



Coral loss alters guarding and farming behavior of a Caribbean damselfish

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Abstract

Coral loss is a major element of global ecological change in the oceans that may shape the behavior of keystone species such as habitat-attached animals. Farming damselfishes cultivate and aggressively protect algal garden within their territory, thereby shaping local fish assemblages and macro-algae diversity. Following the widespread loss of live branching coral throughout Florida and the Caribbean Sea, dusky damselfish (*Stegastes adustus*) have modified their territorial behavior. We compared antagonistic behavior, and size and algal species composition of territories of dusky damselfish on dead branching coral rubble and live boulder coral in the Dry Tortugas National Park, USA. Even though similar numbers of “intruders” entered each habitat type, dusky damselfish on rubble territories chased out significantly more fishes, had larger territories and more species of algae were present in their gardens. This study shows that dusky damselfish successfully occupy living and dead coral areas; however, there are potential trade-offs between defending a larger territory and cultivating fewer algal species.

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Introduction

Coral reefs are one of the most endangered ecosystems on Earth (Carpenter et al. 2008; Ault et al. 2013; Huntington et al. 2017). Indeed, significant reductions in coral cover resulting from anthropogenic activity have been well documented at both local and regional scales (Hughes et al. 2018a,b). Although coral communities vary with natural changes in abiotic and biotic factors, loss of coral cover can have major negative impacts on reef community structure (Boström-Einarsson et al. 2018). Predictions of further community composition and behavioral changes associated with anthropogenic disturbance suggest that understanding the role of species composition and relationships in marine assemblages will be increasingly important moving forward (Di Santo and Bennett 2011; Ault et al. 2013; Di Santo et al. 2016; Di Santo and Lobel 2016; O'Connell et al. 2019). Branching corals provide the topographic complexity necessary to support diverse, resilient fish and invertebrate communities (Roff and Mumby 2012). Architectural complexity of branching corals allows for partitioning of space and critical resources that facilitate the co-existence of multiple species and can result in ecological separation among habitats or along environmental gradients (Alvarez-Filip et al. 2009). Loss

of architectural complexity is one of the most disruptive consequences of coral decline (Alvarez-Filip et al. 2009; Huntington et al. 2017) and can be especially disturbing to habitat-bound animals.

Clownfishes and damselfishes (Family Pomacentridae) have strong associations to sessile invertebrates, such as corals and sponges. Habitat-bound Pomacentridae fishes are especially important to reef ecology as they exert strong localized environmental effects that profoundly shape their communities, and are therefore regarded as a keystone group (Hixon and Brostoff 1983; Ceccarelli 2007; Di Santo and Lobel 2017; Quadros et al. 2019). Clownfishes, for example, actively defend their host-anemone, whereas farming damselfishes cultivate filamentous algal patches that they defend vehemently against intruders and they often reduce large fleshy algae overgrowth of coral (Brawley and Adey 1977). Even though healthy coral reefs are traditional damselfish habitat, as many reef systems in the Caribbean Sea and Florida reef tract have been in a serious and steady state of decline, damselfish have successfully established territories in these degraded environments (Carpenter et al. 2008).

Several species of tropical damselfishes establish well-defined territories on live branching corals (Brawley and Adey 1977; Wallman et al. 2004) where they cultivate high levels of algal biomass (Lobel 1980; Sammarco 1983). Cultivated algae make up the bulk of the nutritional needs of most farming damselfishes, and fish will continuously and strongly defend against intruders, especially free-roaming herbivores such as parrotfishes (Family Scaridae) and tangs (Family Acanthuridae), as well as neighboring damselfish (Foster 1987; Letourneur 2000; Hata et al. 2002; Eurich et al. 2018). Damselfish activities can influence coral structure, growth, and survival (Kaufman 1977; Precht et al. 2010; Boström-Einarsson et al. 2018) by interrupting grazing activities of other herbivores (Williams et al. 2001; Boström-Einarsson et al. 2014), and by controlling algal diversity (Hixon and Brostoff 1983; Hata and Kato 2003, 2006; Zemke-White and Beatson 2005). Numerous studies have also shown that there is a considerable interspecific variation on how farming damselfish may shape the diversity of algae and fauna in their territories (Hata and Kato 2004; Emslie et al. 2012). In fact, farming damselfishes are categorized based on these effects in three different guilds: “intensive” farmers, which select a small number of algal species and tend to be very aggressive towards intruders, “extensive” farmers, which tend to occupy larger territories with a wider range of algal species that are loosely defended against intruders, and “indeterminate” farmers, less aggressive than either intensive or extensive farming fishes that do not influence significantly the diversity of algae inside their territories (Hata and Kato 2004; Emslie et al. 2012). Therefore, different type of farming damselfish may exert dramatically different effects on coral reefs.

In the winter of 1976–77, a severe cold front moved across the Florida peninsula and the Florida Keys killing approximately 96% of branching coral within two meters of the surface (Porter et al. 1982; Bohnsack 1983). The cold damage to corals was further compounded by devastating mass mortality of *Diadema antillarum* in the mid-1980’s (Lessios 1988; Carpenter 1990), resulting in a 97% decrease in algal grazing. In the wake of the successive stress from cold, algal overgrowth (Williams et al. 2001), and *Diadema* populations that have still not rebounded (Pomory et al. 2014; Cramer et al. 2018), the staghorn coral *Acropora cervicornis* suffered widespread collapse across the south Florida reef tract to the Dry Tortugas National Park, DTNP (Davis 1982; Aronson and Precht 2001; Di Santo et al. 2009). The transition from standing live coral to dead coral rubble was rapid, culminating in massive architectural and spatial changes across large sections of reef, and disrupting ecological functions (Davis 1982). While many aspects of damselfish guarding behavior have been extensively investigated on healthy, or at least marginally disrupted reef sites, it is unclear what effect loss of branching coral might have on key aspects of damselfish behavior and ecology, specifically, territory size, algal garden species diversity, and intra/inter-specific interactions as they relate to guarding behavior. In Florida, the once extensive branching coral formations in the DTNP have been reduced to rubble (Davis 1982; Wallman et al. 2004) leaving damselfish two discrete habitat types on which to establish territories—dead branching coral, *Acropora cervicornis*, rubble (hereafter referred to as “rubble”), or live boulder corals (hereafter referred to as “live coral”). The DTNP is a no-take protected marine area with abundant live coral habitat in close proximity to rubble fields making it an ideal site for our study.

The purpose of our study was to test the hypothesis that habitat type would affect aggressive behavior and gardening in the dusky damselfish *Stegastes adustus*. In fact, a change in habitat type could alter their territorial and gardening activity, thus changing how their farming behavior is categorized (i.e., in which guild they are placed). To test our hypothesis, we quantified territory characteristics and guarding behavior of the dusky damselfish living on rubble and live coral sites. Specific objectives of our study were to (1) estimate damselfish territory size, (2) determine the number and diversity of intruder fishes defended against, and (3) identify any differences in damselfish algal garden composition (as total number of species) between live coral and rubble sites. A better understanding of damselfish defense strategies in heavily disturbed and live reef patches can provide useful insights into damselfish ecology and possible changes in their role as a keystone group on Caribbean reef environments.

Materials and methods

Study site

In May 2008, damselfish territory size, guarding behavior, and algal garden diversity was quantified in shallow waters (1–2.5 m) on the northwest side of Loggerhead Key (24°37'55" N 82°55'17" W, Fig. 1), DTNP, near the Little Africa coral formation. All observations were made between 0800 and 1700 local time on either rubble *Acropora cervicornis* or live boulder coral by pairs of snorkelers. Both habitat types were sampled concurrently so that time was not a confounding variable in the study (Sikkel et al. 2004, 2005; Sikkel and Kramer 2006). The different boulder corals where dusky damselfish were present in the DTNP were *Orbicella faveolata*, *Orbicella annularis*, *Montastraea cavernosa*, *Siderastrea siderea*, *Diploria labyrinthiformis*, *Pseudodiploria strigosa*, *Pseudodiploria clivosa*, and *Porites astreoides*.

Territory size, damselfish behavior, and algal diversity

Our study focused on the Dusky damselfish (*Stegastes adustus*). The initial visual survey of the study site reef area revealed that dusky damselfish were present on both live boulder and rubble branching coral patches. Dusky damselfish were abundant on the northwest side of Loggerhead Key, DTNP, and a total of 50 h of underwater observations and measurements of territory size, garden algal species diversity, and antagonistic/chasing behavior were undertaken across 34 territories ($n = 17$ for each

rubble and live coral habitat types). Specific sites were selected haphazardly by slowly swimming in a straight line until encountering a dusky damselfish actively guarding a territory. A minimum distance of 30 m was maintained between teams of observers to minimize potential disturbance from other observers. After a dusky damselfish territory was selected, the fish was allowed to become accustomed to the presence of observers for 10 min (Wallman et al. 2004; Di Santo et al. 2009). After the initial 10-min pre-observation period, the area of the territory was delineated using eight weighted marker pins that were placed at equidistant intervals around the approximate center point of the fishes' territory. Pins were adjusted inward or outward from the center point as dictated by fish movement over a 20-min period. Territory area (m^2) and shape were estimated by measuring from the center of the area occupied by the resident dusky outward to each final marker pin position. All area measurements were then reduced to a 1:20 scale and plotted onto constant weight paper, which was massed (g), and mass values (g/m^2) converted into territory area (m^2). As territory delineation was completed, the site was marked with a labeled transect flag and photographed to avoid duplicating the observations in the same territories. The site was then left undisturbed for 2 h. A pair of researchers returned to the site, and dusky damselfish behavior was observed over 15 min (after a 10-min pre-observation period) and recorded using a digital Sony Handycam DCR-SR40 in a waterproof housing. A territorial behavior was considered to be an aggressive movement toward an intruder, i.e., conspecifics, other herbivores, and non-herbivores, showing lateral display, chasing, or biting (Draud et al.

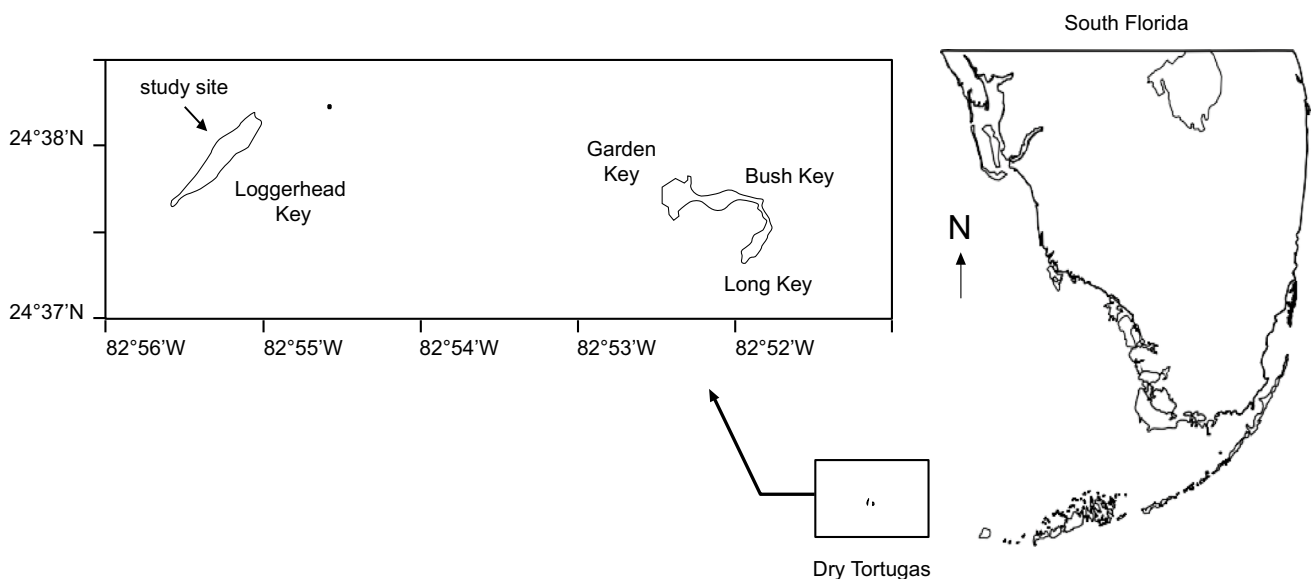


Fig. 1 Location of the field observations in the Dry Tortugas National Park, Florida, USA

1990; Di Santo et al. 2009). Intruders that entered the resident damselfish range but did not provoke an aggressive response were also documented. We compiled a list of species that penetrated the territory of our focus individual, whether challenged or unchallenged (Table 1). Videos of each 15-min observation were analyzed in the lab to confirm the annotations taken in situ. After the behavioral observations were concluded, algal material was scraped from a standardized 5 cm × 5 cm area in each garden to identify the total number of algal species (algal richness) present in each territory. Algal material was preserved in 70% ethanol for later identification (Taylor 1960). Each algal sample was placed under a dissecting microscope and identified at least at genus level (Table 2). Algal richness was calculated as the total number of species identified in each sample.

Statistical analysis

One-way ANOVA was used to compare territory size, algal diversity and number of fishes encountered (challenged and unchallenged), on rubble and live coral habitats. Percent data of chased intruders were arcsine sqrt-transformed prior to analysis. The assumptions of normality, independence and homogeneity of variance were met. All statistical comparisons were based on $\alpha = 0.05$. All analyses were performed in JMP Pro v. 13 (SAS Institute).

Table 2 Species of algae collected in each habitat type (live coral and rubble) occupied by dusky damselfish (*Stegastes adustus*)

	Habitat type	
	Live coral	Rubble
Species of algae	<i>Anotrichum</i> spp	<i>Anotrichum</i> spp
	<i>Ceramium</i> spp	<i>Ceramium</i> spp
	<i>Cystoseira myrica</i>	<i>Cystoseira myrica</i>
	<i>Dictyota dichotoma</i>	<i>Dictyopteria delicatula</i>
	<i>Halimeda</i> spp	<i>Dictyota bartayrensis</i>
	<i>Rosenvingea intricata</i>	<i>Dictyota dichotoma</i>
	<i>Wrangelia</i> spp	<i>Dictyota linearis</i>
		<i>Halimeda</i> spp
		<i>Lobophora variegata</i>
		<i>Rhipilia tomentosa</i>
		<i>Rosenvingea intricata</i>
		<i>Rosenvingea sanctae-crucis</i>
		<i>Wrangelia</i> spp

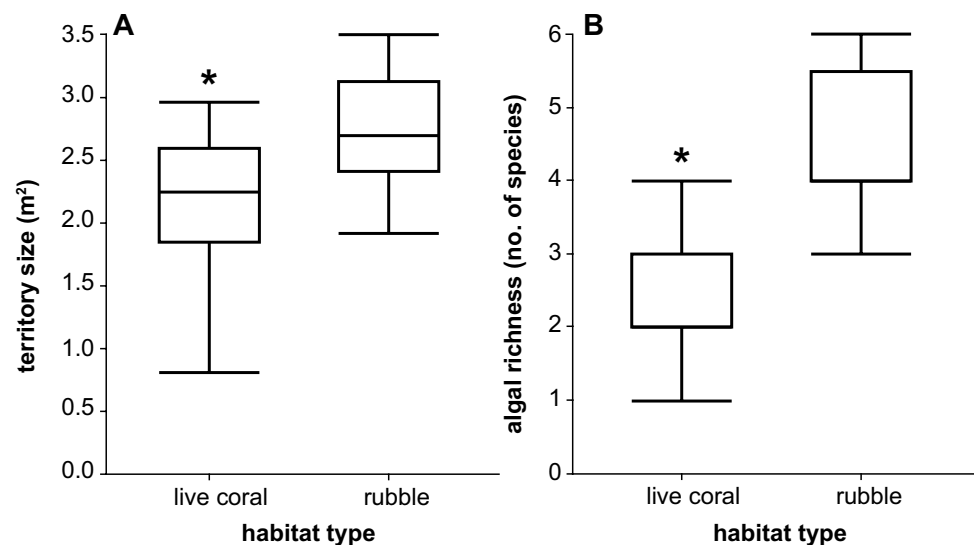
Results and discussion

Territory size comparisons found that damselfish on rubble held significantly larger territories than those occupying the live coral habitat (one way ANOVA $F_{(1,32)} = 10.56$; $P = 0.002$; Fig. 2a). Similarly, algae richness (total species found in a garden) was significantly different between habitat types (one-way ANOVA, $F_{(1,32)} = 15.56$; $P = 0.0004$),

Table 1 Count of species of intruders encountered and chased in each habitat type (live coral and rubble) by resident dusky damselfish (*Stegastes adustus*) during observations

Species	Live coral		Rubble	
	Encountered	Chased	Encountered	Chased
<i>Abudefduf saxatilis</i>	13	5	5	4
<i>Abudefduf saxatilis</i> (juvenile)	2	0	0	0
<i>Acanthurus coeruleus</i>	19	3	27	18
<i>Aplysia</i> spp	3	1	5	3
<i>Diadema antillarum</i>	15	0	16	0
<i>Haemulon flavolineatum</i>	15	4	11	0
<i>Halichoeres bivittatus</i>	2	2	6	1
<i>Halichoeres bivittatus</i> (juvenile)	5	0	14	2
<i>Halichoeres pictus</i>	4	0	3	0
<i>Lutjanus griseus</i>	6	0	8	0
<i>Microspathodon chrysurus</i>	5	0	3	0
<i>Ophioblennius macclurei</i>	18	0	23	0
<i>Scarus iserti</i>	14	4	12	7
<i>Sparisoma rubripinne</i>	0	0	7	4
<i>Sparisoma viride</i>	11	8	3	3
<i>Stegastes adustus</i>	24	19	43	42
<i>Thalassoma bifasciatum</i>	18	4	29	1
<i>Thalassoma bifasciatum</i> (juvenile)	19	2	24	0

Fig. 2 Comparison of territory size (**a**, m²) and algal richness (**b**, as total number of species) between two habitat types, live boulder coral and rubble ($n=17$ per type). Asterisks represent significantly different means (one way ANOVA, $\alpha=0.05$)



with number of species on rubble territories nearly twice that seen on live coral (Fig. 2b, Table 2).

Damselfish from both habitat types received statistically equal numbers of intruders, (one-way ANOVA, $F_{(1,32)}=3.24$; $P=0.080$, Fig. 3a), suggesting that intruders did not prefer, or benefit from either habitat. Although antagonistic pressure from conspecifics, herbivorous, and egg-eating fishes was statistically similar for the two habitat types, dusky damselfish occupying rubble territories chased out statistically more herbivorous fishes than dusky damselfish on patch reef sites (one-way ANOVA on transformed data $F_{(1,32)}=9.98$; $P=0.003$, Fig. 3b,c). Non-herbivores fishes, including wrasses and grunts, however, were chased from the two habitat types at similar rates (one-way ANOVA, $F_{(1,29)}=2.63$; $P=0.100$, Fig. 3c). No significant differences were seen between habitat types when the intruder was a neighboring dusky damselfish (one-way ANOVA, $F_{(1,27)}=2.37$; $P=0.100$, Fig. 3d). Yellowtail damselfish (*Microspathodon chrysurus*) and redlip blenny (*Ophioblennius macclurei*) were present in several territories, regardless of habitat type (Table 1). It is noteworthy that although dusky damselfish defended territories against solitary herbivorous fishes more frequently when located on rubble, they virtually ignored long spine sea urchins that occurred in their territories (Table 1). Our results suggest that dusky damselfish behave differently on rubble and live coral. Territory size was significantly larger on rubble habitat and gardens hosted a greater array of algal species. In addition, dusky damselfish defend their territory more aggressively on rubble habitat even though the intruder pressure was statistically equal on both habitat types.

Until its collapse 30 years ago, staghorn coral constituted more than fifty percent of total coral coverage in the DTNP (Davis 1982; Ault et al. 2013), and was the primary habitat for damselfish territories. The remarkably slow recovery of

the vast staghorn formations in the DTNP has most likely affected damselfish distribution (de Boer 1978; Wallman et al. 2004). Patch reefs may better conceal fish and nesting sites from predators (Chabanet et al. 1997; Almany 2004), but dimensional complexity is only one of many factors influencing reef fish distributions (Nagelkerken et al. 2005). Following the collapse of staghorn coral, competitive interactions among herbivorous fishes for shelter, feeding, or nesting sites may have affected space partitioning (Emery 1973). Dusky damselfish appear to have adjusted to the changes in reef structure. The fishes were abundant on both rubble and live coral but occupied larger territories on rubble. It is possible that high competition for patch reef space would push dusky damselfish to colonize flat rubble fields. Although previous studies suggest that different farmer species use algal resources differently (Hata and Kato 2004; Ceccarelli et al. 2005; Hoey and Bellwood 2010; Emslie et al. 2012) we found that individuals of the same species located just meters apart, may exhibit characteristics of different farming guilds. In fact, dusky damselfish on live boulder coral, by weeding intensively and leaving only a narrow range of algal species in a relatively small territory, fit into the category of typical intensive farmers, while the same species on rubble habitat have larger territories with higher diversity of algae typical of an extensive farmer. However, in the latter case, damselfish show “hybrid” characteristics. Even though the same amount of intruder pressure was experienced in both habitats, dusky damselfish on rubble showed significantly stronger antagonistic behavior, which is a typical characteristic of fishes fitting under the intensive farmers’ guild. This finding suggests that as coral complexity collapses as a result of coral loss, damselfishes could adopt diverse strategies creating novel combinations of behaviors where neither algal selectivity nor a relaxed antagonistic behavior are observed.

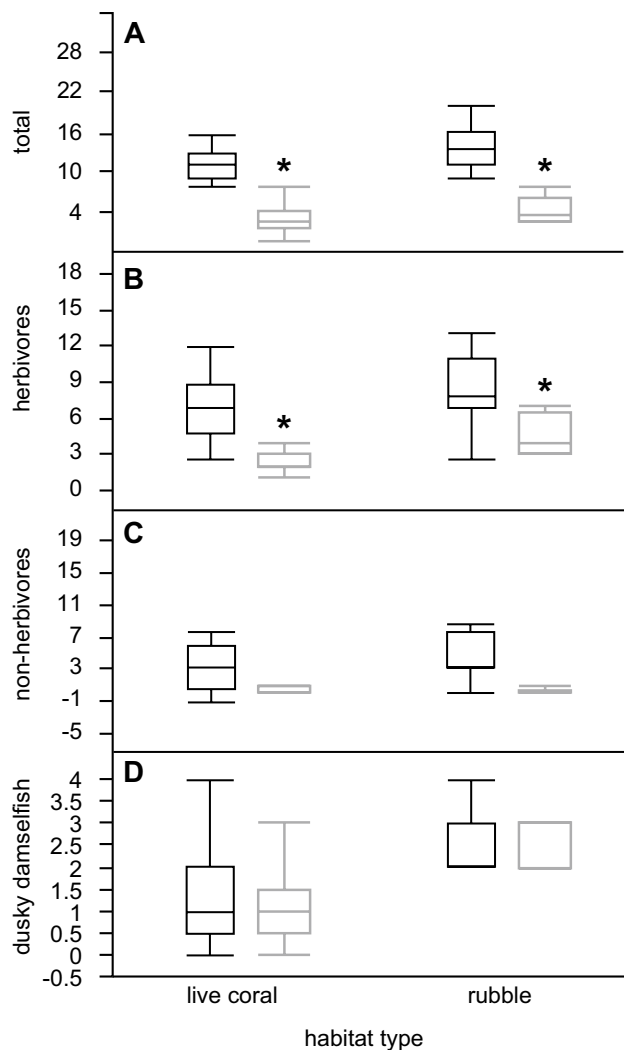


Fig. 3 Dusky damselfish (*Stegastes adustus*) encounters (black) and aggressive behavior (grey) towards intruders compared between two habitat types, live boulder coral and rubble ($n=17$ per type). Mean total encounters and chased intruders were analyzed using a one-way ANOVA (asterisks represent significantly different means between habitat types; $\alpha=0.05$) in all type of intruders (a, total), herbivores (b), non-herbivores (c), and neighboring dusky damselfish (d)

Territory size is, to a great extent, influenced by the abundance and type of competitors, i.e., conspecifics and intruders (de Boer 1978; Hixon 1980). Territory size of tropical damselfishes has been extensively examined and quantified in light of optimal territory size models (Hixon 1980; Souza et al. 2011). According to optimal territory size models first proposed by Hixon (1980), the benefits of greater food resources derived from larger territory size must exceed the costs of protecting them by chasing intruders (Dill 1978; Ebersole 1980; Krebs 1980; Schoener 1983; Grant and Noakes 1987; Catano et al. 2014). It has been proposed that the optimum size of a territory may increase with the benefits obtained from excluding

intruders predated on the algal turf (Grant 1997; Souza et al. 2011). Our study found approximately equal amounts of intruder pressure in both live coral and rubble territories with dusky damselfish on rubble chasing out more intruders than dusky damselfish on live coral. Perhaps, dusky damselfish inhabiting flat rubble are better able to detect intruders, typically seeing them before they penetrated territory boundaries, suggesting that flat territories are easier to patrol than complex patches. It has also been suggested that dusky damselfish on three-dimensional structures exhibit higher levels of boldness, allowing intruders to enter deeper into the territory (Quadros et al. 2019). It is possible that dusky damselfish exhibiting a bold personality may tend to occupy territories on boulder corals. This hypothesis needs to be tested by relocating damselfish to test their aggressive behavior on different habitat types. Interestingly, our video footage often showed intruder herbivorous fishes entering live coral territories and picking on algae while the tenant dusky was busy defending the other side of their territory. Perhaps the larger selection of algae, i.e., resources, in rubble territories may allow dusky damselfish to display more costly intense aggressive behavior (as aggressive displays per unit of time).

Defensive behavior of dusky damselfish varied markedly depending on the type of intruder detected. Non-herbivorous fishes were attacked less frequently than herbivorous fishes. Egg-eating bluehead wrasses (*Thalassoma bifasciatum*) were not systematically chased from territories, possibly because damselfish were not nesting. Wrasses were typically chased 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 often chased off as they likely represented a constant threat to the algal garden. Other studies have shown the only way these fishes could effectively graze in dusky damselfishes' territories 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 tolerate and share territories with smaller damselfishes like the dusky damselfish (Foster 1987). It is unclear why dusky damselfish would tolerate the constant presence of redlip blennies. Perhaps the belligerent demeanor of the small blenny combined with its probable low impact on algal mats (Nursall 1977), makes the fish an inconsequential intruder. Interestingly, neighboring dusky damselfish were challenged more promptly than other herbivorous fishes. In a field experiment (Jan et al. 2003), dusky gregory (*Stegastes nigricans*) were removed from their territory, causing the adjacent dusky gregory to immediately occupy the vacant area suggesting 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, as we quantified in the present study. The algal diversity response to herbivory varies among studies of habitat-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). However, there seems to be no effect of algal biomass present in the garden on the intensity of aggressive behavior (Jan et al. 2003).

In conclusion, our study investigated previously unstudied aspects of behavioral ecology of dusky damselfish in response to coral loss. Our data suggest that rubble territories resulting from the collapse of staghorn coral in the DTNP represent an alternative habitat space for dusky damselfish, one in which, fish spend more time defending larger territories, and leaving a wider range of algae in their garden.

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Data availability The data set supporting this study is provided as supplementary material.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable institutional and governmental guidelines for the care and use of animals were followed. The work was conducted under the NPS permit # DRTO-2008-SCI-0004.

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References

- Almany GR (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc Royal Soc B* 276:3019–3025
- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38
- Ault JS, Smith SG, Bohnsack JA, Luo J, Zurcher N, McClellan DB, Ziegler TA, Hallac DE, Patterson M, Feeley MW, Ruttenberg BI, Hunt J, Kimball D, Causey B (2013) Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. *Fish Res* 144:28–37. <https://doi.org/10.1016/j.fishres.2012.10.007>
- Bohnsack JA (1983) Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. *Environ Biol Fish* 9:41–53
- Boström-Einarsson L, Bonin MC, Munday PL, Jones GP (2014) Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. *Ecology* 95:3056–3067. <https://doi.org/10.1890/13-1345.1>
- Boström-Einarsson L, Bonin MC, Munday PL, Jones GP (2018) Loss of live coral compromises predator-avoidance behaviour in coral reef damselfish. *Sci Rep* 8:7795
- Brawley SH, Adey WH (1977) Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Environ Biol Fish* 2:45–51
- Carpenter R (1990) Mass mortality of *Diadema antillarum*. *Mar Biol* 104:67–77
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, DeVantier L (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560–563
- Catano LB, Shantz AA, Burkepile DE (2014) Predation risk, competition, and territorial damselfishes as drivers of herbivore foraging on Caribbean coral reefs. *Mar Ecol Prog Ser* 511:193–207. <https://doi.org/10.3354/meps10921>
- Ceccarelli D (2007) Modification of benthic communities by territorial damselfish: a multi-species comparison. *Coral Reefs* 26:853–866
- Ceccarelli DM, Jones GP, McCook LJ (2005) Effects of territorial damselfish on an algal-dominated coastal coral reef. *Coral Reefs* 24:606–620. <https://doi.org/10.1007/s00338-005-0035-z>
- Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16:93–102
- Cramer KL, O'Dea A, Carpenter C, Norris RD (2018) A 3000 year record of Caribbean reef urchin communities reveals causes and consequences of long-term decline in *Diadema antillarum*. *Ecography* 41:164–173. <https://doi.org/10.1111/ecog.02513>
- Davis GE (1982) A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. *Bull Mar Sci* 32:608–623

- de Boer BA (1978) Factors influencing the distribution of the damselfish *Chromis cyanea* (Poey), Pomacentridae, on a reef at Curaçao, Netherlands Antilles. *Bull Mar Sci* 28:550–565
- Di Santo V, Bennett WA (2011) Effect of rapid temperature change on resting routine metabolic rates of two benthic elasmobranchs. *Fish Physiol Biochem* 37:929–934. <https://doi.org/10.1007/s10695-011-9490-3>
- Di Santo V, Lobel PS (2016) Size affects digestive responses to increasing temperature in fishes: physiological implications of being small under climate change. *Mar Ecol* 37:813–820. <https://doi.org/10.1111/maec.12358>
- Di Santo V, Lobel PS (2017) Body size and thermal tolerance in tropical gobies. *J Exp Mar Biol Ecol* 487:11–17. <https://doi.org/10.1016/j.jembe.2016.11.007>
- Di Santo V, Pomory CM, Bennett WA (2009) Algal garden cultivation and guarding behavior of dusky damselfish on coral rubble and intact reef in Dry Tortugas National Park. *Proc Am Acad Underw Sci* 2009:222–228
- Di Santo V, Tran AH, Svendsen JC (2016) Progressive hypoxia decouples activity and aerobic performance of skate embryos. *Conserv Physiol* 4:cov067. <https://doi.org/10.1093/conphys/cov067>
- Dill LM (1978) An energy-based model of optimal feeding-territory size. *Theor Popul* 14:396–429
- Draud M, Itzkowitz D, Itzkowitz M (1990) Co-defense of territory space by two species of coral reef fishes. *Bull Mar Sci* 47:721–724
- Ebersole JP (1980) Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *Am Nat* 115:492–509
- Emery AR (1973) Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull Mar Sci* 23:649–770
- Emslie MJ, Logan M, Ceccarelli DM, Cheal AJ, Hoey AS, Miller I, Sweatman HPA (2012) Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Mar Biol* 159:1293–1304. <https://doi.org/10.1007/s00227-012-1910-0>
- Eurich J, McCormick M, Jones G (2018) Habitat selection and aggression as determinants of fine-scale partitioning of coral reef zones in a guild of territorial damselfishes. *Mar Ecol Progr Ser* 587:201–215
- Foster SA (1985) Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Anim Behav* 33:782–792
- Foster SA (1987) Territoriality of the dusky damselfish: influence on algal biomass and on the relative impacts of grazing by fishes and *Diadema*. *Oikos* 50:153–160
- Grant JWA (1997) Territoriality. In: Godin JGJ (ed) *Behavioural ecology of teleost fishes*. Oxford University Press, Oxford, UK, pp 81–103
- Grant JW, Noakes DL (1987) A simple model of optimal territory size for drift-feeding fish. *Can J Zool* 65:270–276
- Hata H, Kato M (2003) Demise of monocultural algal farms by exclusion of territorial damselfish. *Mar Ecol Progr Ser*. <https://doi.org/10.3354/meps263159>
- Hata H, Kato M (2004) Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. *J Exp Mar Biol Ecol* 313:285–296. <https://doi.org/10.1016/j.jembe.2004.08.009>
- Hata H, Kato M (2006) A novel obligate cultivation mutualism between damselfish and *Polysiphonia* algae. *Biol Lett* 2:593–596
- Hata H, Nishihira M, Kamura S (2002) Effects of habitat-conditioning by the damselfish *Stegastes nigricans* on community structure of benthic algae. *J Exp Mar Biol Ecol* 280:95–116. [https://doi.org/10.1016/S0022-0981\(02\)00395-7](https://doi.org/10.1016/S0022-0981(02)00395-7)
- Hixon MA (1980) Food production and competitor density as the determinants of feeding territory size. *Am Nat* 115:510–530
- Hixon MA, Brostoff WN (1983) Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. *Science* 220:511–513
- Hoey AS, Bellwood DR (2010) Damselfish territories as a refuge for macroalgae on coral reefs. *Coral Reefs* 29:107–118. <https://doi.org/10.1007/s00338-009-0567-8>
- Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018a) Global warming transforms coral reef assemblages. *Nature* 556:492–496. <https://doi.org/10.1038/s41586-018-0041-2>
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018b) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80–83. <https://doi.org/10.1126/science.aan8048>
- Huntington BE, Miller MW, Pausch R, Richter L (2017) Facilitation in Caribbean coral reefs: high densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia* 184:247–257
- Jan R, Ho C, Shiah F (2003) Determinants of territory size of the dusky gregory. *J Fish Biol* 63:1589–1597
- Kaufman L (1977) The threespot damselfish: effects on benthic biota of Caribbean coral reefs. In: Taylor DL (ed) *Proceedings of third international coral reef symposium, vol 1*. Rosenstiel School of Marine and Atmospheric Science, Miami, FL, pp 559–564
- Krebs JR (1980) Optimal foraging, predation risk and territory defence. *Ardea* 68:83–90
- Lessios H (1988) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annu Rev Ecol Syst* 19:371–393
- Letourneur Y (2000) Spatial and temporal variability in territoriality of a tropical benthic damselfish on a coral reef (Reunion Island). *Environ Biol Fish* 57:377–391
- Lobel PS (1980) Herbivory by damselfishes and their role in coral reef community ecology. *Bull Mar Sci* 30:273–289
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu Rev Ecol Syst* 12:405–437
- Montgomery WL (1980) The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal communities in the Gulf of California, Mexico. *Bull Mar Sci* 30:290–303
- Nagelkerken I, Vermonden K, Moraes O, Debrot A, Nagelkerken W (2005) Changes in coral reef communities and an associated reef fish species, *Cephalopholis cruentata* (Lacepede), after 30 years on Curaçao (Netherlands Antilles). *Hydrobiologia* 549:145–154
- Nursall J (1977) Territoriality in redlip blennies (*Ophioblennius atlanticus*-Pisces: Blenniidae). *J Zool* 182:205–223
- O'Connell KA, Di Santo V, Maldonado J, Molina E, Fujita MK (2019) A tale of two skates: comparative phylogeography of north American skate species with implications for conservation. *Copeia* 107:297–304. <https://doi.org/10.1643/CG-18-114>
- Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. *Environ Biol Fish* 3:49–63
- Paine RT, Vadas RL (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnol Oceanogr* 14:710–719
- Pomory CM, Wright JE, Dabruzzi TF, Howsden D, O'Boyle L, Beddick D, Bretana W, Onjukka L, Somers C, Bennett WA (2014) Density of *Diadema antillarum* (Echinodermata: Echinoidea) on live coral patch reefs and dead *Acropora cervicornis* rubble

- patches near Loggerhead Key, Dry Tortugas National Park, Florida, USA. *Caribb J Sci* 48:1–8. <https://doi.org/10.18475/cjos.v48i1.a2>
- Porter JW, Battey JF, Smith GJ (1982) Perturbation and change in coral reef communities. *PNAS* 79:1678–1681
- Precht WF, Aronson RB, Moody RM, Kaufman L (2010) Changing patterns of microhabitat utilization by the threespot damselfish, *Stegastes planifrons*, on Caribbean reefs. *PLoS ONE* 5:e10835
- Quadros ALS, Barros F, Blumstein DT, Meira VH, Nunes JACC (2019) Structural complexity but not territory sizes influences flight initiation distance in a damselfish. *Mar Biol* 166:65. <https://doi.org/10.1007/s00227-019-3508-2>
- Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. *TREE* 27:404–413
- Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Mar Ecol Prog Ser* 13:1–14. <https://doi.org/10.3354/meps013001>
- Schoener TW (1983) Simple models of optimal feeding-territory size: a reconciliation. *Am Nat* 121:608–629
- Sikkel PC, Kramer DL (2006) Territory revisits reduce intrusion during spawning trips by female yellowtail damselfish, *Microspathodon chrysurus*. *Anim Behav* 71:71–78
- Sikkel PC, Cheney KL, Côté IM (2004) In situ evidence for ectoparasites as a proximate cause of cleaning interactions in reef fish. *Anim Behav* 68:241–247
- Sikkel PC, Herzlieb SE, Kramer DL (2005) Compensatory cleaner-seeking behavior following spawning in female yellowtail damselfish. *Mar Ecol Prog Ser* 296:1–11
- Souza AT, Ilarri MI, Rosa IL (2011) Habitat use, feeding and territorial behavior of a Brazilian endemic damselfish *Stegastes rocasensis* (Actinopterygii: Pomacentridae). *Environ Biol Fish* 91:133–144. <https://doi.org/10.1007/s10641-010-9765-z>
- Taylor WR (1960) Marine algae of the eastern tropical and subtropical coasts of the Americas. Dissertation, University of Michigan
- Wallman HL, Fitchett KJ, Reber CM, Pomory CM, Bennett WA (2004) Distribution of three common species of damselfish on patch reefs within the Dry Tortugas National Park, Florida. *Fl Sci* 67:169–176
- Williams ID, Polunin NV, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Mar Ecol Prog Ser* 222:187–196
- Zemke-White LW, Beatson EL (2005) Algal community composition within territories of the damselfish *Stegastes nigricans* (Pomacentridae, Labroidae) in Fiji and the Cook Islands. *SPJNAS* 23:43–47

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