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## Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation

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### Abstract

Abundances of the surgeon fish *Acanthurus lineatus* (Linnaeus) within a single reef-system were estimated using a hierarchical sampling design during 1982. Additional sampling was carried out during 1983 and 1984 at a restricted number of sites. This species is aggressive toward other herbivorous fishes and is strongly site-attached. On the study reef (Lizard Island; 14°40'S; 145°28'E), *A. lineatus* was restricted to reef-crest sites below mean low water, mainly on reefs not directly exposed to prevailing winds. Within this reef zone and depth-defined stratum, *A. lineatus* was distributed heterogeneously with high abundance, (approximately 14 fish per 300 m<sup>2</sup>) at a single sample-locality covering 600 m of reef crest. Abundances of herbivorous species (members of the families Acanthuridae and Scaridae) at other localities did not correlate with abundance patterns of *A. lineatus*. Subsampling within study localities revealed considerable heterogeneity in the abundance patterns of herbivorous fishes, especially within the area of high *A. lineatus* density. A detailed behavioural study of interactions among herbivorous fishes at two adjacent sites within the locality of high *A. lineatus* abundances revealed a complex pattern of site-general and site-specific features. *A. lineatus* excluded smaller scarids from its feeding territories at one site, but not at another. Scarids attaining large size (>350 mm standard length) were present at one site and consistently fed within *A. lineatus* territories; large scarids were rare at the second site, even though the distances involved were small. In addition, the small surgeon fish *A. nigrofusus*, a consistent target for *A. lineatus* aggression, was rare at one site but moderately common at the other. Finally, the abundant surgeon fish *Ctenochaetus striatus* was present at high densities at both sites and fed within *A. lineatus* territories. This species was not attacked by *A. lineatus* nor did it attack other herbivorous fishes within the vicinity. Small but consistent differences in reef structure were detected at each site. Local-scale heterogeneity in these interactions makes

it difficult to develop generalizations concerning the role of territorial herbivores such as *A. lineatus* within reef systems. We hypothesize that very local differences in the within-habitat component of acanthurid and scarid abundances and distributions may reflect site-associated variability in recruitment patterns, post-recruitment mortality or behaviour that is independent of *A. lineatus* activities. Replicated removal experiments which include explicit tests for local site-effects and better descriptions of recruitment in larger herbivorous fishes are required before these interpretations can be evaluated.

### Introduction

The herbivorous fishes of coral reefs constitute an abundant and diverse assemblage of grazing and browsing species (Russ, 1985a, b). A large proportion are vagile, often schooling species, which graze and browse over the exposed calcareous surfaces of the reef (Choat and Robertson, 1975; Robertson *et al.*, 1979). This feeding may be intense (Robertson *et al.*, 1976; Hay, 1981). A number of reef workers have concluded that such feeding may have a major influence on the character of the reef sessile-biota (Ogden and Lobel, 1978) and play an important role in determining patterns of energy flow and nutrient cycling in the reef environment (Hatcher and Larkum, 1983). Many of these studies have employed field experiments to investigate details of the interaction between herbivorous fishes and the sessile biota (Brawley and Adey, 1977; Hay, 1981; Miller, 1982; Hatcher and Larkum, 1983; Hixon and Brostoff, 1982).

Reef habitats may be subdivided into distinct zones based on depth, aspect, and exposure (Done, 1982; Williams, 1982). The distribution patterns of herbivorous fishes may be conveniently described with reference to these (Williams and Hatcher, 1983; Russ, 1985a, b). Within such zones one may encounter extensive, appar-

ently homogenous areas of similar habitat, a reflection of the relatively predictable biogenic processes that produce shallow reefs. How uniformly are herbivorous fishes distributed within such areas? Is the influence of their feeding similar across extensive areas within the same type of habitat? Are the patterns that have been discerned clear-cut and consistent, or do they blur and lose definition when slightly different combinations of sites, observation times, and species assemblages are considered? Russ (1985b) has provided evidence of an among-reef component of variation in abundance and species composition. Other studies (Sale and Douglas, 1984) suggest that similar variation may occur within the same habitat on a single reef.

Tropical herbivorous fishes show a variety of feeding activities, reflecting their movement patterns and behavioural traits. Some species within the families Acanthuridae, Scaridae and Siganidae feed over a relatively wide area, frequently forming mixed feeding-schools and rarely displaying aggression toward other species. In sharp contrast, a number of acanthurids and pomacentrids remain within and actively defend specific areas of reef substratum against the feeding activities of other herbivores, especially the more vagile acanthurids and scarids (Low, 1971; Vine, 1974; Robertson *et al.*, 1976, 1979). As this class of interactions appears to be widespread where acanthurids, scarids, and pomacentrids co-occur, it serves as a convenient focus for studies on the abundance and feeding behaviour of herbivorous fishes. If territorial aggressive species occur in large numbers, they should create conspicuous gaps in the local distribution of other herbivores and thus influence the assemblages of sessile organisms on which they feed.

The present study seeks to assess variation in herbivore abundance and behaviour within some habitats of a single reef-system on the northern Great Barrier Reef. We have chosen to collect information over relatively small areas. This reflects the spatial scale of most experimental studies recorded in the literature. Such localized within-habitat variation would be most likely to influence experimental results, especially in cases where replication was limited. Our focus is the interaction between an aggressive site-associated acanthurid *Acanthurus lineatus* (Linnaeus) and a fauna of grazing acanthurids and scarids. Relatively large-size, well-developed caudal knives, and a tendency to aggregate in groups all suggest that *A. lineatus* or related species would have a demonstrable influence on the abundances of other herbivore species (Nursall, 1974; Vine, 1974; Robertson *et al.*, 1979; Robertson and Polunin, 1981). Our specific questions are as follows.

What is the distribution pattern of *Acanthurus lineatus* within and among habitats on a single reef?

Is there a consistent negative relationship between the abundances of *Acanthurus lineatus* and other acanthurids and scarids in habitats where they co-occur?

Is the aggressive behaviour of *Acanthurus lineatus* directed toward all acanthurids and scarids or are there distinctions relating to size and identity?

Are behavioural interactions similar among different sites harbouring equivalent numbers of *Acanthurus lineatus*?

We have included here information on the most abundant acanthurid in the study area, *Ctenochaetus striatus*, which shows some degree of site-attachment but is not consistently aggressive toward other species. It is, however, debatable as to whether this abundant and widespread species can be classified as a herbivore. We do not include pomacentrid fishes in this study. Our observations on acanthurids and scarids all refer to adult individuals.

This study was conceived as a pilot sampling regime in anticipation of experimental manipulation of herbivore abundances. Planned emphases were on comparisons of herbivore abundance and feeding between areas with, and areas lacking groups of *Acanthurus lineatus*. However, preliminary sampling detected unexpectedly high variation in herbivore abundances and activity among different sites within areas of high *A. lineatus* occurrence. These occurred within adjacent, relatively homogenous sections of reef. Accordingly, the major sampling and investigative effort was directed to such sites.

## Materials and methods

### Study areas and organisms

The observations and sampling programme were carried out at Lizard Island (14°40'S; 145°28'E), a continental island 30 km off the mainland coast and 18 km from the outer Barrier Reef. A major sampling programme was carried out during the period June to December 1982. Additional sampling at specific sites was made during December 1983 and August 1984. The island is surrounded by an extensive and varied reef system which includes both rocky and living coral reefs. It has the typical complement of mid-shelf species of herbivores (Williams, 1982; Russ, 1985a). We concentrated on the two major families of reef herbivores, the Acanthuridae and the Scaridae with 14 and 20 species, respectively, being recorded from our transect counts. Siganids were present in low numbers at our study sites. Other numerous, smaller herbivores such as pomacentrids and blennies were present but not dealt with in this study.

### Fish sampling programme

The reef was initially divided into three zones based on structure and degree of exposure to prevailing winds (Fig. 1A). These were: exposed reef fronts – steep reef areas facing southeast and exposed to the prevailing trade-wind flow; oblique reef fronts – areas of coral reef with the main axis perpendicular to prevailing trade-winds; and granite reefs – in which granite rock, not coral, formed the primary intertidal and subtidal substratum. Within each

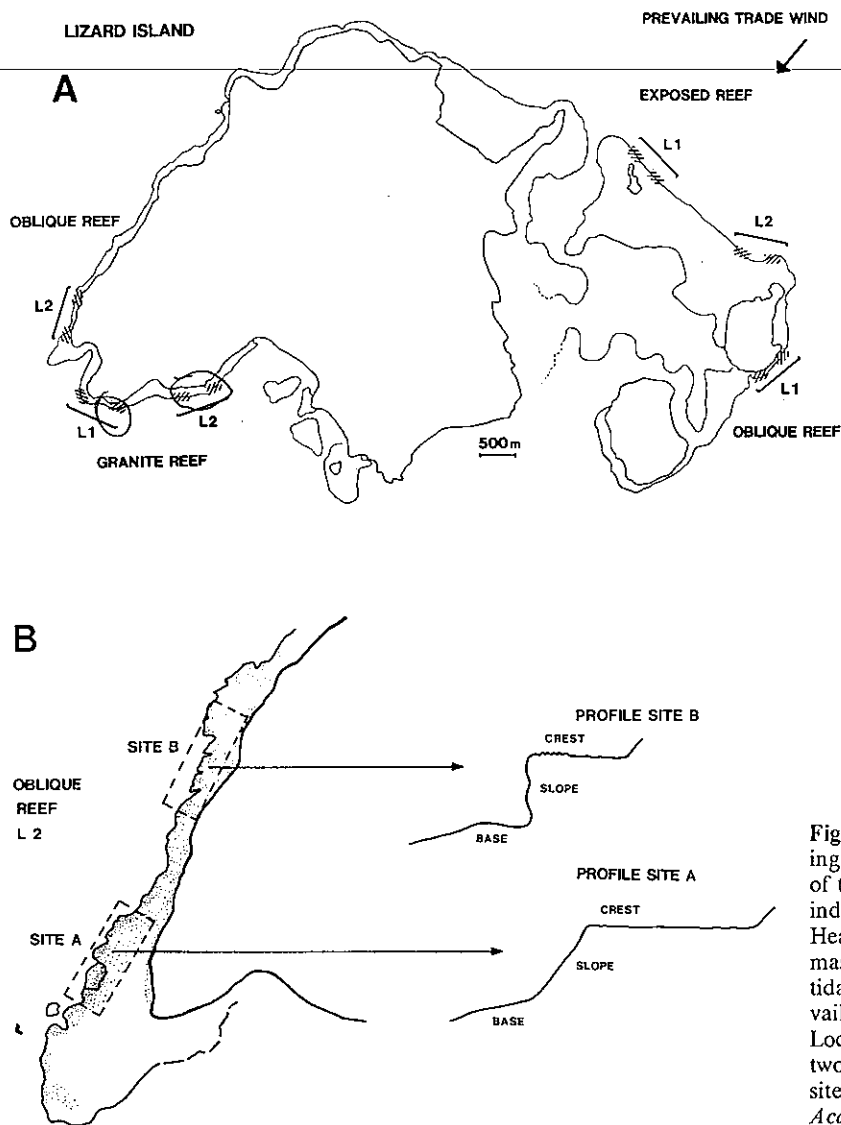


Fig. 1. (A) Plan view of Lizard Island Study area, showing the disposition of two localities (L1, L2) within each of three reef-zones. Hatched areas within each locality indicate positions of two sites within each locality. Heavy outline indicates extent of continental island masses, fine contour indicates extent of mid-depth sub-tidal reef areas; the exposed reef zone is subject to prevailing southeast winds. (B) Detail of main study area at Locality 2 of the oblique reef zone; disposition of the two sites within this locality and the reef profile at each site are shown; stippled area represents distribution of *Acanthurus lineatus* territories

reef zone, three depth strata were identified: shallow – extending through the intertidal; mid – the crests and immediate frontal areas of reefs; deep – reef basal areas where rock or reef matrix met the surrounding sediment floor. Water depth at mid-areas varied between 0.5 and 2.5 m, depending on tidal state; deep-areas were between 8 and 12 m in depth.

These reef structure and depth combinations defined a series of habitats. Abundances of herbivorous fishes were estimated by replicated visual counts within each of these habitats. We employed a hierarchical sampling scheme to examine within-habitat variability at two spatial scales. *Localities* were areas within habitats extending approximately 500 m along the main axis of the reef. The positions of localities were constrained, so that the minimum distance between them was greater than 600 m. These were initially selected randomly from aerial photographs but, in some instances, distance and travelling considerations required some modifications of the original

selection. On account of the island structure and orientation there was a probability that the distance among localities in some habitats would be greater than in others. Within each locality, two adjacent *sites* were established. The distance between adjacent sites was approximately 150 m (Fig. 1).

Visual counts were made along replicated 30×10 m strip transects within each site. Transects were run parallel to the reef edge. Initially, counts were made in transect areas where the dimensions were delineated as 30×10 m rectangles by tapes. These were compared with transects run in the same area by using a single 30 m tape and estimating the requisite 5 m each side of the line. Comparisons suggested that the 5 m distance was initially underestimated by the diver (J.H.C.) but there was also a tendency to include larger fish in the transect when they were in fact outside. Analysis of count information suggested however that the major source of variability was the clumped distribution of the fishes in question. Small

differences in transect dimensions seemed less important than replication of counts within and among areas (J.H.C. in preparation). Accordingly, transect counts were made using a single 30 m tape which permitted many more replicate counts and less disturbance than procedures which involved setting out rectangular areas bounded by tapes.

Behavioural observations were made in randomly placed 3×3 m areas within *Acanthurus lineatus* (Linnaeus) territories on adjacent areas of reef. Territories were recognizable by the presence of distinct algal mats (Robertson *et al.*, 1979). Observation areas were marked out and left for a 5 min period. For the following 15 min any passage or feeding by non-resident herbivorous fishes plus interactions with residents was recorded. In some of these areas the feeding of *A. lineatus* and *Ctenochaetus striatus* was examined with respect to their feeding microhabitats. Five categories of feeding microhabitat were recognized in observations of *A. lineatus* and *C. striatus*, and three in observations on scarid feeding. The feeding microhabitat selected by individuals of the different species for each of 200 bites was recorded. Fishes of comparable size were selected in each area. Additional behavioural and feeding data were obtained by following individual scarids and recording the relationship to *A. lineatus* territories, the microhabitats of all bites taken, and any aggressive interactions. Feeding observations were made as close as possible to midday and early afternoon, and timed to avoid major reproductive events, as described by Robertson (1983). Most transect counts were made during summer months, so care was taken to avoid, as far as possible, the distorting effects of migration to and the presence of spawning aggregations. Spawning aggregations were clearly visible on some occasions, especially during ebb-tide periods. Transect counts made during these periods were excluded from general summaries.

#### Estimates of reef structural properties

Depth profiles were recorded from transect tapes run perpendicular to the reef front from the reef crest to the reef base. Combinations of substratum type and angle-of-slope information were collected at predetermined points down these transects. Depth at each point was estimated using oil-filled depth gauges. Replicated transects were used to obtain depth, angle, and composition of reef-slope estimates at different sites on the reef.

Habitat structure and heterogeneity within *Acanthurus lineatus* grazing areas were assessed by a hierarchical sampling design. Estimates of percentage cover of different substrata and structural heterogeneity of the grazing surfaces were obtained from three 10 m transects separated by a minimum distance of 10 m within each site. Within each transect, five randomly placed 5 m subtransects perpendicular to the main transect axis were randomly subsampled at five points. At each point, substratum identity, its height above the reef platform, and the degree of

horizontal complexity (shrubbiness) were assessed. This design was a modification of the method of Wiens and Rotenberry (1981). It provided 75 random sampling points at each site and allowed estimates of variation in reef structure at two spatial scales (within and among transects) within each site.

#### Results

We have employed the following sequence for presentation of results: (a) An examination of general patterns of herbivorous fish distribution over the whole reef-system based on the totals and means of counts; the initial focus is on *Acanthurus lineatus* abundance. (b) Hierarchical analyses of these data to establish the within-habitat component of variation in the abundance of the commoner species and groups; here we address the problem of relating patterns of herbivore abundance to the presence of *A. lineatus*. (c) Behavioural studies of herbivorous fish at a series of sites within specific localities as indicated by the analyses in (b). (d) An analysis of within-habitat differences in reef structure at the different study sites.

#### General patterns of herbivore abundance

Total numbers of *Acanthurus lineatus* counted at each combination of reef zones and depth-defined habitats are shown in Table 1. *A. lineatus* was abundant only on reef crests of intermediate depth at oblique-reef areas. This species was not abundant in intertidal areas (cf. Robertson *et al.*, 1979), but in areas adjacent to reef crests covered by approximately 0.5 m of water at mean low-water. These numbers translate into an average of 14 *A. lineatus* per 300 m<sup>2</sup> at the mid-depth, oblique-reef habitat-combination. These densities are similar to those reported from other *A. lineatus* groups (Robertson and Polunin, 1981). The next most abundant combination supported an average of only two *A. lineatus* per 300 m<sup>2</sup>. A series of transect counts within the lagoonal area revealed no *A. lineatus*. Accordingly, the focus of our distributional and behavioural studies was at different localities within the mid-depth reef stratum.

A herbivorous fish fauna comprising 14 species of acanthurids and 20 species of scarids was sampled at each

**Table 1.** *Acanthurus lineatus*. Total numbers from 20 transect counts at each combination of structurally defined reef zone and depth stratum

Depth stratum	Reef zone		
	Exposed	Oblique	Granite
Shallow	0	34	0
Mid	11	273	0
Deep	0	0	0

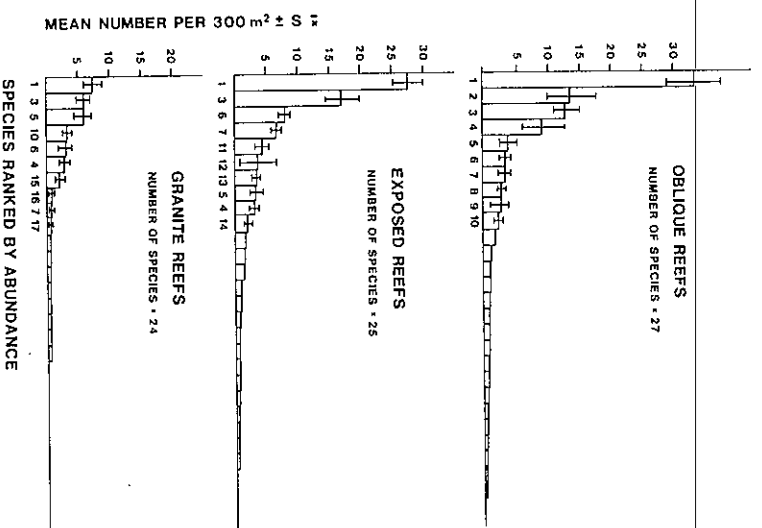


Fig. 2. Frequencies of acanthurids and scarids sampled at mid-depth region of three reef-zones. Data are mean numbers per 300 m<sup>2</sup>,  $n=20$ . Standard errors of means for ten most abundant species at each zone are shown. 1: *Ctenochaetus striatus*; 2: *Acanthurus lineatus*; 3: *A. nigrofasciatus*; 4: *Scarus rivulatus*; 5: *S. psittacus*; 6: *S. sordidus*; 7: *Zebriasoma scopas*; 8: *S. globiceps*; 9: *A. triostegus*; 10: *S. schlegelii*; 11: *S. frenatus*; 12: *S. niger*; 13: *A. dasymicri*; 14: *A. mata*; 15: *Scarus* sp.; 16: *A. olivaceus*; 17: *Naso brevirostris*.

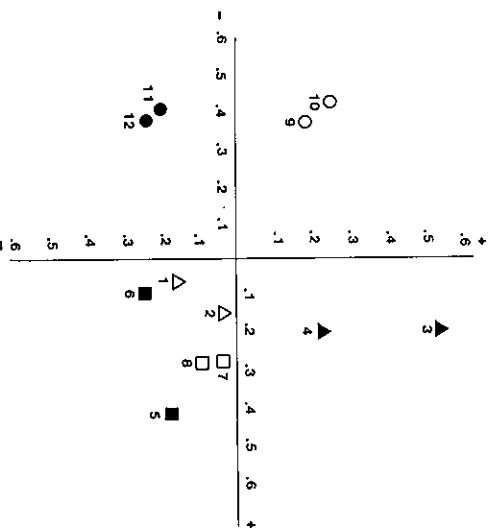


Fig. 3. Principle-coordinate analysis on results of five transect counts of 34 species of acanthurid and scarid fishes from each of twelve sites at the mid-depth stratum. Plot displays the degree of faunal similarities among sites (see "Results: General patterns of herbivore abundance" for details). Exposed reefs = ■ 5, ■ 6: Locality 1, Sites A and B, respectively; □ 7, □ 8: Locality 2, Sites A and B. Oblique reefs = △ 1, △ 2: Locality 1, Sites A and B; ▲ 3, ▲ 4: Locality 2, Sites A and B. Granite reefs = ○ 9, ○ 10: Locality 1, Sites A and B; ● 11, ● 12: Locality 2, Sites A and B.

reef zone. The general trends in abundance are shown in Fig. 2, for the ten most abundant species at each zone. With one exception, the general patterns of species' occurrence were the same in the three reef types. On oblique reefs, *Acanthurus lineatus* comprised the second most abundant species but was virtually absent from other areas. All areas sampled were characterized by acanthurids, with *Ctenochaetus striatus* consistently dominating. Reef areas dominated by coral had higher abundances of fishes than reefs composed of granite slopes. Relative abundances in coral areas followed a negative exponential function; in granite-reef sites relative abundance patterns were described by a linear function.

Our sampling design (Fig. 1A), allowed for subsampling at two spatial scales within each structurally defined reef area. Fig. 3 shows the results of an ordination treatment of our main data set. The means of five transect counts from two sites at each of two localities in the mid-depth region of the three reef-zones were examined. Principle-coordinate analysis was performed on a similarity matrix of 34 species of herbivores from twelve sites using Gower's similarity index (GENSTAT, General Statistical Program, Rothamstead Experimental Station, 1980). The relationships among the twelve sites as revealed by this analysis are shown in Fig. 3. These may be summarized as follows: (a) Granite-reef sites were distinct from coral-reef sites; there was a clear distinction between the faunas at each locality within this reef zone. (b) Herbivorous fish assemblages at exposed reefs and one of the oblique-reef localities showed strong similarities. (c) The second oblique-reef locality was distinct from other areas; the sites within this locality were also distinct from each other.

One element of this sampling design suggests the possibility of a confounding influence of two factors. The localities within the oblique-reef habitat were separated by a considerable distance and consequently closer to other habitats than each other. Any scale-associated phenomenon such as patches of settling postlarvae might override habitat differences. Indeed, Locality 1 of the oblique-reef series was more similar to the adjacent exposed-reef areas than to the other locality on oblique reefs. However, the important result was the marked difference among sites at the second oblique reef locality (Fig. 3). The localities and sites within oblique reefs were examined in greater detail to investigate the relationship between *Acanthurus lineatus* and other herbivores.

#### Within-habitat variation in herbivorous fish abundances

The trends reported above represent summaries of mean values. In most instances variances were large. A hierarchical analysis of variance permitted comparisons among localities within oblique reefs to be made simultaneously with comparisons at smaller spatial scales; among sites within localities and among transects within sites. In this way, the contribution of the different elements within the sampling design to the total variation in herbivorous fish

abundance was assessed. The relevant data set is shown in Table 2. Analyses concerning four categories of herbivorous fishes are shown in Table 3.

Tables 2 and 3 reveal major differences in *Acanthurus lineatus* abundances among localities on oblique reefs. Analysis of variance confirms that *A. lineatus* abundances were greater at Locality 2 and that differences within sites at each locality were not significant and accounted for only a minor proportion of the total variation. This spatial bias in the abundance of *A. lineatus* accounts for the among-locality differences for oblique reefs seen in Fig. 3. However, it should be noted that the adjacent exposed-reef locality (Fig. 1A) did not harbour any *A. lineatus*. The ubiquitous acanthurid *Ctenochaetus striatus* was abundant at all localities and sites on oblique reefs, differences among localities and transects within sites accounting for most of the variation; higher numbers of *C. striatus* occurred at Locality 2. All other acanthurids were considered as a single group, which was dominated by the small schooling-species *A. nigrofasciatus*. Differences among sites were significant; there were fewer acanthurids at Site A, Locality 2 than at Site B (Student-Newman-Keuls analyses). The scarid fauna showed considerable local variation. Dif-

ferences among transect counts within sites (possibly a reflection of schooling tendencies) accounted for most of the variation in this group. There was no systematic trend in the abundance data that could be attributed to the presence of *A. lineatus*. Both the principle coordinate analysis and the analyses of variance confirm the following patterns of herbivore-abundance—*A. lineatus* achieved high abundances at a single locality, but had no consistent influence on the other herbivorous species. There was evidence of reduced numbers of small acanthurids in the presence of *A. lineatus*, but only at a single site within this locality. *C. striatus* was, if anything, more numerous in areas of high *A. lineatus* abundance.

It appears that behavioural patterns of the herbivores such as the temporary formation of schools as well as the activities of *Acanthurus lineatus* might have contributed to the high variability. In addition, local differences in species abundance-patterns and composition, especially in the scarid fauna, could have been an important source of variation.

For these reasons, a more detailed study of the herbivore feeding process and the associated interactions were initiated at the adjacent sites within Locality 2.

#### Herbivore activity and behaviour patterns

The most abundant acanthurid at all sites examined was *Ctenochaetus striatus*. Many individuals appeared to occur and feed in *Acanthurus lineatus* territories without eliciting any aggressive response. Table 4 summarizes the patterns of abundance of both species from counts within territories at each site. Abundances of both species were almost identical within territories at each site; the small differences followed the trend revealed by line transects. Only one instance of an aggressive interaction directed by *A. lineatus* toward *C. striatus* was recorded (Table 5) despite the high, spatially overlapping densities of each species. In addition, although both species displaced measurable intraspecific aggressive interactions, only *A. lineatus* consistently attacked other species. Intraspecific aggression for both species was higher at Site A, and was most marked in *A. lineatus*.

**Table 2.** Variation in abundance of herbivorous fish within and among localities on oblique-reef zones at mid-depth stratum. Values are means ( $\pm$  SE) per 300 m<sup>2</sup>,  $n=5$

Species	Locality 1		Locality 2	
	Site A	Site B	Site A	Site B
<i>Acanthurus lineatus</i>				
$\bar{x}$	0.6	5.4	30.0	18.6
(SE)	(0.2)	(2.5)	(8.3)	(3.7)
<i>Ctenochaetus striatus</i>				
$\bar{x}$	23.0	32.4	36.4	43.4
(SE)	(3.7)	(6.6)	(3.2)	(5.9)
Other acanthurids				
$\bar{x}$	17.2	32.2	7.4	25.6
(SE)	(4.7)	(8.7)	(3.1)	(4.4)
Scarids				
$\bar{x}$	47.0	21.8	19.4	23.8
(SE)	(13.6)	(8.7)	(7.1)	(3.4)

**Table 3.** Summary of hierarchical analysis of variance results on four categories of herbivores in mid-depth stratum of the oblique-reef zone. Variance components are expressed as percentages of the total variation.  $n=5$

Groups	Proportion of variation explained			Significant terms
	Localities	Sites (L)	Transects (S)	
<i>Acanthurus lineatus</i>	77.2	3.9	21.4	Localities L2 > L1
<i>Ctenochaetus striatus</i>	29.9	0	69.5	None
Other acanthurids	0	50.5	49.5	Sites L2SA < L2SB
Scarids	0	14.5	85.4	None

**Table 4.** *Acanthurus lineatus* and *Ctenochaetus striatus*. Abundances within territories at each site (Locality 2, oblique-reef zone). Values are mean numbers ( $\pm$  SE) of individuals per sample area;  $n = 12$ . (Note: in some instances  $3 \times 3$  m area covered more than one territory)

	<i>A. lineatus</i>	<i>C. striatus</i>
Maximum numbers		
Site A	$3.8 \pm 0.2$	$3.9 \pm 0.3$
Site B	$3.1 \pm 0.2$	$3.1 \pm 0.5$
Constant numbers		
Site A	$1.4 \pm 0.1$	$1.6 \pm 0.2$
Site B	$1.2 \pm 0.1$	$1.5 \pm 0.4$

**Table 5.** *Acanthurus lineatus* and *Ctenochaetus striatus*. Summary of inter- and intraspecific interaction rates at each site (Locality 2, oblique-reef zone). Values are mean numbers ( $\pm$  SE) of interactions per 15 min observation period;  $n = 12$ 

	<i>A. lineatus</i>	<i>C. striatus</i>
Interspecific interactions		
Site A	$1.9 \pm 0.5$	$0.08 \pm 0.08^a$
Site B	$1.6 \pm 0.6$	$0.2 \pm 0.1^b$
Intraspecific interactions		
Site A	$0.9 \pm 0.3$	$0.8 \pm 0.3$
Site B	$0.08 \pm 0.08$	$0.5 \pm 0.2$

<sup>a</sup> Attacked by blenny<sup>b</sup> Attacked by *A. lineatus*

The scarid fishes in the study area could be divided into a number of categories reflecting size, feeding rate, and movement. Species such as *Scarus sordidus*, *S. globiceps*, *S. spinus*, *S. frenatus*, *S. schlegelii*, *S. rivulatus* and *S. psittacus* are relatively small, vagile or occasionally site-attached species, with a tendency to form feeding-schools. A second group may be differentiated on the basis of size. These may be schooling or solitary, and include *Cetoscarus bicolor*, *S. gibbus*, *S. rubroviolaceus* and *Bolbometapon muricatum*. Initial observations suggested that, while the two adjacent study sites supported similar numbers of scarids, there were differences in species composition and size-frequency. Moreover it was clear that the reactions of *Acanthurus lineatus* to intruding herbivores varied with their identity.

An examination of the scarid transect-count data for each site (Table 6) revealed the following differences. Site A contained relatively few small schooling scarids and more large scarids than Site B. Did *Acanthurus lineatus* react differently to different types of scarids or were the scarids indiscriminately attacked as they attempted to feed in *A. lineatus* territories? We made a series of observations in *A. lineatus* territories at each site. Twelve  $3 \times 3$  m areas within *A. lineatus* territories were observed for 15 min each at Sites A and B. The results (Table 7) confirmed the transect-count data; at Site A, many large scarids entered *A. lineatus* territories but none were observed to do so at Site B. Many small schooling scarids entered territories at Site B, but few did so at Site A. Large

**Table 6.** Composition of scarid fauna at Sites A and B, Locality 2, of the oblique-reef zone. Values are mean numbers per 300 m<sup>2</sup> ( $\pm$  SE);  $n = 5$ 

Species	Site A	Site B
Large		
<i>Scarus gibbus</i>	$2.6 \pm 0.7$	$0.2 \pm 0.2$
<i>S. rubroviolaceus</i>	$0.8 \pm 0.2$	$0.2 \pm 0.2$
<i>Cetoscarus bicolor</i>	$0.2 \pm 0.2$	$0.2 \pm 0.2$
Totals	$3.6 \pm 0.3$	$0.6 \pm 0.2$
Small		
<i>Scarus sordidus</i>	$1.4 \pm 1.4$	$6.6 \pm 2.7$
<i>S. globiceps</i>	$2.2 \pm 1.7$	$4.6 \pm 0.4$
<i>S. spinus</i>	$0.4 \pm 0.2$	$2.2 \pm 0.7$
<i>S. frenatus</i>	$2.2 \pm 0.7$	$3.2 \pm 0.7$
<i>S. schlegelii</i>	$1.6 \pm 1.4$	$2.0 \pm 1.6$
<i>S. rivulatus</i>	$3.0 \pm 1.4$	$2.2 \pm 0.5$
<i>S. psittacus</i>	$0.8 \pm 0.4$	$0.8 \pm 0.6$
<i>S. niger</i>	$1.6 \pm 0.5$	$0.6 \pm 0.2$
<i>S. brevifilis</i>	$1.0 \pm 1.0$	$0.2 \pm 0.2$
<i>S. ghobban</i>	0	$0.4 \pm 0.2$
<i>Scarus</i> sp.	0	$0.4 \pm 0.4$
<i>S. oviceps</i>	$1.0 \pm 0.5$	0
<i>S. bleekeri</i>	$0.6 \pm 0.4$	0
Totals	$15.6 \pm 6.7$	$23.4 \pm 3.4$

**Table 7.** Interactions and feeding behaviour by site and scarid size-category within *Acanthurus lineatus* territories (Locality 2, oblique-reef zone). Values are totals from 15 min observations of replicated 9 m<sup>2</sup> areas; means  $\pm$  95% confidence interval;  $n = 12$ 

Scarid category	Site A	Site B
Large		
Passes through territory	$14 (1.2 \pm 0.7)$	0
No. attacked by <i>A. lineatus</i>	$1 (0.1 \pm 0.2)^a$	0
Feeding episodes	$6 (0.5 \pm 0.5)$	0
Small schooling		
Passes through territory	$19 (1.7 \pm 0.8)$	$81 (7.1 \pm 7.4)$
No. attacked by <i>A. lineatus</i>	$12 (1.0 \pm 1.3)$	$13 (0.8 \pm 0.2)$
Feeding episodes	0	$7 (0.5 \pm 1.1)$

<sup>a</sup> Small *Scarus gibbus*

scarids (mainly *Scarus gibbus* and *S. rubroviolaceus*) entering *A. lineatus* territories at Site A were not attacked, and 40% of those that entered actually fed within the territories. The only aggressive interactions observed with this group involved a small individual (less than 300 standard length) of *S. gibbus*. A majority of the smaller scarid species entering territories were immediately attacked and none was able to feed within them. In contrast, a total of 81 small scarids entered territories at Site B and a minority of these were able to graze. Only a small proportion (16%) of the invading scarids was attacked. For small scarids, approximately the same number of attacks by *A. lineatus* occurred at each site (12 and 13 at Sites A and B, respectively), but far more individuals entered territories and fed at Site B.

A breakdown of aggressive interactions by *Acanthurus lineatus* against species- in seven families of reef fishes revealed further evidence of site-specific patterns. Small



scarids (*Scarus sordidus*, *S. globiceps*, *S. spinus*, *S. rivulatus* and *S. psittacus*) were the major targets at Sites A and B, where they received 52 and 49% of the observed aggression, respectively. There were differences with respect to other groups. At Site A, the pomacentrid *Abudefduf whiteleyi*, which often forages in the water column but also feeds on the reef substratum, was attacked with the next greatest frequency, 30% of observed attacks. There were no interactions with acanthurids at Site A, with the exception of a single attack on *Ctenochaetus striatus*. However, acanthurids were frequent targets of aggression at Site B, with the focus on *Acanthurus nigrofusus*, 37% of observed attacks.

In addition to fixed-time observations within and adjacent to *Acanthurus lineatus* territories, we maintained a more informal schedule of observations on scarids within Site A. The attack rate on scarids was biased toward certain species; *Scarus globiceps* led, with 2.6 attacks per hour, followed by *S. frenatus* (1.8), *S. sordidus* (1.1), *S. gibbus* (less than 300 mm; 0.6), *Scarus* sp. (0.6), and *S. oviceps* and *S. spinus* (0.5). These are approximations, but suggest that certain species are attacked more frequently than their relative abundances alone (Table 6) would suggest.

The above results suggested that some species fed within the territories of *Acanthurus lineatus*. These included *Ctenochaetus striatus*, *Scarus gibbus*, *S. rubrovittatus*, and *Cetoscarus bicolor*. Feeding by these species was not interrupted by attacks from *A. lineatus*. One explanation argues that these species were selecting different components of the reef substratum as grazing sites; overlap in food resources may have been minimal. To clarify the relationship between grazing location, species identity, and substratum selection we observed the feeding of the various herbivores within and adjacent to *A. lineatus* territories.

The grazing substratum was subdivided into five structural microhabitat categories and the number of bites made by each species on the different categories recorded. For both *Acanthurus lineatus* and *Ctenochaetus striatus*, 200 bites of four individuals of each species at each site were so recorded (Fig. 4). Both species showed clear biases in the grazing substratum selected. There was a well developed tendency to graze flat or dome-shaped components of the substratum rather than the other categories observed. These results were subjected to a three-factor analysis of variance (Table 8). The species term was not significant; the sites  $\times$  grazing categories interaction was highly significant. The absence of any significant interaction term involving species suggests that, in feeding, both species are responding to minor structural differences at each site in a similar fashion. We provide a quantitative description of these structural differences in the following section concerned with within-habitat differences in reef structure (Tables 10 and 11).

Comparisons were also made between the feeding patterns of *Acanthurus lineatus* and two categories of scarids, large species of scarids which fed within *A. lineatus* territories and small species which generally fed outside.

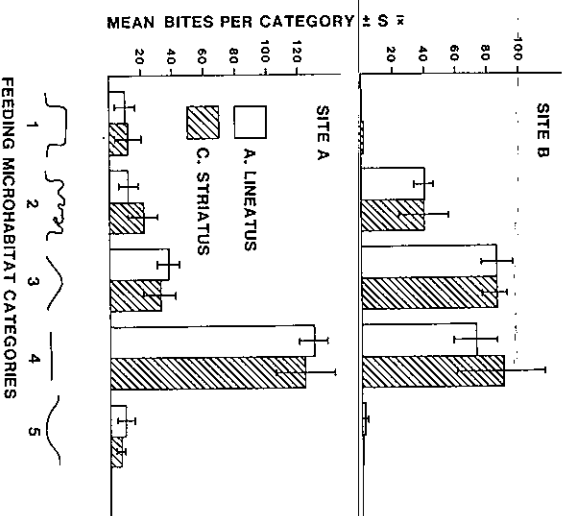


Fig. 4. *Acanthurus lineatus* and *Ctenochaetus striatus*. Feeding, expressed as mean number of bites, on five microhabitat categories at two sites (Locality 2, oblique-reef zone). 200 bites were monitored per individual;  $n = 4$ .

Table 8. *Acanthurus lineatus* and *Ctenochaetus striatus*. Analysis of variance feeding microhabitat data from Fig. 4. The analysis is a mixed model with three factors: species are fixed, sites random, and feeding-microhabitat categories fixed. \*  $p < 0.05$ ; no tests performed for the factors "Sites" and "Categories", as the interaction was significant; ns: non-significant  $F$  value,  $p > 0.05$ . D.F.: degrees of freedom; MS: mean square

Source	DF	MS	F
Species	1	45.0	ns
Sites	1	45.0	—
Categories	4	28 167.7	—
Species $\times$ sites	1	44.9	ns
Species $\times$ categories	4	61.3	ns
Sites $\times$ categories	4	5 157.2	10.5*
Species $\times$ sites $\times$ categories	4	162.8	ns
Residual	60	491.8	

Table 9. Summary of feeding-microhabitat categories used by species in two size-classes of scarids at Site A. Locality 2, oblique-reef zone. Values are percentage of bites on each of three feeding-microhabitats. A: minutes observed; B: percent of size-class feeding in *Acanthurus lineatus* territories; C: number of attacks by *A. lineatus*

Scard size categories	Feeding microhabitats			A	B	C
	Convex	Flat	Concave	(min)	(%)	(n)
Large						
<i>Scarus gibbus</i>	96.1	3.9	0	37	100	4*
<i>S. rubrovittatus</i>	24.2	75.1	0.7	29	100	0
Small schooling						
<i>Scarus sordidus</i>	77.3	16.6	6.0	49	0	0
<i>S. frenatus</i>	28.8	40.4	30.8	44	0	0

\* Three attacks on < 300 mm individual

We made the assumption that large species of scarids feeding within the surgeon-fish territory would be selecting different grazing microhabitats than those used by the resident *A. lineatus*. In this instance we considered three grazing microhabitats, convex, flat and concave. The large scarids kept under observation for a cumulative period of 66 min of observation at Site A in December 1983 fed exclusively within *A. lineatus* territories. Table 9 shows that these large scarids selected convex and flat grazing microhabitats. Their grazing microhabitats thus showed a major overlap with those of *A. lineatus* (Fig. 4), with all species concentrating on convex and flat grazing surfaces. This overlap was most marked between *A. lineatus* and large *Scarus rubrovittatus*. Grazing on similar substrata in association with *A. lineatus* and within their territories did not elicit an aggressive response from the acanthurid, nor between these scarids and *Ctenochaetus striatus*. In addition to these observations we also followed a number of large scarids including terminal-phase *Cetoscarus bicolor* over Site A feeding areas in 1984. During 27 min of observation including nine on *C. bicolor*, all recorded feeding occurred in *A. lineatus* territories.

Smaller species of scarids such as *Scarus sortidus* and *S. frenatus* which were usually attacked by *Acanthurus lineatus* also showed considerable overlap in grazing microhabitats with both the acanthurid and the large scarids. *S. frenatus* was the only species which showed some differences in grazing microhabitat using concave substrata (Table 9). It also showed overlap with *A. lineatus* by

grazing flat substrata. All categories of grazing fish examined used very similar grazing microhabitats.

#### Within-habitat differences in reef structure

Our counts and observations suggest that differences exist between the two adjacent sites in terms of herbivore abundances, behaviour, and feeding patterns. Despite similar characteristics of the reef at both sites, it is possible that subtle differences in habitat structure were present in this apparently homogenous area. Here we consider two aspects of reef structure; the degree of surface heterogeneity and the proportion of living coral on the reef crest areas where the fishes held territories and grazed, and the character of the reef (degree of slope, overhang etc.) itself.

The reef crest was sampled for estimates of structural heterogeneity and cover at three equidistant sampling areas within each site. This permitted estimates of the structural differences and of the spatial scale on which they occurred. Tables 10 and 11 suggest that the reef-crest areas were relatively homogenous within each site, but that there were differences among the two sites in a number of features. The data were analysed so as to provide estimates of the proportional variation explained at each level of sampling, between sites, within sites and within the subsampling areas. Site A was characterized by a greater amount of flat substratum. Most of the variation in this feature was explained by differences between the

Table 10. Estimates of percentage cover of live coral and the dimensions of continuous flat-areas within reef-crest herbivore feeding-areas at Sites A and B, Locality 2, oblique-reef zone

	Site A	Site B
% sampling points on live coral	21%	32%
Continuous no. of sampling points on flat areas per transect (means $\pm$ SE)	2.3 $\pm$ 0.2	1.3 $\pm$ 0.2

Table 12. Estimates of height and angle of reef profiles at Sites A and B. Values are means ( $\pm$  SE)

	Site A	Site B
Height of reef front (m, $n=6$ )	5.1 (0.4)	5.5 (0.5)
Angle of reef slope (degrees, $n=6$ )	59.2 (2.3)	84.2 (5.5)

Table 11. Summary of hierarchical analysis of variance results on two categories of reef-crest structure at Sites A and B. Variance components are expressed as percentages of total variation. Na: no estimate of the variation associated with subtransects was possible for the structural variable "flat area", as data are expressed as proportion of flat area per transect

Structural variable	Percentage of variation explained		
	Sites	Transects	Subtransects
Height above substratum	80.1	0	1.4
Shrubiness	36.1	0.3	4.1
Proportion of area flat	38.0	0	NA
			Residual
			Significant terms
			18.4 Sites A < B
			59.7 Sites A < B
			59.7 Sites A > B

**Table 13.** Patterns of herbivore abundance over time at Sites A and B, Locality 2, oblique-reef zone. Values are mean numbers ( $\pm$  SE) per 300 m<sup>2</sup>. *A. lineatus* and *C. striatus* not counted at Site A in 1983. No counts (NC) of other acanthurids in 1983

Herbivores	1982 (n=5)		1983 (n=4)		1984 (n=4)	
	Site A	Site B	Site A	Site B	Site A	Site B
<i>Acanthurus lineatus</i>	30.0 (8.3)	18.6 (3.7)	NC	21.0 (5.6)	26.7 (4.1)	16.5 (3.2)
<i>Ctenochaetus striatus</i>	36.4 (3.2)	43.4 (5.9)	NC	27.7 (9.3)	37.5 (4.4)	21.7 (3.7)
Other acanthurids	7.4 (3.1)	25.6 (4.4)	NC	NC	7.7 (1.8)	16.0 (1.7)
Scarids						
Large	3.6 (0.3)	0.6 (0.2)	1.9 (0.6)	1.0 (0.4)	2.0 (0.7)	0 (-)
Small schooling	13.2 (5.4)	22.8 (3.6)	9.2 (2.1)	23.2 (9.3)	5.0 (2.5)	28.7 (3.7)

two sites and by the residual term which reflected the local scale-differences within each subsampling area. There was a slightly lower proportion of live coral and less surface heterogeneity (two measures) at Site A compared with Site B. In all the measures taken, there is a pattern of both broad-scale (among sites) and very local scale (within transects) variation. At Site A there was a series of large flat areas interspersed with aggregations of dead coral bases and live corals; at Site B, the dead and live coral was more continuous, higher, and structurally complex. These structural properties reflect patterns of feeding-substratum selection in Fig. 4. Both *Acanthurus lineatus* and *Ctenochaetus striatus* appear to select feeding substrata on the reef crests in the proportions that they occur at each site. Extensive flat areas of reef at Site A were associated with a greater spread of contiguous *A. lineatus* territories. At Site B, the reef-crest area was narrower (Fig. 1B) and *A. lineatus* territories did not extend so far shoreward.

The sites also differed in a series of more obvious structural features. Reef height, or the vertical distance from the crest edge to the start of the rubble slope at the base was similar at each site; the reef front was about 5 m high in each case (Table 12). However, the slope of the reef was much steeper at Site B. At Site A, the reef sloped more gradually down to an extensive rubble plain which, in turn, extended gradually out into deeper water; at Site B, the reef was close to vertical or undercut, with an abrupt transition to the rubble base (Fig. 1B).

#### Temporal changes in abundance

To determine whether the site-associated patterns of abundance we observed were consistent, we carried out limited additional sampling at other times and in other areas of *Acanthurus lineatus* territories. Replicate samples taken in the study sites in 1983 and 1984 showed no changes in the major species groupings (Table 13). During the 1984 series,

local areas of group spawning-activity by scarids (the adjacent North Point) were carefully monitored before transect counts at Site A. Counts were made only when it was established that no aggregations of scarids were present at North Point. Similar trends in herbivorous fish abundances between sites over time suggest that the behavioural interactions that we observed are consistent features of this locality. However, sampling in other localities provided little evidence that the observed behavioural interactions are consistent with those between individuals at other sites. Observations at the other oblique reef locality suggested that some species of small scarids fed undisturbed in *A. lineatus* territories. Four territories at Locality 1, Site A, were observed for 10 min each. During this time terminal phase *Scarus sordidus* and *S. frenatus* fed within the territories in the presence of *A. lineatus*, but were not attacked. This information is limited in scope as so few samples were taken, but it tends to reinforce the idea of spatial lability in herbivore interactions. In this context, it is interesting to note that Nursall (1974) observed species-specific responses in interactions among *A. lineatus* and scarids. The species which "escaped attention" from *A. lineatus* at his Heron Island study site were species (*S. sordidus*, *S. globiceps*, *S. rivulatus*) which were frequently attacked at our Lizard Island, Locality 2, oblique-reef study sites.

#### Discussion

Our discussion deals with two related sets of observations:

- (i) We detected differences in abundance and species composition in the fauna of herbivorous fishes at two adjacent study sites. These were associated with small but measurable differences in reef structure. Both sites were characterised by relatively high abundances of *Acanthurus lineatus*. Visual sampling, repeated over a period of 2.5 yr, suggests that these patterns are fairly stable.

(ii) Aggressive behaviour by *Acanthurus lineatus* was not directed uniformly against other herbivorous fishes. The size and identity of these fishes clearly influenced this interaction. This was most noticeable in scarid fishes.

Large scarids were commoner at Site A, and were not only ignored by *Acanthurus lineatus* but carried out the majority of observed feeding within their territories. Smaller scarids were relatively rare, as was the acanthurid *A. nigrofasciatus*, and were attacked at the borders and adjacent to *A. lineatus* territories. We observed no feeding within or adjacent to *A. lineatus* territories. At Site B, small schooling herbivores including *A. nigrofasciatus* were abundant, invaded *A. lineatus* areas more frequently, and some fed within these areas. These feeding episodes did not occur in the context of "swamping" the *A. lineatus* defenses (Robertson *et al.*, 1976). No large scarids were observed to feed within the observed territories. The attack rate by *A. lineatus* on small scarids was similar at both sites despite different intrusion rates. Differences between study sites would be even more pronounced if scarid biomass rather than numbers were used. The acanthurid *Ctenochaetus striatus* was equally abundant at both sites, and showed a considerable overlap with *A. lineatus* in territory distribution and feeding microhabitats.

Our attempts to generalize about the influence of *Acanthurus lineatus* were constrained by this site-associated variation. To clarify an initially confusing picture, we have subdivided our discussion so as to consider numerical and behavioural aspects of this interaction separately.

We address the numerical aspect of the question first; does *Acanthurus lineatus* have an easily recognizable and consistent effect on the fish fauna of our study reef? The clear answer is that it does not. While our results suggest that significant variation in herbivorous fish abundance exists on the study reef, this could not be related to the distribution of *A. lineatus* in any consistent way. The presence and activities of this species did not generate predictable patterns at any of the scales considered.

Given its behavioural and distributional characteristics, why does *Acanthurus lineatus* not have a more clear-cut influence on the local abundances of other herbivorous species? One explanation is that other processes acting relatively early in the life cycle may play a more important role in establishing observed abundances. The numerical patterns we describe may be more the result of settlement and recruitment events. Settling scarids may be responding to particular structural and biological features of the reef which are prerequisites for successful recruitment into adult populations.

Preliminary information suggests that for some species of scarids this is true. Recently settled individuals of *Scarus gibbus*, *S. rubroviolaceus* and *Cetoscarus bicolor* were observed only in deeper water on the gently shelving reef slopes and basal areas that were characteristic of Site A (Fig. 1B; Table 12). With increase in size, juveniles of these species move up the reef slopes and eventually establish themselves on the reef crests and adjacent flats

which constitute the major adult feeding areas (Bellwood, in preparation).

Smaller schooling species (*Scarus sordidus*, *S. rivulatus*, *S. psittacus*) occurred in greater abundance in shallower areas behind the reef crest, especially in coral debris adjacent to flat feeding-areas as seen at Site B. The combined processes of settlement and recruitment into populations of grazing adults appear to be complex, involving sequential movement through a series of habitats. The interaction with *Acanthurus lineatus* commences after many of these events have been completed. Although this interaction is readily observable, it may not have any influence on the numerical status of herbivore populations. Removal of *A. lineatus* may result only in a very local redistribution of herbivores, but not a real increase in numbers either in the short- or long-term.

*Acanthurus lineatus* is also associated with the acanthurid *Ctenochaetus striatus*. Although large numbers occur within *A. lineatus* territories we see no obligatory elements in this association. *C. striatus* is one of the most abundant species on the study reef, and most occur in areas not occupied by *A. lineatus*. Although *C. striatus* living in association with *A. lineatus* may have better growth rates or condition, there appear to be no general numerical or distributional features of this association.

Behavioural interactions were also complex. *Acanthurus lineatus* attacks were directed only toward some elements of the acanthurid and scarid fauna. The feeding of *Scarus gibbus* and *S. rubroviolaceus* in *A. lineatus* territories was strongly size-dependent. Small individuals (less than 300 mm) were consistently attacked; larger individuals were ignored. This was seen in the first instance as the inability of *A. lineatus* to evict the larger, heavier scarids from the feeding territories. However, such size-dependent arguments do not stand up to comparisons with other species combinations. Small pomacentrids (*Pomacentrus flavicauda*) successfully evict moderate-sized scarids (250 to 300 mm) from their feeding areas (Low, 1971). The ratio of intruder to defender size or weight is far greater in these species than in the scarid: *A. lineatus* interaction.

Size in scarids is correlated with a number of other features related to feeding activities. Larger species such as *Scarus gibbus* and *S. rubroviolaceus* have a relatively low feeding rate (bites per minute), greater movement between feeding episodes, and a greater home range (Bellwood, in preparation). These individuals are likely to feed briefly and move on to other areas, irrespective of *Acanthurus lineatus* activities. Their range of movement is usually far greater than an *A. lineatus* territory. Smaller scarids feed more intensively, and are likely to occur in schools or have a limited range of movement. These represent preliminary observations, but we suggest that size alone is important only as it relates to other aspects of feeding behaviour. These predictions require observations at other areas before they can be evaluated.

The attack rate on smaller schooling scarids was similar at Sites A and B and therefore not predictably related to abundance. The higher rate of intrusion at

Site B did not result in more attacks. A testable idea concerning the attack-rate-data concerns the type of grazing substrata sought by scarids and the probability of attack by *Acanthurus lineatus*. Scarids attempting to graze flat or gently concave surfaces (characteristic of Site A) may be attacked more readily than those seeking heterogeneous grazing-surfaces. Some of the variability in attack-rate among sites may therefore be explained by the substratum differences (Tables 10 and 11). Further feeding observations are required to clarify these points.

There are a number of records of a high degree of spatial overlap in different species of territorial herbivorous fishes (Robertson and Polunin, 1981; Robertson, 1984). This has been termed "cohabitation" and usually involves pomacentrid fishes as either one or all of the group. The species involved share similar food requirements and the task of repelling other herbivorous species. The participants may behave aggressively toward one another and, depending on the status of the different cohabitants, these associations have been termed parasitic or mutualistic. Similar associations may occur at Lizard Island. The most striking pattern of spatial overlap in the species studied involved the acanthurids *Acanthurus lineatus* and *Ctenochaetus striatus*. At our study sites this association involved a high degree of overlap in feeding sites, but we found no evidence of aggression among these species or shared defense of feeding areas. *C. striatus* was a passive member of this association.

Preliminary examination of adult *Ctenochaetus striatus* alimentary tract contents revealed no evidence of algae; the contents comprised fine sedimentary material. This confirms the observations of other workers on members of this characteristic genus (Jones, 1968; Robertson, 1983). However, there was no evidence that *C. striatus* sought feeding microhabitats in which sediment or detritus might accumulate. They fed over the same algal-rich microhabitats grazed by *Acanthurus lineatus*. At these sites, *C. striatus* was extracting some element from the algal turf environment, utilizing its characteristic combing and suction-feeding mode. At this stage we cannot identify this element, which may be bacterial or detrital, nor would we accept the argument that *C. striatus* and *A. lineatus* are seeking different food sources and avoiding resource overlap. Both species may be targeting the same food source but have very different ways of harvesting it. There was no evidence of any general dependence of *C. striatus* on territorial herbivores and their associated algal mats.

Our data from the two study sites includes information on both habitat structure and faunal composition. The reef-fish literature provides evidence of relationships between relative abundances, species composition and distinct elements of reef structure. Such relationships are most obvious when one compares faunas from structurally diverse reef areas (Kaufman and Ebersole, 1984). The situation described in this study concerns fish faunas within localized and structurally similar habitats where we found marked differences in herbivore abundances. One explanation would argue that the subtle within-habitat

differences in reef structure presented in Tables 10, 11, 12 were responsible for the observed differences in fish faunas. It is equally probable, however, that the patterns observed are due to chance recruitment events occurring on a very localized scale. This argument is also supported by empirical evidence from other reef situations (Sale and Douglas, 1984). An examination of a wider range of sites within the same habitat type may not show any consistent relationship between fish faunas and quantitative differences in reef structure. Our intention is twofold. Firstly, to focus attention on the desirability of collecting recruitment data over a number of sites within similar habitats. Secondly, to suggest that the processes of settlement and recruitment into adult populations of the larger herbivores may involve sequential occupation of a series of habitats, and thus be more complex than those reported for smaller species (Doherty, 1983).

The behavioural features of the *Acanthurus lineatus*/herbivore interaction that we have described are open to a variety of interpretations. As Losey (1982) has pointed out, the literature has tended to emphasize the adaptive nature of interspecific territoriality in fishes. Aggressive interactions may be correlated with the degree of overlap in ecological requirements. A refinement of these arguments extends to a cost/benefit perspective (Robertson and Polunin, 1983; Robertson, 1984). For example, benefits which accrue to the continued exclusion of larger scarids must be balanced against the costs of maintaining such a defense. Such costs and benefits are seen in evolutionary terms, resulting in changes in survival and fecundity that will ultimately influence fitness. However, the process of interspecific defense amongst herbivores may be exceedingly complex, involving learned elements of behaviour. Recognition of potentially competing species may be moulded by early experience (Losey, 1982).

Two elements in the reef-fish environment must complicate a strict application of cost/benefit arguments. Dispersive episodes of larvae coupled with patchiness and local variability in reef-fish distributions could result in fishes being exposed to very different behavioural environments each generation (Eckert, 1984; Sale *et al.*, 1984). Differing interspecific behaviour-patterns may be the result of locally learned responses, rather than the general fine-tuning of a process by selection acting on heritable behaviour-patterns. Patterns of aggression or tolerance might reflect the influence of early chance encounters with particular species at different density thresholds. The behaviour patterns that we have described (especially, the interactions with large scarids) must be checked for consistency in other localities.

One of our initial aims was to survey study areas as a prerequisite for experimental manipulations; specifically, the removal of *Acanthurus lineatus*, followed by an evaluation of herbivore response in experimental and control areas. These experiments would be more complex and logistically expensive than our preliminary surveys suggested. We were able to identify a relatively homogeneous section of reef, 600 m in length, supporting a high density

of *A. lineatus* and schooling herbivores. Within this area replicated removal and control areas for an *A. lineatus* removal experiment could be set up. However, localized variation in herbivore abundance and feeding behaviour suggest that such experiments would have been confounded. Other factors besides the presence of *A. lineatus* appear to be influencing herbivore abundances, and a simple *A. lineatus* removal experiment would not have accommodated these. The results of such an experiment would be potentially misleading for this reason. One conclusion is that the most appropriate error-term for the testing of such experimental hypotheses would involve the mean square associated with within-habitat variation collected over several spatial scales, rather than from the replicates at one site. A further and very tentative conclusion is that short-term temporal changes might not be such an important source of variation. More comprehensive monitoring schemes which target both short-term (behavioural) and long-term (recruitment-associated) changes are required to resolve this.

Our results complement other studies on herbivorous-fish distribution patterns. Williams (1982), Williams and Hatcher (1983) and Russ (1985a) demonstrated major latitudinal trends in fish distribution across the continental shelf of the Great Barrier Reef. Russ (1985b) also demonstrated major differences among habitats within reefs for herbivorous-fish abundances. More importantly, he showed differences in abundance in the same habitat for adjacent reefs on the continental shelf. Miller (1982) showed very local differences in herbivorous-fish distribution at Enewetak Atoll, and suggested that this had a major influence on the sessile biota in his study areas. Structural differences in the reef environment were considered to be important factors in his study. Our data provide a finer scale perspective of herbivorous-fish distribution. It is at this scale that most experiments and detailed observations of reef-fish behaviour are carried out. A general conclusion of our study was that a strong site-specific component was present in reef-fish abundance and behaviour, a fact which complicated our proposed experiments. One criticism of our conclusions might be that Lizard Island is "atypical" in the sense that it is a continental island surrounded by large numbers of coral cays. Undoubtedly there are some environmental differences, but coral reefs associated with rock substrata are a significant element in many reef regions. The important question is to determine whether the within-habitat variation of the type that we describe is typical of other reef types, or whether they are characterized by a more predictable pattern of herbivorous-fish abundance. Sale *et al.* (1984) monitored recruitment within similar habitats on a series of platform reefs. Their analysis suggests that for the species concerned (mainly small labrids and pomacentrids) significant variation occurred among reefs but not at sites within a reef. Similar studies on the recruitment patterns of larger herbivores would be of considerable interest.

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