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Damselfish Territoriality: Influence on *Diadema* Distribution and Implications for Coral Community Structure

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ABSTRACT: Experiments were performed in Discovery Bay (Jamaica, W.I.) to determine the relationship between behavior of threespot damselfish *Eupomacentrus planifrons* Cuvier, and distribution of the common shallow-water echinoid *Diadema antillarum* Philippi. *E. planifrons* actively excludes *Diadema* from its algal lawn, causing a distinct alteration in local distribution of *Diadema* on the reef. Physical attacks on the urchin were usually sustained for ≥ 5 min. The damselfish's agonistic behavior occurred only during the day. *Diadema* densities were higher within algal lawns at night than during the day but were always significantly lower than the mean density outside. The size of the damselfish's algal lawn was positively correlated with damselfish density, implying that damselfish which occur in aggregations are able to defend larger territories together than they would when occurring alone. The impact of interactions between fishes, urchins and sessile epibenthos are predictable from experimental data derived from a concurrent study. *E. planifrons* territories are probably sites of locally high mortality in coral spat, particularly in *Agaricia* and *Porites* spp. This would result from competition for space with algae and encrusting epifauna. The algal lawns, however, may also represent refuges for other corals such as *Favia fragum* which are well-adapted to survive competition with other sessile epifauna as well as with algae. Thus, the algal lawns could represent discrete patches in the environment within which mortality of dominant species is high and that of rarer species is relatively low, causing an increase in the latter's representation in the benthic community. The net effect of this would be an overall increase in coral diversity within the community. This interpretation is consistent with hypotheses concerning the role of patch-formation in determining community structure.

INTRODUCTION

Territorial behaviour can greatly reduce the density of intruders within a territory (e.g. Dow, 1977; Williams, 1979). The damselfish *Eupomacentrus planifrons* Cuvier is one of the most aggressive territorial pomacentrids in the Caribbean (Robertson et al., 1976; Itzkowitz, 1979). It has been observed to defend successfully its territories against conspecifics, heterospecific fish, and certain benthic invertebrates – in particular *Diadema antillarum* Philippi (Kaufman, 1977; Williams, 1977, 1978, 1980). This urchin is known to be an important shallow-reef grazer (Ogden et al., 1973a, b,; Sammarco et al., 1974; Lawrence, 1975; Sammarco, 1977, 1980a, in press; Lawrence and Sammarco, in press). Interspecific interactions are common between pomacentrids and other fish and have been widely studied (Myrberg and Thresher, 1974; Sale, 1975; Thresher, 1976; and others), but only rarely have cases of a pomacentrid demonstrating aggression towards non-piscine members of the community been recorded (Albrecht, 1969; Clarke, 1970; Williams, 1977, 1978, 1980). Interphyletic interactions such as this have received little attention in behavioral ecology (Pearson, 1977).

Territorial populations are known to alter local community structure in the shallow reef environment. By excluding many herbivorous fish, some territorial damselfish allow algae to proliferate within their territories, causing an increase in biomass of algae and a shift in algal community structure (Ogden and Lobel, 1978; Lassuy, 1980; Montgomery, 1980a, b; Hixon and Brostoff, in press; Wilkinson and Sammarco, in press). This is particularly true of *Eupomacentrus planifrons*,

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the territories of which possess 5 times (to 40×) as much algal biomass by wet weight (Brawley and Adey, 1977) or 1.7 times as much by dry weight (Williams, 1977, 1981) as areas outside their territories.

Vine (1974) has demonstrated that the aggressive behavior of *Pomacentrus lividus* and *Acanthurus sohal* affects not only the distribution of algae but also that of sessile epibenthic invertebrates such as spirorbid polychaetes. According to Potts (1977), *Dischistodus perspicillatus* can be responsible for mortality of adult colonies of the coral *Acropora palifera* in shallow water, and Kaufman (1977) demonstrated that *Eupomacentrus planifrons* has a similar effect on *Acropora cervicornis.*

Diadema antillarum is known to influence the structure of shallow reef communities on a much broader scale. Its grazing activities significantly alter algal community structure (Ogden et al., 1973a; Sammarco et al., 1974). In addition, it can control the success of settlement and survival in both juvenile and adult corals, significantly affecting coral species composition, abundance, and diversity (Sammarco, 1975, 1977, 1980a, in press). This effect is most dramatic at high densities where food is scarce and grazing intense.

If the agonism of *Eupomacentrus planifrons* is sufficiently intense to inhibit the grazing activities of *Diadema antillarum* within its territory, then a small patch within the habitat will have been formed which exhibits characteristics differing from those of surrounding community. Patch formation and small-scale disturbances of this sort are known to have significant effects on community structure (Grassle, 1973; Levin, 1974; Levin and Paine, 1974; Menge, 1976; Whittaker and Levin, 1977; Vance, in press).

Here we demonstrate that *Eupomacentrus planifrons* exerts a significant effect on the local distribution of *Diadema antillarum.* We also suggest that this alteration in distribution has important secondary effects on shallow-reef community structure, causing a shift in the success and pattern of recruitment in scleractinian corals.

MATERIALS AND METHODS

Experiments were performed in 3 sites within the area of Discovery Bay, Jamaica, W.I. (77°24'W, 18°28'N; Fig. 1), herein referred to as Sites A, B and C. Site A was a set of 2 lagoonal patch reefs – Crosby and Stills Reefs – in the southern portion of the bay, ranging in area from 250 to 5,800 m^2 and in depth from 2 to 5 m. These reefs were chosen for their conspicuously high densities of *Diadema antillarum* and *Echinometra viridis* (A. Agassiz) in comparison to densities observed on similar Caribbean patch reefs (e.g. Tague

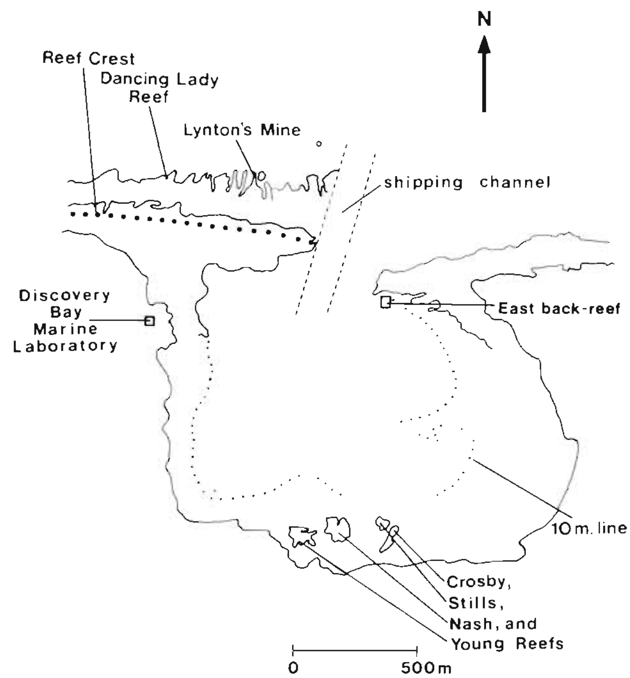

Fig. 1. Map of Discovery Bay, Jamaica, W.I. depicting study sites

Bay, St. Croix, U.S.V.I.; see Sammarco et al., 1974). The echinoids *Lytechinus williamsi* (Chesher) and *Eucidaris tribuloides* (Lamarck) were also present, although in much lower abundances. Site B was a backreef on the eastern side of the bay, 3 to 5 m in depth with a high abundance of threespot damselfish and a similar complement of echinoid species (Williams, 1978); it was characterized by the staghorn coral *Acropora cervicornis.* Site C was located on the forereef at a depth of 15 m, specifically Dancing Lady Reef and Lynton's Mine.

Baseline information of *Diadema antillarum* densities was collected at Sites A and C with 1 m^2 quadrats placed along uniform linear transects. Site C was sampled during the day and at night; 10 to 20 evenly spaced quadrats were examined along each transect.

The *Eupomacentrus planifrons* populations were censused at Site A in April 1975 with the aid of belt transects 1 m in breadth. At least four 10 m transects were used and repeated 3 times each. The number of *Diadema antillarum* within the algal lawn of each damselfish territory was also recorded. The number of damselfish and urchins within 52 marked *Acropora cervicornis* patches of known dimensions at Site B were also recorded daily from August 1975 to July 1976.

Sizes of algal lawns were estimated by calculating surface area (m^2) from length and width measurements. *Diadema antillarum* density within territories was estimated by dividing the mean number of *D.*

antillarum within territories by the mean size of *Eupomacentrus planifrons* territories and standardizing to no. m^{-2}. In this way, any variation in size of algal lawn due to clumping of damselfish would be averaged out.

In order to test the hypothesis that differences in *Diadema antillarum* distribution were due to damselfish interference, urchins were experimentally added to damselfish algal lawns at Sites A and C. The urchins were added by prodding to which they reacted with an alarm response (Snyder and Snyder, 1970), or by direct placement with the aid of a diver's hand-tool. The damselfish's response took the form of nipping and displays and was recorded as either positive or no response. Each individual was observed for 5 min, and the duration of response was recorded. Observations were made on > 125 damselfish at various times of the day, including dawn and evening periods and under new and full moon conditions (also see Williams, 1979).

All experiments were performed in the field with the aid of SCUBA.

RESULTS

Diadema antillarum densities were very high on Crosby Reef, intermediate on the forereef, and low within the algal lawns of the damselfish (Table 1). *D. antillarum* densities within algal lawns of damselfish territories on Dancing Lady Reef were significantly higher at night than during the day. However, *D. antillarum* densities within algal lawns were significantly lower than those outside in all cases observed.

Table 1. Densities of *Diadema antillarum* in no. individuals/m^2 inside and outside damselfish territories. Diurnal vs. nocturnal data also shown. Nocturnal *Diadema* densities within territories significantly higher than diurnal ones ($p < 0.005$, Kruskal-Wallis Test) but significantly lower than nocturnal densities outside territories ($p < 0.005$)

		Diadema density (no m^{-2})			
		Outside algal lawns		Within algal lawns	
Site		Day	Night	Day	Night
Dancing Lady Reef (Site C)	$\bar{X}$	16.2	22.6	0.0	7.6
	s	5.35	7.49	0.00	5.86
	n	20	10	16	7
Crosby Reef (Site A)	$\bar{X}$	72.8	•	0.0^{+}	•
	s	21.93		0.00	
	n	20		123	

• Data not available
($^{+}$) Includes data from back-reef (Site B)

Similar supporting observations were made at the back-reef site.

Adult *Eupomacentrus planifrons* densities on Crosby and Stills Reefs were estimated to be 5.1 10 m^{-2} (s = 3.06, n = 12) and 7.2 (s = 2.00, n = 24), respectively. Densities in the back-reef were 2.8 m^{-2} (s = 1.38, n = 36), and algal lawns were estimated to cover an average of 0.19 m^2 (s = 0.18, n = 36). This meant that the algal lawns of this damselfish accounted for 53 % of the surface area at this site. A significant positive correlation was found between the density of damselfish and the size of their individual algal lawns (Fig. 2).

Each *Diadema antillarum* introduced into a damselfish territory immediately elicited an agonistic response from the fish, consisting of a lateral approach and a grasping of the spine with its mouth. It would then abruptly twist and sever the tip of the spine and

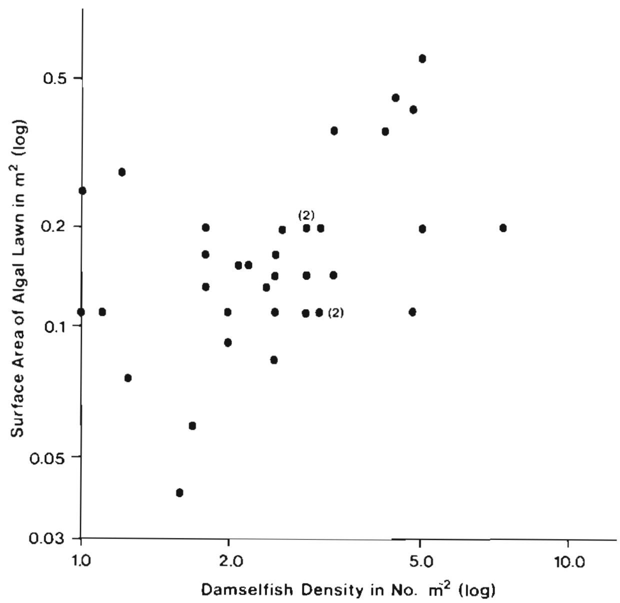

Fig. 2. Relationship between *Eupomacentrus planifrons* density and surface area of algal lawn within *Acropora cervicornis* patches (Site B). Significant positive correlation (r = 0.49, $p < 0.01$, Pearson's correlation analysis). Multiple points represented in parentheses

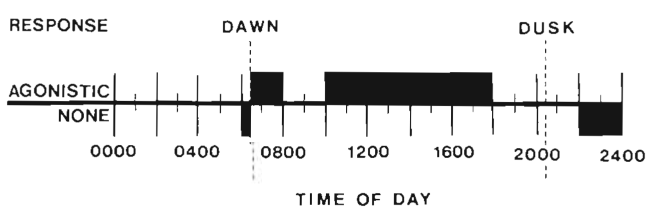

Fig. 3. Diurnal pattern of agonistic responses elicited from *Eupomacentrus planifrons* by *Diadema antillarum*. Urchins were experimentally introduced into territories. Data presented only for those hours specifically tested. N > 100 individual damselfish, 1 trial per individual

Table 2. Diurnal *vs.* nocturnal responsiveness of *E. planifrons* to intrusion by *Diadema* into its territory. Frequency of diurnal response significantly greater than nocturnal responses ($p < 0.005$, Model II 2×2 contingency G-test)

Response	Day	Evening	Total
Agnostic response	102	0	102
No. response	1	16	17
Total	103	16	119

swim away, releasing it. Each attack was short in duration ($\overline{X} = 3$ s; $s = 1.6$, $n = 20$). The attacks were repeated in rapid succession randomly over the urchin's test. After continuous harassment, the echinoid usually exhibited a strong, randomly directed alarm response and quickly left the territory.

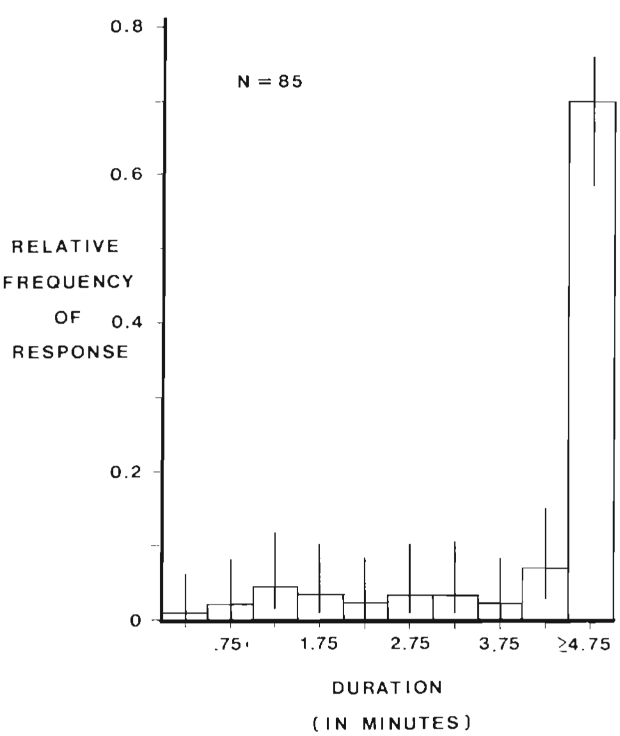

Fig. 4. Relative frequency distribution of duration of agonistic response in *Eupomacentrus planifrons* against *Diadema antillarum* with 95 % confidence intervals

When tested, the fish responded aggressively only during daylight hours (post-dawn, pre-dusk; Fig. 3, Table 2) with approximately 70 % of the timed responses continuing for > 5 min (Fig. 4). In contrast to their daytime habits, the damselfish were consistently timid during the evening hours, irrespective of phase of the moon and resultant light levels.

DISCUSSION

Eupomacentrus planifrons actively defends its territory against *Diadema antillarum* only during the day. Similar observations have been made on congeners such as *E. partitus* (Myrberg, 1972) and *E. fuscus* (Itzkowitz, pers. comm.), as well as on other pomacentrids (e.g. Ebeling and Bray, 1976). For a general discussion of diurnal vs. nocturnal activities in fish, see Hobson (1965, 1972) and Collette and Talbot (1972).

The removal of all *Diadema antillarum* by the fish tested here indicates that threespot damselfish are capable of clearing these urchins from their lawns and creating the observed heterogeneity in their distribution. Spatial partitioning of *Acropora cervicornis* patches by both *D. antillarum* and *Echinometra viridis* has been attributable partially to threespot interference with these urchins (Williams, 1979).

The density of damselfish may also affect the scope of grazing by *Diadema antillarum* within *Acropora cervicornis* patches. The positive correlation between algal lawn size per territory and damselfish density implies that damselfish occurring in higher densities or in aggregations have a positively synergistic effect on the area of substrate which is defended from grazing fish. This is implied from the data collected here but requires experimental verification.

The urchin is primarily a nocturnal grazer (Lewis, 1964; Randall et al., 1964) but also feeds during the day when occurring at densities such as those found on Crosby Reef (P.W.S., pers. obs.). Once territorial defence has been relaxed in an area, one might expect an intruder to take advantage of this ready access to food, particularly if it is in short supply. Echinoids are known to have well developed chemosensory powers (Leighton, 1966; Garnick, 1978). *Diadema antillarum* in particular is known to respond to chemical stimuli involving repulsion from predated conspecifics (Snyder and Snyder, 1970) and attraction to algae (Sammarco, 1972; Carpenter, 1979). Despite this, *Eupomacentrus planifrons* territories did not experience a high influx of *D. antillarum* during the early evening, the urchin's peak period of activity (Ogden et al., 1973a, b; Smith, 1975). *D. antillarum* densities were higher on algal mats within the territories at night than during the day but still remained well below the surrounding natural density.

Eupomacentrus planifrons is not 100 % effective at excluding *Diadema antillarum* from its territories. Averaged over a 24-h period, the *D. antillarum* density within algal lawns is not $0\ m^{-2}$ but slightly higher. This is important in light of the effects of the grazing activities of *D. antillarum* on coral community structure. Earlier studies demonstrated that reduction in the density of *D. antillarum* can result in an increase in coral spat diversity under primary succession conditions (Sammarco, 1975, 1977, 1980a). Through grazing, the urchins deter successful coral recruitment in a species-specific manner. They also strongly influence competitive outcomes between juvenile corals and other epibiota by changing the array of competitors with which the spat must compete for space. Optimal conditions for settlement, survival, growth, and competitive success in such coral genera as *Agaricia* and *Porites* occur at intermediate *D. antillarum* densities. *Favia fragum*, on the other hand, is an excellent competitor against algae and thrives at negligible grazing intensities (Sammarco, 1977, 1980a). The sum of these effects results in an increase in spat diversity (as measured by H'; see Pielou, 1967, 1969, 1975) in the absence of grazing under primary succession conditions. These conditions of reduced grazing on newly provided primary substrate – freshly killed coral – are created by the colonization of *E. planifrons* and its defense of the area (Kaufman, 1977). This has also been demonstrated to occur in other damselfish (Potts, 1977).

Fish grazing is not entirely absent within these territories. *Eupomacentrus planifrons* is itself an omnivore, browsing on algae as well as sessile and vagile invertebrates within its algal mat (Randall, 1967; Robertson et al., 1976). The impact of this grazing on the benthic community, however, is probably trivial in comparison to that of the urchins (Williams, 1981). Recent experimentation has demonstrated that fish grazing in Discovery Bay has little if any impact on success of coral settlement in the absence of echinoids (Sammarco, in press).

Territoriality by *Hemiglyphidodon plagiometopon* Bleeker (Pomacentridae) on the Great Barrier Reef has been correlated with an increase in local diversity of adult corals (Sammarco, 1980b, and work in progress). In addition, the reduced grazing characteristic of these territories has been experimentally demonstrated to cause an increase in the number of coral genera within the algal lawns of this fish (Sammarco, 1980b; Sammarco and Carleton, in press).

Eupomacentrus planifrons may affect coral community structure in a similar manner, both at the adult level and at the earliest stages of succession. *E. planifrons* territories may remain distinct for extended periods of time, for long-term serial territories (those re-invaded by a series of males through time) are common in *E. planifrons* (Itzkowitz, pers. comm.). The territories of another pomacentrid, *Hypsopops rubicunda*, common in eastern Pacific waters, have been observed to be maintained for > 13 y (Clarke, 1970).

Considering the density of these fish on the reef and the area of their algal lawns, their potential impact becomes evident. In areas such as the back reef, over 50% of the reef surface is under the influence of *Eupomacentrus planifrons*. We suggest here that their indirect effect on community structure may be an important factor contributing to the maintenance of high coral diversity on the reef.

CONCLUSIONS

(1) *Eupomacentrus planifrons* defends its territory against *Diadema antillarum* through attacks usually sustained for ⩾ 5 min. Local urchin distribution is affected, causing patches where grazing by *D. antillarum* is reduced.

(2) Territorial defense occurs only during daylight hours; the lack of nocturnal defense is unaffected by changes in lunar phase.

(3) Densities of *Diadema antillarum* within the algal lawns of threespot damselfish are always lower than the natural density outside.

(4) Size of algal lawns within territories of threespot damselfish is positively correlated with damselfish density.

(5) Areas within *Eupomacentrus planifrons* territories represent local patches in the environment where grazing by *Diadema antillarum* is reduced and stands of algae are maintained. This, in turn, may influence coral community structure by causing the mortality of some adult corals, susceptible to overgrowth by algae while allowing others which are better competitors for space under these conditions to survive.

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