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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# Damsel in defense: The effect of *Stegastes planifrons* on invertebrate densities

Matthew T. Burke and Benjamin B. Risk

*Abstract:* The threespot damselfish (*Stegastes planifrons*) is a highly territorial species that increases macroalgal productivity on coral reefs throughout the world by excluding other herbivorous fish. Damselfish also deter fish that prey upon invertebrates from their territories, but the effects of damselfish on invertebrates are not well-documented. We examined the effect of damselfish on the density of motile invertebrates (primarily arthropods and polychaetes) on a species of red algae (*Gelidiella acerosa*). We hypothesized the following: (1) fish size would affect invertebrate density, as larger fish may be more effective defenders of their territories and consequently decrease invertebrate predation; (2) territories with a greater density of invertebrates would be smaller, since higher resource density may allow individuals to obtain sufficient resources from small territories; (3) invertebrate density would be higher inside of damselfish territories than outside, as damselfish may chase away invertebrate predators. We found that higher densities of invertebrates were associated with larger fish, possibly because larger fish better defend their territories. Territory size and invertebrate density were independent. We also found no significant pattern in invertebrate density in and outside of damselfish territories. *S. planifrons* seems to affect invertebrate density, and these effects depend on fish size. Territories of large damselfish may serve as a refuge for invertebrates, as high levels of defense by large damselfish may result in low levels of predation. In contrast, territories of smaller damselfish seem to have the least density of invertebrates, possibly due to the combined effects of predation by the resident damselfish and intruding fish.

*Key Words: algal turf, Discovery Bay Marine Laboratory, fish size, invertebrate refuge, macroalgae, resource defense, territoriality, territory size, threespot damselfish*

## Introduction

Damselfish of the genus *Stegastes* generally increase macroalgal diversity and productivity on coral reefs by excluding other fish from their territories (Hixon and Brostoff 1983, Klumpp et al. 1987). *Stegastes* is typically omnivorous, primarily consuming algae and detritus, but also preying upon invertebrates (Randall 1983). For one species of damselfish, *Stegastes planifrons*, motile invertebrates (primarily arthropods and polychaetes) comprised 16% of gut content volume (Randall 1967). Among damselfish, *S. planifrons* is especially territorial, aggressively chasing out other species of fish from their macroalgal "gardens" (Deloach 1999). Although it is widely known that *S. planifrons* increases algal productivity (Klumpp 1987), the interactions between *S. planifrons* and other trophic levels, such as invertebrates, are not well documented.

We examined the effects of *S. planifrons* on invertebrate densities by sampling invertebrates on *Gelidiella acerosa* , a red alga common to the reef of Discovery Bay, Jamaica. Specifically, we examined the relationships between motile invertebrate density (isopods and amphipods, other crustaceans and polychaete worms) and fish size, territory size and frequency of occupancy by *S. planifrons* (proportion of time spent in a given area). We hypothesized the following: (1) Larger fish are associated with a higher density of invertebrates, perhaps because larger fish are better able to defend areas from predatory fish than are smaller fish. (2) Territory size is negatively correlated to invertebrate density. Higher densities of invertebrates support damselfish on smaller areas. Additionally, larger territories are more difficult to defend, and thus are associated with decreased density of invertebrates. (3) The density of invertebrates decreases from frequently occupied areas of the

territory, to less frequently occupied areas of the territory, to non-territory areas, as interspecific aggression creates a refuge for invertebrates. Alternatively, it is possible that damselfish predation on invertebrates leads to lower densities in frequently occupied areas, and the highest invertebrate densities occur outside of damselfish territories.

We also examined how size of invertebrates varied with damselfish occupancy, specifically comparing larger invertebrates (>5 mm in length) to all invertebrates (<5 mm in length). We hypothesized that preferential feeding by damselfish on certain size classes of invertebrates results in a non-random size distribution of invertebrates between territory and non-territory algal samples.

## Methods

Research was conducted on 23 - 25 February 2002 near the crest of the west back-reef of Discovery Bay, Jamaica. Ten focal *S. planifrons* were haphazardly selected from different areas of the reef, and their activity was observed for 5 min each. We made a sketch of fish length and height to estimate fish size. Territory size was determined by 5 min observations of focal fish movement and interactions with other fish. Territory area in $m^2$ was gauged by dividing the observed territory into easily measured geometric shapes (rectangles and triangles). To determine invertebrate density, three samples of *Gelidiella acerosa* were collected from each territory, placed in a sealed bag and brought back to the lab for analysis. One algal sample was collected from an area of frequent occupation in an individual's territory (an area in which the individual spent a large proportion of the 5 min observation period), one from a less frequently occupied area and another from an area outside the territory not lying in any other damselfish territory. In five instances, the non-territory samples were collected from areas adjacent to the fish's territory (<2 m away), but otherwise, they were collected from any

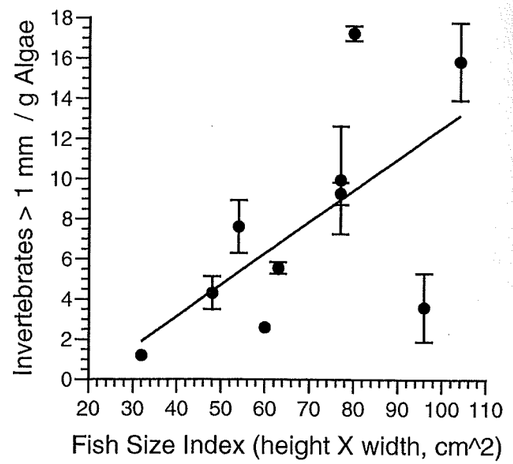


FIG. 1. Effect of *S. planifrons* on invertebrate density (>1 mm long) within damselfish territories. Algal samples from areas frequently occupied and less occupied by the damselfish averaged, except for two cases (one frequently occupied, one less occupied) where only one sample from the territory was available. y = -3.13 + 0.157x

undefended alga in the general vicinity (<15 m away). We collected samples of just one species of alga to control for variation in invertebrate density across species of algae. *Gelidiella acerosa* was chosen because it is common throughout the reef crest and could be found in all damselfish territories. In the lab, algal samples were washed with freshwater and invertebrates were removed with a 200 µm filter. The total number of invertebrates was counted using a dissecting microscope, and individuals were separated into three size classes: <1 mm, 1 – 5 mm and >5 mm. The algae was patted dry and weighed to determine number of invertebrates per gram wet weight of algae.

We used least-squares linear regression to analyze invertebrate density versus fish size index, where fish size index was calculated as fish height multiplied by length, and territory size versus invertebrate density. Invertebrate density corresponding to each fish size was the average of the two algal samples (frequently and less frequently occupied) from that fish's territory, although in two instances





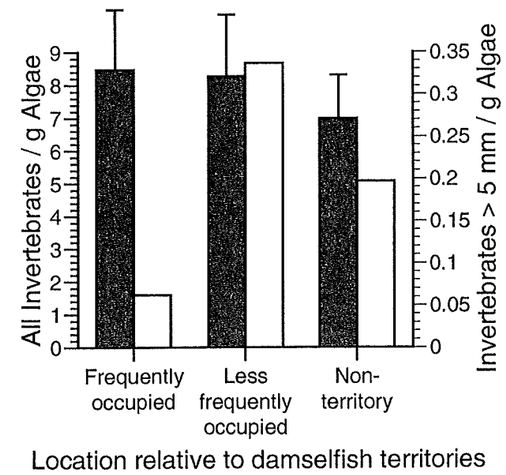


FIG. 2. (a) Density of all invertebrates (solid bars) or >5 mm (open bars) in frequently occupied areas, less frequently occupied areas, or non-territories of *Stegastes planifrons*.

only one sample from the territory was available. Pooling this data was justified because there was no significant difference in invertebrate density between frequently occupied areas and less frequently occupied areas (t = 0.389, df = 16, P = 0.70). We also compared territory size and fish size using least-squares linear regression. Differences in densities of all invertebrates and invertebrates >5 mm in length between the three levels of damselfish occupancy were analyzed using two one-way randomized complete block ANOVAs incorporating the effect of individual fishes as the block.

Invertebrates <1 mm were excluded from analyses due to differences in observer counting; invertebrates >1 mm will hereafter be termed "all invertebrates". In addition, the labels on four samples were indistinguishable and were thus excluded from analyses.

## Results

Density of all invertebrates increased with increasing fish size ($r^2 = 0.40$, n = 10, P < 0.05; Fig. 1). Territory size was independent of invertebrate density (r = 0.05, n = 10, P = 0.90), and independent of fish size ($r^2 = 0.049$, n = 10, P = 0.54). Frequency of occupancy by damselfish had no significant effect on the density of all invertebrates (F = 0.096, df = 2, P = 0.91), although there was a trend of increased invertebrate density with increased damselfish occupancy (Fig. 2). Additionally, there was no significant relationship between frequency of occupancy and density of invertebrates >5 mm (F = 1.79, df = 2, P = 0.20). In contrast to the density of all invertebrates, invertebrates >5 mm tended to decline in density within high-occupancy areas of damselfish territories (Fig. 2).

## Discussion

The positive relationship between fish size and invertebrate density supports the hypothesis that larger fish may better defend their territories against other fish that prey on invertebrates (Fig. 1). Alternatively, it is possible that larger fish select and competitively exclude smaller fish from territories with high invertebrate densities. Itzkowitz (1979) found evidence that larger threespot damselfish exclude smaller fish from higher quality territories, where territory quality was related to amount of staghorn coral (*Acropora cervicornis*). But because fish, especially large fish, may hold territories for up to several years, it seems more likely that the fish are directly increasing invertebrate density.

Territory size was independent of invertebrate density, indicating that invertebrate density is not determining territory size and/or that territory size does not affect invertebrate density. Additionally, fish size and territory size varied independently, suggesting that territory size may be unrelated to fish defensibility. Territory size may reflect algal resources rather than invertebrate density, as damselfish are more herbivorous than predatory (Deloach 1999), or territory size may be more influenced by coral, as *Acropora sp.* is a major determinant of territory quality (Itzkowitz 1979). Other factors affecting dam-

selfish population size, such as recruitment limitation, weather patterns, predation and other factors affecting habitat quality (such as spatial heterogeneity) may be greater predictors of territory size. Estimates of territory size including three-dimensional space (not examined in this study) could reveal relationships between territory size and resource base or fish size.

Although there was a trend of increasing invertebrate density with increasing frequency of occupancy by *S. planifrons* (Fig. 2), the trend was not significant, suggesting that *S. planifrons* does not create invertebrate refuges. However, larger fish were associated with higher densities of invertebrates (Fig. 1). It appears that size of the damselfish determines whether or not damselfish territories function as invertebrate refuges. Territories of large fish may be well defended, such that the invertebrates suffer predation from only the resident damselfish. Territories of small damselfish may be poorly defended; consequently, invertebrates suffer from damselfish predation and predation by other fish. Non-territory areas would suffer medium levels of predation, as they lack a concentration of damselfish activity. Consistent with this hypothesis, invertebrate density in territories defended by the four smallest fish was less than invertebrate densities on algal samples from outside of damselfish territories, although the small sample size precluded significance ($x_{small} = 3.92 \pm 1.34$, $n = 4$; $x_{non\text{-}territory} = 6.97 \pm 1.32$, $n = 8$; $t = 1.43$, $df = 10$, $P = 0.18$). Larger sample sizes would better establish the differential effect of damselfish size on creating invertebrate refuge in territories.

In contrast to the trend in decreasing density of all invertebrates with decreasing frequency of damselfish occupancy, the density of invertebrates >5 mm was lowest in algal samples from the frequently occupied sections of the territories (Fig. 2). Although the difference was not significant, *S. planifrons* may preferentially feed on larger invertebrates, and thus differentially impact the density of different sizes of invertebrates. In this way damselfish may confer different advantages to different-sized individuals, with smaller invertebrates gaining greater refuge in damselfish territories than larger invertebrates.

We sampled only one algal species, with samples ranging from 1.9 – 24.1 g, which was an extremely small proportion of total biomass in a territory. At this scale, invertebrate densities are likely subject to a large degree of variation from abiotic factors such as wave action, which may affect recruitment success, and biotic factors such as detritus deposition (a food source). Sampling invertebrate density or abundance across the entire territory could decrease the variation due to microhabitats. Additionally, the interior versus peripheral position of a territory in a cluster of territories may affect algal resources (Alexander et al. in this volume), and consequently also affect invertebrate density. Our sampling method did not standardize for the effect of position. Lastly, invertebrates may prefer some species of algae to others; sampling across species of algae could reveal patterns undetected by the scope of this study.

The effect of fish size on invertebrate density indicates that *S. planifrons* affects the invertebrate community; territories of larger damselfish may provide invertebrate refuge. Territories of small damselfish may have a lower density of invertebrates than non-territories due to predation from the resident damselfish and ineffective defense. Future research should quantify directly the effects of the intensity of damselfish defense invertebrate diversity and abundance, thereby further assessing the effects of damselfish territoriality on the invertebrate communities of coral reefs.

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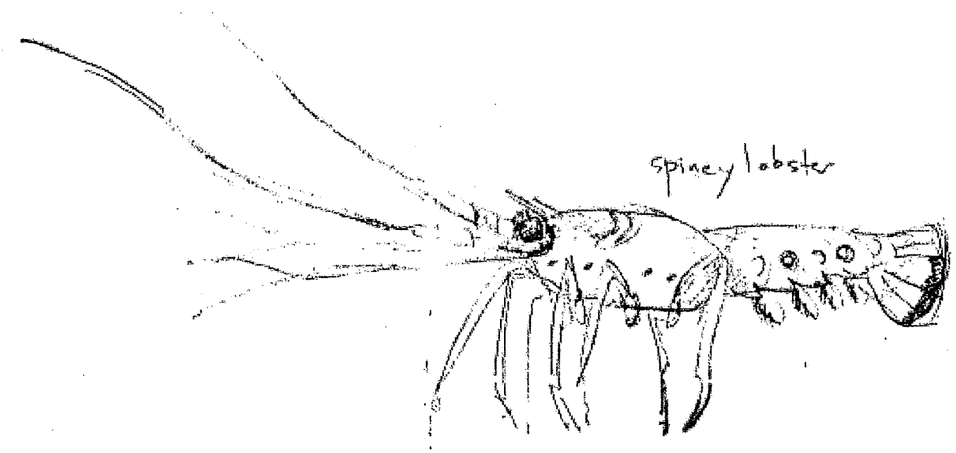
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