

## Damsel-fishes and their Algal Lawns: a Case of Plural Mutualism

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### Abstract

Damsel-fishes (Pisces: Pomacentridae) are known for their aggressive defense of territories that contain well developed, typically multispecific, algal lawns. The damselfish maintains the lawn by defending it against potential herbivorous intruders, and by "weeding out" undesirable algal species. Although the damselfish-algal association generally has not been considered in the context of a symbiosis, it not only fits the original definition of a symbiosis (de Bary 1879), but also is significant to the well-being of both symbiotes (Starr, 1975). Here, the association is proposed as a mutualism which includes multiple substrate species (plural mutualism), and is classified using a published scheme for specifying symbiotic associations by multiple criteria. The interactions between the damselfish-algal mutualism and associated coral substrates are then used as a contrast to the proposed mutualism.

Interactions between the Acapulco Damselfish, *Stegastes acapulcoensis* (Fowler), and the sea urchin, *Diadema mexicanum* A. Agassiz, are used in a case study of the proposed mutualism to demonstrate the defense of algal lawns by damselfish. A significant positive correlation was found between the responsiveness of damselfish to invading urchins and three variables: lawn quality, fish size and urchin density. I hypothesize that larger damselfish are able to control territories in locations that are somehow better for algal growth, but which require greater effort to defend from intruding herbivores, than smaller damselfish which control locations less suited to the growth of algal lawns.

Keywords: *Stegastes acapulcoensis*, *Diadema*, sea urchins, territoriality, Panama, behavioral symbioses, Pomacentridae, *Acanthaster planci*, damselfish-coral interactions, coral mortality

## 1. Introduction

Symbiosis, as originally defined by de Bary (1879), is the living together of differently named organisms. This term has suffered many attempts at change, but today remains an important concept which exists in nearly its original form (Starr, 1975). By the original definition, and most modern interpretations, symbiosis includes any intimate association between two or more partners (symbiotes, Hertig et al., 1937), including parasitism (Starr, 1975; Lewis, 1985). One of the few changes that improves the application of de Bary's concept, without changing its meaning, is the requirement that the association be significant to the well-being of at least one of the participants (Starr, 1975). This eliminates "casual" associations without necessitating a degree of permanence, and can be applied when the association either improves or reduces fitness.

Many symbiotic assemblages involving coral reef fishes have been described (reviews in: Dales, 1966; Davenport, 1966; Feder, 1966; Fricke, 1975; Losey, 1978b), but the behavioral nature of most of these interactions has slowed the progress of their study. Unlike associations based on physiological adaptations, behavioral symbioses often are difficult to describe in the context of metabolic dependency, and relative fitness has been used as an alternative measure (Roughgarden, 1975). Unfortunately, discussion of behavioral symbioses often have been based on conjecture (Colin and Heister, 1973; Hanlon et al., 1983; Hanlon and Hixon, 1986), with few cases of quantitative analyses of behavior (Davenport, 1966; Karplus et al., 1972; Losey 1972, 1978a; Preston 1978) or detailed studies of physiological adaptations (Schlichter, 1976; Brooks and Mariscal, 1984; Lubbock, 1981).

Here I will propose a new symbiotic assemblage, the damselfish and its algal lawn, in the context of modern schemes of classifying symbiotic assemblages (Starr, 1975; Lewis, 1985). This association will be contrasted with the interactions between the damselfish-algal mutualism and associated coral substrates. The defense of the algal lawn by damselfishes will be discussed as a case study, using new data from field experiments on the removal of "invading" *Diadema* by damselfish.

*The Damselfish-algal lawn mutualism: proposal and classification*

Many damselfishes aggressively defend territories containing well developed, typically multispecific, algal lawns. Generally, the damselfish-algal association has not been considered in the context of a symbiosis. However, this association not only fits the original definition of a symbiosis (de Bary 1879), but also is significant to the well-being of both symbiotes. Because the algal lawn is often multispecific (Lobel, 1980; Lassuy, 1980; Montgomery, 1980; Irvine, 1981), it should be considered a case of "plural" symbiosis (Starr, 1975). Finally, because the association benefits both species (see below), I propose that the association should be considered a case of plural mutualism.

In light of the confusion which has existed over the meaning of symbiosis, it is not surprising to find confusion over the characteristics that specify associations as symbioses. It was not until Starr (1975) developed his "generalized scheme for classifying organismic associations", that a systematic means was established to classify symbiotic associations through the use of multiple criteria. Unfortunately, Starr's original scheme was somewhat biased towards physiological associations in which the interaction is primarily based upon direct nutritional exchange. This method has been improved recently (Lewis, 1985), and better describes interorganismic associations at the behavioral level. A technical description according to these schemes follows (Table 1):

(1) The association results in increased fitness for both the damselfish (nutrition) and the algae (protection, nutrient enrichment suggested). Both behavioral observations and gut content analyses have shown that most territorial pomacentrids primarily feed on algae and the invertebrate epiphytes living in the algal lawn (Randall, 1967; Lobel, 1980; Montgomery, 1980; Irvine, 1981). The algae in the territories are preferentially farmed, and benefit as a population from the territorial exclusion of transient herbivores. The resulting intermediate level of grazing permits them to grow in dense stands of higher biomass and in more erect forms than would be possible on the heavily grazed reef surfaces outside of territories (Brawley and Adey, 1977; Lobel, 1980; Montgomery, 1980; Lassuy, 1980; Irvine, 1981; Hixon and Brostoff, 1983). (2) The association is of prolonged duration. Once damselfishes reach a size at which they maintain a territory with a lawn, they will continue to do so throughout their lives. Although damselfish may move into new territories which become vacant, the old lawn will be reoccupied rapidly (Lobel, 1980; Wellington and Victor, pers.comm.; Eakin, unpublished). (3) The two symbiotes are very different in size (anisymbiotic).

Table 1. Classification of the damselfish-algal lawn association by means of a heuristic scheme for specifying symbiotic associations (based on Lewis, 1985).

Criterion	Position of damselfish-algal association
1. Fitness	mutualism
2. Duration	prolonged
3. Relative size	anisymbiotic
4. Physical contact	exhabitational (physical contact essential)
5. Specificity	highly to somewhat specific
6. Nutrition	necrotrophic/saprotrophic <sup>1</sup>
7. Interdependence	
degree	semi-obligate/facultative
mode	organismic/"population" level
mechanism <sup>2</sup>	behavioral
8. Integration	
degree	mostly independent
modes	ecological

<sup>1</sup> A/B indicates condition for damselfish/algal lawn where different.

<sup>2</sup> This is a new subcategory that ranges from subcellular through biochemical and physiological to behavioral levels (c.f. Lewis, 1985, p. 36).

(4) Physical contact is essential, although the association is exhabitational. Contact is necessary both for nutritional flow, and for the damselfish to tend to the algal lawn; actual "weeding" behavior has been documented (Lassuy, 1980; Irvine, 1981). (5) Damselfishes vary in host-specificity among species and probably by geography. Some damselfishes maintain monospecific lawns (Montgomery, 1980), others multispecific lawns with a different composition than in surrounding areas (Lobel, 1980; Lassuy, 1980; Montgomery, 1980; Irvine, 1981). (6) Nutrient transfer is known to occur through damselfishes feeding on their algal lawns (necrotrophy in Lewis' scheme) (Randall, 1967; Lobel, 1980; Montgomery, 1980; Irvine, 1981). Recent works suggests that nutrients defecated by reef herbivores may be directly incorporated by lawn algae (Polunin, 1984; Carpenter and Williams, 1986; Fitzgerald et al., 1986), so algae also may utilize nutrients excreted by damselfishes (saprotrophy). (7) The amount of interdependence between the damselfish and the lawn is far less certain. Although damselfish species which maintain algal lawns can be kept in captivity without an algal lawn, they are seldom found living without them in the field. Even though there is often considerable variation in lawn quality, adult damselfishes are dependent upon the algal lawn for spawning as well as for feeding (Myrberg and Thresher, 1974; Wellington and Victor,



pers.comm.). The algae are strictly facultative. The same species are found outside of damselfish territories, but typically not in such high biomass or diversity. The mode of interdependence also differs between the symbiotes; single damselfish (organisms) are found with mats of algae ("populations"). I add a new subcategory to describe the mechanism by which the symbiotes interrelate. Mechanism of interdependence ranges from subcellular through biochemical and physiological to behavioral levels (c.f. Lewis, 1985), with the damselfish relating to the algae at the behavioral level. (8) Finally, the symbiotes are mostly independent, although the damselfish-algal symbiosis may act as a unit in reef community dynamics. Impacts of damselfish and their lawns on coral substrates contributed to differences between the coral communities found in shallow and deep habitats (Wellington, 1982a), and the algal lawn has been implicated both in increasing mortality in young coral colonies (Potts, 1977) and in reducing settlement by many benthic invertebrates (Vine, 1974).

The association between the damselfish-algal symbiosis and live coral substrates serves as a contrast to the mutualism which exists between the damselfish and its algal lawn. The former association is primarily either amensalistic or agonistic, as corals are often killed to create substrates for algal lawns (Kaufman, 1977; Wellington, 1982a). However, all the effects of damselfishes on corals are not harmful. Recent observations in Tahiti and Panama suggest that damselfishes may protect corals from direct predation by *Acanthaster planci* Linnaeus (Tahiti: Glynn and Colgan, pers. comm.; Panama: Glynn, pers. comm.; Eakin, unpublished), and Wellington (1982a) has observed *S. acapulcoensis* to defend its territories against the corallivorous fish, *Arothron meleagris* (Bloch and Schneider). Thus, it is uncertain whether corals realize net benefit or harm.

The association with coral substrates also lacks the aspect of significance proposed by Starr (1975). Damselfish have not been shown to kill corals preferentially, and subordinate damselfish often establish territories on dead coral substrates while nearby live coral colonies remain unoccupied. However, it has been suggested that damselfish which establish new lawns may have greater reproductive success than those which maintain older lawns (Wellington, pers. comm.). And although damselfishes can affect coral community structure, other factors, such as light and zooplankton densities, also are important (Wellington, 1982b). Finally, while damselfish have been shown to prefer habitats with higher topographic complexity (Wellington, 1982a), high topographic complexity can be found in both live branching

coral and dead coral rubble. Thus, unlike the algal lawn which is an important resource protected by the damselfish, there is little evidence that the association with corals is significant to the well-being of the damselfish.

#### *Defense of the algal lawn: a case study*

The algal lawn is maintained by the damselfish not only by defending against invading conspecifics, but also by the exclusion of a wide array of potential herbivore intruders. Herbivorous and omnivorous fishes which have been observed to be attacked include: heterospecific pomacentrids, scarids, acanthurids, siganids, tetraodontids, chaetodontids, labrids, lutjanids, pomadasyids, mullids, canthigasterids, scolopsids, blenniids, gobiids, parapercids and eleotrids (Low, 1971; Myrberg, 1972; Ebersole, 1977; Montgomery 1980; Mahoney, 1981; Wellington, 1982a; Robertson, 1984; Eakin, pers. obs.). In addition, quantitative studies of interspecific territoriality have shown that damselfishes exhibit varied levels of aggression against different intruder species (Myrberg and Thresher, 1974; Thresher, 1976; Moran and Sale, 1977; Mahoney, 1981; Losey, 1982; Harrington and Losey MS), and that the levels varied seasonally (Myrberg and Thresher, 1974; Moran and Sale, 1977) and with recent exposure to potential competitors (Losey, 1982).

Damselfishes have been shown not only to direct territorial aggression against other fishes, but also to direct interphylal territorial aggression against slowly moving herbivorous echinoids (Williams, 1978, 1981; Glynn and Wellington, 1983) and the corallivorous asteroid *Acanthaster planci* (Glynn and Colgan, pers. comm.; Glynn, pers. comm.; Eakin, unpublished). The sea urchin *Diadema* is known to enter damselfish territories and feed on algal lawns (Williams, 1978, 1981). Here I discuss experiments performed on the ejection of *Diadema* urchins from damselfish lawns.

## 2. Methods

Experiments were performed to test the interactions between the Acapulco Damselfish, *Stegastes acapulcoensis* (Fowler), and the sea urchin, *Diadema mexicanum* (A.Agassiz), in a shallow coral reef habitat (2–5 m, Uva Is., Pacific Panama; [see Glynn, this volume Figure 1b]). Here, *Diadema* exist in densities which have become elevated since the 1982–1983 El Niño (Glynn, pers. comm.). *Diadema*, suspended by monofilament line from the end of a clear acrylic rod, were introduced into the lawns of 28 damselfish, divided among four different sites, for a total of 106 tests over a 3 day period. Experiments were performed at various times throughout the day, from

just before dawn to just after dusk. The damselfish were observed as they repeatedly bit at, and finally carried the *Diadema* from the algal lawn.

The data consisted of the distance that the damselfish carried the urchin in three successive trials. Because of the rapid changes in illumination during dawn and dusk observations, only observations made during full daylight are discussed in this paper (162 trials total). Defensive effort was calculated as the mean of the distances measured (usually 6 values).

Data on several environmental parameters were collected at each damselfish's lawn. Among these were the number of *Diadema* in the square meter centered on the algal lawn, and a qualitative index of lawn quality. The latter is a subjective assessment which ranges from 1 (sparse algal growth with poorly defined margins) to 4 (lush algal growth with clearly defined margins). After the conclusion of the experiments, as many fish as possible were collected. The standard length (snout tip to caudal peduncle) was measured on each of these (to mm) and estimated for the other individuals (to 0.5 cm).

### 3. Results and Discussion

Damselfish at Uva Is. reacted territorially to both naturally and introduced invading urchins from shortly after dawn to shortly after dusk. Their behavior was sharply divided into fish which responded to the presence of urchins and those which did not, and the four sites varied in the proportion of responsive fish (Table 2). Therefore, the relationship between responsiveness and the above variables was analyzed by means of the nonparametric rank biserial correlation (Goldman, 1982), which tests for trends in a binary variable along a continuous axis.

Biserial correlation analysis yielded a highly significant positive correlation between responsiveness and each of: lawn quality ( $r = 0.88$ ,  $p < 0.001$ ), fish size ( $r = 0.96$ ,  $p < 0.001$ ) and urchin density ( $r = 0.73$ ,  $p < 0.001$ ). Cumulative frequency curves demonstrate that the proportion of responsive fish increases with each independent variable, and that this increase is sharpest in response to damselfish standard length and lawn quality (Fig. 1). This suggests that larger damselfish are able to control territories in locations that are somehow better for algal growth than smaller damselfish. Additionally, these locations appear to be more attractive to intruding urchins, and thus require greater defensive effort, than locations inhabited by smaller fish. This would explain the high urchin densities immediately outside of the lawns defended by large damselfish and agrees with field observations by Williams (1978).

Table 2. Distance which urchins were carried by each fish, and responsiveness value used in biserial correlations.

Site #	Fish #	Response	Distance Carried		
			Mean	s	n
1	1	yes	26.17	8.45	6
	2	no	0.00	0.00	6
	3	no	0.00	0.00	6
	4	yes	50.83	18.28	6
	5	no	0.00	0.00	3
	6	no	0.00	0.00	6
	7	no	0.00	0.00	6
2	1	yes	68.33	29.10	6
	2	yes	28.33	10.41	3
	3	yes	70.00	16.92	6
	4	yes	18.17	1.83	6
	5	yes	45.00	28.28	6
	6	yes	50.00	14.49	6
	7	yes	41.17	20.00	6
	8	yes	54.67	9.69	6
3	1	no	0.00	0.00	6
	2	no	0.00	0.00	6
	3	no	2.50	6.12	6
	4	no	0.00	0.00	6
	5	no	0.00	0.00	6
	6 6b*	no	0.00	0.00	6
4	1	yes	75.00	28.14	6
	2	yes	27.17	27.06	6
	3	yes	52.17	12.25	6
	4	yes	49.33	19.98	6
	5	yes	52.83	12.97	6
	6	yes	63.33	37.51	6
	7	yes	37.50	10.37	6

\* Fish 6b represents the secondary algal lawn defended by fish 6.

Most fish under 65 mm standard length did not demonstrate a territorial response to the intruding urchins. These were individuals which held territories in habitats of apparently lower quality (lawn on rubble bottom several meters from shelter hole) with less developed algal lawns and fewer urchins in the surrounding area than those above 65 mm. Future work is needed to determine if the lack of response is due to a lack of regular stimulation



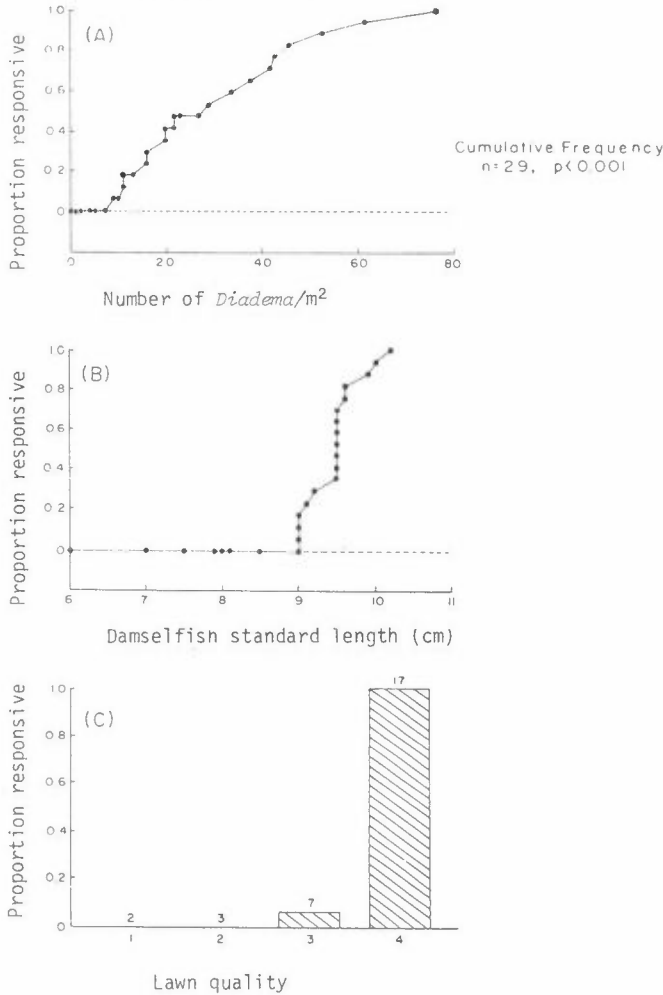


Figure 1. Cumulative frequencies of the proportion of those damselfish which were responsive to experimentally introduced *Diadema* (17 of the 29 total fish). Responsiveness was highly significantly associated with all three dependent variables ( $p < 0.001$ , rank biserial correlation): A. damselfish standard length; B. number of *Diadema* in the square meter centered on the algal lawn; C. subjective lawn quality index (n for each group appears over the bars).

from invading urchins (Losey, 1982) or if the territory contains a resource level too low for it to be energetically economical to defend (Carpenter and MacMillen, 1976).

While there is still some question of how these and other factors influence damselfish responsiveness, most of the damselfish seem to expend a great deal of effort to defend their lawns from invading urchins. Among the responsive

damsel fish, the mean distance that they carried urchins was  $48.2 \pm 2.5$  cm. In one case, a damselfish of approximately 90 mm standard length carried an urchin 195 cm from its lawn, with a mean distance of 75 cm per ejection (Table 2). This behavior is not restricted to Uva Is., as *S. acapulcoensis* have been found to carry urchins from their territories elsewhere in Pacific Central America (Costa Rica: H. Guzman, pers. comm.). For such behavior to be selective, it must confer some increase in overall fitness. While fitness has not been determined directly, by securing exclusive use of the primary food source, dominant damselfish should have an advantage over subordinates which have greater losses from lower quality lawns.

#### 4. Final Considerations

The damselfish-algal symbiosis is a well developed association that demonstrates many of the attributes used to describe mutualisms. However, the recognition of this system as a mutualism calls attention to new questions. Further work is needed to determine the extent of the benefit to the algal partner. Increased biomass is not advantageous to the population unless such maintenance increases algal populations. The reproductive condition of the algae and rates of both sexual and vegetative recruitment need to be compared in and out of damselfish territories to help resolve whether this association is a true reciprocal mutualism, or simply a "gentle parasitism" (Roughgarden, 1975).

There is still a question why only large *S. acapulcoensis* respond to invading *Diadema*. Cost-benefit analyses of this system would help to determine if this is due to energetic economization (Carpenter and MacMillen, 1976) or to the influence of differential urchin densities (Losey, 1982). In addition, this system has the advantage that the "currency" in which the damselfish receives benefit (food energy) is directly comparable to that in which costs arise (defensive effort). This makes this system a good candidate for cost-benefit analysis of the mutualism (Addicott, 1984).

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