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# Interference Behavior and Ecology of Threespot Damselfish (*Eupomacentrus planifrons*) *

A. Houston Williams [1]

Department of Zoology University of North Carolina, Chapel Hill, North Carolina 27514, USA

**Summary.** Interference behavior by threespot damselfish directed at the sea urchins, *Diadema antillarum* and *Echinometra viridis*, differed in levels of aggression and discrimination. Higher aggression towards and recognition of *Diadema* by threespots was correlated with the distribution of *Diadema* along edges of coral patches. Lower aggression levels combined with lower recognition levels of *Echinometra* were correlated with a distribution of *Echinometra* closer to damselfish algal lawns. Differences in behavior of the urchins stimulated differing levels of aggression by the damselfish directly affecting the distribution of the urchins in the back-reef environment.

## Introduction

The importance of interspecific interference behavior by the territorial threespot damselfish, *Eupomacentrus planifrons* Cuvier, in maintaining food resources and reproductive sites has been documented by Myrberg and Thresher (1974). Recognition of competitive reef fish species by threespots has been analyzed further (Thresher, 1976) and found to be the result of discriminations based on the form and color of the intruding individual. Although competition between reef fish, particularly Pomacentrids, has been shown to occur frequently (Clarke, 1970; Fishelson, 1970; Low, 1971; Sale, 1975; Itzkowitz, 1977; Williams, 1978a), competition between highly divergent taxa such as herbivorous fish and sea urchins has not been evaluated adequately. Experimental studies I have completed (Williams, 1977) have examined the competitive interactions between a threespot damselfish population and two abundant sea urchin species, *Diadema antillarum* and *Echinometra viridis*, at Discovery Bay, Jamaica. Such competitive interactions between threespots and *Diadema antillarum* also have been observed by Kaufman (in preparation) and Sammarco (in preparation).

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[1] Present address: Duke University Marine Laboratory, Beaufort, North Carolina 28516, USA

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Behaviors of these abundant species in the back-reef provided mechanisms for both active and passive forms of competitive interactions. Threespot damselfish were observed to maintain either solitary or clustered territories on three-dimensional patches of *Acropora cervicornis* coral dependent on coral patch size (Williams, 1978a). Individual damselfish territories were found to be centered around an "algal lawn" as described by Brawley and Adey (1977) found on the upper and outer branch tips of the ramose coral. Both the algal lawn and the immediately surrounding coral substrate were protected from intruders by the damselfish (see Itzkowitz, 1974; Myrberg and Thresher, 1974). *Diadema* and *Echinometra* exhibited sharply contrasting behaviors when disturbed. *Diadema* exhibited an increased spine agitation and mobility as compared with decreased activity, spine tension, and grasping of the substrate by *Echinometra*.

In this paper I present experimental field studies of interference behavior between *Eupomacentrus planifrons* and the above mentioned sea urchins. Measures of urchin species' discrimination and levels of aggression directed at the competitors by the damselfish provide an estimation of differences in levels of competitive interactions. Field observations of spatial partitioning of the habitat by *Diadema* and *Echinometra* indicate an avoidance of interference proportional to the aggression level exerted by the damselfish toward the urchin species. Thus, the distributions of the dominant herbivorous sea urchins, an important component of the structure of the community, are directly affected by the interference behavior of the territorial threespot damselfish.

## Methods

The observations and experiments reported here were conducted during the period from August 1975 to July 1976 at the Discovery Bay Marine Laboratory, Discovery Bay, Jamaica, West Indies. The populations studied were those inhabiting the shallow (−3 to −5 m) back-reef environment on the east side of Discovery Bay. The back-reef area provided a highly heterogeneous mixture of large living head corals (*Montastrea* spp. and *Diploria* spp.), dead rubble, and discrete patches of living staghorn coral, *Acropora cervicornis*. The threespot damselfish and the sea urchins were found to inhabit this area in large numbers (Williams, 1978b).

All observations and experimentations were accomplished by use of SCUBA. Because *A. cervicornis* has been shown (Itzkowitz, 1974, 1977) to be the primary substrata for threespot damselfish, all observations on distributions of urchins have been gathered from patches of this coral within the back-reef.

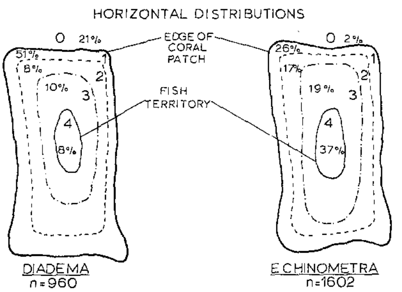
Vertical distributions of *Diadema* and *Echinometra* were estimated by use of a weighted plumb line measuring the distance of each individual's position within the network of coral branches in 5 cm intervals above the substrate floor. Horizontal distribution was evaluated for each urchin as a function of its position along a radius of the coral patch extending from the center of the resident damselfish's territory to the edge of the coral patch (i.e., 0 = located immediately outside the coral patch boundary, 1 = within the edge of the coral boundary, 2 = deep within the coral patch but not adjacent to the resident damselfish territory, 3 = located on the edge of the resident damselfish territory, and 4 = located centrally within the damselfish territory). Data on distributions from ten (horizontal) and eleven (vertical) sampling days were compared between species by utilizing a three-way G-test of independence (Sokal and Rohlf, 1969). This allowed an evaluation of the question of whether or not an association existed between each species and its observed distribution. Thus, a comparison of daily distributions across all zones for both species in two dimensions enabled the analysis of differential habitat use by the urchins.

Damselfish discrimination experiments were carried out on 25 territorial threespots selected randomly in the study area during June. A test consisted of the presentation of a comparable-sized pair of *Diadema* and *Echinometra* or *Echinometra* and the less common *Lytechinus williamsii* individuals (i.e., small *Diadema* and large *Echinometra* etc.) to a resident threespot. The urchins were placed in the center of the algal lawn territory of the damselfish and timed observations were made of the damselfish's aggression level, in terms of its attack on the experimental urchins. The aggression level exhibited by each damselfish was recorded as damselfish bites (of urchin spines)/minute. Experimental test periods were two minutes or less, depending on the rapidity with which the urchins were removed from the territory by the damselfish. Thus, removal of both urchins from a damselfish's territory terminated the experiment. The recipient of the first attack ("primary attack") also was noted as a further measure of the discrimination level of the threespot towards the urchin species. A paired $t$-test was used to compare the level of aggression (i.e., competitive interaction level) exhibited by the threespots toward both species of urchin.

## Observations

Territorial interference behavior during the breeding season by four species of damselfish toward sea urchins and hermit crabs was first noted by Albrecht (1969) and, later, by Sammarco (personal communication) for *E. planifrons* at Discovery Bay. Thus, urchins of several species which invade the territorial boundaries of threespot damselfish were "attacked" by the damselfish's biting their spine tips repeatedly. In the case of invading *Diadema*, spine tips were broken off, resulting in increased activity on the part of the urchin and a hasty retreat from the area of attack. This increased activity on the part of the *Diadema* rapidly carried the urchin out of the territory. However, when *Echinometra* or *Lytechinus* was the invading species, the stouter, less brittle spines of these urchins frequently enabled the threespot to lift the urchin by grasping a spine in its mouth and to carry it out of its territory, releasing it at its boundary.

Spatial partitioning of the three-dimensional *A. cervicornis* patches by *Diadema* and *Echinometra* was apparent. While 72% of the *Diadema* observed were found to aggregate along the outer edge, 56% of the *Echinometra* were found in the central region of the coral patches (Fig. 1). Additionally, 73%

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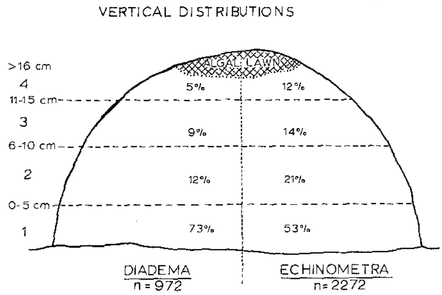


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**Fig. 1.** Horizontal distributions of *Diadema* and *Echinometra* populations found within *Acropora cervicornis* patches. 0–4, zones of occupancy; $n$ = number of individuals

**Fig. 2.** Vertical distributions of percent frequencies of *Diadema* and *Echinometra* found within *Acropora cervicornis* patches. 1–4, zones of occupancy at 5 cm intervals above the substrate; $n$ = number of individuals

**Table 1.** Horizontal distributions of *Diadema* and *Echinometra* populations within *Acropora cervicornis* coral patches. Zones parallel the perimeter of the patch from the periphery (0) to the center (4). Distributions are expressed as percentage of population occupancy for each of 10 daily samples. The distributions were found to be highly associated with each individual species (G = 692.9; 4 df; $P < 0.001$)

| Zone | 0 | 1 | 2 | 3 | 4 | $n$[a] |
|---|---|---|---|---|---|---|
| *Echinometra* | 6 | 52 | 25 | 16 | 0 | 153 |
| | 1 | 40 | 27 | 13 | 18 | 142 |
| | 1 | 32 | 17 | 29 | 21 | 168 |
| | 1 | 36 | 29 | 14 | 20 | 188 |
| | 6 | 9 | 24 | 19 | 41 | 278 |
| | 0 | 6 | 21 | 23 | 50 | 241 |
| | 0 | 29 | 3 | 23 | 44 | 90 |
| | 4 | 12 | 6 | 10 | 68 | 141 |
| | 0 | 22 | 12 | 22 | 45 | 65 |
| | 0 | 21 | 5 | 16 | 58 | 136 |
| *Diadema* | 26 | 59 | 12 | 2 | 1 | 175 |
| | 20 | 49 | 20 | 11 | 1 | 122 |
| | 34 | 47 | 6 | 8 | 5 | 137 |
| | 12 | 61 | 9 | 12 | 6 | 110 |
| | 25 | 36 | 10 | 10 | 18 | 87 |
| | 5 | 55 | 8 | 22 | 10 | 60 |
| | 18 | 46 | 3 | 22 | 10 | 99 |
| | 31 | 57 | 3 | 5 | 5 | 65 |
| | 19 | 59 | 2 | 6 | 14 | 63 |
| | 21 | 52 | 5 | 7 | 14 | 42 |

[a] Sample size

of all *Diadema* were observed to occupy the substrate floor below the coral branches, while 47% of the *Echinometra* were found 5 cm above the substrate or higher within the coral (Fig. 2). Three-way G-tests of independence were performed on numbers of individuals of each species observed on each day. Horizontal distributions of *Diadema* and Echinometra (Table 1) were found to be significantly associated with each species (G = 692.9; 4 df; $P < 0.001$). Vertical distributions (Table 2) also were found to be highly associated with individual urchin species (G = 132.8; 3 df; $P < 0.001$). Thus, *Diadema* appeared to occupy the external and lower regions of *A. cervicornis* patches along the outskirts of threespot territories. *Echinometra,* on the other hand, were found within the interior of the coral patches and frequently amongst higher branches adjacent to the algal lawn.

## Experimental Presentations

Twenty-five discrimination tests of threespots presented with pairs of *Diadema* and *Echinometra* indicated that threespots were seven times more aggressive (measured in bites/minute) toward *Diadema* than *Echinometra* (Fig. 3). This difference was statistically significant at $P < 0.01$ ($t = 11.7$). Ten similar presenta-

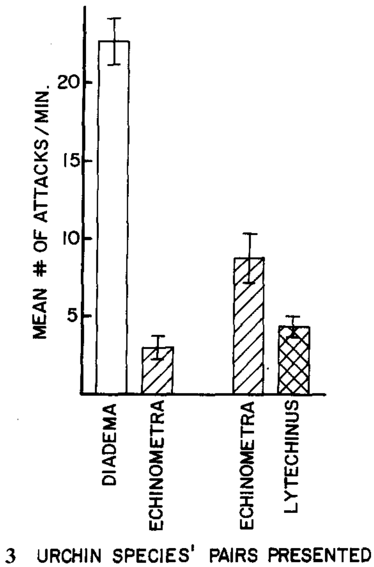
**Table 2.** Vertical distributions of *Diadema* and *Echinometra* populations found within *Acropora cervicornis* coral patches. The zones occur at 5 cm intervals above the substrate base. Distributions are expressed as percentage of population occupancy for each of 11 daily samples. The distributions were found to be highly associated with each individual species ($G = 132.8$; 3 df; $P < 0.001$)

| Zone | 1 (0 – +5 cm) | 2 (+6 – +10 cm) | 3 (+11 – +15 cm) | 4 (> +16 cm) | $n$ [a] |
|---|---|---|---|---|---|
| *Echinometra* | 50 | 32 | 13 | 5 | 152 |
| | 66 | 23 | 5 | 6 | 198 |
| | 79 | 6 | 12 | 3 | 209 |
| | 53 | 30 | 11 | 6 | 187 |
| | 36 | 24 | 15 | 25 | 428 |
| | 61 | 26 | 10 | 4 | 371 |
| | 59 | 21 | 13 | 7 | 250 |
| | 39 | 15 | 26 | 20 | 188 |
| | 47 | 18 | 23 | 12 | 83 |
| | 54 | 20 | 12 | 14 | 76 |
| | 41 | 14 | 16 | 28 | 130 |
| *Diadema* | 69 | 17 | 6 | 8 | 84 |
| | 87 | 8 | 2 | 3 | 134 |
| | 83 | 3 | 6 | 9 | 103 |
| | 69 | 19 | 9 | 3 | 106 |
| | 68 | 25 | 3 | 3 | 88 |
| | 90 | 7 | 3 | 0 | 120 |
| | 91 | 8 | 2 | 0 | 66 |
| | 63 | 9 | 12 | 15 | 117 |
| | 49 | 8 | 27 | 17 | 66 |
| | 62 | 13 | 24 | 2 | 55 |
| | 67 | 21 | 9 | 3 | 33 |

[a] Sample size

tions of pairs of *Echinometra* and *Lytechinus* showed a slightly higher aggression level by the threespots towards *Echinometra* (Fig. 3). However, this level of aggression did not prove to be significantly different from the attacks on *Lytechinus* ($P > 0.05$, $t = 2.13$).

At the onset of each experimental presentation, the urchin species selected by the damselfish to receive the first or primary attack was noted. In all presentations of *Diadema-Echinometra* pairs (25) the threespot selected the *Diadema* first (Fig. 4). This individual received almost total attention by the threespot, although a few attacks intermittently were aimed at the *Echinometra*, until the *Diadema* left the territory. Then the damselfish directed its attention at the *Echinometra*. In 50% of their attempts the damselfish were able to grasp an *Echinometra* spine and carry the urchin outside of the territory for release. The remaining removals were accomplished by a series of lifts and drops of the urchin until it was successfully removed. An examination of the species which received the primary attack in *Echinometra-Lytechinus* pairs indicated no significant trend in discrimination by the damselfish (Fig. 4) and both species were lifted by the damselfish during removals.



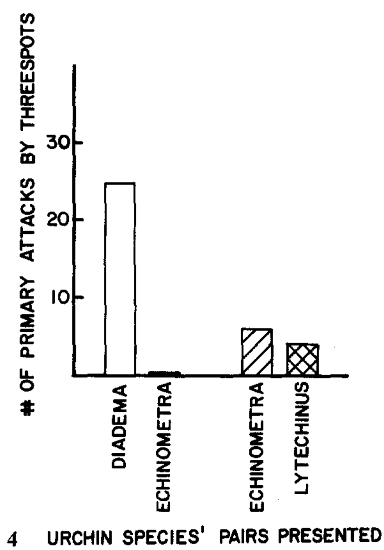




**Fig. 3.** Relative aggression level (mean number of attacks/minute ± SE) exerted by threespot damselfish toward experimentally presented pairs of urchin species (*Diadema-Echinometra* and *Echinometra-Lytechinus*

**Fig. 4.** Relative discrimination level (number of primary attacks) exerted by threespot damselfish toward experimentally presented pairs of urchin species (*Diadem-Echinometra* and *Echinometra – Lytechinus*)

To summarize, differences were observed in damselfish aggression levels, discrimination levels, and methods of removal of the invading species. Threespots exhibited higher levels of interference by aggression towards *Diadema* than either *Echinometra* or *Lytechinus*. Additionally, threespots always discriminated between *Diadema* and *Echinometra*, whereas clear discriminations between *Echinometra* and *Lytechinus* were not observed. And finally, removals of *Diadema* by threespots were aided by the greater mobility of *Diadema* and the greater fragility of its spines as compared with the other urchins.

## Discussion

Case and Gilpin (1974) noted that since interference competition frees resources for the interfering population, the evolutionary cost of interference against a non-competing population would preclude such evolution. Thus, the exhibition of directed interference appears to be indicative of competition for resources. Such competition between the threespot damselfish and sea urchins may be spatial and/or food oriented. The coral substrate, in providing refugia from predators and as a platform for algal growth for all these species, is a potential limiting resource. However, the spatial partitioning demonstrated by this study may ensure coexistence of all species along this resource axis. In terms of direct competition for food, overgrazing of a benthic algal food resource by sea urchins has been documented in many marine systems (Kitching and Ebling, 1961; Paine and Vadas, 1969; Lang and Mann, 1976; Williams, 1977). Since benthic algal growth is confined to dead or dying coral substrate (Potts, 1977; Kaufman, 1977), its settlement and subsequent availability is limited by spatial constraints. The absence of filamentous algae on lower coral substrate (Williams, unpublished data) provides evidence of heavy grazing pressures at the limits of damselfish territories. Thus, the threespot damselfish defends its algal lawn food and coral substrate resources from the herbivorous echinoids which invade its territorial boundaries.

The distributions of *Diadema* and *Echinometra* distinctly separate the two species within the habitat. These distributions in both vertical and horizontal dimensions correlate highly with the discrimination and aggression levels of the damselfish. That is, *Diadema*, which is recognized quite readily by threespots and which receives the greatest aggressive interference, exhibits a distribution which is restricted to the lower edge of the damselfish's territory. *Echinometra*, which is not readily distinguished from other urchins and which receives a moderate to low aggressive interference, exhibits a distribution which more closely approaches the algal lawn of the damselfish.

Case and Gilpin (1974) have suggested that subordinate species, such as these urchins, in a unilateral interference situation may become restricted to habitats in which interference provides no benefit for the dominant species. The highly restricted distribution of *Diadema* is apparently the direct result of a higher level of competitive interference directed towards it than *Echinometra*. This may be stimulated by the greater activity level of *Diadema*. On the other hand, *Echinometra's* relative immobility results in a less restricted distribution because of a lower aggression level stimulated in the damselfish. Thresher's study (1976) indicated similar results for interspecific interactions between *E. planifrons* and invading reef fish. Movement proved to be a critical factor in releasing territorial aggression towards other species. Thresher theorized that a slow moving intruder could encroach more on a territory than if it had been moving faster. Thus, the behavioral differences between the urchins also may affect the interference levels.

Differences in behavioral interference by threespot damselfish stimulated by differing behaviors of competitors have been shown to directly affect the distribution of herbivorous sea urchins in the back-reef environment. Hence, the community structure at the herbivore level is partially determined by the competitive interference of *Eupomacentrus planifrons*.

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