

## Coexistence: Symbiotic Sharing of Feeding Territories and Algal Food by Some Coral Reef Fishes from the Western Indian Ocean

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### Abstract

A symbiotic relationship between a damselfish (*Stegastes fasciolatus*) and 2 surgeonfishes (*Acanthurus lineatus* and *A. leucosternon*) is described. The damselfish, which is about 1/10 the size of the surgeonfishes, is concentrated in, and appears to prefer to be in, the feeding areas of the surgeonfishes. There is an average of one adult damselfish per adult surgeonfish feeding area. All 3 species defend their feeding areas against conspecifics and various other fishes that have similar diets, but there are few aggressive interactions between the cohabitants. Most of the interspecific defense of cohabited areas is provided by the surgeonfishes. The cohabitant species eat the same types of benthic microalgae, but only the damselfish eats microcrustaceans. It appears that the net cost to a surgeonfish of having a damselfish in its feeding area is very low because (1) biomass density of the damselfish is low, (2) it uses some food that the surgeonfishes do not use, and (3) it makes a small contribution to the defense of shared feeding areas. Even if there is a cost to the surgeonfish, the small size of the damselfish would allow it to take shelter from the surgeonfish, thus making it too costly for the surgeonfish to exclude it. Such cohabitation relationships, which may be quite common among reef fishes, represent a means by which the coexistence of species that use the same limiting resources is achieved.

### Introduction

Reef fishes are often involved in symbiotic relationships; some clean parasites from other fishes (Randall, 1958; Feder, 1966), while others live with sea anemones (Verwey, 1930; Mariscal, 1970), sea urchins (Eibl-Eibesfeldt, 1961), corals (Tyler, 1971), sponges (Tyler and Böhlke, 1972), crinoids (Fishelson, 1966), seaweeds (Davis and Cohen, 1969), and in the burrows of shrimps

(Klausewitz, 1960; Polunin and Lubbock, 1977). Some of these symbionts evidently share resources that they may be competing for with each other and with other species. Anemonefishes sometimes take food that the host anemone has captured (Mariscal, 1970), fish-shrimp symbionts share shelter, and some fishes that live in corals share food and shelter with other coral symbionts (Lassig, 1977). Food sharing also occurs among symbiotic carnivorous fishes (Eibl-Eibesfeldt, 1955; Strasburg, 1959; Karplus, 1978). However, we know of no reports in the literature of symbiotic relationships between fishes that share feeding territories and food. Here we describe such a relationship between several algivorous reef fishes: the pomacentrid *Stegastes fasciolatus*, which shares territory space and food with each of 2 acanthurids, *Acanthurus lineatus* and *A. leucosternon*.

Long-term defense of feeding territories is common among coral reef fishes, especially those that eat benthic algae, and ecological studies of interactions among species that are evidently food competitors typically emphasize how territory owners exclude potential competitors of the same and different species from their territories (Low, 1971; Brockman, 1973; Barlow, 1974; Itzkowitz, 1974; Myrberg and Thresher, 1974; Vine, 1974; Reese, 1975; Robertson *et al.*, 1976; Ebersole, 1977; Ehrlich *et al.*, 1977; Itzkowitz, 1977; Nursall, 1977; Sale, 1977; Thresher, 1977; Williams, 1978; Robertson *et al.*, 1979; Lassuy, 1980). The study that we describe here demonstrates that relationships between potential food competitors can be much more complicated than this simple, straight-forward picture.

We present data on the large- and small-scale spatial distribution of the cohabitant species, the habitat preference of the "dependent" species, the population and biomass densities of the cohabitants, their aggressive relations with conspecifics, with each other and with other fishes, and the degree to which they partition food resources. The nature of the symbiotic relationship is then discussed.

## Materials and Methods

### The Study Species

*Acanthurus lineatus* is a moderate-sized surgeonfish that reached a weight of 289 g in the study area, while *Acanthurus leucosternon* is a somewhat smaller (max. 207 g) fish. Both these species are illustrated in Robertson *et al.* (1979). *Stegastes fasciolatus* (= *Eupomacentrus*, Emery and Allen, in press) is a small species of damselfish that attained only 25 g in the study area. A color variant of this species is figured in Allen (1975, p 140).

### The Study Area

We used the same study area (at Aldabra Atoll, western Indian Ocean) as for our concurrent study on the ecology and behavior of surgeonfishes (Robertson *et al.*, 1979). This area consisted of a 25-m-wide belt transect that spanned 90 m of both intertidal and subtidal portions of the outer edge of the reef. Data were collected from July 1975 through January 1976.

### Data Collection

#### A. Spatial Distributions and Biomass Densities of Cohabitants

The number of individuals of each of the 3 study species resident in all 5-m segments of the 90-m length of the transect were counted at the beginning of the study to determine patterns of vertical zonation. The location of each *Stegastes fasciolatus* in the study area was determined relative to the location of the feeding areas of *Acanthurus lineatus* and *A. leucosternon*. Feeding areas of a series of individuals of each species were mapped to obtain information on the degree of overlap in the feeding areas of each pair of cohabitants. Each feeding area was mapped by noting the location of the substrate bites that its owner took during observation periods of 10 to 30 min. In zones in which *S. fasciolatus* and the 2 *Acanthurus* spp. co-occurred, we counted the number of *S. fasciolatus* resident in individual feeding areas of the *Acanthurus* spp. The relative biomass densities of each cohabitant species in shared areas were estimated using (a) mean body weights of speared specimens, (b) mean sizes of the feeding areas of adults of each surgeonfish, and (c) the mean number of *S. fasciolatus* per surgeonfish feeding area.

#### B. Aggressive Relations of the Cohabitants

The mapped feeding areas and our observations on interactions between the cohabitants provided data on intraspecific territoriality and aggressive relations between each pair of cohabitants. All aggressive interactions between the 3 study species and other fish species

were recorded. These data were used to determine the functions of territory defense by each cohabitant species.

The spatial distribution of *Stegastes fasciolatus* could be the result of either its preference for the areas in which it is found to other areas, or its being excluded from other areas by superior competitors or predators. We gathered data aimed at determining whether competitors might be restricting *S. fasciolatus* to the areas it was using. The species most likely to do so are those with which *S. fasciolatus* was mutually aggressive and which had habits and diets similar to those of *S. fasciolatus*. We made observations on several such species to determine the nature of their interactions with and degree of ecological similarity to *S. fasciolatus*. We also performed reciprocal removal experiments with 2 of these species and *S. fasciolatus*. These experiments were based on the following prediction: individuals of a competitively dominant species that we remove should be replaced by either conspecifics or members of the competitively subordinate species, while individuals of the subordinate species that we remove should be replaced only by conspecifics. We mapped the feeding areas of contiguously distributed individuals of *S. fasciolatus* and these "competitor" species, eliminated one species by spearing, and then determined which species took over the vacated area during the next 3 d.

#### C. Food Partitioning by Cohabitants

To determine the degree to which the cohabitant species were partitioning food resources we collected by spearing a series of adult *Acanthurus lineatus* and *A. leucosternon* and a series of *Stegastes fasciolatus* that were living in the feeding areas of those 2 species. Their stomach contents were preserved in 5% neutral buffered formalin in seawater. Each sample (or an aliquot of each large sample) was placed on a glass slide and covered with a cover slip. The relative abundance of each type of material that was in each sample was then determined by noting what materials were present under 150 randomly chosen intersection points of a grid that was superimposed on the cover glass.

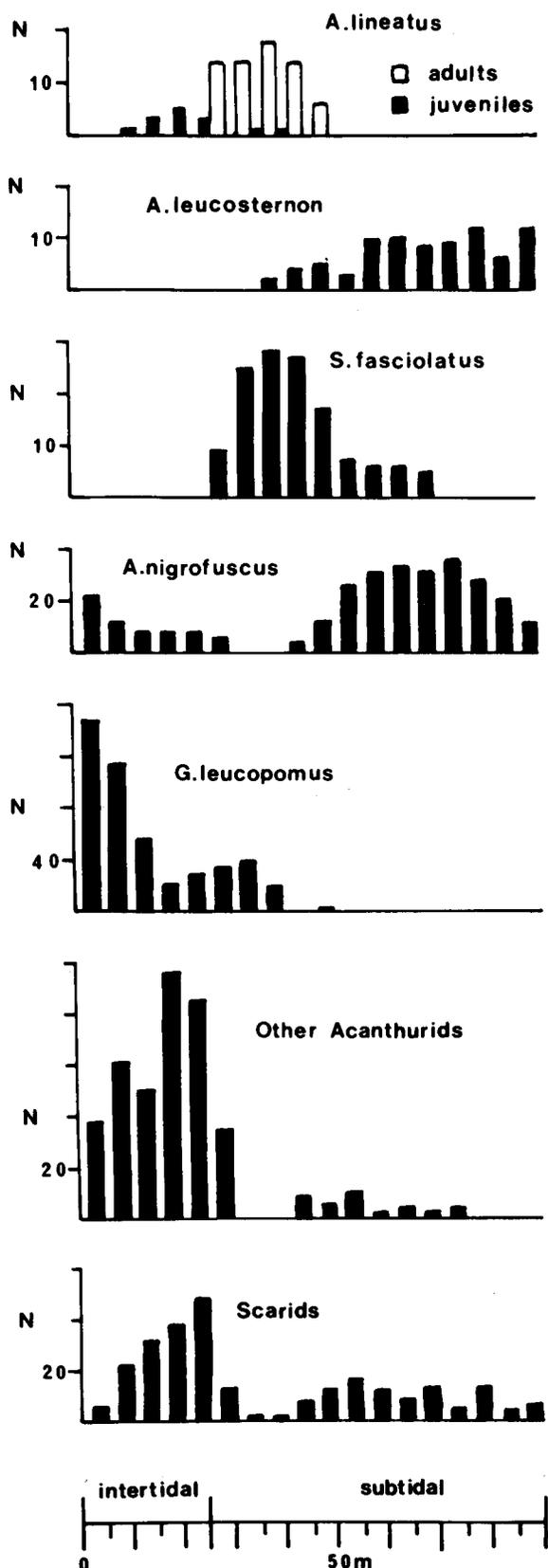
We recorded from which of 9 microhabitats each bite was taken by each of a series of individuals of the cohabitant species over a 10-min observation period. This classification of substrate microhabitats was based on the elevation and attitude of the substrate, and whether it was exposed or concealed. Similarity of microhabitat use between pairs of cohabitant species was determined by comparing the proportions of total bites directed at the different microhabitats.

## Results

### Spatial Distributions of the Study Species

#### Zonation Along Reef Transect

The 3 species did not occur inshore from the transect area and *Acanthurus leucosternon* was the only species



that was found in areas deeper than those the study area covered (Robertson *et al.*, 1979).

Adult *Acanthurus lineatus* were concentrated on the subtidal section of the transect immediately below the intertidal section. *A. leucosternon* were found throughout the remainder of the subtidal segment of the transect. Most *Stegastes fasciolatus* present were in the same zone as the adult *A. lineatus*, while the remainder were living in that part of the *A. leucosternon* zone nearest the *A. lineatus* zone (Fig. 1).

*The Coincidence of the Feeding Areas of S. fasciolatus and the Two Acanthurus spp.*

All *Stegastes fasciolatus* found in the zone they shared with adult *Acanthurus lineatus* were living in the feeding areas of *A. lineatus*. The feeding areas of the 2 species overlapped extensively, although there was no pronounced tendency for the borders of individual feeding areas of the 2 species to coincide (Fig. 2).

The feeding areas of *Acanthurus leucosternon* occupied 51% of the substrate in the part of the transect that *A. leucosternon* and *Stegastes fasciolatus* shared. There was a strong tendency for the *S. fasciolatus* that lived in the *A. leucosternon* zone to be located in the feeding areas of *A. leucosternon* as 28 of the 29 *S. fasciolatus* present were in such feeding areas. The feeding areas of these 2 species overlapped extensively, although the borders of those areas showed little tendency to coincide (Fig. 2).

*Population and Biomass Densities of Space Sharers*

Individual feeding areas of adult *Acanthurus lineatus* and *A. leucosternon* covered a mean of 7 m<sup>2</sup> and 17 m<sup>2</sup> of substrate, respectively (Robertson *et al.*, 1979). The feeding areas of *Stegastes fasciolatus* ranged in size from areas about equal to those of *A. lineatus*, to areas about equal to those of *A. leucosternon* (see Fig. 2). By adding the fractions of *S. fasciolatus* territories that overlapped each *Acanthurus* territory, we found that the feeding areas of adult *A. lineatus* and *A. leucosternon* had 1.2 and 1.1, respectively, adult *S. fasciolatus* residents in them (Table 1). Taking into account the difference in mean body weights of adults of each species we calculate that the average feeding area of each *Acanthurus* species supported a biomass of *S. fasciolatus* that was less than 10% of the biomass of surgeonfish supported by the same feeding area (see Table 1).

◀ Fig. 1. Zonation patterns of various benthic feeding algivorous fishes in the study area. The numbers of fishes in each 5 x 25-m segment of a belt transect are shown. *G. leucopomus* = *Glyphidodontops leucopomus*. Other acanthurids = *Zebrasoma scopas*, *Z. veliferum*, *Naso lituratus*, *Acanthurus triostegus*, *A. nigricaudus* and *A. tennentii*. Scarids = species listed in Table 2. In all species except *A. lineatus* the numbers of adults and juveniles are combined

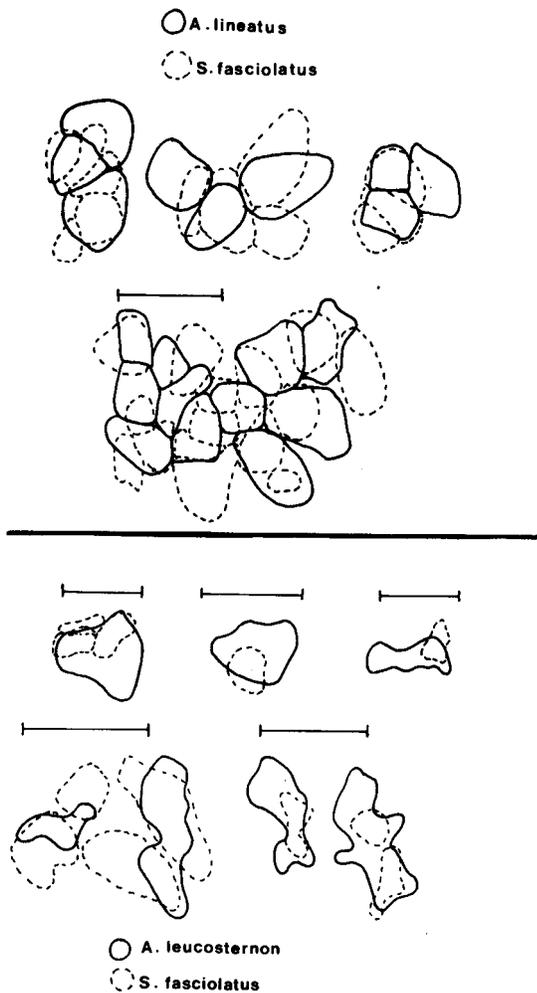


Fig. 2. Overlap in the feeding areas of cohabitant species. Each outline represents 10 to 30 min observation on each fish. Bar = 5 m

### Intra- and Interspecific Aggressive Relations

#### Intraspecific Territoriality

The feeding areas of *Acanthurus lineatus* and *Stegastes fasciolatus* are defended by single individuals of either sex, while those of adult *A. leucosternon* typically are defended jointly by a male and a single female (Robertson *et al.*, 1979). There was virtually no overlap between the feeding areas of neighboring individuals of either *A. lineatus* or *A. leucosternon* (Robertson *et al.*, 1979; Fig. 2). We mapped the feeding areas of 112 *S. fasciolatus*. In only 5 instances was there overlap between the feeding areas; those overlaps were slight, as less than 3% of the bites that those 5 fishes took from the substrate were in the overlap areas (see also Fig. 2).

Table 1. Population density and biomass of *Stegastes fasciolatus* in the feeding areas of adults of *Acanthurus lineatus* and *A. leucosternon*

	Feeding area of	
	<i>Acanthurus lineatus</i>	<i>Acanthurus leucosternon</i>
No. of <i>S. fasciolatus</i> per surgeonfish feeding area <sup>a</sup>		
adults	1.2 ± 0.2 <sup>a</sup>	1.1 ± 0.3
juveniles	0.1 ± 0.1	0.1 ± 0.2
n =	53 feeding areas	35 feeding areas <sup>b</sup>
Biomass of <i>S. fasciolatus</i> per surgeonfish feeding area (g) <sup>c</sup>	20.1	18.5
Biomass of surgeonfish per surgeonfish feeding area (g) <sup>d</sup>	222	258

<sup>a</sup>  $\bar{X} \pm 95\%$  C.I.

<sup>b</sup> Includes only feeding areas in the zone in which both species co-occur

<sup>c</sup>  $\bar{X}$  Weight of *S. fasciolatus* adults = 16.5 ± 1.0 g (n = 56), juveniles = 3.4 ± 1.0 g (n = 8)

<sup>d</sup> from Robertson *et al.*, 1979

#### Relations Between Cohabitants

Aggressive interactions between the cohabitants occurred very infrequently. During 60 h of observations on adult *Acanthurus lineatus*, 53.7 h on adult *A. leucosternon* and 34 h on *Stegastes fasciolatus* we saw only 4 interactions between *A. lineatus* and *S. fasciolatus*, and 3 between *A. leucosternon* and *S. fasciolatus*. In all 7 instances the surgeonfish chased the damselfish. The damselfish retaliated only once, and was then chased. In all cases the damselfish retreated into a hole in the substrate in its feeding area.

#### Cohabitants' Defense of Feeding Areas Against Other Species

**Range of Species Attacked.** All 3 species of cohabitants attacked numerous species of fishes that fed on benthic algae; 96% of *Acanthurus lineatus*' aggressive interactions, over 99% of *A. leucosternon*'s (Robertson *et al.*, 1979) and 89.6% (n = 375) of *Stegastes fasciolatus*' were with such fishes. The remainder of *S. fasciolatus*' interactions were with fishes that fed on small fishes, small benthic invertebrates and, probably, damselfish eggs. The algivorous fishes that the cohabitants attacked included surgeonfishes, damselfishes, parrotfishes, and one balistid (Table 2). Most of the species listed in Table 2 were attacked by all 3 cohabitants. There are 4 possible reasons that some of the species listed in Table 2 were attacked by only 1 or 2 of the cohabitants. First, few observations were made on some species (e.g.

Table 2. Attacks by cohabitant fishes on other fishes that feed on benthic algae

Species attacked	Diet <sup>a</sup>	Number of attacks by			
		<i>Acanthurus lineatus</i>	<i>Stegastes fasciolatus</i>	<i>Acanthurus leucosternon</i>	
Acanthuridae	<i>Acanthurus nigrofuscus</i>	mia	162	74	237
	<i>A. triostegus</i>	mia	798	36	578
	<i>A. nigricaudus</i>	mia,d	7	25	37
	<i>A. tennenti</i>	mia,d	2	8	66
	<i>Zebrasoma scopas</i>	mia	6	23	77
	<i>Z. veliferum</i>	mca,mia	11	43	84
	<i>Naso lituratus</i>	mca	75	7	4
	<i>N. unicornis</i>	mca	22	0	0
	<i>N. brevirostris</i>	mca,zp	18	5	0
Pomacentridae	<i>Glyphidodontops leucopomus</i>	mia,zp	17	37	0
	<i>Plectroglyphidodon dickii</i>	mia,cor	0	11	0
Scaridae	<i>Scarus sordidus</i>	mia,ba	323	25	446
	<i>S. cyanognathus</i>	mia,ba	52	6	153
	<i>S. psittacus</i>	mia,ba	166	7	41
	<i>S. niger</i>	mia,ba	3	0	8
	<i>S. scaber</i>	mia,ba	40	26	42
	<i>S. viridifucatus</i>	mia,ba	21	7	83
	<i>S. frenatus</i>	mia,ba	101	10	95
	<i>S. oviceps</i>	mia,ba	7	0	2
	<i>S. rubroviolaceus</i>	mia,ba	61	1	37
	<i>Hipposcarus harid</i>	mia,ba	28	1	1
	<i>Calotomus spinidens</i>	mia,sg	4	0	0
Balistidae	<i>Melichthys</i> sp.	mia,ba,zp	60	0	32

Sample size (No. fish/No. observation periods of  $\geq 10$  min): *A. lineatus* (232/459), *A. leucosternon* (145/360), *S. fasciolatus* (148/204), *A. nigrofuscus* (217/246), *A. triostegus* (36/72), *A. nigricaudus* (19/62), *A. tennenti* (35/64), *Z. scopas* (51/99), *Z. veliferum* (19/64), *N. lituratus* (57/144), *N. unicornis* (39/45), *N. brevirostris* (21/34), *G. leucopomus* (95/95), *P. dickii* (39/39), *S. sordidus* (59/80), *S. cyanognathus* (25/54), *S. psittacus* (20/40), *S. niger* (2/5), *S. scaber* (26/50), *S. frenatus* (24/47), *S. oviceps* (0/0), *S. viridifucatus* (23/50), *S. rubroviolaceus* (22/45), *H. harid* (20/40), *Calotomus spinidens* (1/3), *Melichthys* sp. (46/55). Observations on scarids were by R. Bruce

<sup>a</sup> mia = microalgae, mca = macroalgae, d = detritus, zp = zooplankton, cor = coral tissue, ba = boring algae, sg = seagrasses, Robertson *et al.*, 1979

*Scarus niger*, *S. oviceps* and *Calotomus spinidens*). Second, some species were restricted to part of the study area away from those parts occupied by a particular species of cohabitant: *Glyphidodontops leucopomus* occurred only in the intertidal portion of the study area (Fig. 1), and 43 of the 46 *Plectroglyphidodon dickii* present were in the *A. leucosternon* zone. *Zebrasoma scopas*, *A. nigricaudus* and *A. tennenti* were also restricted to the *A. leucosternon* zone, while *Naso unicornis* and *N. brevirostris* fed in areas away from the *A. leucosternon* zone (Robertson *et al.*, 1979). Third, the two *Acanthurus* cohabitants move further up in the water column to attack intruders than *S. fasciolatus* moves. As a result, fishes that often move about and feed in midwater, such as the balistid *Melichthys* sp., were more likely to be attacked by the wider ranging surgeonfishes than by the sedentary damselfish. Fourth, some species are actually tolerated in the feeding areas of one species but not in the areas of another. The damselfish *P. dickii* was tolerated by *A. leucosternon*, and both *S. fasciolatus* and *A. leucosternon* generally tolerated feeding by *N. lituratus* in their cohabited areas. *N. lituratus* was, however, excluded by *A. lineatus*. We have attributed this difference in responsiveness of the two *Acanthurus* species

to *N. lituratus* to differences in the degree to which the algae that each defends can be exploited by species, such as *N. lituratus*, that normally feed on macroalgae (Robertson *et al.*, 1979).

*Relative Levels of Defense Activity by Cohabitants.* The cohabitants were normally present in their feeding areas throughout the day. During such times the frequency of attacks on noncohabitant alivorous fishes by *Stegastes fasciolatus* was much lower than the frequency of attacks on them by either *Acanthurus lineatus* or *A. leucosternon* cohabitants (Table 3). Also, the mean frequency of attacks on non-cohabitants by *S. fasciolatus* living in *A. lineatus* territories was less than the mean frequency of such attacks by *S. fasciolatus* living in *A. leucosternon* territories (Student's *t*-test,  $P < 0.001$ ) (Table 3). As there was about one *S. fasciolatus* cohabitant per *Acanthurus* territory (see above), these attack frequencies indicate that the bulk of the defense of each unit area of cohabited substrate is provided by the surgeonfishes.

There were 2 situations in which the burden of defense of shared substrate fell entirely on *Stegastes fasciolatus*. First, both *Acanthurus lineatus* and *A. leucosternon* slept away from their feeding areas in deeper water,

Table 3. Interspecific territory defense activity by adults of cohabitant fishes

Cohabitant pair	No. of attacks per 10 min <sup>a</sup> that an individual cohabitant makes on other algivorous fishes <sup>b</sup>	Sample size	
		No. fish	No. observation periods of $\geq 10$ min
<i>Acanthurus lineatus</i>	1.5 $\pm$ 0.4 to 2.9 $\pm$ 0.4 <sup>c</sup>	150	277
<i>Stegastes fasciolatus</i>	0.4 $\pm$ 0.4	63	89
<i>Acanthurus leucosternon</i>	♂ 4.3 $\pm$ 1.0	78	78
	♀ 2.1 $\pm$ 0.8		
<i>Stegastes fasciolatus</i>	1.0 $\pm$ 0.3	50	78

<sup>a</sup>  $\bar{X} \pm 95\%$  C.I.

<sup>b</sup> Species are listed in Table 2

<sup>c</sup> Range is for fish living in the centers of *A. lineatus* colonies and fish living at the edges of colonies, respectively

leaving their areas at dusk and returning to them at dawn (Robertson *et al.*, 1979). *S. fasciolatus* did not migrate at night but slept in holes in the substrate in areas they shared with the two *Acanthurus* spp. Various algivorous scarids and surgeonfishes, such as *A. triostegus* and *A. nigrofuscus*, slept in and near the feeding areas of *A. lineatus* and *A. leucosternon* and attempted to feed in those areas during the few minutes of dusk when the *Acanthurus* territory owners were absent and the other surgeonfishes and parrotfishes were still active. At these times they were attacked and often driven off by the *S. fasciolatus*. Second, at 20-min intervals (on average) throughout the day many of the larger fishes, including *A. lineatus* and *A. leucosternon*, but not *S. fasciolatus*, stampeded out of the study area into deeper waters. These stampedes were in response to the movement of predatory fishes through the study area (Robertson *et al.*, 1979). The *A. lineatus* and *A. leucosternon* usually were absent from their feeding areas for about a minute during a stampede. Small individuals of other algivorous fishes, particularly *A. nigrofuscus*, *A. triostegus* and small parrotfishes, that had taken shelter in the study area during the stampede, emerged from that shelter and attempted to feed in the areas of *A. lineatus* and *A. leucosternon* while they were absent. They were attacked and often driven away by the cohabitant *S. fasciolatus* at such times.

#### Interspecific Competitive Interactions and Choice of Habitat by *S. fasciolatus*

There were 3 species of fishes that were abundant in parts of the study area outside those occupied by *Stegastes fasciolatus* which often fed on benthic algae and with which *S. fasciolatus* interacted aggressively. These 3 seemed most likely to be species that might be competitively excluding *S. fasciolatus* from certain habitat areas. They were the surgeonfish *Acanthurus nigrofuscus* and the damselfishes *Glyphidodontops leucopomus* and *Plectroglyphidodon dickii*. *A. lineatus*

and *A. leucosternon* were also intolerant of *A. nigrofuscus* in their feeding areas (Robertson *et al.*, 1979). *A. nigrofuscus* was the only surgeonfish that was mutually territorial with *S. fasciolatus*. *P. dickii* was the only other damselfish that defended permanent feeding areas on the substrate and, except for *G. leucopomus*, the remaining damselfishes either fed exclusively on benthic animal material (*Plectroglyphidodon imparipennis*) or mainly or exclusively on plankton (*Chromis margaritifer*, *Pomacentrus pulcherrimus*, *Abudefduf saxatilis*, *C. nigrurus*).

*Relations between A. nigrofuscus and S. fasciolatus.* Almost all of the *Acanthurus nigrofuscus* in the study area were juveniles (Robertson *et al.*, 1979), which were about the same size as *Stegastes fasciolatus* adults. These juvenile *A. nigrofuscus* were abundant in the *A. leucosternon* zone (Fig. 1). There was small-scale habitat segregation between these fish and the *S. fasciolatus* in that zone both inside and outside of the study area: 65% of 77 *S. fasciolatus* in that zone lived on mounds of rock while the remainder were on low areas of substrate; conversely, only 28% of 155 juvenile *A. nigrofuscus* were on high mounds, and the remainder were on low areas ( $X^2$ ,  $P < 0.001$ ).

Our experimental removal of juvenile *Acanthurus nigrofuscus* that had feeding areas contiguous with those of adult *Stegastes fasciolatus* resulted in their replacement by juvenile conspecifics rather than by *S. fasciolatus* (Table 4). Similar removals of *S. fasciolatus* adjacent to juvenile *A. nigrofuscus* led to the vacated feeding areas being filled by both *S. fasciolatus* and juvenile *A. nigrofuscus* (Table 4, Fisher's exact probability,  $P < 10^{-8}$ ).

*Relations Between G. leucopomus and S. fasciolatus.* *Glyphidodontops leucopomus* was very abundant in the intertidal portion of the study area (Fig. 1). There were some ecological and behavioral differences between these two species. First, many of the *G. leucopomus* fed in midwater on plankton (66% of 87 fish that were each observed for 10 min fed in this manner), which *Stegastes fasciolatus* were not seen to do. Second,

Table 4. Replacement of territorial fishes of 3 species that were experimentally removed

Site <sup>a</sup>	Removals		No. fish replacing fish that were removed, in (No.) replicates			
	Species removed	No. replicates	No. fish removed	Adult <i>Stegastes fasciolatus</i>	Juvenile <i>Acanthurus nigrofuscus</i>	Adult <i>Glyphidodontops leucopomus</i>
Under edge of <i>A. lineatus</i> Zone	<i>S. fasciolatus</i>	5	10	11 (4)	0 <sup>b</sup>	8 (3)
	<i>G. leucopomus</i>	4	15	0	0 <sup>b</sup>	4 (2)
Middle of <i>A. leucosternon</i> Zone	<i>S. fasciolatus</i>	7	23	21 (6)	6 (4)	0 <sup>b</sup>
	Juvenile <i>A. nigrofuscus</i>	9	26	0	25 (8)	0 <sup>b</sup>

<sup>a</sup> Zones are those occupied by each species in Fig. 1

<sup>b</sup> None of this species was living in the vicinity of the experimental sites

Note: Vacancies created by the removal of *G. leucopomus* and *A. nigrofuscus* were not invariably refilled, and within a replicate, vacancies created by the removal of *S. fasciolatus* often were filled by 2 species

*G. leucopomus* were more weakly territorial than *S. fasciolatus*. While the feeding areas of *S. fasciolatus* rarely overlapped (see above), adults of *G. leucopomus* typically shared their feeding areas with adult conspecifics: the mean number ( $\pm 95\%$  C.I.) of other adult conspecifics that fed in the feeding area of the average adult *G. leucopomus* was  $1.3 \pm 0.12$  ( $n = 87$ ). Third, the *S. fasciolatus* adults appeared to be aggressively dominant over the *G. leucopomus* as all the aggressive interactions that we saw between these 2 were attacks by *S. fasciolatus* on *G. leucopomus* (Table 2). Fourth, in areas where these 2 species co-occurred there was small-scale habitat segregation between them, with *S. fasciolatus* occupying higher substrate than that occupied by *G. leucopomus*: 40 of 41 *G. leucopomus* that were adjacent to *S. fasciolatus* territories were on substrate that was lower than that used by the *S. fasciolatus*; 47 of 56 *S. fasciolatus* that were living next to *G. leucopomus* were on substrate that was higher than that used by the latter.

We removed a series of *Stegastes fasciolatus* that were living adjacent to *Glyphidodontops leucopomus* and another series of *G. leucopomus* that were living adjacent to *S. fasciolatus*. The vacancies created by the removal of *S. fasciolatus* were filled by both species, while only *G. leucopomus* replaced conspecifics (Table 4, Fisher's exact probability,  $P = 0.0559$ ), and some of the *G. leucopomus* sites were still vacant 3 d after the removal of their original owners.

*Relations Between P. dickii and S. fasciolatus.* *Plectroglyphidodon dickii*, which was less abundant than *Stegastes fasciolatus*, was largely restricted to the *Acanthurus leucosternon* zone. Few aggressive interactions were observed between *P. dickii* and *S. fasciolatus* (Table 2), and all but one of them consisted of attacks by *S. fasciolatus* on the other species. Most (36 of 46) *P. dickii* in the study area were juveniles that were much smaller than, and easily routed by, adult *S. fasciolatus*.

There were some distinct ecological differences between these 2 species, as *Plectroglyphidodon dickii*

used a different habitat and different food to *Stegastes fasciolatus*. All of the *P. dickii* in the study area lived in association with live masses of arborescent *Acropora* spp. corals. Much of the feeding by the *P. dickii* was on the live *Acropora* in which they lived: a mean of 87% (SE = 98,  $n = 34$ ) of the bites that each *P. dickii* took during a 10-min observation period was on live coral. *S. fasciolatus* did not live in the matrices of arborescent *Acropora* corals or feed on living corals.

#### Food Partitioning Between the Space-Sharers

##### *Stomach Content Analyses*

*A. lineatus and Cohabitant S. fasciolatus.* Most of the material ingested by both species was benthic microalgae (Table 5). Most of the species of algae that were eaten by one species also were eaten by the other, and types of algae that were common in the stomachs of one species were common in the other. The most striking difference between the 2 species is that a quarter of the material that *Stegastes fasciolatus* had eaten was microcrustaceans, while those organisms were virtually absent from the stomach of *Acanthurus lineatus* (Table 5).

*A. leucosternon and Cohabitant S. fasciolatus.* Cohabitants of these 2 species had ingested mainly benthic microalgae (Table 5). However, unlike the situation with cohabitant *Acanthurus lineatus* and *Stegastes fasciolatus* (see above), there were often distinct differences in the amounts of a particular alga in the stomachs of *A. leucosternon* and *S. fasciolatus* (c.f. *Laurencia* sp., *Gelidiaceae* sp., *Champia* sp., *Ceramium* sp. a, and diatoms in Table 5). As with the other set of cohabitants, the greatest difference between *A. leucosternon* and their cohabitant *S. fasciolatus* was in the abundance of microcrustaceans in the stomachs of the latter species and their absence in the stomachs of the former species (Table 5).

Table 5. Stomach contents of cohabitant surgeonfishes and damselfish

Food item	Percentage of stomach contents represented by each food item <sup>a</sup>					
	Cohabitant pair		Cohabitant pair			
	<i>Acanthurus lineatus</i>	<i>Stegastes fasciolatus</i>	<i>Acanthurus leucosternon</i>	<i>Stegastes fasciolatus</i>		
<b>Benthic</b>						
<b>Microalgae</b>	<b>Growth form<sup>b</sup></b>					
Red:	<i>Polysiphonia</i> sp.a	Fi	17.1	12.1	19.0	21.0
	<i>Laurencia</i> sp.	F1	13.1	10.7	18.2	5.3
	Unidentified sp.a	F1	12.7	11.0	2.7	3.3
	" sp.b*	F1	8.7	7.8	0.9	0
	" sp.c	Fi	0	7.4	0.1	0
	<i>Gelidiaceae</i> sp.	F1	6.3	0.2	13.5	0.7
	<i>Champia</i> sp.	Fi	10.3	1.4	11.8	3.1
	<i>Centrocerus</i> sp.	Fi	5.5	0	7.2	0
	<i>Ceramium</i> sp.a	Fi	6.0	6.8	3.5	18.4
	Unidentified sp.d	Fi	1.1	0.1	1.0	0
	<i>Polysiphonia</i> sp.b	Fi	0	0	2.2	1.4
	<i>Polysiphonia</i> sp.c	Fi	1.1	0	0.3	0
	<i>Ceramium</i> sp.b	Fi	1.8	1.8	0.9	0.8
	<i>Jania</i> spp.	C	0.4	0	2.8	0.4
	<i>Ceramium</i> sp.c	Fi	0	0	1.0	0
Bluegreen:	<i>Lyngbia</i> sp.	Fi	11.4	6.4	11.8	2.6
Green:	<i>Cladophora</i> sp.	Fi	3.1	0.4	2.0	0.8
	<i>Enteromorpha</i> sp.	F1	0	2.4	0	0
Diatoms:	Unidentified sp.a	Col.	0	3.7	0	0
	Unidentified spp.		0.3	0.9	0.3	11.6
Microcrustaceans	Copepods		0.1	25.4	0	30.0
No. of fish examined			15	15	15	11

<sup>a</sup> Results for all individuals of each species were combined. Only items that represent  $\geq 1\%$  of stomach contents of at least one species are included here

<sup>b</sup> Fil - filamentous; F1 - fleshy; c - upright coralline; Co = colonial

\* Unidentified red alga sp. b = *Colpomenia sinuosa* (a brown alga)

Table 6. Feeding microhabitats of pairs of cohabitant fishes

Cohabitant species pair	Mean proportion of bites taken from each microhabitat <sup>a</sup>								
	Low areas of substrate <sup>b</sup>				High areas of substrate <sup>b</sup>				
	R	HR	VR	SD	HR	VR	SD	DD	O
<i>Acanthurus lineatus</i> <i>n</i> = 21 fish, 31 observation periods	0	0.34	0.29	0.02	0.14	0.17	0.01	0	0
				**					
<i>Stegastes fasciolatus</i> <i>n</i> = 44 fish, 44 observation periods	0	0.29	0.28	0	0.17	0.24	0.01	0	0
<i>Acanthurus leucosternon</i> <i>n</i> = 68 fish, 77 observation periods	0.01	0.16	0.30	0.02	0.13	0.32	0.02	0.01	0.01
		**	**	*			**	**	**
<i>Stegastes fasciolatus</i> <i>n</i> = 16 fish, 40 observation periods	0.01	0.30	0.19	0.01	0.19	0.27	0.02	0	0

Mann-Whitney U Test: \*\* =  $P < 0.01$ , \* =  $P < 0.05$

<sup>a</sup> The mean feeding rates of both *A. lineatus* and *A. leucosternon* were over 200 bites  $10 \text{ min}^{-1}$  (Robertson *et al.*, 1979); *S. fasciolatus* fed at a rate of  $115 \pm 6$  bites  $10 \text{ min}^{-1}$  ( $\bar{x} \pm 95\%$  C.I., *n* = 93 fish, 137 observation periods)

<sup>b</sup> R = rubble and sand, HR = flat horizontal rock, VR = flat vertical rock, SD = shallow depressions, DD = deep depressions, O = under overhangs

### Feeding Microhabitats

*A. lineatus* and Cohabitant *S. fasciolatus*. There was almost no tendency for these 2 cohabitants to segregate their feeding in different microhabitats. The only microhabitat that one species consistently used more than the other species was rarely used by either (Table 6).

*A. leucosternon* and Cohabitant *S. fasciolatus*. One of these species made greater use than the other species of 5 of the 9 microhabitats (Table 6). However, 3 of these 5 were only rarely used by either species and the other 2 were commonly used by both.

### Discussion

Our data show that *Stegastes fasciolatus* is concentrated in the feeding areas of *Acanthurus lineatus* and, to a lesser extent, *A. leucosternon*. We suggest that this distribution is the result of *S. fasciolatus* preferring those areas. Reciprocal removal experiments were performed with the 2 species of fishes that seemed most likely to be its competitors for control of feeding substrates. Because *S. fasciolatus* were replaced by both conspecifics and the "competitors," and the "competitors" were not replaced by *S. fasciolatus*, it is more likely that *S. fasciolatus* excluded those species than vice versa. Further, it seems unlikely that predators excluded *S. fasciolatus* from other parts of the study area because those parts were occupied by the feeding areas of similar sized damselfishes and small surgeonfishes e.g. *Glyphidodontops leucopomus*, *Plectroglyphidodon dickii*, and juvenile *A. nigrofuscus*.

All 3 species of cohabitants defend their feeding areas against algivorous fishes, and we have shown (Robertson *et al.*, 1979) that the 2 *Acanthurus* species hinder feeding by such fishes in their feeding areas. Food is probably a limiting resource for which all three species of cohabitants compete both intraspecifically and with other fishes (Robertson *et al.*, 1979). Data on the frequencies of attacks on other fishes by each cohabitant indicate that most of the defense of shared feeding areas is by the surgeonfishes. Robertson (unpublished data) has found feeding area and food sharing by cohabitant algivorous fishes in the Caribbean, and experimentally demonstrated that differences in the frequencies of attacks on other species by each cohabitant species do reflect their relative contributions to the defense of shared substrate. We suggest that they also do so in the system we have described here, although experimental verification is required.

It seems then that either *Stegastes fasciolatus* is a food parasite that relies on its *Acanthurus* cohabitants to defend (i.e., provide) the food that it and they use, or that the relationship benefits *S. fasciolatus* and has no net effect on the *Acanthurus* spp. *S. fasciolatus* is concentrated in the feeding areas of *A. lineatus* rather than *A. leucosternon*, probably in part because it has to contribute less to the defense of shared resources in *A. lineatus* territories than in *A. leucosternon* territories.

*A. lineatus* is the larger of the 2 *Acanthurus* spp. and appears to dominate *A. leucosternon* aggressively. *A. lineatus* attacks intruders at greater distances outside its feeding areas than does *A. leucosternon* and experiences less feeding by noncohabitant intruders in its territories than does *A. leucosternon* (Robertson *et al.*, 1979). The small size of the damselfish would enable it to take shelter in holes in the substrate where it was inaccessible to an attacking *Acanthurus* sp. cohabitant. As a result it would be costly, in time and energy, for the *Acanthurus* spp. to exclude a small, parasitic damselfish from their feeding areas. The low frequency of attacks on the damselfish by its cohabitants could merely reflect the futility of such attacks rather than indicate the existence of a relationship other than a parasitic one. In any case, the net cost to an *A. lineatus* or *A. leucosternon* of maintaining a damselfish cohabitant is probably quite low. First, because the biomass density of the damselfish is less than 10% of that of either surgeonfish, the drain on resources by the damselfish is relatively low. Second, the damselfish is ingesting appreciable amounts of a food that the surgeonfishes are not using. This represents an additional reduction in its potential drain on shared food items. Third, *S. fasciolatus* does make some contribution to the defense of the shared food, particularly when the surgeonfishes are absent from their feeding areas. Thus, the net cost to an *Acanthurus* sp. territory owner of a damselfish cohabitant may approach zero, or at least is low enough to make it more costly to exclude the damselfish than to tolerate it. Based on the available information, we conclude that the symbiotic relationship benefits *S. fasciolatus* and costs the surgeonfishes little or nothing. Long-term experiments involving the removal of each of the cohabitant species could resolve the questions of net costs and benefits to each species.

The situation that we have described above very probably is not unique to Aldabra. One of us (D. R. Robertson) has observed sharing of feeding areas by *Acanthurus lineatus* and *Stegastes fasciolatus* at several sites in the Pacific Ocean, and territory-sharing by other Pacific species of surgeonfishes and damselfishes of disparate sizes (Table 7). It is possible that some of these relationships are similar to that described here, although we do not expect all of them to be. Robertson (unpublished data) has investigated in detail a cohabitation relationship between 2 dissimilarly sized Caribbean damselfishes. He concluded that the large species' size advantage enabled it to dominate aggressively the small species and force it to share the food that the small species defends against other species of fishes. In these cohabitation relationships, size differences between species seem to be of critical importance. They may allow a small species to parasitize a large one because the large one cannot exclude it; they may also enable a large species to dominate and parasitize a small one.

To understand how a symbiosis is maintained at a particular cost/benefit state to each species, the mechanism(s) by which the population densities of each species are regulated must be determined. Increasing

**Table 7.** Pairs of species of territorial fishes that feed on benthic algae and that cohabit feeding areas at several sites in the Pacific Ocean and Caribbean Sea

Site	Cohabitant species pair	
	Large species <sup>a</sup>	Small species <sup>b</sup>
<b>Pacific</b>		
Heron Island (Great Barrier Reef, Australia)	<i>Acanthurus lineatus</i>	<i>Stegastes fasciolatus</i> , <i>S. apicalis</i> , <i>S. gascoynei</i> , <i>Plectroglyphidodon</i> <i>leucozona</i> , <i>Pomacentrus wardi</i>
Secas Islands (Panama)	<i>Acanthurus glaucopariens</i>	<i>Stegastes acapulcoensis</i>
Hawaii	<i>Acanthurus achilles</i>	<i>Stegastes fasciolatus</i>
Palau (Western Caroline Islands)	<i>Acanthurus lineatus</i>	<i>Stegastes fasciolatus</i>
	<i>Acanthurus glaucopariens</i>	<i>Stegastes fasciolatus</i>
<b>Caribbean</b>		
San Blas Islands (Panama)	<i>Microspathodon chrysurus</i>	<i>Stegastes dorsopunicans</i> , <i>S. planifrons</i> , <i>S. diencaeus</i>

<sup>a</sup> *Acanthurus* spp are Acanthuridae, *M. chrysurus* is Pomacentridae

<sup>b</sup> All Pomacentridae

population density of a parasite could increase the cost to an individual host to the point where it is cheaper for that host to relocate its territory, if suitable space that is unoccupied by other hosts and parasites is available. If the cost of such a relocation is low, the parasite might be expected to maintain its density at a low level by regulating its territory size. Alternatively, as the parasite's density increases the relationship might become more mutualistic or eventually the host/parasite roles might reverse.

These studies show that interspecific relations between fishes that compete for limiting resources on coral reefs can be far more complex than has been previously realized. Such cohabitation, either parasitic or mutualistic, represents a mechanism by which the coexistence of some of the numerous species of coral reef fishes can be achieved.

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