that further study is necessary to understand the effects of UV radiation on cryptic sponge distribution.

Sponges in predator treatments tended to suffer more physical damage than sponges in predator exclusion enclosures, though this pattern was only marginally significant. It is possible that with a longer sampling period, this relationship would become stronger over time. Another explanation might be that while larger sponge-eating fish were able to graze on sponges in the open treatment, our enclosures were too small to allow them to effectively reach the sponges inside. Furthermore, we observed several *D. antillarum* in the vicinity of our experimental setup, leading us to suspect that they were preying on the sponges of the open treatment, since they are too large to fit in the enclosures. However, our findings from the *D. antillarum* predation experiment do not support this theory. As there is no past evidence for grazing on sponges by *D. antillarum*, it is unlikely that this urchin caused the damage seen in open treatment sponges.

We did not observe the rapid and extensive sponge predation recorded by Dunlap and Pawlik (1996). The high macroalgal cover found in nearby parts of the reef at Discovery Bay may explain this unusual result. Parrotfish species previously reported to eat cryptic sponges by Dunlap and Pawlik may prefer these algal food resources.

Interestingly, we recorded sponge disappearances only in treatments exposed to both predation and UV-radiation. This finding might imply that exposure to UV radiation is reducing the effectiveness of sponge predation defense. Thus, the distribution of cryptic sponges in shallow waters of Discovery Bay may be limited by both UV-radiation and predation. Alternatively, other studies have suggested that sponge community distribution above substrate is affected by turbidity and wave action (Gischler and Ginsburg 1996). Future research could observe sponge damage and mortality over longer time periods and examine turbidity and wave action as alternative explanations for the cryptic growth of shallow water sponges.

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Costs and benefits of position in clusters of damselfish territories

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Abstract: Territorial fish may occupy over 80% of coral reef surfaces. *Stegastes planifrons*, the threespot damselfish, is the most aggressive territorial species of damselfish. Their territories are often clustered, forcing them to defend against both foraging intruders and neighboring territorial damselfish. We hypothesized that there are differential costs and benefits associated with an individual's position within these clusters. Specifically, we predicted that the cost of defending against intruder fish would be greater in peripheral than in interior territories, but that the cost of defending against neighboring territorial fish would be greater in the interior. Additionally, we predicted that increasing aggressive interactions would lead to decreased feeding rates. Within clusters of less aggressive congeners, we predicted that threespots would be more likely to occupy interior territories than peripheral territories. We tested these hypotheses by observing focal threespot individuals on patch reefs in mangrove and back-reef habitats of Discovery Bay, Jamaica. As predicted, peripheral individuals engaged in more interspecific aggressive encounters than interior individuals while interior individuals engaged in more aggressive encounters with neighbors. Feeding rates were not correlated with the number of aggressive interactions between intruders and/or neighbors. When found with other *Stegastes* spp., threespots were more likely to occupy interior territories than their congeners. We concluded that interior individuals benefit from these territory clusters, and that the potential benefits for peripheral individuals warrant further study.

Key Words: aggression, Stegastes planifrons *, territoriality, threespot damselfish*

Introduction

Territorial fish occupy a large portion of many coral reefs, in some cases covering more than 80% of the reef surface (Foster 1985). Among the most common territorial fish are damselfishes (Pomacentridae) which maintain individual territories for food resources, protection from predators and nesting (Myrberg 1974, Ebersole 1977, Foster 1985, Robertson 1996, Gutiérrez 1998). There are six territorial *Stegastes* species in the Caribbean that vary in habitat choice, diet and levels of aggressiveness (Robertson 1996).

Territories of individual damselfish often occur in clusters, forcing individuals to defend their territories both from foraging intruders and from neighboring conspecifics (Deloach 1999). In a study of group territories in striped parrotfish, Clifton (1989) found that dominant individuals benefit from having surrounding subordinates to defend the resource, because intruders are more likely to be chased away by peripheral individuals. Robertson (1996) found that in the absence of competition with the threespot damselfish (*S. planifrons*), the bicolor damselfish (*S. partitus*) moved from peripheral territories to those in the center, suggesting that the threespot outcompetes the bicolor damselfish to gain access to the more highly defended interior territories.

We explored possible costs and benefits of territory position for the threespot damselfish, hypothesizing that there would be differential costs and benefits associated with interior and peripheral territories. Specifically, we predicted that peripheral individuals would engage in more interspecific interactions and forage at a lower rate than interior individuals due to frequent encounters with intruders and increased time spent defending. We predicted that interior individuals would engage in more aggressive interactions with neigh-

bors to maintain territory boundaries. We also predicted that when threespot damselfish are found in multi-species territory clusters, the more aggressive threespots would tend to inhabit interior territories while other damselfish species would tend to occupy peripheral territories. Alternatively, other factors such as substrate type and habitat complexity could be a priority in habitat selection regardless of position in the cluster.

Methods

The study was conducted 3 - 8 March 2002 at Discovery Bay, Jamaica. We located discrete patch reefs occupied by territorial damselfish in the back-reef and in mangroves just west of the marine laboratory dock. We selected patches containing at least 1 interior threespot territory (entirely surrounded by other territories) and 1 peripheral threespot territory (Fig. 1). The remaining territories in the patch were occupied by threespot, dusky, beaugregory and longfin damselfish. At each patch reef, observers simultaneously watched two focal threespot individuals (one interior and one peripheral) for 15 minutes (n = 18 pairs). We recorded the number of neighbor interactions and whether the focal individual was the aggressor. For each interspecific interaction we noted whether the intruders were alone or schooling. We also recorded the number of foraging bites taken by the focal individual and by any intruders in the territory.

We estimated focal fish size by sketching the dimensions of the focal fish from 0.5 m, and estimated territory size in cubic meters by measuring length, width and height. We recorded the number of neighbors whose territories were adjacent to the territory of the focal individual. Habitat heterogeneity was scored from 1 to 5, with 5 indicating the greatest three-dimensional structure. For each patch reef, we measured reef size and total number of territorial fish and calculated density of damselfish per unit reef area.

All data for interspecific, intraspecific and total aggressive interactions were log-transformed for normality. We used paired t-tests to compare number of neighbor and interspecific interactions, interactions against solitary intruders and against schools and foraging bites by the focal individual and by intruders between interior and peripheral individuals within a patch. We compared fish size and total number of aggressive interactions between the mangrove and back-reef individuals using Student's t-tests. We tested for a relationship between foraging bites by the focal individual and total aggressive interactions using linear regression. We compared fish size, territory size and habitat heterogeneity between interior and peripheral individuals using paired t-tests.

FIG. 1. Schematic diagram showing a typical patch reef with an interior (I) and several peripheral (P) territories.

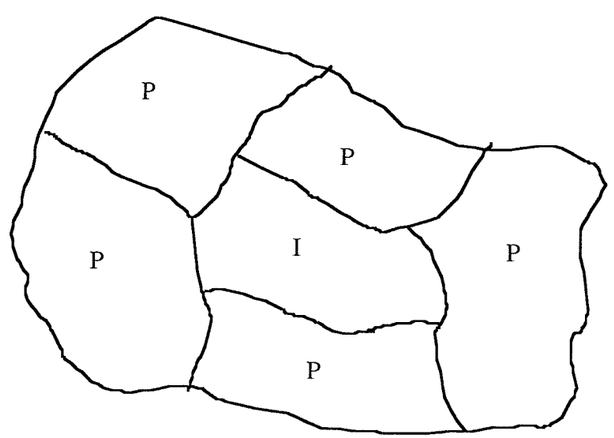

TABLE 1. Summary of costs and benefits of territory position in damselfish clusters per 15 min focal observation.

Cost/benefit	Position effect
Number of interspecific interactions	higher in periphery
Number of neighbor interactions	higher in interior
Bites taken by territory holder	no difference
Bites by intruders	higher in periphery

To assess habitat partitioning among threespot and other damselfishes, we surveyed 14 patch reefs in the back-reef. We recorded the number and species of damselfish in interior versus peripheral territories. We tested for nonrandom distributions of species in interior and peripheral habitat using a chi-square test.

Results

Neighbor and interspecific aggressive interactions varied with fish position in a patch (Table 1). Total number of aggressive interactions with intruders and neighbors was higher for peripheral than interior individuals (paired-t = 3.10, df = 17, P = 0.003). Peripheral individuals engaged in a higher number of interspecific interactions than interior individuals (paired-t = 6.14, df = 17, P < 0.001). Interior individuals engaged in a higher number of neighbor interactions than peripheral individuals (paired-t = 2.89, df = 17, P = 0.005). On a per neighbor basis, neighbor aggression was higher in the interior than periphery, but this difference was not significant (Mean ± SE; 0.93± 0.14 and 0.64 ± 0.16 respectively; t = 1.36, df = 17, P = 0.19). This same pattern was observed in both the mangrove and back-reef areas, although individuals in the mangrove engaged in a higher number of interspecific aggressive interactions than individuals in the back-reef (t = 3.60, df = 34, P = 0.001). The number of neighbor interactions did not differ between the mangrove and back-reef (t = 1.79, df = 34, P = 0.08). Interior individuals (mangrove and back-reef pooled) interacted more often with single intruders than with schools (paired-t = 2.59, df = 17, P = 0.01), while peripheral individuals showed no difference in number of interactions with single intruders versus schools (paired-t = 0.58, df = 17, P = 0.57).

The number of foraging bites taken by focal individuals on their territory did not differ with territory location (paired-t = 0.63, df = 17, P = 0.54) or with the total number of aggressive interactions (r = 0.04, df = 35, P = 0.70). The number of intruder bites on the focal territory was higher in peripheral territories than interior territories (paired-t = 1.78, df = 17, P = 0.05; Table 1).

Territory size and habitat heterogeneity did not differ with position in the patch (paired-t = 0.76, df = 12, P = 0.46; paired-t = 1.64, df = 17, P = 0.12 respectively). Fish size in the mangrove was greater than in the back-reef (t = 3.08, df = 34, P = 0.004). In the mangrove, interior individuals were larger than exterior individuals (paired-t = 4.55, df = 3, P = 0.01), while in the back-reef size did not vary with position in the patch.

There was a non-random distribution of threespot and other *Stegastes* spp. in interior and peripheral territories (χ^2 = 48.45, df = 1, P << 0.001). Threespot individuals were more likely than other species to occur in interior territories and less likely to occur in peripheral territories.

Discussion

As predicted, threespot damselfish on the periphery of a patch reef were forced to

defend their territories from foraging fish more often than individuals in interior territories. Interior individuals interacted primarily with solitary intruders rather than schools, and intruders rarely managed to forage successfully in these territories. Solitary individuals are less conspicuous than a school of fish and could pass to the interior unnoticed. On the other hand, peripheral individuals frequently encountered schools of foraging intruders, and these intruders often overwhelmed the territory defenses and foraged successfully. The higher number of intraspecific interactions for interior individuals did not outweigh the benefit gained from surrounding territorial defenders.

Contrary to our hypothesis, aggressive interactions were not inversely related to feeding rates, suggesting that time spend defending territories is not limiting feeding rates. Individuals on the periphery may have higher energetic needs due to increased number of aggressive encounters, forcing them to forage at higher rates during the brief periods of time when they are not actively defending. Interior individuals may forage consistently at a lower rate. Therefore foraging bites may not be the best measure of feeding rate, and future studies should examine time allocation among foraging, defense and resting.

Given the relative benefits of interior territories, we expected to find more dominant and presumably larger individuals in interior territories. This pattern was observed in the mangrove but not in the back-reef. It appeared that the fish community was more dense in the mangrove, resulting in a higher number of interspecific interactions. Thus the net benefits of interior territories were probably larger in the mangrove than in the back-reef, resulting in a more rigid dominance hierarchy indicated by size.

As hypothesized, in patches where more than one species of damselfish had established territories, threespots occupied the interior territories more often than congeners. Because interior habitats have decreased costs of defense, *S. planifrons* may be competitively excluding its congeners from these preferred territories.

Overall, our results suggest that there are differential costs and benefits associated with interior and peripheral territories in a cluster. Interior individuals clearly obtain benefits from living in aggregations. Our study provides no evidence of direct benefit to peripheral individuals; however they may benefit from mate availability, or they may eventually replace interior individuals with time. Future studies could explore cluster dynamics over time to better understand the costs and benefits of territory aggregation.

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