

The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebrasoma scopas*): their feeding strategies, and social and mating systems

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Keywords:

Coral reefs, Coexistence, Algae cropping, Behavior, Territoriality, Zonation, Fish morphology, Reproduction

Synopsis

The relationship between the morphology, feeding strategies and social and mating systems of three surgeonfishes was investigated. Adults of each defend feeding territories, intra- and interspecifically. The largest species, because of its morphological limitation, relies on food that has to be defended against many other species. It forms large colonies in which fishes singly defend small territories containing high standing crop algal mats. Colony formation is a mechanism by which the efficiency and effectiveness of interspecific territory defense is increased. The smallest species, because of its morphological adaptations, is able to rely most on food that other species cannot efficiently exploit. It forms pairs that defend large territories containing a thin algal mat. It is restricted to the poorest quality habitat by the aggressive activities of more dominant species. The third species, which also forms pairs, has an intermediate feeding strategy. The local coexistence of these three and other surgeonfishes results from a combination of (i) their partitioning both habitat and food resources, and (ii) the populations of two of the most dominant species apparently being below the carrying capacity. Territoriality and the absence of parental care facilitates pair formation in surgeonfishes. Permanently territorial species usually form pairs. The colonial species does not form pairs because the colonial habit facilitates interference of males in each other's spawnings.

1. Introduction

Surprisingly little work has been undertaken on the behavioral ecology of the surgeonfishes (Acanthuridae). In contrast, much attention has been directed at

the two other major, pantropical groups of coral reef fishes that eat benthic algae, the damselfishes (Pomacentridae) and the parrotfishes (Scaridae). The efforts of Randall (1961a) and Jones (1968) remain the most comprehensive on surgeonfish ecology to date. More recent information has tended to be conjectural (Nursall 1974, Vine 1974, Barlow 1974a, b). Barlow (1974a), in preliminary explorations of the ecological significance of the social systems of some acanthurids, regards the structure of a species' social and mating systems as being ultimately a consequence of its feeding ecology. Little is known of the reproductive behavior and structure of mating systems of surgeonfishes (Randall 1961b).

At Aldabra Atoll, in the Indian Ocean, surgeonfishes are very abundant. We decided to examine the behavioral ecology of a number of them with a view to gaining insight into (1) what the determinants, ecological and otherwise, of their patterns of social organization might be, and (2) by what mechanisms their coexistence was achieved. Although comprehensive data were collected on 13 species of surgeonfishes found in the study area, this paper deals in detail with only three of those species, that have strongly differentiated morphologies, feeding ecologies and social and mating systems — *Acanthurus lineatus*, *A. leucosternon* and *Zebrasoma scopas*. These three were chosen because they were the only species present in the study area whose adults defended permanent feeding territories containing turfs of the microalgae on which they fed. We present data on their gross morphology, spatial distribution patterns (on different scales), feeding behavior and diets, social systems

Received 8.6.1978 Accepted 16.10.1978

Table 1. Summary of comparisons between three surgeonfishes.

	<i>A. lineatus</i>	<i>A. leucosternon</i>	<i>Z. scopas</i>
Morphology			
Size	Largest	Intermediate	Smallest
Body shape	Elongate	Oval	Rounded
Fin shapes	Small fins, lunate tail	Intermediate	Large fins, truncate tail
Caudal knife	Largest	Intermediate	Smallest
Color	Changeable	Poster	Cryptic
Mouth	Flat, wide, no rostrum	Intermediate	Rounded, long rostrum
Zonation	Shallow subtidal	Below <i>A. lin.</i>	With <i>A. leuc.</i>
Territory substrate	Flat rock	High mounds	Low rubbly areas
Diet	Filiform and fleshy algae	Filiform algae	Filiform algae
Algal mat	Thick	Moderate	Thin
Feeding microhabitats	Narrow range	Intermediate	Broad range
Feeding rate	Low	Intermediate	High
Colonial	Yes	No	No
Sexual dimorphism	Nil?	Male < Female	Male > Female
Social unit	Single fish	Pair	Male + 1 - 2 Females
Spawning pattern	Group?	Pair?	Pair
Territory size	Small	Medium	Large
Social unit biomass density	High	Moderate	Low
Aggressiveness	High	Moderate	Low
Non-owner feeding in territory	Very little	Intermediate	Much
Range of fishes excluded from territory	Broad	Moderate	Narrow

(the nature of their territoriality), and mating systems. These data are summarised in Table 1.

2. Materials and methods

The study was conducted at Aldabra Atoll (9°25'S, 46°22'E) from July 1975 through January 1976.

2.1 The study area

The main study area was located on the outer edge of the reef flat directly in front of the Research Station (Fig. 1). The particular site used was chosen for convenience and because acanthurids of a variety of species were numerous. All of the species present were commonly encountered elsewhere within a couple of kilometers either side of our site. We feel it was reasonably typical of much of the western face of the atoll near the research station. The study area consisted of a 25 m wide vertical transect, running across 25 m of intertidal reef flat and 65 m of subtidal reef slope. The bottom end of this transect had a low tide depth of about 7 m. The tidal range was up to several meters. The reef crest portion consisted of a flat rock pavement containing very few large crevices and holes. The main part of the reef slope portion, which

as a whole contained little live coral, consisted of two series of eroded groove-and-spur coralline rock formations rising 1–2 m above flatter rock and shingle areas. At its deep end the transect ran into a sandy trough. As is shown in Figure 2, the shallowest part of the subtidal in the study area was flatter than the deepest parts.

2.1.1 Acanthurids present in the study area

The following species of acanthurids were encountered in the main study area:

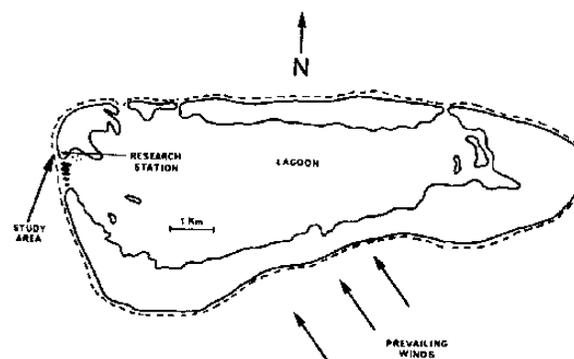


Fig. 1. Site of the study area at Aldabra Atoll.

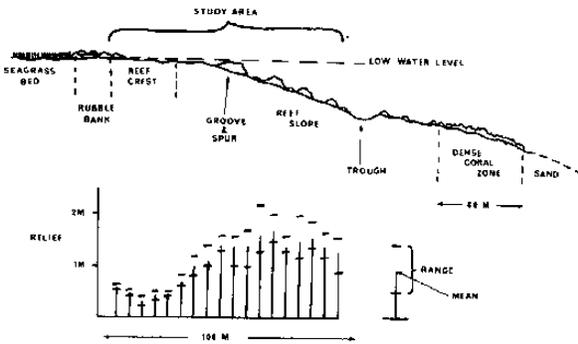


Fig. 2. Substrate types and relief along the transect of the main study area: relief = difference in height (measured by a line weighted at one end and floated at the other) between the lowest and highest points in each 5 x 5 m square of the study area; mean and range are for each series of 5 of these squares across the 90 x 25 m transect.

<i>Acanthurus lineatus</i>	(Linnaeus)
<i>A. leucosternon</i>	Bennett
<i>A. triostegus</i>	(Linnaeus)
<i>A. nigrofuscus</i>	(Forsk.)
<i>A. gahhm</i>	(Forsk.)
<i>A. dussumieri</i>	Cuvier & Valenciennes
<i>A. tennenti</i>	Günther
<i>Zebrasoma scopas</i>	(Cuvier)
<i>A. veliferum</i>	(Bloch)
<i>Naso lituratus</i>	(Bloch & Schneider)
<i>N. unicornis</i>	(Forsk.)
<i>N. brevirostris</i>	(Valenciennes)
<i>Ctenochaetus striatus</i>	(Quoy & Gaimard)
<i>C. strigosus</i>	(Bennett)

[These identifications and names are after Randall 1955a, b, c, 1956).]

2.1.2 Factors determining the availability of food and shelter in the study area

The face of the atoll on which the study area was located, although relatively protected from the prevailing winds, was intermittently subjected to short bouts of heavy wave action that resulted in readily noticeable, and often very pronounced, substrate abrasion. In one such instance we estimate crudely that substrate in about a third of the study area had been heavily eroded. Examination of local meteorological station records, which extend back to 1968, indicates (conservatively) that during that eight-year period, the study area experienced an average of five

such heavy weather episodes per year, each lasting up to a week. We suggest that such periodic substrate disturbances have been instrumental in severely reducing coral coverage in the study area and regularly providing clean rock surfaces suitable for algal growth; and thus that such disturbances have ultimately been responsible for the large population of surgeonfishes.

Several observations showed quite clearly that the shallower parts of the study area did not provide suitable shelter for larger fishes, either against predators or for sleeping sites. Firstly, when large predatory fishes, such as carangids, moved through the reef crest and upper reef slope areas, fishes of many species, including *A. lineatus*, *A. leucosternon* and *Z. scopas*, regularly rushed, en masse, out of that area into deeper water. There coral cover was much greater and shelter presumably more available. These stampedes occurred quite frequently: mean = 2.8 ± 0.7 stampedes per hour (95% confidence interval), $n = 24$ observation periods totalling 68 hours. After a stampede these fishes usually returned to their territories within several minutes, although occasionally they stayed away from them for up to half an hour. Secondly, many of the adult acanthurids present did not sleep in the study area but moved off into deeper areas. These included *A. lineatus* and *A. leucosternon*. None of the 29 different individuals of the former species and 48 of the latter that we chose at random and observed for one crepuscular period each, slept in the territories they used during the day. Less intensive observations on *Z. scopas* showed that at least some individuals resident in the study area also spent the night outside the study area.

2.2 Techniques

Almost all of our observations were made within three hours of high tide. A few low-tide dives were made on the subtidal portion of the study area to check that social organization patterns observed at high tide were not breaking down at low tide. Snorkelling, rather than SCUBA, was used almost exclusively.

A map of the transect study area was made by laying out lines in a 5 x 5 m grid and drawing details of these squares on a 2.5 x 2.5 cm scale on a sheet of roughened white plexiglass. Larger scale maps were made of some sections of this and other smaller study areas. Data were recorded using wax and carbon pencils on sheets of transparent plastic film laid over

these maps. This main study area was used for obtaining counts of numbers of fishes of various species and for mapping some territories.

Small fishes were collected using a small Hawaiian-sling-type speargun, and larger specimens with a small conventional speargun. For stomach content analyses fishes were killed immediately after collection, and taken to the laboratory for dissection within an hour of being shot. Their stomach contents were preserved in 5% neutral buffered formalin in seawater.

Unfortunately, the only practicable method available at the time for catching specimens for tagging was by spearing them. For this a 3 mm diameter, unbarbed, stainless steel shaft was used in a simplified Hawaiian-sling. After being approached to within about one meter, the specimen would be shot through its dorsal musculature and immediately grasped. Surgeonfishes have tough skin and the wound caused by such a spear normally covered much less than 5 cm². While being held underwater the fish would be tagged and released as rapidly as possible. For tagging, small plastic clothing tags were injected subcutaneously with a special 'gun' (Tack-it, Morris Co., London). Each tag was anchored below the skin and a small piece of nylon line protruded externally. Approximately normal behavior of these fish resumed within a few hours of their being handled in this manner, although the fish no longer permitted

close approaches by a diver. These spear wounds almost invariably healed quickly, with no marked external scarring.

Five *A. lineatus*, nine *A. leucosternon* and six *Z. scopas* were tagged in this manner. Other members of the former two species could also be recognized individually by apparently permanent differences in their color patterns.

3. The general composition of the Aldabran benthic algivore assemblage

The three major families of benthic-algae eating fishes present in our study area were the surgeonfishes, parrotfishes and damselfishes. Blennies (Blenniidae) were small and not very common. Rabbitfishes (Siganidae) only rarely entered the study area.

As Table 2 shows, this Aldabran assemblage was dominated by surgeonfishes, in terms of numbers of species, numbers of individuals, and biomass of fishes. Surgeonfishes were also at the top of the interspecific aggressive dominance hierarchy. The parrotfishes were the next most strongly represented group in terms of numbers of species, abundance of individuals, and total biomass. Damselfishes that fed on benthic algae were not abundant. In fact only two of the five species that did feed on such algae seemed to be strongly

Table 2. Abundance and standing crops of fishes of three families that consumed benthic algae in the main study area in August 1975.

Family	Number of species present	Number of species consuming benthic algae	Approximate number of individuals per hectare	Approximate kg fish per hectare ¹
Acanthuridae	14	12 ²	4400 ³	402 ³
Scaridae	10 ⁴	10	1170	276
Pomacentridae	8 ⁵	5 ⁶	2970	19
(Exclusively benthic feeding species)		(2 ⁷)	(640)	(8)
Total All fishes	32	27	8560	697
Exclusively benthic feeding species		24	6230	686

¹. Standing crop of each species = number of individuals counted in study area x mean weight of speared specimens. Data on scarid weights from Robin Bruce.

². Not including two roving species: *N. unicornis* and *N. brevirostris*.

³. Includes 100 schooling *A. triostegus*.

⁴. For species list see Table 10.

⁵. *Stegastes fasciolatus**, *Plectroglyphidodon dickii****, *Glyphidodon leucopomus***, *Chromis margaritifer***, *Pomacentrus pulcherrimus*, *Abudefduf saxatilis***, *Plectroglyphidodon imparipennis***, *Chromis nigrurus*. Identifications: *G. R. Allen pers. comm. 1978, **after Allen 1975, remainder after Smith 1960.

⁶. First five species on list 5 above.

⁷. First two species on list 5 above.

Table 3. Abundance and standing crops of the main fishes eating benthic algae on two Caribbean reefs (data from Randall 1963).

Family	Number of species	Number of species eating benthic algae	Approximate number of individuals per hectare	Approximate kg fish per hectare
Acanthuridae	2	2		
Reef 1			1060	50
Reef 2			1580	64
Scaridae	8	8		
Reef 1			670	280
Reef 2			1210	390
Pomacentridae	9	7 ¹		
Reef 1			2630 ²	98 ²
Reef 2			4920 ²	133 ²
Blenniidae	3	3		
Reef 1			2130	14
Reef 2			10200	36
Total				
Reef 1	22	20	6490	442
Reef 2			17910	623

¹ Did not include *Abudefduf saxatilis* and *Chromis multilineata* (see Emery 1973 for diets).

² Represents virtually only the 7 benthic algivores.

reliant on benthic food. The remaining three ingested large amounts of zoo- and phytoplankton.

Very few comprehensive data are available on the composition of assemblages of benthic-algae eating fishes on coral reefs in other areas. Randall's (1963) study of two Caribbean reefs provides the only detailed information we can locate. We have summarized his pertinent data in Table 3. Our estimate of 697 kg hectare⁻¹ total standing crop of algivores is about the same as his (442–623 kg hectare⁻¹). Few other estimates of standing crops of such fishes on coral reefs are available. Goldman & Talbot (1976) obtained 370 kg hectare⁻¹ on the leeward reef slope of a western Pacific reef (a reef slope which corresponds roughly to our study area). Bardach's (1959) estimate of 140 kg hectare⁻¹ on a Caribbean reef is much lower. Our estimate is thus on the high end of the scale.

In Randall's (1963) areas the algivore assemblage differed radically in composition from the assemblage in our area. Among the three main families, parrotfishes dominated Randall's sites in terms of biomass, parrotfishes and damselfishes dominated in numbers of species, and damselfishes in numbers of individuals. Of these three groups the surgeonfishes had the

lowest standing crop, and the fewest species. Large numbers of blennies were present, but, as these were small fishes, they did not contribute much to the total standing crop. Further, in the Caribbean sites, damselfishes reliant on benthic food, rather than a mixture of such food and plankton, were important contributors in numbers of species, numbers of individuals and biomass to the totals for both the damselfish assemblage and the entire assemblage. A variety of studies have shown that, in the Caribbean, territorial damselfishes are much more important than surgeonfishes as controllers of substrate, the reverse of our Aldabran situation (e.g. Myrberg 1972, Brockman 1973, Thresher 1976a, b, 1977, Robertson et al. 1976, Ebersole 1977, Brawley & Adey 1977).

4. Morphology of the three species

4.1 Absolute sizes

A. lineatus was the largest of the three species, reaching at least 289 g, while the heaviest *A. leucosternon* we collected was 207 g. *Z. scopas* was much smaller, the largest fish obtained weighing only 78 g.

4.2 Sexual dimorphism

Although males and females of *A. lineatus* apparently grew to the same size, males of *A. leucosternon* were much smaller than the females. On the other hand, males of *Z. scopas* were distinctly larger than the females (Table 4).

4.3 Body and fin shapes

The three species are quite different in the shapes of their bodies and fins, with *A. lineatus* and *Z. scopas* representing the extremes (Fig. 3). *A. lineatus* has the most elongate body with the largest, most lunate tail and the largest, widest mouth, situated low in a rounded face. *Z. scopas* has the most rounded body, with large sail-like dorsal and anal fins, and a small truncate tail. Its small mouth, which is the most semi-circular in shape of the three, is at the end of a long rostrum, situated more centrally in the face. *A. leucosternon* is intermediate in each respect.

4.4 Coloration

The three differ radically in their color patterns. *Z. scopas* is a dull black fish. *A. leucosternon*, with its powder blue body, black and white face, and bright yellow and white fins is very strikingly colored, in a pattern that is extremely conspicuous at all distances. *A. lineatus*' body pattern consists of a series of fine blue and black stripes on a yellow background with an orange belly and pelvic fins. While to a human observer this pattern is conspicuous and striking at close proximity, it is cryptic at more than a few meters.

A. lineatus has the greatest facility for color change of the three species. While both of the others maintained essentially the same color pattern at all times, *A. lineatus* was able rapidly, and often radically, to alter its coloration in a variety of ways. For example, when attacking other species of fishes, and especially feeding schools of *Acanthurus triostegus*, its normal color pattern often changed to one in which the body was pale and the head dark. This

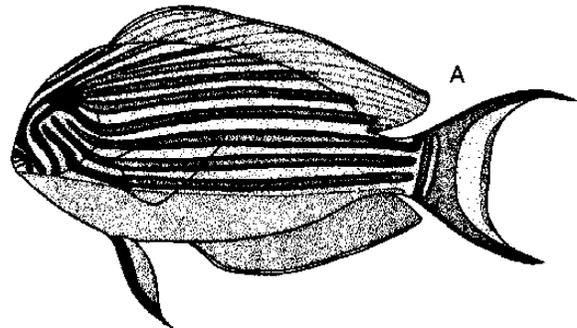
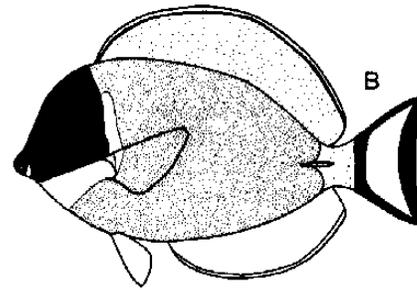
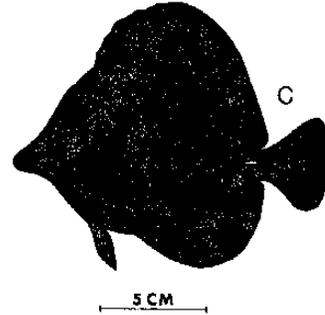


Table 4. Sizes of large of three surgeonfish species.

Species	Males		Females	
	Standard length (mm)	Mass (g)	Standard length (mm)	Mass (g)
<i>Acanthurus lineatus</i>	171 ± 8* n = 11	222 ± 28	168 ± 5 n = 12	206 ± 19
<i>Acanthurus leucosternon</i>	120 ± 2 n = 20	81 ± 4	153 ± 2 n = 21	177 ± 7
<i>Zebbrasoma scopas</i>	114 ± 3 n = 12	65 ± 2	102 ± 3 n = 12	49 ± 4

* Mean with 95% confidence limits.

Fig. 3. The three surgeonfishes: A = *A. lineatus*, B = *A. leucosternon*, C = *Z. scopas*. Maximum sizes of collected specimens.

pattern is similar in form to the permanent pattern that *A. leucosternon* bears.

4.5 Caudal spines

Of the three species, the adults of *A. lineatus* have the largest caudal spines and *Z. scopas* the smallest: the length of those of five *A. lineatus* varied from 10.6–12.7% of the fish's standard length, of 11 *A. leucosternon* from 7.8–10.4% and of 37 *Z. scopas* from 4.9–8.3%. Also, while the caudal spines of the two *Acanthurus* species were sharp and blade-like those of *Z. scopas* were small and thorn like.

5. Distribution in space

5.1 Vertical zonation patterns

5.1.1 Adults

Adult *A. lineatus* were found only in the shallowest, 25 m wide band of the subtidal reef slope, while *A. leucosternon* and *Z. scopas* were restricted to the area below the *A. lineatus* zone (Fig. 4). Relatively very few other algal feeding fishes were observed living in the *A. lineatus* zone, the exception being the damselfish *Stegastes fasciolatus*, which was concentrated here (Fig. 4). Outside the main study area the ranges of both *A. leucosternon* and *Z. scopas* did extend up to the edge of the reef crest. There was one distinct difference in the vertical distributions of *A. leucosternon* and *Z. scopas*. No adult *A. leucosternon* were

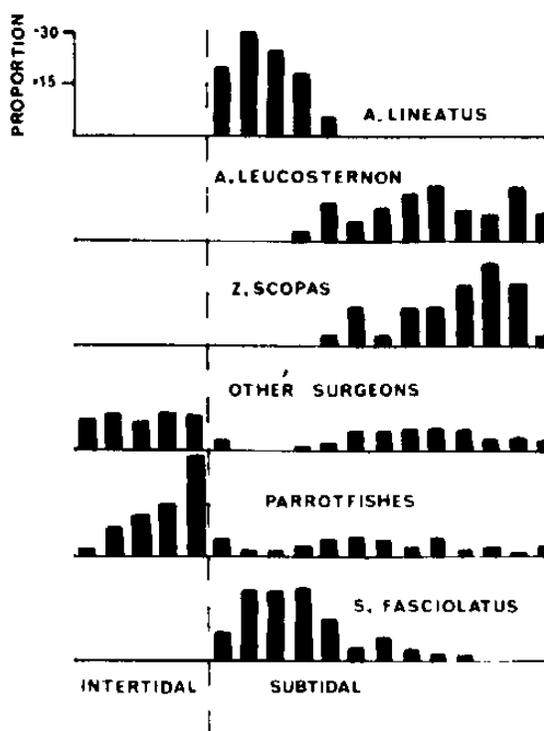


Fig. 4. Vertical zonation of resident algivorous fishes in the main study area: proportion = proportion of the total number of fishes counted in the study area that were present in each 5 x 25 m segment of the study area transect; sample sizes = 79 adult *A. lineatus*, 77 adult *A. leucosternon*, 38 *Z. scopas*; other surgeons = 174 *A. triostegus*, 167 *A. nigrofuscus*, 4 *Z. veliferum*, 8 *N. lituratus*, parrotfishes = 266 of 10 species listed in Table 10, 99 *Stegastes fasciolatus* (Pomacentridae). Counts were made at high tide.

Table 5. Distribution of *A. leucosternon* and *Z. scopas* along a 10 meter wide vertical transect running through the main study area.

Segment no.	Number of fish per 10 m segment of transect																	
	Intertidal section									Subtidal section								
	Main study area ¹									Outside main study area								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>A. leucosternon</i>																		
Adults	—	—	—	0.8	4.4	5.6	6.8	8.4	6.4	4	4	1	1	—	—	—	—	
Juveniles	—	—	—	—	—	—	0.4	—	0.4	—	1	3	1	—	—	—	1.6	
<i>Z. scopas</i>																		
Adults	—	—	—	—	—	1.6	2	5.6	2.8	3	3	2	5	3	7	4	3	1.8
Juveniles	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	2.5

¹. Numbers of fishes in main study area segments calculated from numbers present in 25 m wide segments.

found beyond the zone of scattered coral growths that ended about 40 m beyond the bottom of the study area. *Z. scopas* adults, however, were found throughout that zone and another of dense coral growths, that ran into bare sand about 90 m out beyond the bottom edge of the study area. Both the data presented in Table 5 and the results of a survey along two 200 m long strips of substrate deeper than the study area show that: in one strip, up to 25 m out beyond the bottom of the main study area, 72 adult *A. leucosternon* and 47 adult *Z. scopas* were counted. In the second strip, 25–100 m out from the bottom of the study area 68 adult *Z. scopas* were noted, but no adult *A. leucosternon*.

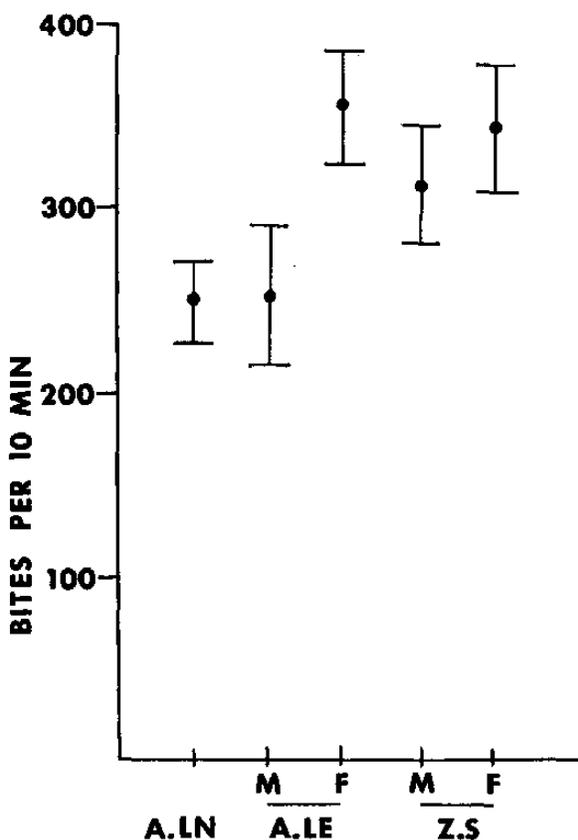


Fig. 5. Feeding rates of adults of three surgeonfishes. Mean (with 95% confidence limits) number of bites on substrate per 10 mins. A.ln = *A. lineatus* (n = 79, sex not determined); A.le = *A. leucosternon*, M = males (n = 51), F = females (n = 72); Z.s = *Z. scopas*, M = males (n = 50), F = females (n = 41). Sex of *A. leucosternon* and *Z. scopas* determined by the size of the fish being observed relative to that of its mate.

5.1.2 Juveniles

While juvenile *A. lineatus* were found only in shallow water (Fig. 6) those of *A. leucosternon* and *Z. scopas* were mainly restricted to coral-rich areas deeper than the study area. The data in Table 5 show this, as do

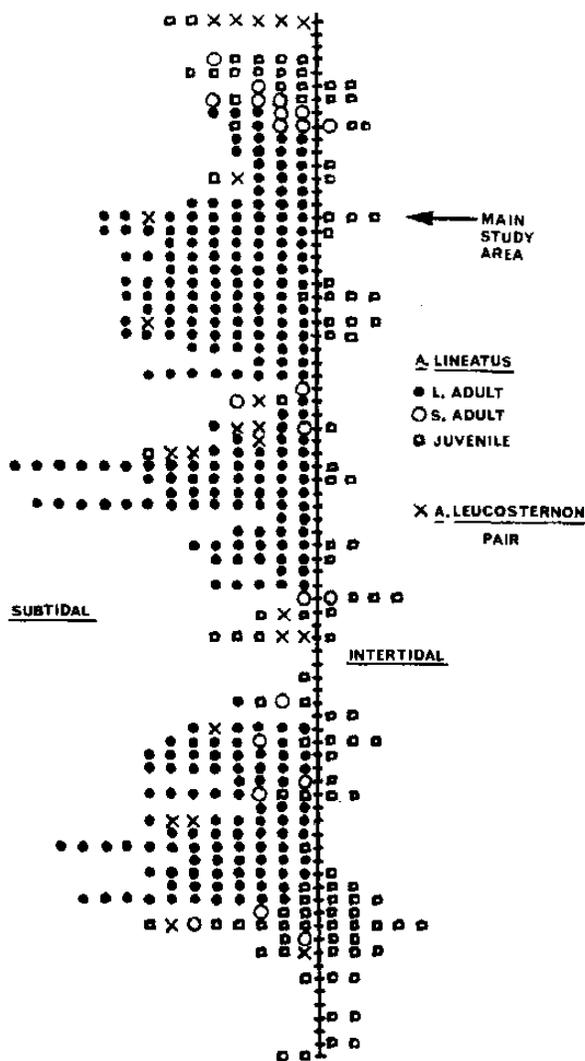


Fig. 6. Colony formation by *A. lineatus*: The identity of territorial surgeonfishes encountered along transect swims made at 5 m intervals along 400 m of reef edge is shown. *A. lineatus* L. adult = adult > 175 mm S. L., S. adult = 100–175 mm S. L., juvenile < 100 mm S. L. Both *A. leucosternon* and *Z. scopas* were encountered along the subtidal edges of these colonies, but only *A. leucosternon* were interspersed with the *A. lineatus*.

the results of the two surveys along 200 m strips referred to above. In the shallow strip the ratio of adult to juvenile *A. leucosternon* was 1:0.57 (n = 113), and of *Z. scopas* adults to juveniles 1:0.09 (n = 51). In the deeper strip the ratios were 0:23 (n = 23) and 1:0.12 (n = 76) respectively. In the main study area the ratio of adult to juvenile *A. leucosternon* was 1:0.025 (n = 79), while no juvenile *Z. scopas* were seen there.

5.2 Habitat segregation in areas of overlap

5.2.1 Between *A. leucosternon* and *Z. scopas*

A. leucosternon and *Z. scopas* were found throughout the lower half of the study area. However, within this zone there was habitat segregation between these two species. *A. leucosternon* territories tended to be centered round the higher points of rock in this zone, while those of *Z. scopas* were in the lower areas. This pattern is clearly reflected in differences in the feeding microhabitats of these two species (see section 6.3).

5.2.2 Between *A. lineatus* and *A. leucosternon*

The substrate of the zone in which *A. lineatus* was concentrated tended to be flatter than that to which *A. leucosternon* was largely restricted (compare Fig. 2 and 4). At the interface of these two species' distributions *A. lineatus* tended to be associated with areas of substrate that were lower than those occupied by *A. leucosternon*: We examined the territories of a series of individuals of each species along this interface and noted the height of each, relative to the height of that of its nearest interspecific neighbour. The territories of 50 of 84 *A. lineatus* were lower than those of neighboring *A. leucosternon*, while those of only three were higher. Twenty-nine of 58 *A. leucosternon* territories were higher than those of neighboring *A. lineatus* and only two were lower.

6. Feeding activity

6.1 Diets

We examined the stomach contents of 33 adult and 29 juvenile *A. lineatus*, 48 adult and 19 juvenile *A. leucosternon* and 31 adult *Z. scopas*. All of those fishes were collected within 1500 m of the main

study area in habitats similar to those in the study area. These specimens had all fed on small, soft benthic algae, and had ingested very few small animals, such as crustaceans. Although we have not attempted to assess quantitatively differences in the diets of the adults of each species, the stomach contents of adult *A. lineatus* were very different to those of the other two. *A. lineatus* adults had eaten larger types of filiform and fleshy algae than the other two, both of which principally had taken in similar types of small filiform and filamentous algae.

Each species fed by cropping algae from the substrate and took in little sediment in doing so. On the rare occasions when dense masses of plankton passed through the study area, they fed intermittently on some of this material. Otherwise all their food was derived from substrate feeding.

6.2 Standing crops of algae in territories

We made no specific measurements of algal standing crops in areas permanently occupied by adults of each of the three species. However, differences were readily discernible to us. Adult *A. lineatus* territories contained distinct mats, about 0.5 cm thick, of small fleshy and filiform algae that covered nearly all of the bare rock present in each territory. Even from a distance of 10 m or more this *A. lineatus* zone mat was quite distinct to the observer, with the substrate being uniformly darker inside this zone than outside. The standing crops of algae in the territories of both *A. leucosternon* and *Z. scopas* were much lower than those of *A. lineatus*. In *A. leucosternon* areas there were large, quite distinct patches of algae (of a finer, redder type than in *A. lineatus* territories) scattered about on the sides of humps of raised coralline rock. These algal patches were less thick, less dense, and much less continuous than those in *A. lineatus* areas. Similar algae were present in *Z. scopas* areas but were sparser, and not in patches that could be easily seen by the observer.

Algal standing crops were thus greatest in *A. lineatus* territories and least in *Z. scopas* territories.

6.3 Feeding microhabitats

We examined the feeding habits of the three species to determine if there were differences in the feeding microhabitats of each that might be correlated with (a) differences in their mouth structures, and (b) dif-

ferences in apparent habitat segregation of species in areas in which they overlapped. Specifically, species with longer rostrums might be expected to feed more in crevices, and, if *Z. scopas* was actually living in lower areas than *A. leucosternon*, it would be expected to feed in lower, more horizontal substrates. As can be seen in Table 6, *Z. scopas*, which has the longest rostrum, did the most feeding in crevices, and *A. lineatus* the least. Also, *A. leucosternon* fed more on higher rock substrates and more on vertical surfaces than did *Z. scopas*. Thus *A. lineatus* fed in the most restricted range of microhabitats, and *Z. scopas* in the broadest range.

6.4 Feeding rates

Feeding rates of the three species were estimated by the frequency of bites on the substrate. Observations were restricted to within three hours of high tide and between 0900 and 1700 hours, as the fish were more quiescent nearer the crepuscular periods.

All three species fed consistently at high rates. *Z. scopas* fed at higher rates than *A. lineatus*. *A. leucosternon* females, but not males, fed at higher rates than *A. lineatus*. While *A. leucosternon* females also fed at higher rates than conspecific males, there were no differences evident in the feeding rates of the sexes of *Z. scopas* (Fig. 5).

7. Social Organization

7.1 Territoriality

The adults of all three species, and the juveniles of the two *Acanthurus* species, defended areas to which they were attached from day to day. We have no data on the juveniles of *Z. scopas*. For the purposes of this paper we are defining a territory as 'the area containing the resources that the territory owner is using and defending.' This definition is more restricted than the usual 'defended area' (Sensu Noble 1939, and see also Myrberg & Thresher 1974) i.e. the area within which intruders are reacted to aggressively by the territory owner. We have chosen to use such a definition because it is functional rather than simply descriptive (see also Carpenter & Macmillan 1976). We do not necessarily think that such a definition has universal application, and use it merely to emphasize the points we wish to make in this paper. This definition is most applicable to multipurpose territories. For reasons that will become clear later (see section 9.1.1) we consider the feeding areas of territory holders of all three species to be equivalent to their territories.

7.2 The social unit

For the purposes of this paper we define this unit as the unit occupying a territory. The unit differed in composition from species to species:

Table 6. Feeding microhabitats of three surgeonfishes.

Feeding microhabitats	Mean proportion of bites taken by each species in each microhabitat type		
	<i>A. lineatus</i>	<i>A. leucosternon</i>	<i>Z. scopas</i>
High rock	—	0.50	0.24
Flat vertical rock faces	0.47	0.62	0.40
Crevices	0.04	0.07	0.31
Sample sizes			
Number of observation periods	31	77	39
Number of fishes	31	76	39

* p values for Sign Test.

7.2.1 *A. lineatus*

Juveniles and adults of both sexes of all sizes held territories as individuals. They attempted to defend those against conspecifics of all classes and a range of other species.

7.2.2 *A. leucosternon*

The adult social unit in *A. leucosternon* was a female/male pair in which the male was invariably smaller than the female, with an average ratio of 1 g male: 2.17 g female ($n = 16$ pairs). We noted several pairs of tagged or individually recognizable fishes remaining together for three or four months. In this species there were also a considerable number of females that were unpaired and which held territories by themselves or with juveniles (fishes less than 100 mm standard length). In the main study area at one stage there were 14% more females than males among the adult fishes (males $n = 44$). A tendency for males to associate with two females was observed, although only two of the six apparently 'excess' females in the study area were involved in such relationships. In such cases the male would spend several minutes in alternation with each female. Often the two females were immediate neighbors and would defend their areas against each other, rather than using a common area. However, twice we found situations in which the areas of the two females were separated by the territory of another female/male pair. The male would rise up over that pair's territory during his movements to and fro between 'his' two females. The male in such trios defended the areas of both females against both conspecifics and other species.

To test two hypotheses: (i) that there was an excess of females in the population; and (ii) that females preferred to be paired with a male rather than remain alone, we removed the male from each of four pairs and the female from each of another four pairs. We predicted that, if these hypotheses were valid, females that had been removed would be more likely to be replaced than males that had been removed, and that females would compete with each other to pair with males. The females that had been removed were all replaced within several days, after considerable female-female fighting. Over a period of one month none of the four males that was removed was replaced permanently and only one was temporarily replaced by a small (presumed) male; instead, each of the females in these experiments became involved in a

trio with a neighboring male. In the main study area we also observed three cases in which a female lost her mate. One became involved in a trio for about seven weeks before a male finally moved in with her. The other two females were intermittently involved in trios for about a month then disappeared. These observations and experiments support these two hypotheses.

Two pieces of information relating to the physiological condition of females show that the physiological condition of unpaired (= lone) females was different to that of paired females: Firstly, while none of the six lone females that we collected had noticeable fat deposits in their gut mesenteries, 20 of 21 paired females had quite visible and often large deposits. Secondly, the percentage of body weight devoted to ovary was much less in the lone females than in paired females: mean = 0.56 ± 0.21 (95% confidence lts) ($n = 6$) and 2.06 ± 0.48 ($n = 12$) respectively. The significance of these differences is discussed in section 9.3.2.

A. leucosternon juveniles were territorial towards each other. Although adult pairs were intolerant of juveniles in their territories, adults were able to move relatively unmolested through the territories of the juveniles. Lone females were also observed living in and defending the same areas as juvenile conspecifics.

7.2.3 *Z. scopas*

With *Z. scopas* the social unit comprised a male plus one or two females. Males were invariably larger than their females, by an average ratio of 1 g male: 0.75 g female ($n = 14$ pairs). The proportion of males with two females was not high: 0.22 of 18 males. Unlike the situation in *A. leucosternon*, both females in trios of *Z. scopas* moved around in a common area, with the larger of the two being aggressively dominant over the smaller. We also saw no indications of male *Z. scopas* visiting two females in widely separated areas, which did occur in *A. leucosternon*, and no indications of females of *Z. scopas* living by themselves. Thus there were basic interspecific differences in the nature of the relationship between females in multi-female social groups of *A. leucosternon* and *Z. scopas*. No observations were made on the behavior of juveniles on the latter species.

Table 7. Territory packing in three surgeonfishes.

Percentage of border of a territory that is contiguous ¹ with the borders of neighbouring conspecifics' territories			
Species	Mean percentage (range)		Number of territories measured
<i>A. lineatus</i>	78	(60-88)	10
<i>A. leucosternon</i>	31	(11-60)	26
<i>Z. scopas</i>	32	(14-50)	10

¹ Borders come to within 25 cm of each other in *A. lineatus* and within 50cm of each other in *A. leucosternon* and *Z. scopas*. Measurements made on *A. lineatus* completely surrounded by conspecifics. At least 30 min observation per territory.

7.2.4 Temporal aspects of territoriality

As described in section 2.1.2 most adults of the three species occupied their territories only during daylight. At least some of the *A. lineatus* juveniles that had territories in intertidal areas behaved similarly and spent their nights in the abandoned subtidal territories of adult conspecifics.

Territory holders of all three species did not spend their entire days within their territories. They left them regularly throughout the day in two main ways. Firstly, they joined in stampedes (see section 2.1). Secondly, they frequently left them for short periods and wandered off up to 100 m or more through the zone occupied by conspecifics. *A. lineatus* adults also left their territories to engage in sexual activity (see section 8). Only with *A. lineatus* could we find evidence that not all members were territorial. Occasionally, individual juveniles and adults of this species were observed wandering back and forth through and near the territories of conspecifics, for periods of up to at least two hours. During these movements they fed in the territories of the conspecifics. One tagged adult *A. lineatus* (which held a territory when first tagged) was regularly seen acting as a wanderer over a ten-week period. Whether such wandering normally extends over such long periods or is more transient is unknown.

Tagged or individually recognizable territory holding adults of each species were observed defending territories in the same sites in the main study area for periods varying up to 4.5 months.

7.3 Colonialism

7.3.1 *A. lineatus*

Adult *A. lineatus* were characteristically found massed in bands along the reef slope immediately below

the reef crest. Within these masses their territories were packed closely together, with each territory normally sharing most of its border with that of the territory of a neighboring conspecific (Table 7). Within these masses few individuals of other fish species that fed on benthic algae (except *Stegastes fasciolatus*) held territories (Fig. 6). *A. lineatus* we thus consider to have formed monospecific colonies, i.e. tightly packed aggregations of territory holding fishes in which neighbors are almost invariably conspecifics, rather than members of different but mutually territorial species.

Within the subtidal colonies the largest adults were found centrally, and the smaller adults and juveniles around the periphery (Fig. 6). The majority of juveniles were concentrated intertidally, on the inshore side of these adult colonies. They were rarest on the deep side of those adult colonies (Fig. 6).

Both on the reef crest, and on the upper reef slope away from the main adult colonies, juvenile *A. lineatus* tended to form colonies of their own. In approximately 1.25 hectares of these two zones that we examined we found 161 juveniles and four adults, whose territories covered only about 5% of that area. Those adults were in the centers of two colonies that each contained at least 15 juveniles. Only 5% of the juveniles occupied solitary territories, while 71% of them were in colonies containing four or more fishes, and 37% were in clusters of ten or more fish.

Adult colonies of this structure could form and persist through time by a combination of (1) territories that become vacant in the center of a colony having (a) a very high probability of being taken over by an *A. lineatus* and (b) a higher probability of being taken over than those that become vacant on the edge; (2) a vacant territory being taken over by fish whose size is nearly equal to, or less than, that territory's original owner; and (3) priority of access to vacated territories being determined by size, with the

advantage being with larger of any two fish attempting to move in.

This three-part-hypothesis was tested by the experimental removal of fishes of various sizes from different parts of colonies. The following results were obtained: (1) All ten large adult *A. lineatus* removed from the centers of colonies were replaced by large adult conspecifics. Only eight of 14 experimentally removed and three naturally disappearing adult fishes that held territories at the edges of colonies were replaced by conspecifics. (2) The relative sizes of conspecifics that replaced 23 adult and 13 juvenile *A. lineatus* that we removed were recorded. Thirteen of the 23 adults were large fish that were replaced by other large fish, four others were replaced by distinctly smaller adults and six by juveniles. None of the 13 juveniles was replaced by an adult. (3) Fishes of all sizes became involved in disputes over vacated adult territories that were eventually taken over by adults. Also, while adult territory holders were able to eject intruding juveniles rapidly adult intruders were able to move through the territories of the juveniles despite harassment from those juveniles. These adults also often retaliated to such harassment by chasing the juveniles. These data support the hypothesis.

7.3.2 *A. leucosternon* and *Z. scopas*

In and near the main study area there was no tendency for either of these two species to form colonies similar to those of *A. lineatus*. The territories of each of these two species shared much less of their borders with the territories of neighboring conspecifics than did those of *A. lineatus* (Table 7). Also, *A. leucosternon* and *Z. scopas* usually acted as contiguous neighbors: 41 of 44 *A. leucosternon* territories that were wholly or partly in the main study area had conti-

guous *Z. scopas* territory neighbors, while all of 19 *Z. scopas* territories had contiguous *A. leucosternon* neighbors. The neighboring territories of these two species also overlapped distinctly (Table 14).

7.4 Territory sizes and biomass densities of fishes in them

The absolute areas of territories of adults of each of the three species differed radically. As, interspecifically, there was an inverse relationship between the size of the animal and the size of its territory, the biomass densities of each species varied considerably. The largest species, *A. lineatus*, had the smallest territories and thus the highest biomass density. *Z. scopas*, the smallest species, had the largest territories, and thus the lowest biomass density (Table 8).

7.5 The multispecific nature of their territoriality

7.5.1 The range of species attacked

All three species were both intra- and interspecifically territorial. This territorial aggression was directed almost exclusively at fishes that fed on benthic algae: 96% of 1 000 aggressive interactions by territorial adult *A. lineatus* were with such fishes, as were 99.9% of 1 663 interactions by paired adult *A. leucosternon* and 99% of 210 interactions by territorial *Z. scopas*.

While the great majority of the interactions that both *A. leucosternon* and *Z. scopas* had were interspecific, *A. lineatus*' interactions were split evenly between intra- and interspecific types (Table 9).

Of the three species, *A. lineatus* defended its territories against the broadest range of species, and *Z.*

Table 8. Territory sizes and social unit biomass densities for three species of surgeonfishes.

	<i>A. lineatus</i>	<i>A. leucosternon</i>	<i>Z. scopas</i>
Territory area ¹ (m ²)	7 ± 1 ²	17 ± 2	37 ± 10
Mean mass of social unit (g)	216	257	125
Social unit biomass density (g m ⁻² of territory)	30	15	3
n =	36	38	11

¹ From mapping individual fishes feeding activity for at least 30 min in *A. leucosternon* and *Z. scopas*, and at least 10 min in *A. lineatus*.

² Mean with 95% confidence limits.

scopas the narrowest range (Table 10). Also, while both *Acanthurus* spp. were occasionally aggressive to the algivorous, territorial damselfish, *S. fasciolatus*, *Z. scopas* was attacked by but did not attack that damselfish. The species that were attacked by *A. lineatus* alone shared the characteristic of being large acanthurids that fed on large fleshy algae. There was a major division in the types of species that were attacked by *A. leucosternon* but not *Z. scopas*, as the latter did not defend its territories against parrotfishes. Although these different species of scarids varied greatly in size, they all fed by scraping or biting

dead coralline rock with their hard beak-like mouths. The triggerfishes (*Melichthys* spp.) that were attacked by *A. leucosternon*, but not *Z. scopas*, fed from the substrate in a similar manner to the scarids.

7.5.2 Levels of defense activity by adult social units

We have measured the amount of activity, or effort, the social unit of each of the three species expended in the defense of its territory in three ways, to pro-

Table 9. Frequency with which territory owning surgeonfishes of three species have aggressive interactions concerned with territory defense.

Territory holder	Number of interactions per 10 min. period		
	Intraspecific interactions	Interspecific interactions	Total
<i>A. lineatus</i> n = 125	1.4±0.4 ¹	1.5±0.4	2.9±0.6
<i>A. leucosternon</i> n = 39 male	0.9±0.3	4.3±1.0	5.3±1.2
n = 39 female	0.6±0.2	2.1±0.8	2.6±0.8
pair ²	1.5	6.4	7.9
<i>Z. scopas</i> n = 61 male	0.5±0.2	2.1±0.6	2.6±0.6
n = 51 female	0.2±0.2	1.5±0.5	1.7±0.6
pair ²	0.7	3.6	4.3

¹ Mean with 95% confidence limits.

² Combined male and female rates.

Table 10. Benthic algae eating fishes that were attacked by three species of territorial surgeonfishes.

Species attacked		Attacks commonly observed from		
Name	Diet ¹	<i>A. lineatus</i>	<i>A. leucosternon</i>	<i>Z. scopas</i>
<i>A. lineatus</i>	larger microalgae	yes*	yes	no
<i>A. leucosternon</i>	microalgae	yes*	yes*	yes
<i>Z. scopas</i>	microalgae	yes	yes	yes*
<i>A. nigrofuscus</i>	microalgae	yes*	yes*	yes
<i>A. triostegus</i>	microalgae	yes*	yes*	yes*
<i>Z. veliferum</i>	smaller, soft macro and larger microalgae	yes*	yes	occasionally
<i>A. gahhm</i>	sediments, a little microalgae	yes	yes*	no
<i>A. tennentii</i>	sediments, a little microalgae	yes	yes	no
<i>N. brevirostris</i>	softer macroalgae, zooplankton	yes	no	no
<i>N. lituratus</i>	larger, harder macroalgae	yes*	no	no
<i>N. unicornis</i>	larger, harder macroalgae	yes	no	no
<i>Melichthys</i> (2 spp?)	coralline rock scrapings, zooplankton	yes*	yes*	no
Scaridae (10 spp. ²)	coralline rock scrapings	yes*	yes*	no

¹ For acanthurids diets based on examination of stomach contents of 20 fish per species, for *Melichthys* spp. (F. Balistidae) and Scaridae direct observations.

² (Names supplied by R. Bruce) *Scarus sordidus* Forskal, *S. cyanognathus* Bleeker, *S. psittacus* Forskal, *S. harid* Forskal, *S. niger* Forskal, *S. oviceps* Valenciennes, *S. viridifucatus* (Smith), *S. frenatus* Lacepede, *S. rubroviolaceus* (Bleeker), *Calotomus* sp.

* Feeding by those attacked species increased in the territories of attacking species following removal of territory owners.

vide for comparisons. These are: (i) the frequency with which the social unit interacts with other fishes, (ii) this frequency expressed per unit territory area, which, because of the radical differences in territory sizes, gives a relative measure of defense expenditure per unit area of the territory, and (iii) where fishes are attacked by the social unit in relation to the territory, i.e. inside it or outside (and at what relative distance outside).

The data presented in Table 9 show that *A. leucosternon* units interacted with fishes of all species more often than did the units of either of the other two species, and that *A. lineatus*' overall frequency of interactions was lower than that of *Z. scopas*. This high level of activity by *A. leucosternon* was due principally to its having a high level of interspecific activity. Although the data presented in that table indicate

that *Z. scopas* had a higher level of interspecific interaction than did *A. lineatus* those data represent two classes of interspecific interactions in *Z. scopas* and only one in *A. lineatus*. While *Acanthurus nigrofuscus* juveniles were absent from *A. lineatus* territories they were present throughout the *Z. scopas* territories in the study area. Interactions between these juveniles and *Z. scopas* constituted a major part (46%) of *Z. scopas*' interspecific interactions. *A. nigrofuscus* of all sizes attacked and were attacked by *Z. scopas*. Although *Z. scopas* invariably won such fights, the *A. nigrofuscus* juveniles, because they were much smaller than the *Z. scopas* adults, were able to retreat into shelters where the *Z. scopas* could not reach them. Thus the juvenile *A. nigrofuscus* were able to remain in (and defend their own territories within) *Z. scopas* territories.

Table 11. Frequency with which territorial surgeonfishes have territory defense interactions, expressed per unit area of territory.

Territory holder	Number of interactions per 10 min per m ² of territory ¹		
	Intraspecific interactions	Interspecific interactions	Total
<i>A. lineatus</i>	0.20	0.21	0.41
<i>A. leucosternon</i> pair	0.09	0.37	0.46
<i>Z. scopas</i> pair	0.02	0.09	0.11

¹. Calculated from figures on interactions in Table 9, and territory sizes in Table 8.

Table 12. Distances at which fishes are attacked by territory-holding adult surgeonfishes of three species.

Territory holder	Attacked fish	n Attacks	Proportion of attacks in which 'intruder' was, when attacked, inside or outside the territory			
			Inside	Outside (distance outside in approx. no. territory diameters)		
				Up to 1 diam.	1-5 diams.	More than 5 diams.
<i>A. lineatus</i>	Conspecific	79	0.82	0.17	0.01	—
<i>A. leucosternon</i>		33	0.88	0.12	—	—
<i>A. lineatus</i>	Single non-conspecifics	102	0.56	0.24	0.20	—
<i>A. leucosternon</i>		147	0.99	0.01	—	—
<i>A. lineatus</i>	<i>A. triostegus</i> feeding school	43	0.02	0.16	0.74	0.08
<i>A. leucosternon</i>		44	0.61	0.39	—	—

Social units of the two *Acanthurus* spp. had the same frequency of intraspecific interactions, and interacted with conspecifics more often than did *Z. scopas*.

Considering the frequency of interactions expressed per unit territory area — (a) *A. lineatus* had the highest intraspecific level, and *Z. scopas* the lowest; (b) *A. leucosternon* had the highest interspecific level and *Z. scopas* the lowest; and (c) *Z. scopas* had the lowest total level and the two *Acanthurus* spp. about the same total level (Table 11). Thus, as measured by interaction frequencies, the two *Acanthurus* spp. expended about the same amount of effort in the defense of each square meter of their territories. However, this effort was mainly directed at conspecifics in *A. lineatus*, and interspecifically in *A. leucosternon*. *Z. scopas* expended the least effort of the three.

Of the three species, territorial adult *A. lineatus* were the most rapid, vigorous and persistent in attacking intruders of any species, and *Z. scopas* the least. While we did not observe *Z. scopas* initiating attacks on intruders outside their territories, both of the *Acanthurus* spp. often did so. *A. lineatus* was also

more likely than *A. leucosternon* to attack intruders outside its territories and to attack them at greater relative and absolute distances (Table 12). *A. lineatus* attacked members of other species, and especially feeding schools of *Acanthurus triostegus*, further outside their territories than they attacked conspecifics. However, while *A. leucosternon* also attacked *A. triostegus* schools at greater relative distances than they attacked any other fishes, they attacked conspecifics at greater distances than they did individuals of other species, rather than vice versa as in *A. lineatus*.

7.5.3 Inhibition of intruder feeding by territory defense

To test if the aggressive activity of territorial adults of the two *Acanthurus* spp. was effective in inhibiting the feeding of other algivorous fishes which they attacked, we removed territory owners of both species and compared the levels of intruder feeding before and after those removals. As is apparent from Table 13 there were large increases in the feeding activity of many species following the removal of the territorial

Table 13. Effects of removal of territory holding surgeonfishes of two species on the amount of non-owner feeding by algivorous fishes in those territories.

Territory holder	Mean number of fishes (other than owner) feeding per unit area of territory ¹			
	Acanthurids ²	Scarids ³	Others ⁴	
<i>A. lineatus</i>				
Experiment ⁵ n = 4	Before owner removal	Std. Dev. 0.02(0.03)	0.08(0.06)	—
	After owner removal	5.75(3.87)	8.07(3.46)	1.43(0.59)
Controls ⁵ n = 4	Before owner removal	—	0.01(0.01)	—
	After owner removal	—	—	—
<i>A. leucosternon</i>				
Experiments n = 4	Before owner removal	0.12(0.12)	0.16(0.04)	0.09(0.09)
	After owner removal	1.26(1.15)	1.27(0.61)	0.18(0.13)
Controls n = 4	Before owner removal	0.47(0.59)	0.15(0.04)	—
	After owner removal	0.43(0.53)	0.27(0.28)	—

¹. Calculated from number of feeding fishes present during 90 spot observations made at one-minute intervals. This expressed per 10 m² of territory area to take into account difference in sizes of territories of the two species.

². See species listed in Table 10.

³. These included: *Scarus sordicus*, *S. psittacus*, *S. viridifucatus*, *S. Sexvittatus*, *S. cyanognathus*, *S. oviceps*.

⁴. *Melichthys* 2 spp? (Balistidae).

⁵. Experiments: After 90 min observations owner speared. Post removal observations were made at same time of day on the following day. Controls: Same two series of observations were made, but without the removal of the territory owners.

A. lineatus and *A. leucosternon*. A broader range of species increased their feeding activity in *A. lineatus* territories than they did in *A. leucosternon* territories (Table 10). The presence (presumably aggressive activity) of territory owners of both species thus does inhibit feeding by intruding algivores in their territories.

Even within the occupied territories of both *Acanthurus* spp. some intruder feeding did occur. More of such feeding (per unit area of the territory) occurred in *A. leucosternon* territories than in those defended by *A. lineatus* (see Table 13 and compare values for controls for both species and also preremoval values in the experimental treatments).

We did not conduct experimental tests of the possible inhibition of intruder feeding by *Z. scopas* territory defense in as detailed a manner as we did with the two *Acanthurus* spp. However, a few pairs of *Z. scopas* were removed for other purposes (see section 7.5.4) and apparent levels of intruder feeding before and after the removals were noted. We noted small increases by only one species (besides *Z. scopas*) following those removals (Table 10).

We have no direct measures of the amount of feeding by other algivorous fish species that normally occurred in *Z. scopas* territories that would enable us to compare, quantitatively, this level with that occurring in territories of the two *Acanthurus* spp. However, we feel confident in stating that the level of such feeding was highest in *Z. scopas* territories, because (i) *A. nigrofuscus* juveniles had territories throughout *Z. scopas* territories but not throughout those of the two *Acanthurus* spp., (ii) *A. triostegus* adults in the main study area intermittently defended feeding territories inside *Z. scopas* territories but not inside those of the two *Acanthurus* spp., and (iii) scarids of all species, and the balistid, *Melichthys* sp., fed unmolested in *Z. scopas* territories but were inhibited from doing so in the *Acanthurus* spp. territories.

All three species were particularly active in defending their territories against feeding schools of adult *Acanthurus triostegus*. Such schools frequently contained in excess of 1 000 fish (one medium sized school that was photographed while spread out on the substrate contained at least 624 fish). They were present in and around the main study area throughout the study period. These schools spent most of their time in the *A. leucosternon*/*Z. scopas* zone, none in deeper water areas, and they went only infrequently onto the reef crest. We made 8.60 hours of observations on schools (7 observation periods): 6.05 hours were spent in the *A. leucosternon* zone, and

0.40 hours on the reef crest. They spent another 1.77 hours along the edges of *A. lineatus* colonies, but little time (0.38 h) actually inside such colonies.

While these feeding schools rolled along the bottom in the *A. leucosternon* zone with no obvious hindrance, *A. lineatus* in colonies reacted very strongly to the movement of schools towards colonies. They rushed out en masse and attacked *A. triostegus* schools as much as 10–15 m outside a colony's area, and often succeeded in turning them away or preventing them from gaining entry into colonies further than into peripheral territories for more than a couple of minutes.

Nonschooling *A. triostegus* individuals, some of which were intermittently territorial, were common in the main study area. However, they were restricted almost entirely to the intertidal reef crest. They were absent from the *A. lineatus* zone, and there were few in the *A. leucosternon* zone. In one count there were 157 nonschooling adult and juvenile *A. triostegus* on the reef crest, and 17 adults in the *A. leucosternon* zone.

Schooling enables various herbivorous reef fishes to overcome, by a swamping effect, the territoriality of food competitors (Jones 1968, Barlow 1974b, Robertson et al. 1976). *A. triostegus* is aggressively dominated not only by *A. lineatus*, *A. leucosternon* and *Z. scopas* but also by *A. nigrofuscus*, a group of species which were abundant in the subtidal parts of the study area. We, therefore, regard feeding school formation by *A. triostegus* in the study area as a tactic that enables large numbers of this species to gain access to food in competitor-dominated, subtidal areas. The fact that schools can be turned away by mass activity of fishes in *A. lineatus* colonies, and only infrequently penetrate into the center of colonies, shows how effective this species is in defending its food resources.

7.5.4 Relations between the three species

(i) Between the two *Acanthurus* spp. — These two species were mutually aggressive to one another and often defended contiguous territories along the deeper edges of *A. lineatus* colonies. While juvenile *A. leucosternon* frequently lived in the same territories as lone female conspecifics, we never saw them similarly situated in any *A. lineatus* territories. However, on six occasions juvenile *A. lineatus* were observed living in the territories of *A. leucosternon* pairs, which harassed them. *A. lineatus* juveniles frequently

shared areas with lone *A. leucosternon* females.

In both species there was negligible overlap in the territories of neighboring conspecifics, and almost no overlap between those of neighboring adults of different species (Table 14). While these data indicate that each species was attempting to prevent the other feeding in (and perhaps taking control of) its territories, the events following the removal of individuals of each species from their territories suggest a more complicated situation. When social units of either species were removed conspecifics invariably came and fed in the vacated territories. However, while *A. leucosternon* also fed in vacated *A. lineatus* territories that were situated along the edges of colonies, almost no feeding by *A. lineatus* occurred in vacated *A. leucosternon* territories.

These results suggested the hypothesis that *A. leucosternon* were 'interested' in gaining control of territories occupied by either *Acanthurus* spp., whereas *A. lineatus* were 'interested' in only those of conspecifics. To test if such was the case we checked which species eventually took over control of these vacated territories. Six of 27 *A. lineatus* adults were replaced by *A. leucosternon*, and the remainder by conspecifics. Of those six fishes, all of which were on the edges of colonies, one was replaced by an *A. leucosternon* pair, while the territories of the remaining five were added to those of neighboring *A. leucosternon* pairs. We checked the territories of nine pairs of *A. leucosternon* that had been shot (seven) or disappeared (two). Five of those nine bordered on *A. lineatus* colonies. All of those pairs were replaced by conspecifics. These results support the hypothesis.

We have pointed out (section 5.2) that while *A. lineatus* territories tended to be in flatter areas, those of *A. leucosternon* were usually centered on patches of high relief on the substrate. This habitat segregation could have been the result of either (a) each species preferring the habitat it is associated with, over that occupied by the other; (b) one species having more specific preferences than the other and excluding the latter from its preferred habitat; or (c) two species preferring the same habitat but one excluding the other from that habitat.

Because the only contests between these two species for control of vacated territories were over *A. lineatus* territories, one might be inclined to think that *A. leucosternon* preferred the type of habitat occupied by *A. lineatus*, and that *A. lineatus* had no interest in the *A. leucosternon*-type habitat. However, the vacated *A. lineatus* territories that were taken over by *A. leucosternon* were added to existing *A.*

leucosternon territories, rather than being taken over as separate intact territories. This would not be expected if they were in a habitat that *A. leucosternon* preferred.

Other data also suggest that *A. leucosternon* did not prefer the *A. lineatus*-type habitat over higher patches of rock: four of the nine vacated *A. leucosternon* territories referred to above were on high relief points and the other five in low flat areas. The first four were taken over by *A. leucosternon* pairs. Of the latter five, four were replaced by lone female + juvenile 'pairs' and the remaining one was divided between a lone female and a neighboring pair that added part of it to their territory.

In summary then, it seems that (i) *A. lineatus* adults prefer a habitat that is flat, but that has also been occupied previously by conspecific adults; and (ii) *A. leucosternon* prefers higher substrate areas over flatter ones, and will take over areas that have been previously occupied by either *Acanthurus* spp.

(ii) Between *A. leucosternon* and *Z. scopas* — Both species defended their territories against each other and often acted as neighbors. However, while there was negligible overlap between the territories of conspecifics, there was quite distinct overlap between those of neighboring *A. leucosternon* and *Z. scopas* (Table 14). This overlap was along the edges of the territories.

Table 14. Degree of overlap in the territories of neighboring acanthurids of the same and different species.

Neighbors	Percentage of their bites that neighbors take from common areas
<i>A. lineatus</i> /conspecific n = 4826 bites; 23 territories	0.2
<i>A. leucosternon</i> /conspecific n = 1135 bites; 9 territories	0
<i>Z. scopas</i> /conspecific n = 1069 bites; 7 territories	0
<i>A. lineatus</i> / <i>A. leucosternon</i> n = 4774 bites; 14 <i>A. lin.</i> territories, 5 <i>A. leuc.</i> territories	0.2
<i>A. leucosternon</i> / <i>Z. scopas</i> n = 2204 bites; 9 <i>A. leuc.</i> territories, 7 <i>Z. scopas</i> territories	18.8

To test if each of these two species would take over control of territories previously occupied by the other, we checked what types of fishes replaced those of each species that we removed or that disappeared. All of nine territories that had been vacated by pairs of *A. leucosternon* were taken over by conspecifics. Four of five *Z. scopas* territories, whose owners were shot, were taken over by *Z. scopas* pairs after a lot of intraspecific fighting. The fifth territory was split up, a neighboring *A. leucosternon* pair adding the only piece of high rock in it to their territory, and a neighboring *Z. scopas* pair adding the remainder to their territory. This last case was the only one in which there was evidence of conflict between the two species for control of *Z. scopas*-occupied space. *A. leucosternon* that were engaged in taking over vacated *A. leucosternon* areas chased *Z. scopas* from near them.

These results, when combined with the results of experiments described in the previous section, can be interpreted in two ways: (1) Each of these two species prefers the habitat in which it normally occurs, or (2) *A. leucosternon* prefers high areas over low ones and excludes *Z. scopas* from such areas when opportunities (i.e. vacancies) arise to do so. In this case *Z. scopas* might have no preference for either habitat, or might even prefer the *A. leucosternon*-type habitat.

(iii) Between *A. lineatus* and *Z. scopas* – Although we often observed *A. lineatus* chasing *Z. scopas* away from the edges of *A. lineatus* colonies, we never saw attacks in the reverse direction. We have no information on the possibility of the territories of these two species overlapping and there were no instances of either attempting to take over vacant territories that had been occupied by the other.

7.6 Sexual differences in activity patterns

7.6.1 Feeding activity

As an index of this activity we will use feeding rates (frequency of bites on the substrate). We have no data on whether or not *A. lineatus* males and females might have been feeding at different rates. As noted earlier (section 6.4) males of *A. leucosternon* fed at much lower rates than paired females did. With *Z. scopas* no such pronounced sex differences were evident.

7.6.2 Territory defense

Again we have no information on *A. lineatus*. *A. leucosternon* males and paired females interacted aggressively with conspecific intruders at the same frequency. Also, males interacted mainly with males (57 of 81 interactions were intrasexual), and females almost exclusively with females – 74 of 80 interactions (the sex of the intruder was gauged from its size). There were also sex differences in this species in the frequency with which paired fishes defended their territories against other species. Males interacted aggressively with fishes of other species at a higher frequency than females did (Table 9). Paired females also interacted with fishes of all species less often than their males did (Table 9).

No marked sex differences in the defense activity (as measured by interaction frequencies) of paired *Z. scopas* were evident (Table 9).

There is one further aspect to this division of defense activity between the sexes of *A. leucosternon* that deserves attention. It concerns the territoriality of pairs as compared to that of lone females. While lone females were as strongly territorial as paired females towards adult conspecifics, unlike pairs they tolerated juvenile conspecifics. Also, lone females were not as strongly interspecifically territorial as pairs. Lone females often ignored members of other algae eating species feeding near them in their territories, fishes that pairs attempted to exclude. For example, pairs vigorously attacked territorial juvenile *A. nigrofuscus* and limited them to the edges of their territories. These juveniles increased their feeding inside and also moved into and set up territories inside *A. leucosternon* pair territories whose owners had been shot. Lone females, unless harassed by the territorial juvenile *A. nigrofuscus*, usually ignored them and did not exclude them from the centers of their territories (Fig. 7).

8. Mating systems

Unfortunately *Z. scopas* was the only one of the three species that we saw spawning. However, based on information derived from several sources, we can make some predictions as to what patterns should be found in *A. leucosternon* and *A. lineatus*.

Randall (1961a, b) observed spawning in three acanthurids, *A. triostegus*, *Ctenochaetus striatus* and *Z. scopas*, each of which released gametes free into the water. All three spawned in groups which, in *Z. scopas*, contained eight-ten fish.

We observed 28 *Z. scopas* spawnings. Each involved only a pair of fish. Despite the numerous other instances of observed premating behavior in areas well away from the main study area, we never saw anything to suggest that more than two fish would be involved in the spawnings of *Z. scopas* at Aldabra.



Fig. 7. Superimposition of territories of *A. leucosternon* adults and *A. nigrofuscus* juveniles. A. leuc. = *A. leucosternon* territory, L = lone female, P = pair; A. ng = substrate covered by territories of *A. nigrofuscus* juveniles (n = 110).

While watching *A. triostegus* spawning Randall (1961a) noticed that males underwent a distinct color change, whereas females retained their normal color. We observed the same type of male color change in that species at Aldabra, and collected four specimens bearing the male and female color patterns as a check. Near our study area this species' spawning activity was concentrated at the shallow mouth of one of the few channels that drained the atoll's lagoon. Spawning occurred on the ebb tide, with fishes migrating up to at least 1.2 km and massing in the tens of thousands at the spawning ground. Within this mass, groups of up to at least a score of fish spawned together. The mass as a whole often spawned synchronously. Based on the colors of the participants, each spawning group consisted of a single female with an attendant cluster of males. Copious sperm release accompanied each spawning act, enough, in fact, to reduce severely water visibility at the surface for a few seconds after a mass spawning bout.

Among the tropical labroid fishes (wrasses and parrotfishes), which are broadcast spawners, like the surgeonfishes, both group and pair spawning are common. Group spawning involves a single female and numerous males. Male labroids that usually spawn in groups consistently have much larger testes (relative to their body weights) than those that pair-spawn. This difference in testis weights, which occurs between males of the same as well as different species, has been attributed to the result of sperm competition: by producing more sperm a male increases the proportion of the female's eggs that he fertilizes, at the expense of the other males present (Robertson & Choat 1974, Choat & Robertson 1975).

We regularly saw premating behavior and spawning by four other surgeonfishes besides *Z. scopas* and *A. triostegus*, two that only pair spawned and two in which group spawning was common (Table 15). We collected males of those six and another four species. As can be seen from Table 15 there were very obvious interspecific differences in the relative sizes of the male's gonads: those of males of the group spawning species were relatively much larger than those of the known pair spawners. This difference we attribute to the same effects of sperm competition on group spawning male acanthurids that have been proposed to be operating in group spawning labroid males.

The three known pair-spawning acanthurids indicated in Table 15 we found consistently to occur in pairs of harems. Based on observations of spawning pairs for several minutes after they had spawned, the pair spawnings occurred within the social unit and in

Table 15. Spawning patterns and relative testis weights in ten surgeonfishes.

Species	Spawning pattern ¹	Testis weight as a percentage of body weight (mean with 95% confidence limits)	n
<i>C. striatus</i>	Group	2.1 ± 0.6	7
<i>A. triostegus</i>	Group	3.7 ± 0.7	42
<i>A. nigrofuscus</i>	Group	1.7 ± 0.7	19
<i>A. lineatus</i>	Group?	1.9 ± 1.2	10
<i>Z. scopas</i>	Pair	0.3 ± 0.1	13
<i>Z. veliferum</i>	Pair	0.5 ± 0.1	9
<i>C. strigosus</i>	Pair	0.5 ± 0.1	8
<i>A. leucosternon</i>	Pair?	0.6 ± 0.2	11
<i>A. gahhm</i>	Pair?	0.7 ± 0.2	8
<i>N. lituratus</i>	Pair?	0.3 ± 0.1	13

¹. Pair = 1 male and 1 female.

Group = 1 female and several or more males.

? = inferred.

the unit's territory. That is, the two fishes resumed feeding quietly on the substrate beneath the spawning site rather than dispersing. Also, one tagged pair of *Z. scopas* was seen to spawn in its territory, and two tagged pairs were seen courting in their territories. Males of three other species, including *A. leucosternon*, whose social units were also pairs or harems, also had small testes (Table 15). This we take as evidence indicating that *A. leucosternon* normally pair spawns, with each male spawning with 'his' female.

Several pieces of information that we gathered indicate that *A. lineatus* normally group spawns: males of that species had large testes (Table 15). No permanent pairs are formed. On several occasions we observed what was probably prespawning behavior. This occurred in groups of fishes moving about, both over colony areas and in deeper water outside of, but within 100 m of, colonies. These groups consisted of one fish (a female?) being closely followed by several others. The latter were behaving very similarly to the characteristic manner in which males of *Ctenochaetus striatus*, *C. strigosus*, *Z. scopas* and *A. nigrofuscus* did immediately prior to spawning.

Barlow (1974a) suggested that school-forming species of acanthurids should group spawn and pair-forming species pair spawn. While we agree with this idea, in the light of the information that we have collected we suggest the following modifications: (1) Group spawning should be the major spawning mode in species that do not characteristically form permanent male-female social units, regardless of whether the species is normally a schooling form, or is territorial. (2) Pair spawning should be the major mode in species that do characteristically form male-female so-

cial units. (3) Both modes should frequently occur when, although many members of the population are in such male-female units, many others are not. [*Ctenochaetus striatus*, in which we commonly saw both spawning modes, is an example of this latter type: besides male + one or more female social groups we also often saw areas in which large numbers of non-territorial fishes of this species were feeding.]

At Aldabra we saw no signs of any acanthurids forming leks, as has been suggested might be the case in some species (Barlow 1974a). Some nonpairing species could well do so, however.

9. Discussion

9.1 Acanthurid feeding strategies

Brown (1964) pointed out that the development of feeding territoriality depends upon the economics of defense of the resources being exploited. Territoriality can develop when the spatial distribution of food resources is such that the benefits exceed the costs of defense. The degree to which an animal maintains exclusive use of the resources in its territory depends upon the defensibility of those resources; exclusive territories being restricted to situations in which concentrated, easily defensible food is being exploited (Brown & Orians 1970).

We think that, to understand the significance of differences in the feeding strategies of *A. lineatus*, *A. leucosternon*, and *Z. scopas*, we must consider the defense requirements of their feeding territories and the economics of such defense: (1) To what degree

does a species rely upon defending its food against other species rather than being able physically to obtain certain food resources more efficiently than other species can? (2) By what mechanisms can resources that require defense be more efficiently and effectively defended?

9.1.1 The functions of acanthurid territoriality

A variety of functions have been proposed for the territoriality of tropical reef fishes, either singly or in various combinations. These include defense of space, shelter (including sleeping sites), food, mates, offspring and spawning sites (Smith & Tyler 1972, 1973a, b, Sale 1974, 1976, Reese 1975, Reinboth 1973, Fricke 1975, Warner et al. 1975, Thresher 1976a, Robertson et al. 1976, Ebersole 1977). Unfortunately, there has been little detailed experimental testing of many of these proposed functions. Further, few attempts have been made to dissect out whether or not certain specific, and plausible, functions are in fact served by a fish's territoriality (Robertson & Sheldon, in preparation).

The territoriality of the three surgeonfishes considered here fairly obviously does not serve some of the functions listed previously.

The possibility of competition for and defense of shelter sites of any type is remote, particularly in the two *Acanthurus* spp. The animals flee their territories at the approach of certain types of predators and do not appear to fight over shelter sites during such flights. They also spend their nights away from their daytime territories. That is, there is no evidence that the territories of adults of many of the species living in the study area contained adequate shelter, let alone shelter that should have benefited a territory's owner by being defended.

All three species undoubtedly spawn in midwater, and, because their eggs are planktonic, do not show extended parental care to their offspring. Males of some midwater spawning labroid fishes momentarily defend their freshly spawned zygotes against egg predators (Robertson & Hoffmann 1977). Although we did not see such behavior by any Aldabran acanthurids, territoriality could conceivably serve such a function in these animals. If so it would be a secondary function.

We know that *Z. scopas* pairs at least spawn in their territories. However, the spawnings and courtship that we observed occurred well up in the water

column, and were not associated with specific substrate features. We predict that the same will be the case with *A. leucosternon*. It seems likely that *A. lineatus* do not spawn over their individual territories, but move about inside the colony's area, or even outside it, to do so. Thus defense of spawning sites would not be expected in any of these species.

A male, *Z. scopas*, by defending the area to which his mate restricts her movements, could reduce the ability of other males to spawn with her. Defense of his mate's egg production is almost certainly a function of male territoriality in both this species and in *A. leucosternon*. The same function, i.e. defense of the mate's gamete production per se, cannot be ascribed to female territoriality in such pair forming species. However, if long term association with a male offered a female advantages, and males were a limiting resource to females, then a female's defense of her mate could be expected to develop. As pair formation does appear to offer benefits to female *A. leucosternon* (see section 9.3.2) and the adult sex ratio is skewed towards females, a female's defense of her mate is very likely in this species. The fact that members of a pair in this species attack mainly members of their own sex argues for mate defense being a function of territoriality of both sexes in this species.

Defense of food, arising from competition for food, is the most likely general function of territoriality by fishes of both sexes of these three species. Each species attacks fishes that are capable of utilizing its food resources. Also, we have shown that the two *Acanthurus* spp., at least, strongly inhibit the feeding of intruders of such species in their territories.

When an animal defends, for an extended period of time, a discrete space that contains the food it requires, and the continuance of supply of that food depends on the fish defending it, it can be difficult to separate out which of the two following situations obtains: is there (i) competition for space, which is limiting or (ii) competition for food alone, with the availability of space not being limiting. To illustrate this difference, consider interactions between mutually territorial fishes. If territories of minimum adequate size filled the available space there would be competition for space, if they filled only a part of it there would not be such competition.

The two questions concerning competition among acanthurids that should be dealt with in this paper then are: (i) is intra- or interspecific competition for space limiting the three acanthurid species, and (ii) are any of the three involved in competition

for space with any other species. Firstly, data that we have gathered on the two *Acanthurus* spp. are consistent with the view that more of each could have been accommodated in the study area than were present (see section 9.1.6). Thus we consider that neither species was limited by either intra- or interspecific competition for space with each other. We have insufficient data on *Z. scopas* to indicate what might have been the case with that species.

Are any of these three species involved in competition for space with other species that use the same type of food resources? They could well be competing for space with, and excluding, *A. nigrofuscus* and *A. triostegus*. Both of these latter species defended feeding territories at times in the same zones as *A. lineatus* and *A. leucosternon* and the removal of *A. lineatus* and *A. leucosternon* from their territories resulted in both *A. nigrofuscus* and *A. triostegus* setting up territories in the cleared areas.

9.1.2 *A. lineatus*' feeding strategy

(i) Feeding efficiency and the type of algal mat — *A. lineatus* is larger than either *A. leucosternon* or *Z. scopas*, and has the largest, flattest mouth of the three. It also has the most elongate body shape of the three, with or without its median fins spread, which probably makes it least able to manoeuvre (Alexander 1967) and pick carefully at food in less accessible sites. We suggest that this combination of morphological characters limits *A. lineatus* to being physically more efficient at feeding on denser stands of algae growing on exposed rock areas than on smaller, more sparsely spread algal growths, and especially growths in crevices. That is, were selection to favor the defense of an algal mat by a fish such as *A. lineatus*, its morphological limitations would favor defense of a comparatively thick mat growing in readily accessible situations.

If the minimum size and thickness of an algal mat that *A. lineatus* can economically feed on is determined in part by its morphology, what determines the maximum thickness and density of the mat? We would expect at least two factors to operate: (1) differences in the productivity of different algae, and (2) differences in the ability of the animal to make metabolic use of different algae. Even if *A. lineatus* could more easily crop a thicker mat, the net return per unit area from a mat with a different algal species composition might be lower. Alternatively, it might be uneconomical to defend such a mat. Physical conditions might also limit mat morphology.

Although we have stressed that *A. lineatus* defends a thick algal mat, it is only a thick mat relative to those of the other two species. Some of the damselfishes (Pomacentridae) maintain and defend algal mats that are much thicker than those of *A. lineatus*. Mats of damselfishes can have algae several centimeters or more long, for example those of the Caribbean species *Eupomacentrus planifrons* (Kaufman 1977, Brawley & Adey 1977), and of its Pacific congeners *E. nigricans*, *E. apicalis*, *Plectroglyphidodon lacrymatis* (D.R.R., unpublished observations), and evidently *E. (Pomacentrus sic) lividus* (Belk 1975, and Allen 1975, p. 141). The ability of these pomacentrids to maintain such thick mats may be facilitated by their defensibility. The presence of shelter in damselfish territories permits them to remain in or very close to their territories at all times and they do not have to abandon them regularly, as does *A. lineatus*. Further, such damselfish mats are often in beds of coral with growth forms that allow the formation of 3-dimensional rather than 2-dimensional mats. Because the diameter of a 3-dimensional mat is less than that of a 2-dimensional one containing the same amount of algae, its owner is probably able to monitor it more easily, and take action to protect it earlier and more rapidly. These damselfish algal mats are also developed in habitats that are much more sheltered than the *A. lineatus* habitat is, where delicate strands of algae would not be torn off by wave surge.

(ii) The significance of colonialism, and colony dynamics — A fish that relies on maintaining for its own use a high standing crop algal mat in an exposed situation, is faced with the problem of preventing other fishes from using it. There are several reasons why a mat of this type is particularly vulnerable to the depredations of competitors. Firstly, as mat thickness and density increases the range of species that are, physically at least, able to exploit it also increases, i.e. the range and number of potential competitors increases. Secondly, having a larger mass of algae in an area, potentially offers increases in return for effort to other competitors, and favors stronger attempts by them to gain access to that food. Thirdly, the mat could be rapidly damaged by intruders. Such damage could represent serious losses to its owner, especially if the mat had specific biological properties that required careful manipulation by the owner to maintain them. A premium would therefore be placed on increasing the effectiveness with which such a mat was defended by its owner.

The ease with which a territory could be both

surveyed by its owner and have an intruder rapidly ejected from it would be expected to increase if the territory became smaller. If a group of fishes, with similar defense requirements and capabilities, occupied adjacent territories that were clustered tightly together, the ability of intruders (other than neighbors) to enter a territory would be reduced, as some of the avenues of entry would be blocked by neighboring territories. The effect of such a clustering of territories on increasing the efficiency with which each territory was defended would be enhanced if each territory holder tended to attack potential intruders (other than its neighbors) outside the limits of its territory. That is, the density of the defense screen over each territory would be increased by the overlapping of adjacent screens. Itzkowitz (1974) has described intraspecific clustering of feeding territories in certain Caribbean damselfishes. He suggested that in such clusters the defense of individual territories would be enhanced by the effect of several fishes simultaneously attacking an intruder.

We suggest, therefore, that selection has favored the development of high density colonies by *A. lineatus* because colony formation increases the efficiency with which individual territories are defended. Colony formation represents a tactic used by a species to overcome a serious problem of interspecific competition for food. It should be emphasized that we consider each fish in such a colony to be acting selfishly, i.e., to be increasing the efficiency with which its food is defended by taking advantage of its neighbors' defense activities. Territorial *A. lineatus* readily attempt to take food from neighbors' territories or those of other fishes in the same colony.

Besides increasing the efficiency with which occupied territories are defended, colony formation could also enhance territory defense in the following ways. Colonial *A. lineatus* probably have to spend less time finding mates and to travel shorter distances from their territories to do so, than would be the case if they were dispersed. Thus the time an individual territory was unprotected (during spawning) could be reduced. Also, if not all members of a colony were sexually active at the same time, the territories of those fishes that had left them to spawn would not be completely unprotected. Obviously, data are needed to determine if these effects could be operating.

Some positive feedbacks should be involved in the process of formation of high colonies as we see it. For example, any factor that increased the efficiency of territory defense would result in a reduced loss of resources to competitors. A smaller area would, there-

fore, be needed to support the fish and a reduction in territory size would be permitted. This would in turn increase the efficiency of territory defense. With such an increase there should be a reduction in the risk of owning an algal mat that was more productive, but also more damageable and exploitable by competitors. A more productive mat would permit a decrease in territory size. Thus, an initial clustering of territories into a colony should result in a gradual condensation of the colony, and an increase in the density of fishes.

How do the data that we have gathered on the defense activity of *A. lineatus* and the other two species bear on what we have proposed about the needs, effectiveness, and costs of food defense by the former species? Firstly, the *A. lineatus* mat is susceptible to exploitation by, and is defended against, the widest range of species. *A. lineatus* defense is also more effective than that of *A. leucosternon*, and apparently *Z. scopas*, as the loss of food to intruders is greater from the territories of the latter two species. The effectiveness of *A. lineatus* defense activity also produces the disjunctions in the zonation patterns of many of its competitors – they are resident above and below the *A. lineatus* zone, but virtually absent within it.

The main quantitative data that we have on the cost of defense for each species are agonistic encounter frequencies. The most relevant comparisons to be made are between the two *Acanthurus* spp. as they have the most distinct algal mats. Consider first defense costs per territory per adult social unit: a higher proportion of *A. lineatus* encounters are intraspecific than are those of the other two species, which should not be surprising in a colonial fish. Even so the amount of intraspecific defense is no higher in *A. lineatus* than in *A. leucosternon*. The amounts of interspecific defense activity and total defense activity are, however, least in *A. lineatus*. In terms of defense costs per unit area of the territory, the patterns among the three species are similar to those described above: intraspecific levels are highest in *A. lineatus*, interspecific levels lower in *A. lineatus* than in *A. leucosternon*, and overall levels about the same in the two *Acanthurus* spp. *A. lineatus* is, however, more aggressive and active in its repulsion of intruders than the other two species and goes to greater relative and absolute distances in attacking intruders than they do. In some ways then, *A. lineatus* defense costs are less than those of *A. leucosternon*, and in other ways higher than or equal to them. Even though *A. lineatus* probably requires much more effective defense of its

Table 16. Relative amounts of interspecific defense activity by adult *A. lineatus* holding territories at the edges of colonies and in the center of colonies, and the amounts of feeding by algivores other than owners in those territories.

	Non-owner feeding	Defense activity by owner
	Number of bites per 10 min period per territory	Number of interspecific attacks per 10 min period per territory
Territories in center of colony	0.9±0.8 ¹ n = 51 periods, 51 fishes	1.5±0.4 n = 125 periods, 75 fishes
Territories at edges ² of colony	11.7±3.6 n = 46 periods, 18 fishes	2.9±0.4 n = 152 periods, 75 fishes

¹. Mean with 95% confidence limits.

². Includes fishes holding isolated territories outside colony limits.

algal mat than *A. leucosternon* does, the cost of its defense does not appear to be much higher than that of the latter's defense. This we attribute to its living in colonies.

If the colonial habit offers advantages to the individual territory holder such as we have proposed, we might expect to find measurable differences in the quality of territories, differences that the animals respond to by having preferences for predictable types of territories. Specifically, we might predict that, since competitors of other species surround a colony, *A. lineatus* territories at the edges of colonies would cost more to defend against such intruders, and would lose more resources to them. As the data presented in Table 16 show, such is the case. This difference in territory quality could also explain why territories in the center of colonies are preferred over those at the edges. There are, of course, other possible reasons why central territories might be preferred. There might, for example, be differences in the quality of the habitat each class was located on. We noted no obvious, consistent differences in the type of habitat on which central and edge territories were situated.

There are at least two other possible explanations for *A. lineatus* colony formation that we should attempt to deal with: (i) Suitable habitat might actually be limited to the area already occupied by colonies. Colonies merely represent individuals tightly packed into the only available space. (ii) Suitable habitat might be available outside the colonies, but, because it is already occupied by another highly aggressive territorial species (*A. leucosternon*), *A. lineatus*

must pack tightly into the only remaining space.

In answer to the first of these two alternative explanations, we can only say that there were noticeable differences between the structure of the substrate outside as compared to inside adult *A. lineatus* colonies in only two of the four uncolonized areas separating the three large colonies shown in Figure 6. That is, large areas of apparently identical, and suitable, substrate were observed outside *A. lineatus* colonies in the same zone. Considering the second alternative, we do not think that *A. leucosternon* is ultimately capable of resisting the expansion of an *A. lineatus* colony. When *A. lineatus* were removed from territories at the edge of colonies and both *Acanthurus* spp. attempted to take over these vacated areas, *A. lineatus* were quite capable of rapidly defeating and chasing out the *A. leucosternon*. When two species are seen defending territories against each other and repelling each other, care must be taken in interpreting the significance of such interactions. We think that *A. leucosternon* are capable of keeping *A. lineatus* out of their territories because the *A. lineatus* have little or no interest in them, because they lack a suitable algal mat. *A. lineatus* certainly do not attempt to take over vacated *A. leucosternon* territories. The development of an *A. lineatus* algal mat undoubtedly requires time and a lot of effort by its owner. Therefore, it is probably more to an individual *A. lineatus*' interest that it remain in an existing relatively poor quality territory and wait for an opportunity to move into a better, conspecific one, rather than to start a completely new one in a vacated *A. leucosternon* territory. Even if adult *A. leucosternon*

were able to compete on an equal basis with *A. lineatus* for possession of a vacated territory, or had an advantage in such struggles, the apparent difference in these two species preferences for substrate types would tend to allow *A. lineatus* colonies to expand if an expansion occurred in its population.

With the colonies of *A. lineatus* juveniles on the reef crest, we saw nothing to indicate that any other territorial species was aggressively forcing aggregation of territories. *A. leucosternon* were uncommon there, and very large areas of unoccupied substrate that appeared identical to that covered by *A. lineatus* territories were available.

The spatial distribution of *A. lineatus* of different sizes in colonies we attribute to larger fish being able to sequester the most preferred, central territories. By establishing territories at the edges of colonies juveniles benefit by living under part of the adults' defense screen. This adhesion of juveniles to the edges of colonies also provides the means for colony expansion into previously unoccupied space as they grow up. A colony's integrity can be maintained by the willingness of fishes to move into vacated conspecific territories; regardless of where inside a colony a fish death occurs, the net loss of a territory is at the colony's edge. A colony expands and contracts then by the accretion and decurtion of peripheral territories. New colonies can probably form by juveniles initially establishing themselves in clumps outside existing adult colonies.

Itzkowitz (1977) has considered the formation of monospecific 'colonies' of several territorial damselfishes in the Caribbean. He suggests that three factors are involved: (1) Juveniles of territorial damselfishes, other than the colony species, suffer higher rates of mortality than do those of the colony species in the habitat in which colonies form. (2) Colonies are maintained in a preferred habitat by the recruitment of adults from surrounding nonpreferred areas when mortality creates vacancies in a preferred habitat. The species composition of clusters of fishes is strongly influenced by the type of substratum on which it occurs. (3) Competition is more intense between congeners than between conspecifics, and congeners tend to repel each other more strongly than do conspecifics. Thus, a conspecific is more likely to be accepted as a recruit into a colony than is a member of another species. 'A behavioral system inhibits other species from sharing a common territorial border on a homogeneous substratum' (Itzkowitz 1977).

With *A. lineatus*, at least, we think different processes are involved in colony formation and maintenance.

It is unlikely that differential mortality of juveniles of different species of surgeonfishes in different habitats would be involved since juveniles and adults occur in different habitats. Habitat preferences of *A. lineatus* influence the location of colony formations. However, limitations in the availability of preferred habitat do not appear to bring about the aggregation of territories. We consider *A. lineatus* colonies to be colonies in the general sense that Brown & Orians (1970) have used the term — the clumping of individuals that is 'greater than would be expected on the basis of resource patchiness,' with the selection of territory sites being 'positively influenced by the prior residence of other individuals'. Whether or not Itzkowitz's damselfish 'colonies' are colonies in this sense remains to be determined. The monospecific nature of *A. lineatus* colonies is, we think, maintained by their having priority of access to vacancies in colony areas. This priority is the result of *A. lineatus* dominance abilities rather than a tendency for existing colony residents to repel potential recruits of other species (e.g. *A. leucosternon*) more strongly than they repel conspecific recruits.

(iii) Vertical zonation — There are two questions we wish to consider here. (1) Why should adult *A. lineatus* colonies be subtidal rather than intertidal, while all-juvenile colonies are concentrated in the intertidal zone? (2) Why should adult *A. lineatus* colonies be in strips along the shallowest parts of the subtidal zone rather than in deeper areas?

Several factors may operate to restrict adult *A. lineatus* to subtidal areas. Firstly, for a fish to defend an algal mat adequately, it must be able to remain with the mat whenever other potential users of it are in the vicinity. Small fishes can remain in intertidal areas for larger proportions of the tidal cycle than can larger fishes, such as adult *A. lineatus*. Thus they would be able to exploit an intertidal mat owned by a large fish when the latter was forced into deeper water. Juvenile *A. lineatus* are small enough to remain on their intertidal territories much longer than adult conspecifics, and can thus adequately defend their mats. Secondly, intertidal areas may be physically unfavorable to the growth of types of algae that occur in the mats of adult *A. lineatus*, although the edges of mats of adults along the shallow edges of colonies were often barely awash at low tide. Thirdly, intertidal areas were even farther from shelter than were subtidal areas. Consequently, the risks of maintaining territories there may have been too high for adult *A. lineatus*.

Any or all of several possibilities may have made shallow subtidal areas preferable to deeper areas for *A. lineatus* colonies: (1) The shallower areas contained the largest, most continuous expanses of relatively, bare rock, with the least amounts of sand and rubble patch admixtures. As sand and rubble are unstable, they are less suited to sustained algal growth than bare rock. Flat rock in these shallow, surgier areas was also less subject to covering by sediment than it was in deeper areas. Substrate conditions were thus best in these shallow areas for the formation of large, continuous areas of algal matting, and thus for the formation of large, high density colonies. (2) Physical conditions, such as light availability, may be most favorable to high productivity of algae (or of specific types of algae) in shallower water. (3) Subtidally, the lowest relief areas are in the zone occupied by *A. lineatus*. Territories on such a substrate can be more efficiently defended than can those in high relief areas, because a fish in the former type of habitat is better able to monitor continuously the greatest proportion of its territory. The following is an example of this effect in operation: Adult, wandering *A. lineatus* that moved back and forth through conspecific colonies stealing algae from territories had mixed success in doing so, depending on whether or not they were hidden from the view of a territory owner by a substrate irregularity. Of the bites six wanderers took in occupied conspecific territories in two hours of observations, 65% were obtained while the intruder was hidden from the owner's view. These wanderers also managed to take far fewer bites per feeding bout when visible to the territory owner at the start of such a bout than when hidden from the owner's view [mean number of bites per bout = 3.2 ± 0.5 ($n = 74$) and 26.4 ± 6.8 ($n = 17$), respectively.]

9.1.3 *A. leucosternon*'s feeding strategy

(i) Feeding efficiency and the type of algal mat – We think that the morphological differences between the two *Acanthurus* spp. (*A. leucosternon*'s smaller size, smaller mouth, oral rostrum, more ovoid body with larger median fins, and more truncate tail) give *A. leucosternon* greater physical flexibility in its feeding behavior than *A. lineatus* has. That is, while *A. leucosternon* can feed as efficiently as *A. lineatus* on the same types of algae taken from the types of microhabitats that the latter uses, *A. leucosternon* can feed more efficiently than *A. lineatus* on smaller, more sparsely scattered algae and small growths in

crevices. *A. leucosternon* is then capable of more generalized feeding than *A. lineatus*.

(ii) The absence of colonialism, and the dictation of an alternative strategy – Given that *A. leucosternon* can more efficiently feed on a lower standing crop mat than *A. lineatus*, what factors might be involved in bringing about *A. leucosternon*'s maintenance of such a mat, rather than one of either lower or higher standing crop?

Firstly, we suggest that because of its morphological limitations *A. leucosternon*'s feeding efficiency would be less on a lower standing crop mat (see section 9.1.4). Secondly, we suggest that *A. leucosternon* does not possess a higher standing crop mat because it could not economically defend such a mat. We have previously emphasized that a high level of defensibility is of major importance to the maintenance of a high standing crop algal mat, and that defensibility is determined, in part, by the quality of the habitat in which a territory is located. In a habitat in which a territory owner was unable economically to maintain a high standing crop mat of algae and ensure that a high proportion of the territory's production was reserved for its own use, one economically viable alternative strategy could take the form of relying on a combination of (a) maintaining a moderate standing crop algal mat that (i) could not be efficiently exploited by certain species, (ii) could be cropped (i.e. drained) at only a low rate by intruding competitors, and (iii) was less readily damageable (and quicker to regenerate?) than a high standing crop mat; and (b) feeding in certain microhabitats more efficiently than other species that use the same types of algae. The intensity of interspecific competition for food that such a species was involved in would be lower than one using an *A. lineatus* type of mat. By utilizing the proportion of the territory's production that was least accessible to other species, and 'abandoning' the most accessible proportion to those species, a territory owner could 'afford' less efficient defense. The drain of resources to other species, competitors and otherwise, could be offset by the territory owner having a comparatively large territory, i.e. a territory in which the owner's biomass density was low. This we suggest is *A. leucosternon*'s strategy.

How does the information that we have on (i) the nature of the habitat zones in which *A. leucosternon* is predominantly found and (ii) the amount and effectiveness of *A. leucosternon* pairs' defense activity bear on this hypothesis?

Firstly, reduced defensibility of a territory could be the result of either increased territory size or increased isolation of territories. The zone in which *A. leucosternon* lived was structurally more heterogeneous than the *A. lineatus* zone, particularly in deeper areas. Thus, substrate that we think was best suited to the sustained production of algae used by *A. leucosternon* was distributed in smaller, more dispersed patches than in the *A. lineatus* zone. This substrate was bare rock, and especially the higher points of such rock, which were least subject to movement, sedimentation, and abrasion by rubble movement. *A. leucosternon* territories were centered on such isolated high points, on which most of the territory holder's feeding was done. Because *A. leucosternon* extended into deeper water than *A. lineatus*, the territories of the former might have tended to be in zones of lower productivity (because of reduced light availability and altered light quality?). A larger territory would be required to support the same mass of fish in such a case. In the *A. leucosternon* zone then we can see how certain factors may dictate that territories should be relatively isolated and enlarged.

Secondly, *A. leucosternon* pairs defend their territories against fewer species of algivorous fishes than does *A. lineatus*. Despite this, in several respects *A. leucosternon* social units expend more effort than *A. lineatus* in the defense of their territories, but are less effective in preventing losses of algae to competitors that the latter species: (1) *A. leucosternon* expend more defense effort (as measured by the frequency of encounters per territory, and per unit area of the territory) against members of other species and members of all species than either *A. lineatus* or *Z. scopas* do, although *A. lineatus* is more vigorous in each defensive action. (2) *A. leucosternon* have more feeding in their territories by competitors than do *A. lineatus*, competitors such as resident *A. nigrofuscus* juveniles, *A. triostegus* schools, neighboring *Z. scopas* and individuals of species such as *Melichthys* sp.

9.1.4 *Z. scopas*' feeding strategy

Our ideas about *Z. scopas*' feeding strategy and how it compares to those of the two *Acanthurus* spp. can be summarized as – the *Z. scopas* pattern represents an extreme form of the *A. leucosternon* pattern.

The morphological characteristics of *A. leucosternon* that we think give *A. leucosternon* greater physical flexibility in its feeding than *A. lineatus* has, are even more pronounced in *Z. scopas*. These, we think,

enable *Z. scopas* to feed efficiently on a lower standing crop mat of more dispersed algae, and to feed more efficiently in a wider range of microhabitats than *A. leucosternon* can.

Why should we see *Z. scopas* living in even larger territories than *A. leucosternon* and feeding in a wider range of microhabitats and from a lower standing crop mat than the other two species? In part we suggest that this may be the result of *A. leucosternon* having preempted the patches of higher quality substrate in the zone it shares with *Z. scopas* (see section 9.1.6). A restriction to a low quality habitat would result in *Z. scopas* requiring more substrate area per unit mass of fish than is required by *A. leucosternon* in the same zone. Consequently *Z. scopas* has larger and less defensible territories than *A. leucosternon*. Because *Z. scopas* can probably more efficiently exploit certain resources than most other species in the area, it could offset the loss of that part of the territory's production that is more exploitable by other species. The drain on the substrate's algal production to both dissimilar and similar species, which is higher from *Z. scopas* territories than from those of either *Acanthurus* spp., could also be offset by *Z. scopas* maintaining larger territories (both absolutely and relative to body weight) than either *Acanthurus* spp. *Z. scopas* defense effort is the lowest of the three species because it is able to ensure itself of an adequate food supply by means other than intense defense of a widely exploitable resource.

The ideas that we have presented above on the differences in the abilities and feeding strategies of *Z. scopas* and *A. leucosternon* are consistent with the differences that exist in the patterns of zonal distribution of these two species. In the deep, coral-rich zone that contained both juvenile and adult *Z. scopas*, but only juvenile *A. leucosternon*, hard substrate suitable for algal growth was available in even smaller and more dispersed patches than in the study area. We think that in such a low-defensibility habitat only a small, *Z. scopas* sized fish that was efficient at obtaining food resources that were unavailable to many other species could exist. We suggest that juvenile *A. leucosternon* can also exist in this zone because their small size allows them to exploit food in the same way as *Z. scopas*.

9.1.5 Morphological variation in relation to feeding strategies

In preceding sections (9.1.2–4) of this discussion we have considered how morphological differences be-

tween the three species affect their ability to feed efficiently on algal mats of differing physical structures and in different types of microhabitats. We considered size, structure of the trophic apparatus, and body and fin shapes. Morphological differences between the three species probably also influence the efficacy with which their different feeding strategies operate in a variety of other ways:

(i) Size differences – The comparatively large size of *A. lineatus*, could prove advantageous in two ways. Firstly, because larger fishes can swim faster than small ones (other factors being equal) large size could be important to a fish defending a territory in a shelter-poor habitat from which it has to flee quite regularly, when predators approach. Secondly, although larger size does not necessarily provide an advantage in intra- and interspecific aggressive interactions it often can do so. For instance, large *A. lineatus* dominate smaller conspecifics, and adult *A. leucosternon* often dominate smaller juvenile and subadult *A. lineatus*. [On the other hand, many species of damselfishes successfully defend their feeding territories against fishes of a wide range of species, including some up to several orders of magnitude larger.] An advantage in size could be important to *A. lineatus* in the maintenance of territories that require highly effective defense. *A. lineatus*' larger size could also give it an advantage in any disputes with *A. leucosternon*, for example, over access to vacated space. Because *A. lineatus* apparently has more precise requirements than *A. leucosternon* for the type of space it will take over, any factor that contributed to its having priority of access to vacated space would be useful to *A. lineatus*.

Similarly, *A. leucosternon*'s size advantage could give it an advantage over *Z. scopas* in interspecific contests for vacated space. In view of the apparently greater precision of *A. leucosternon*'s requirements this could be a useful advantage.

Conversely, small size could be advantageous to *Z. scopas*. A fish that, because of its morphological limitations, was unable to flee rapidly would be able to make better use of shelter in the vicinity of its territory if it were comparatively small. In relation to the other two species, *Z. scopas* appears to require a larger area to support each unit of its mass. Increased size in *Z. scopas* might prove disadvantageous, by obliging an increase in territory area beyond a size that can be efficiently patrolled and defended. Small size may also increase the efficiency with which it obtains food in less accessible microhabitats.

(ii) Body and fin shapes – *A. lineatus* has the most fusiform body and the largest and most lunate tail of the three species. These characteristics, which are most pronounced in fishes capable of rapid movement (Alexander 1967), should enable it to flee from shelter-poor habitats more rapidly than either *A. leucosternon* or *Z. scopas* could. Thus, *A. lineatus* can probably safely exploit environments that are too dangerous for the other two species to live in.

(iii) Caudal spines – Barlow (1974b) drew attention to a relationship between the relative size of the caudal spines of different acanthurid species and the position of each species in interspecific dominance hierarchies. He pointed out that *A. triostegus*, one of the least aggressive and most subordinate species, had a very small caudal spine. Of the three species that we have studied *Z. scopas*, with the smallest spine, is the least aggressive species, and *A. lineatus*, with the largest spine, the most aggressive. In some of the fighting that we observed surgeonfishes appeared to be using these spines as weapons. The possession of relatively large spines could provide species such as *A. lineatus* with an advantage during interspecific fights.

(iv) Color patterns – The significance of the bright distinctive colors of many reef fishes and the abilities of fishes to perceive such colors has been the focus of work by reef fish biologists for more than fifty years (Longley 1914, Townsend 1929, Cott 1940, Hamilton & Peterman 1971, Peterman 1971, Munz & McFarland 1975, Thresher 1977). The proposal by Lorenz (1962, 1966) that the striking poster-colors of many reef fishes, including *A. leucosternon*, serve as intraspecific signals functioning in territory defense has aroused considerable attention, much of it recently in the form of adverse criticism (Brockman 1973, Brown et al. 1973, Thresher 1976a, 1977, Hamilton & Peterman 1971, and especially Myrberg & Thresher 1974 and Ehrlich et al. 1977). While the accumulated data have shown clearly that Lorenz overstated the case, we can see how his idea can be applied to explaining the significance of the differences in the color patterns of the three species that we are dealing with here.

Firstly, we suggest that to be properly applied the poster-coloration hypothesis needs to be restated, because in its original form it was oversimplified. Such a restatement should take into account not only the physical properties of poster colors, but also the general nature of the presumed signal function they serve. Poster patterns are relatively permanent, highly

conspicuous patterns, that are usually of comparatively simple design. They serve to communicate, with a high degree of precision, the identity of the bearer at a great distance. Lorenz proposed that poster patterns served in intraspecific territorial interactions. However, the multispecific nature of the territoriality of many reef fishes, including some of the species Lorenz considered, necessitates an alteration of this proposition to one in which the colors serve for territory advertisement of either an intra- or interspecific nature.

Such a restatement should not only take into account what factors might favor the development of poster coloration but also what might act against it. We might expect the development of poster coloration for territory-advertisement in a strongly aggressive species when intruders into its territories could rapidly do significant damage to the resources being defended and should therefore be strongly 'warned' away. We might also expect to see it when a territory owner tends to be relatively isolated from the fishes with whom it 'needs' to communicate. However, the development of such coloration would be less likely to occur if color crypticity was important as an anti-predator defense than if other effective defense mechanisms (morphological or behavioral) were available. We should also less likely see such poster coloration in carnivorous fishes that feed on prey with well developed vision than in fishes that feed on plants or on other types of animals.

Are the differences in the color patterns of the three acanthurids, which are all herbivores, consistent with the poster coloration hypothesis? Firstly, *Z. scopas* appears to be less reliant on interspecific defense of food than either of the other two species. Its color pattern might, therefore, be expected to have the fewest poster characteristics of the three. It is in fact the most dully and cryptically colored species.

A. leucosternon needs much more effective and continuing defense than does *Z. scopas* and *A. leucosternon* expends a greater defense effort against a wider range of species. Also, the *A. leucosternon* territory is reasonably large and relatively isolated. Therefore, it could be advantageous for the territory owner, in this case, to use poster colors to indicate its presence to potential intruders. *A. leucosternon* epitomizes the poster colored fish. Lorenz (1962) used it as an example of this form of coloration.

With *A. lineatus* the situation is more complicated. We have emphasized above that this species requires the most continuous and effective defense of the three, because of the exploitability and fragility of its territory's resources. Therefore, we might expect *A.*

lineatus to have a poster pattern. Instead *A. lineatus*' pattern is intermediate in conspicuousness between those of the other two species, and is the most changeable pattern of the three. This apparent anomaly can be resolved, we think, by considering the results of its living in high density colonies in a shelter-poor habitat. *A. lineatus* can afford to rely less than *A. leucosternon* on advertising to defend its territory because (i) it is a large, aggressive fish that occupies a small, easily monitored and patrolled territory; and (ii) each territory is protected in part by the presence of contiguous colony neighbors. Also, to some degree, the colony acts as an advertising unit: a potential intruder can be made aware of the existence of a concentration of a highly aggressive fish by the sum of a series of individual advertisements that are each not as strong as an *A. leucosternon* advertisement. *A. lineatus* live in a habitat in which avoidance of attracting a predator's attention may be important. Thus, not only does this species require poster coloration less than *A. leucosternon* does, but poster coloration could prove disadvantageous to it.

The flexibility of *A. lineatus*' coloration, and the possession of a basic pattern that is most visible at close proximity (to humans at least) are also a reflection of its colonial habits, and pronounced territory defense requirements. By being able to make basic changes in the structure of its pattern and exhibit a pattern resembling the *A. leucosternon* pattern when a serious intruder-threat develops (the approach of *A. triostegus* schools for instance) *A. lineatus* can advertise when it is most useful to do so, without having the disadvantage of a permanent pattern. Possession of a pattern that is useful for near distance communication and the capacity to alter the pattern in subtle ways (Nursall 1974) also enables *A. lineatus* to deal with the complexities of communication that are necessitated by colonial life — life in a monospecific group of highly aggressive competing individuals living in close proximity to one another.

9.1.6 Interspecific competitive interactions and zonation patterns

(i) Among adult surgeonfishes — We think that there is an interspecific dominance hierarchy among the three species, a hierarchy that can determine which of them takes control of disputed areas of substrate. We see *A. lineatus* as being aggressively the dominant species and *Z. scopas* as the most subordinate. It is also very likely that each species prefers a different type

of habitat, or, at least, that *A. lineatus* has the most precise habitat requirements of the three and *Z. scopas* the least precise.

If such is the case why should we have found such distinct overlaps in the zonation patterns of the three species? This can be accounted for by the following combination of two factors: (1) that the habitats preferred by each were not perfectly zoned, and (2) that the two *Acanthurus* spp. were not at the carrying capacity, i.e. that more of the adults (at least) of these two species than were actually present could have been accommodated in the habitat preferred by each and that a higher proportion of the relevant zones could then have been occupied by each. If a dominant species was kept below the carrying capacity (by predation?, Paine 1966) a subordinate species would be able to extend its range into habitat of a type that the dominant species would otherwise be expected to occupy.

We know of no studies to date that show clearly, or even indicate strongly, that the population of any coral reef fish is below the carrying capacity of its habitat. The evidence that *A. lineatus* was below the carrying capacity is circumstantial. Some areas adjacent to *A. lineatus* colonies, and in the same depth zone, had a substrate similar to areas occupied by colonies. Because of *A. lineatus*' requirement of an algal mat of a particular nature, this expansion would be expected to be a slow process that was most efficiently accomplished by gradual accretive growth of existing colonies or the formation of new ones. We also could not see a competitor capable of preventing such a gradual expansion.

With *A. leucosternon* the data are stronger. Later we argue that the normal adult social unit of *A. leucosternon* is a pair and that it is disadvantageous for a female to remain unpaired (see section 9.3.2). We think that the presence of unpaired females in the population is a reflection of an imbalance in the adult sex ratio produced by differential mortality on the sexes. Males, we suggest, run a higher risk of being eaten, perhaps because of their greater social activity and smaller size. If this biased sex-ratio is caused by such mortality then the population is probably below the carrying capacity. Although it is possible that an increase in the number of males sufficient to balance the sex-ratio, would bring the population up to the carrying capacity, we suspect that the *A. leucosternon*/*Z. scopas* zone could accommodate more *A. leucosternon* pairs than merely equalizing the sex ratio would add. This would result in a reduction of the number of *Z. scopas* there. Whether or not the *A. leucoster-*

non population in the *A. leucosternon*/*Z. scopas* zone could rise to a level at which *Z. scopas* would be totally excluded from that zone is another matter.

(ii) Between juveniles and adults of the same species – Habitat segregation of juveniles and adults of the same species occurred in all five species of microalgae consuming surgeonfishes – *A. lineatus*, *A. leucosternon*, *A. nigrofuscus*, *A. triostegus* and *Z. scopas*. Three factors were probably involved in the production of these patterns of spatial distribution:

(1) The requirements of one age class are met in a wider range of habitats than were those of the other age class: Juveniles of *A. lineatus* and *A. leucosternon*, for instance, seem to have had their requirements met in a broader range of habitats than did their respective adults.

(2) Only one age class is competitively excluded from a habitat: It appears very likely that adult *A. nigrofuscus* were almost completely excluded from the *A. leucosternon*/*Z. scopas* zone. Juveniles of the same species were able to maintain a much stronger presence in that zone (see section 9.2.1).

(3) Predator pressures (or risks) exclude only one age class of a species from a particular habitat. Predation risks may be one reason why adult *A. lineatus* extended only to the outer periphery of the reef crest (see section 9.1.2) while juveniles were common throughout that zone. Predation risks, in combination with competitor pressures, may have excluded juvenile *A. triostegus* from subtidal areas in the following way. Because of the abundance of more dominant species of both the same and larger sizes it seems unlikely that juvenile *A. triostegus* could have gained access to food in that area other than by forming feeding schools. However, perhaps because of high predation risks, feeding schools of small herbivores formed only rarely in that area (see section 9.2.1i).

9.1.7 Geographic variation in feeding strategies

The discussion given to the feeding strategies of the three species that we have presented above should not be regarded by the reader as an attempt to make definitive statements about the characteristics of species throughout their geographic ranges. Among the few other herbivorous reef fishes that have been examined in sufficient detail, there is evidence that such fishes are capable of employing different strategies in the same area and hints that they may also do so in

different areas (Ogden & Buckman 1973, Barlow 1974a, b, Vine 1974, Robertson et al. 1976).

A few data are available on the occurrence of geographic variation in the feeding strategies used by *A. lineatus* and *A. leucosternon*.

(i) In *A. lineatus* – One of us (D.R.R.) has made some short-term observations on *A. lineatus* that are relevant to this discussion, at a site well removed from Aldabra. These were made during November 1977, at Heron Islands, on Australia's Great Barrier Reef, at the same site where Nursall (1974) studied the territoriality of that species. Heron Reef is a large oval reef with its long axis (and that of Heron Island) running roughly east-west. Nursall made his observations on the southwestern face of the reef (to the south of the research station). There he found *A. lineatus*, which was not very common, defending individual territories at the upper edge of the reef slope, at the interface of intertidal and subtidal areas. D.R.R. found *A. lineatus* to be much more common on the outer face of the reef edge to the north-northwest of Heron Island. This latter face is much more exposed to heavy wave action than the face containing Nursall's study area and is subject to repeated episodes of erosion by storm and cyclone action (e.g. see Connell 1973). Although *A. lineatus* was not as common in that area as at the Aldabra site, several colonies of up to about a hundred adults were found. These were located on stretches of flat coralline-rock substrate, at the interface of inter- and subtidal areas. Distinct algal mats were present in these fishes' territories, and their owners were actively attacking a wide range of herbivorous fishes – at least 14 species of parrotfishes, surgeonfishes and rabbitfishes (Siganidae).

What these observations suggest is that in widely separated areas this species applies the same feeding strategy in the same type of habitat, a habitat that is produced by the same physical mechanisms in both sites. This does not mean that the feeding strategy that we have described here is an invariable characteristic of the species, throughout its geographic range. Hiatt & Strasburg (1960) described *A. lineatus* as being 'locally abundant' at one site in the central western Pacific, 'where it occurred in large schools on the seaward reef flats as the tide rose ... When the seaward reef flats are largely exposed during low tide, schools of this species swim back and forth just beyond the outer reef margin.' Different feeding strategies are evidently applied by this species in different localities. What factors determine which of more than one strategy is applied in any one site we do not know.

(ii) In *A. leucosternon* – The only information available to us on the behavior of *A. leucosternon* in other localities is a photograph taken by R. Salm in the Seychelles islands, not far from Aldabra. This shows what appears to be part of a feeding school of adult *A. leucosternon* containing at least a few dozen fishes. The significance of such behavior, which we never saw at Aldabra, escapes us at the moment.

9.2 Community organization in the study area

9.2.1 Acanthurid feeding strategies in the study area

(i) The availability of strategies based on the use of small soft algae – *A. lineatus*, *A. leucosternon* and *Z. scopas* were the only species in the subtidal portion of the study area that (1) relied exclusively on turfs of microalgae, (2) were territorial, and (3) whose adults existed in significant numbers in that zone throughout the study period.

The only other acanthurid species with similar diets that occurred in the study area were *A. nigrofuscus* and *A. triostegus*. Fishes of all sizes of these two species were aggressively dominated by *A. lineatus*, *A. leucosternon* and *Z. scopas*. Both juvenile and adult *A. nigrofuscus* were also dominant over *A. triostegus*. Of the territorial individuals of these two species, *A. nigrofuscus* predominated in the *A. leucosternon*/*Z. scopas* zone. The great majority of these *A. nigrofuscus* were juveniles (190 out of 196 when we first began the study). While they were abundant at the start of our study the numbers of those juveniles decreased gradually over the next 12 months. Just before we left Aldabra their numbers had declined by 26%. Six months later Robin Bruce found no juveniles at all on the reef slope and only nine adults. It seems quite possible, therefore, that juveniles of this species were only ephemerally present in significant numbers in such subtidal areas; either that or they were present cyclically, in what could be considered to be a nursery ground. Not only were the adults of this species uncommon subtidally but those that were present in that zone were small for the species. Also, while the territorial *A. nigrofuscus* adults that we saw there were repeatedly noted at the same sites in the study area (at the edges of and in the interstices of *A. leucosternon* and *Z. scopas* territories) those sites were occupied only intermittently by such fishes.

With *A. triostegus* a similar situation obtained, al-

though no juveniles entered the *A. leucosternon*/*Z. scopas* zone. The few territorial adults present were found in between *A. leucosternon* and *Z. scopas* territories in areas not occupied by *A. nigrofuscus* adults or juveniles. Like *A. nigrofuscus*, they occupied their territories only intermittently. Observations on eight tagged individuals showed that, over periods of up to several months, they would repeatedly leave their territories (after remaining on them for an hour or two) and join feeding schools of conspecifics in the same zone.

This pattern of the spatial distributions of the adults of both *A. nigrofuscus* and *A. triostegus* suggests to us that adult *A. lineatus*, *A. leucosternon* and *Z. scopas* had effectively occupied the available range of feeding strategies that were based on the defense of the type of algal resources they use. That is, three more aggressively dominant species had almost totally preempted certain alternatives that adult *A. nigrofuscus* and *A. triostegus* could have used, and neither of the latter species was sufficiently morphologically specialized to have exploited any class of algal resources more efficiently than any or all of those three species.

The only remaining territorial alternative apparent to us involved an animal avoiding expulsion by aggressively more dominant species by relying in small size to shelter in sites that were inaccessible to larger fishes. This alternative was occupied by juvenile *A. nigrofuscus*.

In the intertidal part of the study area, which was largely unoccupied by our species trio, there were many territorial adults and juveniles of both *A. nigrofuscus* and *A. triostegus*. Probably because of its nonavailability for part of the tidal cycle, the paucity of shelter, and perhaps the effects of regular lowtide exposure on algae, it seems to have been a habitat that the adults of all five acanthurids considered here preferred less than other habitats. The adult *A. nigrofuscus* present there were small for the species. We regularly saw carangid fishes attempting to prey on surgeonfishes there. The movement of large feeding schools of adult *A. triostegus* into subtidal areas also suggests that *A. triostegus* was not particularly successful in the type of intertidal habitat represented in the study area.

Subtidally, the remaining strategy that appeared to be available to acanthurids with this type of diet was employed by adult *A. triostegus*. These fishes formed feeding schools that territory holders of the more dominant species could not totally prevent entering their territories. This schooling met with mixed suc-

cess, and obtained better results in the *A. leucosternon*/*Z. scopas* zone than in the *A. lineatus* zone. If schooling represents a successful counter to territoriality, colony formation represents a successful counter tactic to schooling.

One aspect of feeding school formation puzzles us – why juvenile *A. triostegus* and *A. nigrofuscus* of any size class did not form feeding schools in subtidal areas, or join adult *A. triostegus* schools there. Barlow (1974b) has reported that *A. nigrofuscus* forms such schools in other parts of its range, and very infrequently we saw small groups (of up to a score of fish) of small *A. nigrofuscus* feeding together. On several occasions we noted small feeding schools of juvenile parrotfishes moving into the *A. leucosternon*/*Z. scopas* zone for short periods. During these excursions they did little feeding, and were continually harassed by attacks from small predatory groupers that followed them about. Contrary to what might be expected schooling did not appear to provide protection to subtidal *A. triostegus* against all classes of predators. While such schools typically condensed when attacked by groupers, at the mere approach of large carangids to within 25 m they characteristically shattered as their members fled in all directions.

(ii) Strategies based on benthic macroalgae and their relation to those based on small algae – The foraging habits of the remaining nine species of surgeonfishes present in our main study area on Aldabra were of two types. (We examined the stomach contents of at least 20 subadults and adults of each of these species.)

(1) The sand feeders (*Ctenochaetus striatus*, *C. strigosus*, *Acanthurus gahhm*, *A. tennenti* and *A. dussumieri*) consumed large quantities of sand and sediment (see also Jones 1968), and very little sessile algae of the type eaten by *A. lineatus*, *A. leucosternon* or *Z. scopas*. We shall not deal further with these in this discussion, beyond pointing out that (a) the first two species were extremely abundant in the study area, and the latter pair rare there, but abundant elsewhere; and (b) in and near the study area the first three species were permanently territorial and formed pairs (Table 17), while *A. tennenti* defended territories either solitarily, or in 'pairs' (of what sexual composition is not known). In shallow subtidal areas at Dune D'Messe, on the southern face of the atoll, *A. tennenti* was one of the most abundant surgeonfishes in a type of habitat not represented in our study area. There it did not appear to be territorial.

(2) The browsers on benthic macroalgae (i.e. al-

gae larger than those used by *A. lineatus*, *A. leucosternon* and *Z. scopas*) comprised *Naso lituratus*, *N. unicornis*, *Z. veliferum* and *N. brevirostris*. All four species reached sizes greater than that of *A. lineatus*. The first two *Naso* spp. fed on larger tougher types of algae than the latter two, while *Z. veliferum* took in smaller softer types than *N. brevirostris*. *N. brevirostris* also ingested large amounts of zooplankton during its frequent, prolonged, episodes of midwater feeding.

Of those four species, only *N. lituratus* and *Z. veliferum* defended feeding territories in the study area. Their territories were centered in subtidal areas, although those of *N. lituratus* also extended into intertidal areas. Outside the study area some *N. lituratus* adult social units had their entire territories in the zone equivalent to the intertidal portion of our study area. However, not all adults of that species living in intertidal areas appeared to be territorial. The territories of both these species were very large, the study area being divided between territories of two-three adult social units (Table 17) of each species. The territories of both of these species overlapped interspecifically with each other and also with those of *A. leucosternon* and *Z. scopas*. While territorial *A. lineatus* repulsed intruders of both these species *A. leucosternon* and *Z. scopas* reacted aggressively to only *Z. veliferum*. Even so, *Z. veliferum* often fed relatively unmolested in the territories of both *A. leucosternon* and *Z. scopas*. We never observed *Z. veliferum* for-

aging in the manner described by Jones (1968), i.e. in large schools roaming in intertidal areas. He also described *N. lituratus* as forming small schools that fed in intertidal areas, something that we did not see in the vicinity of our study area. Barlow (1974a) described *N. lituratus* as forming both territorial groups and small schools.

The remaining two browsers, *N. unicornis* and *N. brevirostris*, roamed widely while feeding, either singly, or in schools of up to several dozen fishes. Both Hiatt & Strasburg (1960) and Jones (1968) described similar behavior by *N. unicornis* in the western Pacific Ocean. *N. unicornis*, which is morphologically very similar to *N. lituratus* was also regularly attacked by territorial adults of the latter species, but did accomplish some feeding in that species' territories. Both these nonterritorial *Naso* spp. restricted their substrate feeding to intertidal areas: 96% and 98% of substrate bites taken by *N. brevirostris* and *N. unicornis* respectively ($n = 4.5$ and 8.5 h observations) were from such areas. The aggressive activities of both *A. lineatus* and subtidal *N. lituratus* (which seemed to be more aggressive towards *N. unicornis* than intertidal *N. lituratus* were) probably played a part in producing that pattern of feeding in *N. unicornis*. In subtidal areas *N. brevirostris* fed on plankton in midwater. It was not attacked by other species in the *A. leucosternon*/*Z. scopas* zone.

The feeding strategies of these four browsing species relied primarily on the use of algal resources that

Table 17. Sexual dimorphism in size in pair-forming¹ Acanthurids at Aldabra.

Species	Maximum size	Number of females per pair	Number of pairs examined	Mean difference in size of male and his largest female
<i>A. gahhm</i> mass standard length	377 g 202 mm	1-2	9	male heavier ² by 63%
<i>G. striatus</i> ³	205 g 161 mm	1-4	8	male heavier ³ by 25%
<i>C. strigosus</i>	120 g 133 mm	1-3	9	male heavier by 47%
<i>Z. veliferum</i>	342 g 198 mm	1	9	female heavier by 46%
<i>N. lituratus</i>	610 g 265 mm	1 ⁵	4	male heavier by 27%

¹. Pair = apparently long term association of a male and one or more females.

². In one of the nine cases, the female was slightly heavier but shorter than the male.

³. As for 2 in one of eight cases.

⁴. Many individuals of this species were not in pairs.

⁵. Barlow 1974a reported that this species formed pairs containing more than one female.

were not used by those surgeonfishes that dominated the assemblage in numbers and biomass. Each of the four used a different strategy:

Z. veliferum's morphology, which closely resembles that of *Z. scopas*, probably both restricts it to subtidal areas where shelter is most available and at the same time allows it to concentrate in feeding on algae that are growing in microhabitats that are less accessible to other species with similar diets. Jones (1968) found that in his study areas in central western Pacific both *Z. veliferum* and its congener *Z. flavescens* (which is very similar in morphology and size to *Z. scopas* — see Randall 1955b) fed on filamentous algae. The segregation in the types of algae the two *Zebrasoma* spp. ate at Aldabra could have been due to a combination of (1) the *Acanthurus* spp. being competitively superior to the *Zebrasoma* spp. in using a larger proportion of the small turf algae resource, and (2) *Z. scopas* small size giving it an advantage over *Z. veliferum* in using the remaining proportion, which represented the *Acanthurus* 'leftovers.' That is, *Z. veliferum* may have been outcompeted in the use of microalgae, and, therefore, been 'forced' to rely on somewhat larger algae that were scattered about in its very large territories. Alternatively, of course, its Aldabran diet could have represented some sort of optimal diet.

N. lituratus adults seemed to have only one inter-specific competitor for the same type of food resource, *N. unicornis*. Although there are no external differences in the morphology of these two species that would suggest one was able to exploit certain resources more efficiently than the other, Jones (1968) did find differences in the diets of these two species in some of his study areas. He suggested that differences in the structure of the teeth of these two species gave *N. lituratus* an advantage over *N. unicornis* in feeding on at least one alga. At Aldabra *N. lituratus* seems to have relied to a large extent on aggressively excluding *N. unicornis* from certain areas or moderating its feeding activity in those areas.

N. unicornis grew to over three times the size of *N. lituratus* at Aldabra. The larger individuals of the former species foraged outside the study area on the intertidal reef flat much further in from the seaward edge than *N. lituratus* did. Their large size may have enabled them to do so by reducing their vulnerability to predators (by permitting increased flight speed and increasing the effectiveness of morphological defenses such as fin-spines, caudal knives and tough skin).

The absence of territoriality in *N. unicornis* for-

aging in intertidal areas could have been due either to algae not being economically defensible there, or being sufficiently abundant so that they were not competing for food. To us the latter situation seemed distinctly possible. Macroalgae were abundant on many intertidal areas, where there were few fishes feeding on them. Pieces of such algae that were dislodged and carried out over the edge of the reef on the ebbing tide were readily picked out of midwater and eaten by a variety of subtidal acanthurids. We think that high predation risks in shelter deficient intertidal areas prevented the build up of populations of many (all?) species of acanthurids in such areas well away from the reef edge.

The remaining species, *N. brevisrostris*, foraged heavily on other food besides benthic algae, and may not have been competing to any significant degree with acanthurids that were relying exclusively on benthic algae.

Thus, the two of these four species that relied on benthic algae growing in or close to subtidal areas were much more obviously involved in both intra- and interspecific competition for food than the two that foraged in other areas or on other food. This we attribute to the presence of sufficient shelter in subtidal areas permitting the build up of populations of a variety of algivorous fishes to the point where a high proportion of the substrate's production was being continuously used. As most of that productivity was being directed into other species of algivores, many of which (surgeonfishes, parrotfishes and damselfishes) fed on other than macroalgae, it is not surprising that both *N. lituratus* and *Z. veliferum* had very large territories. Their food was probably available in quite low densities.

9.2.2 Mechanisms of coexistence of browsing acanthurids

Classically, one answer to the question 'how does the multitude of species present in many tropical communities coexist, in the face of the possibility of competition and competitive exclusion?' would be couched in terms of specialization. It might take the following form: each species has a different set of resource requirements and abilities that give it an advantage over all potential competitors under some circumstances. The coexistence of a large number of species of reef fishes in both relatively large areas (whole reefs) and small areas (arbitrarily defined 'habitats') would then be explained in terms of fine scale parti-

tioning of resources (for reviews see Sale 1977, and Connell 1978).

These notions of high degrees of resource partitioning between species of reef fishes and species differentiation in terms of habitat and dietary requirements and competitive abilities have been criticized by Sale, in a series of papers on territorial algivorous damselfishes (Sale 1974, 1975, 1976, 1977, 1978, also Sale & Dybdahl 1975). Sale maintains that the data available on algivorous reef fishes do not indicate that sufficient resource partitioning exists to explain the coexistence of so many species by that mechanism, and has cited Jones' (1968) work as providing some support for his argument (Sale 1977).

In his 1968 paper Jones addressed in detail the problem of the coexistence of a set of sympatric acanthurids. He found evidence of a considerable degree of ecological segregation of the different species in combinations of their diets, morphological adaptations to feeding and habitat distributions. He also suggested that the overlaps in diets that he observed were due to an absence of competition in certain areas, a point that seems to have been overlooked in Sale's (1977) paper.

The results of the present study are pertinent to the discussion on mechanisms of coexistence that has been presented by Sale. The study we undertook constitutes the most detailed examination of interspecific relations between a group of closely related algivorous reef fishes living in one small area to date [Jones (1968) worked over much larger areas]. In this paper we shall consider only the nine species that browsed on benthic macroalgae and microalgal turfs since there was evidence of pronounced competition for food and feeding areas between many of those species. Our remarks are also largely directed at adults' interspecific relations, because most of our data deals with them rather than juveniles. This does not mean that we consider the ecology of juvenile acanthurids to be irrelevant to the question of the coexistence of species.

These nine species segregated quite clearly into two classes on the basis of whether they ate macro- or microalgae. The four macroalgae eaters also demonstrated partitioning of resources, either in (i) their food habits (*Z. veliferum* and *N. brevisrostris* differed from each other and from the two other *Naso* spp.) or (ii) habitat distributions (*N. lituratus* largely excluded *N. unicornis* from areas to which the former seemed more likely to be restricted, and in which competition for food seemed most evident). Even though *N. unicornis* was often present in the study

area it probably should not be considered a resident of that area. It was a highly mobile species that often fed in habitats outside the study area. It was present and feeding in the study area only intermittently, and did so mainly in areas in which competition for food with *N. lituratus* was most likely to have been reduced (or absent?). Thus, *N. unicornis* probably existed in the study area only because it relied on obtaining from elsewhere those resources that were limiting in the study area.

Among the five microalgae consumers the three territorial subtidal species were segregated from the remaining two and from each other on the basis of habitat partitioning. This partitioning was the result of a combination of each species having different habitat requirements and species with more precise requirements tending to exclude those with less precise requirements from certain habitats. The overlaps in the zonal distributions of these three species are probably brought about largely by a combination of small scale patchiness in the distribution of habitat types, and the populations of more dominant species being below the carrying capacity. The possibility that predation may promote the coexistence of competing or potentially competing reef fishes by limiting their population sizes has already been noted by other workers (Goldman & Talbot 1976, Roughgarden 1974).

The two remaining species (*A. nigrofuscus* and *A. triostegus*) showed distinct dietary overlaps with both the three territorial subtidal species and each other. They both apparently had less precise habitat requirements than that subtidal trio, which largely excluded single adults of both species from subtidal habitats.

A. nigrofuscus adults probably should not be considered to have been persistently resident in subtidal parts of the study area. Juveniles of that species were able to exist there in abundance because their small size enabled them to find refuge from larger fishes and thus to avoid being excluded by more dominant competitors. [This pattern is also instructive in a general sense: when considering the coexistence of species in a small area the structure of the population of each cannot be disregarded, and it may be more relevant to compare age/size classes separately rather than whole species.] The ephemeral coexistence of a few nonschooling adults of *A. nigrofuscus* (and also *A. triostegus*) in subtidal parts of the study area we attribute to a combination of (i) the presence there of a few patches of habitat that were of lower quality than that preferred by the territorial trio, and (ii) the populations of at least two of those more dominant species being below the carrying capacity.

Adult *A. triostegus* were able persistently to maintain a much more significant presence in subtidal areas by employing a feeding strategy that the interference techniques of at least some of the more dominant species there could not adequately cope with. Given that schooling *A. triostegus* gained access to food they otherwise would have been denied, we might ask why a higher proportion of the population of this species did not join subtidal schools and completely overwhelm all resident competitors. There may be limits to the returns that schooling offers a species such as *A. triostegus*. Does schooling provide protection against all classes of predation as well as competitors or does it in fact facilitate some predators' activities? What are the optimum sizes of schools for both efficient feeding and efficient competitor swamping? How does optimum school size relate to the spatial distribution and density of algal foods, and to the possibility of depletion of algae? The relationship between feeding schools and territorial competitors require further examination to determine if, in any particular cases (such as *A. triostegus* and *A. leucosternon/Z. scopas*) their coexistence represents a stable equilibrium condition or not. What prevents the density of schooling fishes rising to a point at which territory holders are so swamped that territories become too costly to maintain? What prevents the density of territory holders increasing to the point at which schools cannot gain access to the substrate, as is nearly the case in *A. lineatus* colonies?

We do not have sufficient information to suggest how the coexistence of *A. triostegus* and *A. nigrofuscus* was mediated, on either the reef crest portion of our study area or Aldabra as a whole. We cannot show clearly whether or not they have distinctly different dietary and habitat requirements. There are some morphological differences between the two (Randall 1956, Jones 1968) and the indications from both our work and that of Jones are that *A. triostegus* is more generalized than *A. nigrofuscus* in its habitat requirements. We certainly observed *A. triostegus* in a wider range of habitats than we did *A. nigrofuscus*. We know that *A. nigrofuscus* is able to dominate aggressively *A. triostegus*, and think that it can probably reduce the latter's numbers in some habitat types.

In summary, the situation as we see it, is that among the five feeders on microalgae there is good evidence for differences in resource requirements of most of them and for the partitioning of resources, particularly space. There is a hierarchy in the degree of specialization of this set of species, with a more

specialized species being able to control a certain habitat and exclude a more generalized species from it. Overlap in spatial distributions is brought about by small scale patchiness of preferred habitats, the employment of feeding strategies that tend to circumvent the interspecific dominance hierarchy and low population levels of more dominant species. The present study essentially reinforces Jones' (1968) conclusions of distinct ecological segregation of different species of acanthurids and the presence of an interspecific dominance hierarchy that determines priority of access to certain habitats. However, we cannot say yet whether certain overlaps in spatial distributions represent equilibrium conditions. The picture is a clearer one than Jones (1968) presented, but an interesting set of problems on interspecific competitive relationships remains to be resolved.

9.2.3 Composition of the Aldabran algivore assemblage

In our study area benthic feeding surgeonfishes were much more strongly represented than benthic feeding damselfishes. At Randall's (1963) Caribbean site the reverse applied. We suggest that these differences result from the relative success of one of these groups being dependent upon the success of the other.

Damselfishes that live in intimate association with the substrate have fairly small territories or home ranges and are strongly reliant on shelter being available in the immediate vicinity of their feeding areas. Our work shows that surgeonfishes are evidently less reliant on such a pattern of shelter availability to be able to live in an area. The Aldabran study area was deficient in shelter on a variety of scales, including, we suggest, the scale that medium to large damselfishes would require. While only small benthic damselfishes were present in our study area (the largest specimen of the five species weighed 23 g) surgeonfishes equivalent in size to medium to large damselfishes were abundant. In Randall's (1963) two areas damselfishes reached weights of about 200 g. Both benthic damselfishes and surgeonfishes are interspecifically territorial and can be quite aggressive. It may be that, gram for gram, damselfishes are able aggressively to dominate surgeonfishes. If such is the case, in areas where adequate shelter is available, damselfishes may be able to establish themselves in large numbers, to the detriment of many surgeonfishes. Four species of surgeonfishes are known from the Caribbean area (Randall 1968, p. 254, and Bohlke & Chaplin 1968,

p. 654), three of them being common and widespread. The main damselfish species that consume benthic algae and defend 'permanent' feeding territories on the substrate are all able aggressively to dominate the three common surgeonfishes and exclude them from their territories (Brockman 1973, Thresher 1976, Robertson et al. 1976, Ebersole 1977, D.R.R. unpublished observations).

Whereas the ecological 'success' of the surgeonfishes was inversely related to that of the algivorous damselfishes, parrotfishes were evidently nearly equally 'successful' in Randall's sites and ours. In part at least, this is probably due to many parrotfishes being able to forage in a basically different manner from that by which damselfishes and surgeonfishes forage. Parrotfishes often scrape and bite into coral-line rock, making use of boring and encrusting algae as they do so (Randall 1967). Surgeonfishes and damselfishes, on the other hand, are both limited to cropping benthic algae and ingesting surface sediments. Therefore, competition may be more likely to lead to damselfishes excluding surgeonfishes, or vice versa, than to either of these groups excluding parrotfishes, because damselfishes' and surgeonfishes' food requirements are likely to be more similar to those of each other than to those of parrotfishes.

These suggestions represent only a first approximation, and are limited by the fact that we are making comparisons that involve the faunas of two different seas. These faunas differ radically in composition, with the Caribbean having relatively very few species of surgeonfishes (Randall 1955a, b, 1956). Such differences in the 'availability' of species presumably also play a part in determining the structure of communities in different areas.

9.3 The structure of social units

The composition of adult social units, while fairly consistent within each of the three species, varied greatly between them. There are two aspects to this interspecific variation that we propose to examine in this discussion: (1) Why do *A. leucosternon* and *Z. scopas* form 'pairs' (i.e. long-term associations of one male and one or more females) while each individual *A. lineatus* comprises a unit? (2) Why do we find that males of *A. leucosternon* are smaller than females, and tend to associate with only one female, while *Z. scopas* males are larger than conspecific females, and often associate with two females?

9.3.1 The significance of pair formation

There are two parts to the question – why does pair formation occur in surgeonfishes? (1) What set of factors facilitates the formation of pairs? (2) When pair formation is facilitated, what factors favor it?

For pair formation to occur both sexes must benefit over remaining unpaired. For a male to be paired he must be assured of a relatively exclusive access to his mate's gametes. As Perrone & Zaret (in press) have pointed out, external fertilization by fishes allows the male to assess the paternity of the offspring his mate is producing, and male territoriality facilitates a male's defense of his mate's gamete crop. Besides ensuring his mate's fidelity by preventing other males from gaining access to her during spawning, the male could, alternatively, do so by preventing the female from leaving him to spawn with another male. This second situation could be arrived at in either of two ways. Firstly, a male, by being able aggressively to dominate a female, might be able adversely to affect her access to a limiting resource. This appears to be occurring in at least one wrasse (Robertson & Hoffman 1977). Alternatively, a male could conceivably enhance a female's access to some limiting resource. Males of one hummingbird species, for instance, defend food which their mates require to rear broods (Wolf & Stiles 1970). In either situation a female that was uncooperative at spawning time could be penalized. Thus, we can see how pair formation might be maintained in species in which competition for limiting resources is occurring.

(i) Territoriality and the development of pair formation – Both Fricke (1974, 1975) working on anemone fishes and Lassig (1976) working on gobies have recognized that the basis of pair formation in certain types of coral reef fishes is the long-term attachment of members of both sexes to specific patches of habitat. The fishes that both these authors studied have their movements restricted to very small, well isolated pieces of habitat that are vital to them for shelter: sea-anemones and small clumps of arbore-scent corals. They have argued that pair formation under such circumstances enables both sexes to find mates without having to risk leaving their home sites to do so each time they want to spawn.

This argument is perfectly reasonable when applied to animals that are so strongly reliant on shelter that is distributed in space in such a manner. However, neither the pair forming acanthurids that we have studied nor wrasses and parrotfishes that form

'pairs' (Ogden & Buckman 1973, Robertson & Hoffman 1977, Warner & Robertson 1978, Robertson & Warner 1978), live in intimate association with such small patches of shelter. While both sexes of such species are often site attached and territorial, they could safely leave their territories to spawn. Thus it seems that strong site attachment, for whatever reason it arises, is the prerequisite for pair formation. However, as we shall see, it does not automatically follow that such site attachment leads to pair formation. Perhaps relatively permanent general purpose territoriality is of greater importance to the development of pair formation than site attachment per se. Territorial defense of limiting resources may provide one or both sexes of a pair with better opportunities to manipulate the sexual success of the other and thus ensure a high degree of spawning fidelity. Spawning fidelity can best be assured when spawning occurs in the pair's territory. As we see it, ensurance of female fidelity facilitates pair formation in acanthurids, not risks involved in finding mates.

The limited data available on reef fishes that have planktonic eggs support this notion that strong, permanent territoriality is important to the development of pair formation: Firstly, pair formation occurs in one wrasse that defends permanent feeding territories but not in another that is site attached but not permanently territorial (Robertson & Hoffman 1977). Secondly, we have information on 14 Aldabran acanthurids. Seven species that hold territories form pairs: *A. leucosternon*, *Z. scopas*, *Z. veliferum*, *A. gahhm*, *N. lituras*, *C. striatus*, and *C. strigosus*. One territorial species (*A. lineatus*) does not (for reasons that we consider below). *N. brevirostris* and *N. unicornis* were nonterritorial. We do not know to what extent they were attached to home ranges. Barlow (1974a) has stated that, in the central Pacific, *N. unicornis* forms groups composed of a male and several females. We did not see any behavior that would have indicated pair formation in either of these *Naso* spp. Insufficient data are available on *A. tennenti* and *A. dussumieri*, although the former species was occasionally territorial and formed 'groups' of one to two (or more?) individuals.

While many individuals of both the remaining species, *A. triostegus* and *A. nigrofuscus*, were territorial, many others were not. Also, those individuals that were territorial were typically only intermittently so, in both inter and subtidal areas. Near our study area the number of individuals in social units of both of these species varied from one to four, and there were no consistent patterns in the sexual structure of mul-

ti-individual groups of either species: All of eleven solitary territorial *A. triostegus* were males, while only six of sixteen solitary *A. nigrofuscus* holding territories were males. Only five of eleven *A. triostegus* duos were male + female pairs, while four were male + male 'pairs' and two were female + female 'pairs'. In the heterosexual pairs of *A. triostegus* males were larger than females in only two of the five cases. Two *A. triostegus* trios comprised one large male + two smaller females and two females + one smaller male respectively. Three 'pairs' of *A. nigrofuscus* comprised a male and female of equal size, a female with a smaller male and two females of different sizes. One group of four *A. nigrofuscus* contained two males + two smaller females. Thus, weak, intermittent territoriality in surgeonfishes was not associated with distinct pair formation.

(ii) Pair formation and the lack of parental care by surgeonfishes – The possession of a permanent feeding territory by a surgeonfish is a reflection of its feeding strategy. Thus, whether or not such fishes form pairs is determined to some extent by their feeding strategies. However, we think that the absence of parental care of offspring by the members of this group has also facilitated pair formation.

While surgeonfishes that defend permanent feeding territories usually form pairs, damselfishes that defend such territories normally do not form pairs (unless such is dictated by special circumstances, e.g. the anemonefishes, see above). In nonpairing damselfishes males guard eggs on the substrate and females have no parental role. Perrone & Zaret (in print) have considered why, when egg guardianship occurs, both sexes may gain by males alone exhibiting parental care. Although their arguments were developed to explain why both parents do not remain together to care for the particular brood they have produced, they can be extended to explain the absence of permanent pair formation. When egg guardianship occurs males may be able to care for many more broods than a single female produces, and thus increase their spawning success by remaining unpaired and competing freely for females. Females may be able to produce broods more frequently by not becoming involved in brood guarding, and may gain by being able to choose more carefully prior to each spawning act from a wider range of mates. Because the surgeonfishes do no brood guarding, certain factors that tend strongly to favor independent activity by each sex in brood guarders do not operate.

(iii) Factors favoring pair formation in *A. leucosternon* and *Z. scopas* – Given that permanent territoriality (or at least strong site attachment) facilitates pair formation in fishes such as acanthurids, how could a male benefit by forming a long-term association with one or more females rather than competing for access to them during each spawning period, and how could a female benefit by joining such an association rather than choosing between competing males at each spawning period?

A mating system characterized by relatively permanent pair formation could have developed from at least two other types of mating systems that incorporated greater choice between mates at each spawning.

Firstly, consider a species with a mating system so structured that all males experience about the same level of spawning success. Males, by pairing permanently, might be able to compensate (and very possibly overcompensate) for the advantages (e.g. spawning at a spawning ground that was a good site for egg dispersal – Johannes 1978) that such a system had over spawning in a permanent territory. Such pairing could assure a male of a mate. It might enable him to achieve greater spawning success than he would otherwise attain by being able to increase the spawning success of an individual female (see sections 9.3.1 and 9.3.2) or by forming an association with more than one female. Pairing might also reduce mortality rates if there were predation risks associated with leaving a permanent territory to travel to and spawn in less familiar areas.

Secondly, pair formation could also develop as an alternative male mating strategy in a species in which, as a result of male-male competition for mates, there were pronounced differences in the spawning success of males of different classes. Males that were less successful might be able to offset their disadvantage by inducing females to spawn with them in permanent territories, by being able to influence those females' access to limiting resources.

Brown & Orians (1970) and Schoener (1971) have pointed out that the formation of a social group that defends a common territory might occur if, in such a territory, the resources being used by each group member were defended more efficiently than if that member defended those resources by itself. Pair formation could be favored in acanthurids in this way. A doubling of the area of a regularly shaped territory is accompanied by less than proportionate increases in both territory diameter and circumference. Therefore, two fish may be able more effi-

ciently to monitor and patrol an area twice the size of that occupied by one fish. Two fishes might also be better able to harass certain types of intruders. In species that have relatively large, isolated territories that require a lot of defense activity but that are not intrinsically highly defensible, the gain in efficiency arising from pair formation could be important (e.g. *A. leucosternon*).

Among certain reef fishes, which, like the territorial acanthurids, spawn planktonic eggs, small scale migrations to sites that are favorable for the dispersal of eggs are common (see Johannes 1978 for a review). Such migrations were observed in two nonpairing acanthurids at Aldabra (*A. triostegus* and *A. nigrofuscus*). It is reasonable to expect such behavior to develop in other species that did not form pairs. However, in permanently territorial species, regular abandonment of territories during spawning periods that could last up to several hours could be distinctly disadvantageous. If such territoriality functioned for the defense of food, competitors could be expected to adapt their activity patterns to enable them to make maximum use of cyclically abandoned territories. The effects of territory defense during the rest of the day could be negated during spawning periods. As a factor favoring pair formation, such avoidance of regular evacuation of territories would be expected to be more important in species whose resources required continuous and highly effective defense.

Conceivably also, an animal that left its territory to engage in spawning activity for a period of hours might have difficulty regaining it upon its return if a competitor had established itself there during its absence.

(iv) The absence of pair formation in *A. lineatus* – Even if pair formation was advantageous in some ways to *A. lineatus*, we can see one reason of overriding importance that precludes the possibility of its occurring.

In surgeonfishes, fertilization is external. This provides the same potential for more than two fish to participate in a spawning that it does among the labroid fishes. Thus, it provides the same potential for male surgeonfishes to readily interfere in the spawnings of other males that it does in male labroids (Warner et al. 1975). In a dense colony of fishes holding small territories, conditions would be ideal for males to interfere in each other's spawnings as a male of such a relatively large species could rapidly move the short distance necessary to join a spawning pair. In at least one species of parrotfish, *Sparisoma radi-*

ans, small territory size does appear to facilitate such interference (Robertson & Warner 1978). We feel that an inability of a male *A. lineatus* to prevent other males from interfering in his pair spawnings negates any potential advantage to pair formation.

9.3.2 Patterns of sexual dimorphism and pair composition

We have discussed how, among surgeonfishes, pair formation per se might offer both participants benefits of one type or another in terms of assured or increased zygote production. Modifications from the simplest situation (one male with one equal sized female) might be expected to occur (before or after pair formation had developed) as a result of selection favoring the development of characteristics that tend to increase the spawning success of one or both sexes. Specifically, we might expect changes in the relative sizes of males and females and/or increases in the number of females in the social unit. It can readily be seen how an increase in female size relative to male size should benefit both members of the pair, since, among fishes, female fecundity generally increases with increasing size (Bagenal 1967). Although the absolute size of the female is what is important from the point of view of female fecundity whether one sex can change size may depend upon what size the other is, or a change in the size of one sex may 'induce' a change in the size of the other. If a pair's territory can efficiently support only a certain mass of fish then how that mass is distributed between the sexes affects the spawning success of both. Relative changes in mass of the sexes must, therefore, be considered. While increasing the number of females in a group would also obviously seem to be to the advantage of the male, it may not be as advantageous to the individual female as increasing her size relative to that of her mate. To form harems males presumably compete among themselves. One result of such competition could easily be selection for large male size and an increase in the size of males relative to that of females. Large relative male size could also be selected for if it enabled males to restrict the activities of their mates or defend the resources used by their mates more effectively. Large male size in *Z. scopas* might, in one sense, be detrimental to individual females: It might represent an energetic loss to females if a higher proportion of the territory's productivity was being channeled into the male than would be the case if the female was larger. Alternatively, the size that

females attain might be the optimum for conducting activities that were more important to females than males.

In *A. leucosternon* the sexual dimorphism in size is much more pronounced than it is in *Z. scopas* or the other surgeonfishes we found to exhibit the *Z. scopas* pattern of dimorphism and 'pair' composition (Table 17). Thus a high proportion of the territory's production is channeled into the individual *A. leucosternon* female. Such channeling is reflected in differences in male and female feeding rates in this species. It is also reflected in the division of interspecific defense labor between the sexes. Female *A. leucosternon* do not seem to be territorially competent by themselves. They appear to lose reproductively if they are not paired and to compete to form pairs with males. It seems, therefore, that in this species female participation in pair formation is favored because it actively offers benefits to the female that she could not otherwise obtain.

The existence of unpaired females in *A. leucosternon* suggests to us that a male can adequately cope with the defense burden of only one female. The instances in which one male shared its time between two females, were the result we think, of a biased sex ratio rather than males competing for additional mates, because in a competitive system it seems unlikely that unmated females would have been found as commonly as they were. A combination of small male size and a requirement for highly effective territory defense may severely limit the number of females a male can successfully cope with.

We think it is extremely interesting that the sex-ratio of *A. leucosternon* was biased in the manner it was at Aldabra (see section 9.1.6). This information prompts several questions: Was this purely a temporary or local phenomenon, or is it generally characteristic of the species? If the latter situation obtains, is such a sex ratio generally characteristic of surgeonfishes with the *A. leucosternon* pattern of sexual dimorphism and social unit composition?

In *Z. scopas* there were no clear indications that individuals of one sex were receiving a higher proportion of the territory's food resources. The feeding rates of the sexes were about the same, and both were active in interspecific territorial defense. We cannot say whether the small relative size of females of this species is disadvantageous: if only one much larger female was present in the territory being used by two females, she could have made use of the territory's food more efficiently than a smaller female and could have been a more successful spawner than

those two. Small size may be advantageous in a species employing the type of feeding strategy *Z. scopas* uses. Males might be able to afford a size that is suboptimal in some respect, if their food requirements (particularly for gamete production?) are less than those of females. Whether female participation in *Z. scopas* pairs results from males being able to dominate them and limit their access to food, or because males actively provide 'services' that females require is not clear at present.

All but one of the other five pair forming Aldabran acanthurids that we examined exhibited the *Z. scopas* pattern of sexual dimorphism in size, and social unit composition (Table 17). We do not know how closely the remaining one, *Z. veliferum*, followed the *A. leucosternon* pattern. This leads us to consideration of three questions concerning these patterns:

(1) Is the pattern we see largely a consequence of past evolutionary events? Pair formation could have been preceded by a phase during which the species' mating system selected for a particular pattern of dimorphism. If conditions then became favorable for pair formation the already existing dimorphism may have determined which pattern of pair composition developed.

(2) Are the social and mating systems of a species variable enough in structure that the relative sizes of males and females are determined by factors that are not operating at Aldabra? As in the previous case, the structure of the social unit would be determined by the type of size dimorphism. This possibility could be tested by examining the structure of various species' social and mating systems throughout their geographic ranges.

(3) Do species generally tend to take one alternative unless certain specific (and uncommon) factors make it inefficient? There may be a tendency to move in the direction of 'large male + several smaller females' because the upper limit of potential benefits to the male is greater than with the 'small male + one larger female' case. Presumably male size can be efficiently decreased only so far. Thus the 'small male + one large female' unit may be the most advantageous system when a male can associate efficiently with only an extremely limited number of females. To present a hypothetical example: The type of feeding strategy that *A. leucosternon* employ may mean that the maximum number of females whose food could adequately be defended by a male is two. However, one female larger than twice the size of her mate might have a higher fecundity than two females smaller than him. Thus, a complex of interactions be-

tween such factors as (i) female size and fecundity, (ii) food resource type, (iii) territory size and defensibility and (iv) the size and spatial distribution of habitat patches, may determine optimum group size and, through it the pattern of sexual dimorphism.

Finally, we should also not rule out the possibility that intraspecific geographic variation in feeding strategies and social organization patterns of acanthurids might be accompanied by intraspecific geographic variation in the degree and type of sexual dimorphism and the structure of social units.

10. Conclusions

The defense of territories that are primarily feeding territories is widespread among surgeonfishes. In pair forming species they also serve to ensure that the pair spawns together. Adult acanthurids' territories, in our study, area provided little or nothing of the shelter requirements of their owners.

There are pronounced differences in the feeding strategies of the three main species that defend 'mats' of microalgae. These we think are reflections of differences in the degree to which each (i) relies on interspecific defense of its food rather than an ability to exploit certain resources more efficiently than other species, and (ii) employs certain tactics that increased the efficiency with which its food could be defended. Differences in the morphology of the three species seem to limit what feeding strategy options are available to each by determining its ability to (i) feed efficiently on algal mats of different densities; (ii) feed efficiently in different microhabitats; (iii) exploit shelter-deficient habitats; and (iv) defend territories against other species.

A. lineatus has the most specialized requirements. It apparently feeds most efficiently on high density algal mats growing in exposed microhabitats. This type of mat, which is probably not easily established, can be exploited by the widest range of species. Thus the threat from competitors is a very serious one for this species. *A. lineatus* occupies the zone and habitat that allows the formation of territories of maximum defensibility, and (possibly) maximum productivity. This species is the most reliant of the three on interference to obtain food. Even though it is the largest of the three species *A. lineatus* can rely on the smallest (both absolutely and relatively) territories because they are highly productive and because the high efficiency of their defense ensures that a high proportion of the territory's production is used by the owner.

The high-density colonies of territories of this species are seen as developing in response to the threat of competition from other species, as they increase the efficiency and effectiveness with which individual territories are defended. Such colonies develop as the result of the mutual attraction of individuals rather than either physical or biological limitations in the availability of suitable habitat. If the formation of feeding schools by herbivorous fishes represents a sound tactical response to the territoriality of many competitors, high-density colonies may well represent the ultimate in defense tactics by a territorial species. Feeding schools of another acanthurid have very limited success in entering such colony areas.

The species with the algal mat that is least exploitable by other species, *Z. scopas*, occupies zones and habitats in which territories are least reliably productive, and least defensible. It is least reliant on interfering with the feeding of other species to obtain its requirements. It is most reliant on morphological specializations that enable it to exploit food that is apparently less accessible to other species. Although it is the smallest of the three species, *Z. scopas* has the largest territories, both absolutely and relatively, with the lowest standing crop algal mat, because much of the substrate's production is diverted to other algivorous fishes.

The feeding strategy of *A. leucosternon* is intermediate between those of *A. lineatus* and *Z. scopas*.

Members of the same species of surgeonfish can adopt different feeding strategies, at either the same or different localities.

Interspecific variations in the color patterns of territorial acanthurids are consistent with a modified version of the 'poster-coloration' hypothesis. To what degree a species develops a permanent, conspicuous color pattern that serves to advertise the presence of its territory depends on (i) the degree to which highly effective defense is required; (ii) the range of species and numbers of fishes that the territory is defended against; (iii) the importance of long distance visual communication to territory defense; (iv) the defensibility of the territory (as influenced by its size and location relative to other territories); (v) predation risks to conspicuously colored fishes in different habitats; and (vi) whether the fish feeds on organisms that use well developed vision to avoid their predators.

Subtidally, our trio of strongly territorial species occupies the full range of feeding strategies available to adult surgeonfishes that defend microalgal mats. One other species may be using that area as a nursery, the small size of its juveniles enabling them to take

refuge from the adults of more dominant species. The remaining consumer of turf microalgae gains limited access to subtidal areas by forming feeding schools. Possible limits to the effectiveness of such schooling need to be explored, to determine if there are stable equilibria in the relationships between the amounts of schooling and territorial activity in an area that would result in the stable coexistence of fishes using these two strategies.

There is little dietary overlap among the four species that consumed benthic macroalgae and the five species feeding on microalgae. Two species of macroalgae eaters that rely exclusively on food resources generated in the study area habitats defend feeding territories. The remaining two appear to rely largely on either planktonic material or benthic algae generated elsewhere, and are nonterritorial.

Competition for benthic algae and space to grow such food is a major organizing factor in the Aldabran acanthurid community. The coexistence of nine species that feed by cropping benthic algae can be explained largely on the basis of differences in resource requirements, and resource partitioning. Space and food are the partitioned resources. Among those species that use the same types of algae, more specialized species have priority of access to habitats that, we think, are at the upper end of their preference scales. A fairly well defined interspecific dominance hierarchy exists, with the most specialized species at the top. Overlap in small scale spatial distributions of species is the result of both (i) microhabitat segregation, and (ii) the populations of at least two (of the most dominant) species apparently being below the carrying capacity.

Adults of several of the aggressively more dominant species are concentrated in the shallowest parts of the subtidal. This zone probably offers several advantages: good conditions for algal growth, an abundance of substrate for algal growth, continuous occupancy (and therefore, defense and use) of a territory, and proximity to shelter.

The Aldabran benthic algivore community is dominated by acanthurids, in terms of species, numbers of individuals and standing crop. This pattern, we think, is due to the existing habitats not providing adequate shelter of types used by larger species of benthic, territorial damselfishes. In other areas where members of the latter group predominate they may do so at the expense of surgeonfish activity.

Pair formation only occurs in permanently territorial (or at least permanently site attached) acanthurids. It does so because territoriality enables female

fidelity to be assured. Female fidelity can be brought about by males providing services useful to females, or by males actively being able to restrict females' access to limiting resources. Pair formation is precluded in species forming high-density colonies, because the close proximity of males facilitates their interference in each other's spawnings. Whether or not pair formation occurs in a surgeonfish depends in part upon its feeding strategy. The absence of parental care by members of this group also facilitates pair formation because certain factors that favor independence of both sexes in brood guarders do not act in broadcast spawners such as surgeonfishes.

Pair formation may develop because (i) it represents an alternative male mating strategy in species whose members are involved in competition for limiting resources, (ii) it increases the efficiency of defense of resources, (iii) regular evacuation of territories for spawning is disadvantageous in terms of efficient defense of resources.

Both members of a pair in which the female is much larger than the male would seem to benefit, since, in fishes, female fecundity is positively correlated with female size. While the alternative surgeonfish pattern of sexual dimorphism and 'pair composition' — a large male with two or more smaller females — also seems to offer obvious advantages to the male, it is less clear how it may benefit individual females. Which of these two patterns a species exhibits may be determined by (i) whether, in its evolutionary past, pair formation was preceded by a phase during which one pattern or another of size dimorphism was selected for, i.e. one option was ruled out when pairs began to form; (ii) selection pressures currently operating outside our study area are maintaining one form of size dimorphism, and determining pair structure as a result; or (iii) which pattern is more advantageous being dependent on the number of females a male can efficiently associate with. How many females a male can efficiently associate with may depend upon the species' feeding strategy. If the male can only associate with very few females it may be more advantageous to take the small male + one large female option.

Acknowledgements

This work was largely made possible by a grant from the National Geographic Society to D.R.R., who was also supported by the Smithsonian Tropical Research Institute. N.V.C.P.'s participation was supported by

the Pantin and Pryor Funds of Trinity College and his parents. We are indebted to the Royal Society for the use of facilities at the Research Station on Aldabra Atoll. We thank Peter W. Glynn, Neal G. Smith, and an anonymous reviewer for their criticism of a draft of the manuscript.

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