish distribution (Wallman *et al.*, 2004). Following the collapse of staghorn coral, competitive interactions among herbivores for shelter or feeding and nesting sites could have influenced space partitioning (Emery, 1973). In our study, dusky damselfish seemed to have adjusted to changes in reef structure and were abundant on both patch and coral rubble. Ferer *et al.* (personal communication) found that dusky damselfish in DTNP show significantly higher density ($p < 0.05$) on patch reef ($0.785 \cdot \text{m}^{-2}$) than rubble ($0.596 \cdot \text{m}^{-2}$). A more complex structure, patch reef could provide refuge from predators and nesting sites that are more concealed (Chabanet, 1997; Almany, 2004). However, Nagelkerken *et al.* (2005) found dimensional complexity to be only one of many factors influencing coral reef fish distribution. Moreover, in our study dusky damselfish occupied larger territories on flat rubble field than on patch reef. Patch reef may be better suited for nesting; however the high competition for a concealed nesting space could push dusky damselfish to colonize two-dimensional rubble fields.

Territory size is, to a great extent, influenced by abundance and type of competitors, *i.e.*, conspecifics, and intruders. According to the optimal territory model, the benefits deriving from guarding behavior must surpass the costs of chasing intruders. Videos recorded on site illustrate approximately equal amounts of intruder pressure in both patch and rubble territories. However, dusky damselfish inhabiting flat rubble may have been better able to detect intruders, typically seeing them before they penetrated territory boundaries. It is plausible that flat territories are easier to patrol than complex patches, but perhaps the larger territories were more difficult to defend. Our video footage often showed intruder herbivorous fishes entering patch territories and picking on algae while the tenant dusky was busy controlling the other side of the area.

Dusky damselfish defensive behavior varied markedly depending on the type of intruder detected. For example, non-herbivorous fishes were attacked less frequently and with less vigor than herbivorous fishes. Egg-eating bluehead wrasses, *Thalassoma bifasciatum*, for example, were not always chased from territories, possibly because damselfish were not nesting. The wrasses were typically run off only if they became a disturbing presence by picking on algal mats to obtain invertebrates (Ogden and Lobel, 1978). Individual blue tangs, *Acanthurus coeruleus*, and parrotfishes, *Scaridae* spp, on the other hand, were chased off successfully at all times as they likely represented a constant threat to the algal garden. The only way these fishes could effectively graze in dusky territory was by invading as

a group (Foster, 1985). Yellowtail damselfish and redlip blenny, both algal grazers, were never chased from dusky damselfish territory. Yellowtail damselfish are known to share a territory with dusky's (Foster, 1987); however, it is unclear why dusky damselfish would tolerate the constant presence of redlip blennies. It is possible that the belligerent demeanor of the small blenny combined with its probable low impact on algal mats, makes the fish an 'ignorable' intruder. Interestingly, neighboring dusky's were challenged more promptly than other herbivorous fishes. In a removal experiment, Jan *et al.* (2003) found that when dusky gregory, *Stegastes nigricans*, were removed from their territory, the adjacent dusky gregory immediately occupied the vacant area. These data suggest that conspecifics represent a greater threat to a territory tenant than other herbivorous fishes.

By keeping intruders outside territories, dusky damselfish likely influence algal diversity of their gardens. The responses of diversity to herbivory, however, vary among studies of site-bound fishes (Sammarco, 1983). For instance, Hixon and Brostoff (1983) observed that algal diversity is enhanced by farming behavior of Pacific gregory, *Stegastes fasciolatus*. Conversely, Hata and Kato (2003) found that dusky gregory in the North Pacific tend a monoculture of palatable algae. At the same time Zemke-White and Beatson (2005) described dusky gregory as farming up to ten species around Rarotonga, Cook Islands, and Fiji. Several factors may in fact result in increased algae diversity including species availability and palatability (Zemke-White and Beatson, 2005), differing levels of herbivory (Paine and Vadas 1969) farming behavior (Montgomery, 1980), and type of intruders (Lubchenco and Gaines, 1981; Sammarco, 1983). Whatever the cause, it is clear the recently formed rubble territories resulting from the collapse of staghorn coral in DTNP represent the chance for dusky damselfish to defend bigger spaces and cultivate a larger variety of algae.

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