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CHAPTER FIVE

THE BEHAVIOURAL ECOLOGY OF ADULT SCARIDS

Introduction

From the functional considerations of the morphological analyses in Chapter 1, two morphological and functional groups were described in the genus *Scarus*. This raised the question: is there any correlation between the functional morphology and behavioural ecology of scarids? This question will be addressed in this chapter.

The two functional groups described in Chapter 1 are primarily separated by the form of their feeding apparatus, the 'sordidus' group as 'biters' and the 'frenatus' group as 'scrapers'. Any ecological differences between the two groups are therefore, likely to include differences in their feeding biology. For this reason, the feeding biology of the two groups will be considered in most detail.

Part A – Feeding Biology

5.1 Introduction

Several aspects of the feeding biology of scarids have been investigated. These include analyses of: 1) intestinal contents (Gohar & Latif, 1959, Hiatt & Strasberg, 1960, Choat, 1966, 1969, Randall & Bishop, 1967, Gygi, 1969, 1975, Glynn *et al.*, 1972, Hobson, 1974, Frydl & Stearn, 1978 and Bruce, 1979), 2) differential utilization of grazing substrata (Choat & Robertson, 1975, Bruce, 1979 and Frydl, 1979), 3) feeding rates (Barlow, 1975, Itzakowitz, 1977, Bruce, 1979 and Hatcher, 1981), and 4) bite types (Bruce, 1979).

Analyses of the gut contents of scarid fishes are difficult due to the nature of the ingested material (primarily turf algae and inorganic particles), and the grinding action of the pharyngeal mill which turns ingested material into a thick slurry. Nevertheless, consistent dietary differences have been found between both genera and species. *Leptoscarus vaigiensis*, *Calotomus* spp. and *Sparisoma radians* (C & V) predominantly feed upon angiosperms and fleshy algae (Suyehiro, 1942, Bruce, 1979 and Lobel & Ogden, 1981), whilst *Scarus* species, *Cetoscarus bicolor*, *Hipposcarus* species and *Sparisoma viride* (Bonnaterre) predominantly feed upon the algae covering calcareous rocks (Choat, 1966, Gohar & Latif, 1959, Gygi, 1975 and Bruce, 1979). However, within the genus *Scarus*, the detailed comparative analyses of Choat (1969) and Bruce (1979) revealed little difference between the diet of several species and a large degree of overlap between species in the 'sordidus' and 'frenatus' groups.

One aspect which has received considerable attention is the inclusion of living coral in the diet. Darwin (1845) first reported scarids feeding upon living coral (the species included *S. gibbus* [Randall & Bruce, 1983]). These observations were later questioned by Wood-Jones (1910), who stated that scarids feed upon algae growing on boulders rather than living corals. This confusion has persisted for many years. Several authors have indicated the importance of live corals in the diet of scarids (Al Hussaini, 1945, 1947, Gohar & Latif, 1959, Hiatt & Strasburg, 1960, Bakus, 1964, Glynn *et al.*, 1972, Glynn, 1973 and Frydl, 1979), whilst others have emphasised the herbivorous nature of scarids, and that live corals, if eaten, form only an insignificant part of the diet (Stephenson & Searles, 1960, Randall, 1961, 1965, Choat, 1966, 1969, Bakus, 1967, Randall & Bishop, 1967, Hobson, 1974, Choat & Robertson, 1975 and Bruce, 1979). The only species that has been reported to include large quantities of live coral in its diet is *Bolbometopon muricatum* (Randall, 1974, Bruce, 1979 and Randall & Bruce, 1983).

Analyses of utilization of grazing substrata, feeding rates and bite types have revealed differences between species within the genus *Scarus*. Bruce (1979) described a preference for sand covered rock (versus bare rock or rubble) in *S. psittacus* and *S. taeniurus* (=?) and a preference for bare rock in *S. scaber* Valenciennes, *S. sordidus*, *S. tricolor* (as *S. cyanognathos*, see Randall & Bruce, 1983), *S. virifundicatum* (Smith, 1956), *S. frenatus*, *S. rubroviolaceus* and *S. niger*. Further subdivision of bare rock into shallow crevice, deep crevice and open rock revealed little difference in substratum utilization, with all species feeding predominantly on open rock, except terminal phase (TP) *S. tricolor* (as *S. cyanognathos*). The similarity between species may, however, be a result of the limited number of substratum categories considered and/or unequal abundances of the substratum types in the study area. Choat and Robertson (1975) considered the substratum types in more detail and described preferences for certain grazing substrata by scarids as a whole, and differential utilization of grazing substrata by abundant species. However, these preferences may be the result of differences in the distribution of scarids and substratum types. Neither of the two studies indicated any differences in the utilization of grazing substrata that reflect the morphological differences between the 'sordidus' and 'frenatus' groups. Both groups are 'grazers' (ingesting large quantities of inorganic matter) rather than 'browsers' (ingesting only algal material) as defined by Hiatt and Strasburg (1960) and Jones (1968).

Feeding rates differ markedly within the genus *Scarus* and between other scarine genera. Bruce (1979) quantified the feeding rates of several scarid species (in bites per 10 minutes) and divided species into those with high or low feeding rates. Species with high feeding rates (approx. 200–400 bites per 10 min.) include *S. niger*, *S. taeniurus* (=?), *S. globiceps*, *S. psittacus*, *S. virifundicatum*, *S. scaber* and initial phase (IP) *S. frenatus* and *S. tricolor* (as *S. cyanognathos*). Species with low feeding rates (below approx. 200 bites per 10 min.) include *S. gibbus*, *S. sordidus*, *S. rubroviolaceus*, *Hipposcarus harid* (Forsskål) (as *S. harid*) and terminal phase (TP) *S. frenatus* and *S. tricolor* (as *S. cyanognathos*). With the exception of the low feeding rates in terminal phase individuals which may reflect sexual rather than morphological constraints (Hoffman & Stouder, 1980 and Hoffman, 1983), there is a marked difference between 'sordidus' group and 'frenatus' group species. Species with a high feeding rate are restricted to members of the 'frenatus' group or species provisionally included in that group (Section 1.3.4.2), whilst *Scarus* species with a low feeding rate include only 'sordidus' group members and *S. rubroviolaceus* which is the most robust 'frenatus' group species examined (Sections 1.3.4.1 & 1.3.4.2). Similar differences in the feeding rates of species within the two proposed groups have been recorded by Choat (pers. comm.) and between some *Scarus* and *Sparisoma* species by Itzakowitz (1977, 1980) and Frydl and Stearn (1978).

There are several reports of substratum scarring as a result of grazing by scarids (*e.g.* Hiatt & Strasburg, 1960, Gygi, 1975, Frydl & Stearn, 1978 and Frydl, 1979). Comparative surveys have shown differences in the extent of substratum scarring by scarids. Frydl and Stearn (1978), working on Caribbean species, found that *Sparisoma viride* regularly scars the substratum, whilst *Sparisoma aurofrenatum* (C & V) and terminal phase *Scarus vetula* (Bloch & Schneider) only occasionally produce scars or scratches. No scars or scratches were found, by these authors, as a result of grazing by *Scarus taeniopterus* Desmarest, *S. iserti* (Bloch) and initial phase *S. vetula*.

Bruce (1979) described the bite types of several Aldabran (Indian Ocean) scarid species. Species producing deep scars during grazing included: *S. sordidus*, *S. gibbus*, *Cetoscarus bicolor*, *Bolbometopon muricatum* and *S. rubroviolaceus*. It is interesting to note that in the present study, *S. sordidus* and *S. gibbus* are included in the 'biting' 'sordidus' group (Section 1.4.1), whilst *C. bicolor* and *B. muricatum* are described as 'proto-biters' (Sections 1.4.3) and *S. rubroviolaceus* is considered one of the most robust members of the 'frenatus' group (Section 1.4.2). Species that leave no marks on the substratum or produce only shallow scars included *S. globiceps*, *S. ghobban*, *S. psittacus*, *S. frenatus*, *S. virifundicatum*, *S. taeniurus* (=?) and *H. harid* (as *S. harid*). This group is composed solely of species in, or provisionally included in, the 'scraping' 'frenatus' group (Section 1.4.2) and *H. harid* which is described as a 'proto-scraper' (Section 1.4).

From previous studies, no notable differences in intestinal contents or substratum preference which reflect the morphological and functional differences between the 'sordidus' and 'frenatus' groups have been reported. The only parameters that indicate differences which may be correlated with the proposed functional adaptations of the 'sordidus' and 'frenatus' groups are the feeding rate and bite type. These observations and the functional interpretations in Chapter 1 strongly suggest that differences between the 'sordidus' and 'frenatus' groups are likely to be demonstrable at a small (*i.e.* cm^2) scale, rather than at a large (*i.e.* m^2) scale. Studies in this section were therefore focused on small scale events (*i.e.* bites) to investigate the ecological implications of the proposed functional differences between the 'sordidus' and 'frenatus' groups.

In this section, detailed observations were restricted to *S. sordidus* and *S. frenatus*, as representative species of the 'sordidus' and 'frenatus' groups. These species were chosen for the following reasons: a) they are of approximately similar size, b) they have overlapping distributions, with common feeding areas in the study sites on reefs around Lizard Island, and c) they were the principal species examined in the morphological analyses in Chapter 1.

5.2 Materials and Methods

Field observations were made at the North Reef study site at Lizard Island (Fig. 5.1) during November 1982 to February 1983 and November 1983 and January 1984. All observations were made using SCUBA, with notes recorded on PVC sheets. In each of the following analyses, an equal number of observations on *S. sordidus* and *S. frenatus* were recorded from the same area. Individual fish were followed for periods of approximately five minutes and the number of bites per foray was recorded (a 'foray' is defined as a feeding event with no discernible interval between successive bites, other than that necessary to reapply the jaws to the substratum). These data were used to assess both feeding rates and periodicity.

Analyses of bites and bite locations were initially made by following individual fish and recording the site and type (*i.e.* scarring or scraping) of each bite. These factors were later quantified by following known individuals and measuring the site and location of the first clearly observed bite each time the individual was located. A vernier caliper was used to take measurements (to the nearest 0.1 mm) of the length (L) and width of the scar or dislodged algae, of the maximum and mean scar depth (if appropriate) and of the height of the substratum above the site of the bite (H) (Fig. 5.2 A). The ratio of (H) divided by the bite length (L), was used as an estimate of the curvature of the substratum. If $H/L = 0$, the substratum bitten was approximately planar, whilst values above 0 indicate an increasing prominence or curvature of the substratum. Data were analysed using T-tests unless they had unequal variances or markedly non-normal distributions. In these cases Mann Whitney

Figure 5.1

The location of the major study sites in the lagoon and at North Reef, Lizard Island.

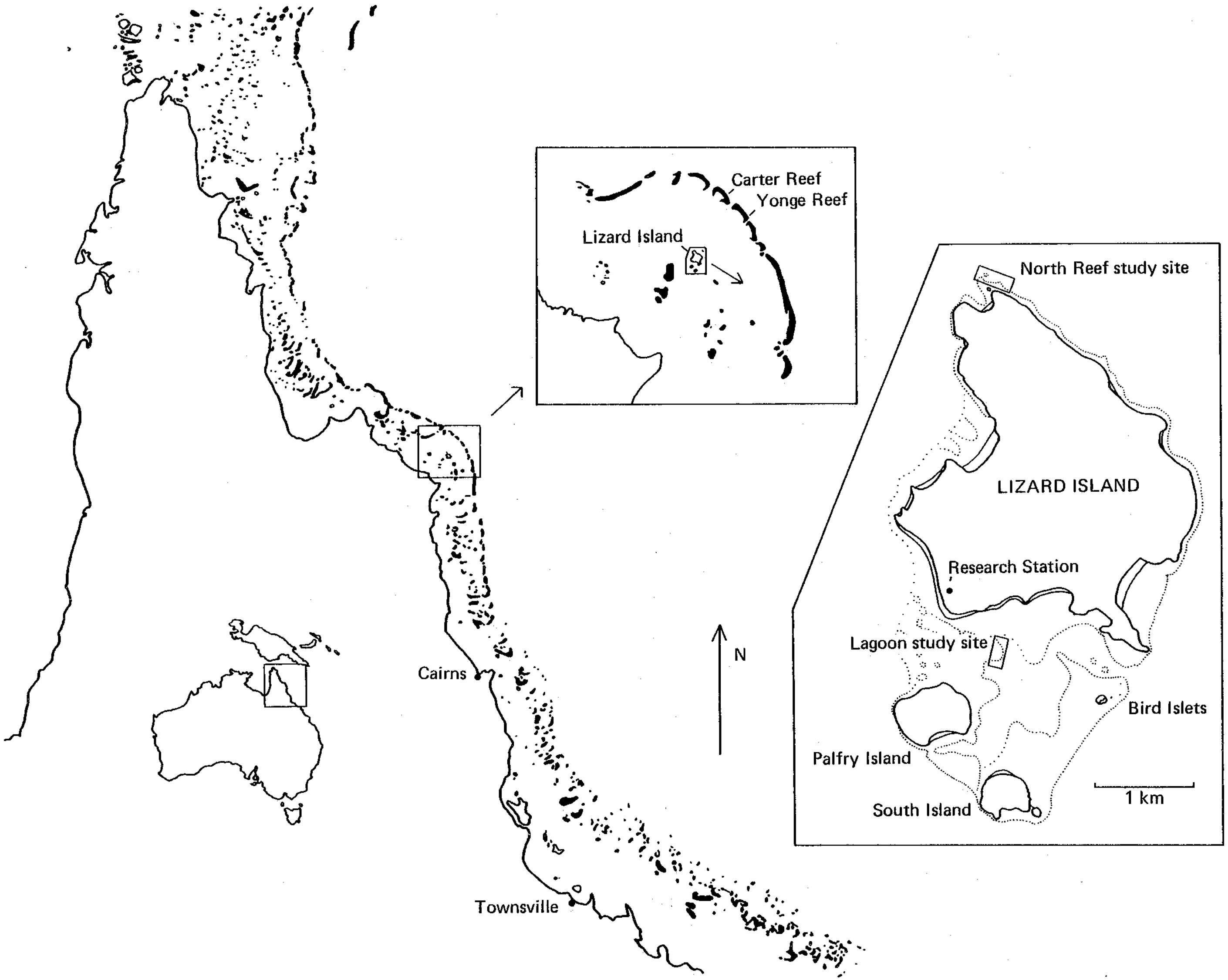

Carter Reef
Yonge Reef
Lizard Island
North Reef study site
LIZARD ISLAND
Research Station
Lagoon study site
N
Cairns
Bird Islets
Palfry Island
1 km
South Island
Townsville

Figure 5.2 A

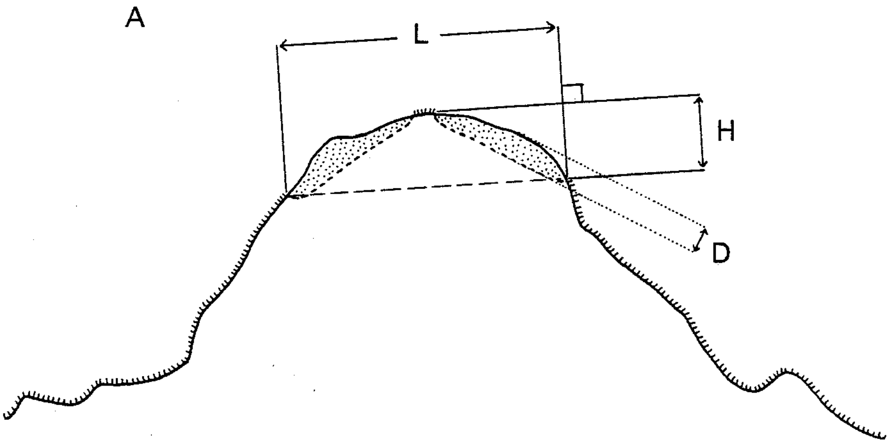
A diagramatic figure of three parameters measured when quantifying scarid feeding scars.

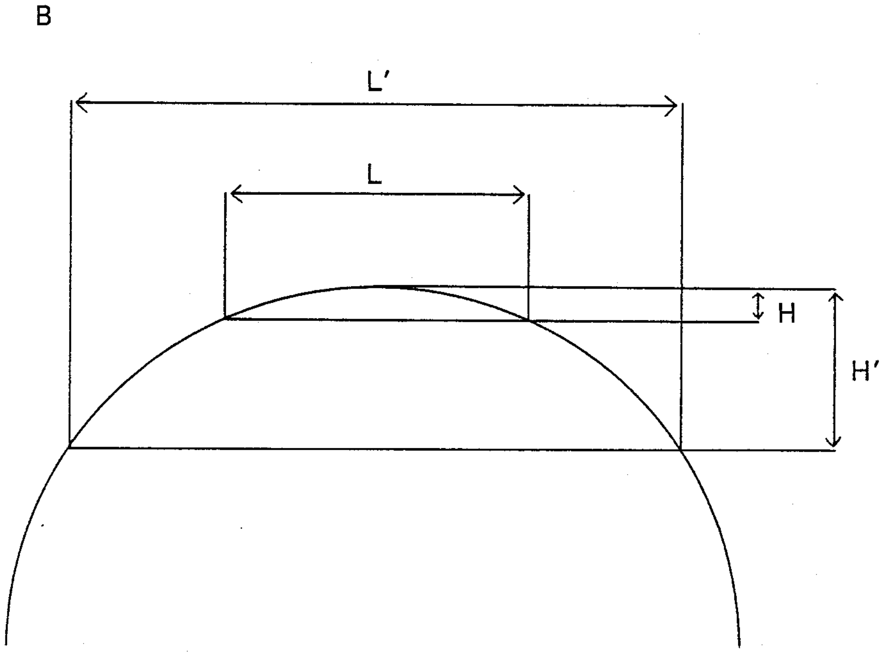
Legend:
L = Length of the bite
H = Height of the substratum above the bite site
D = Depth of the bite (the mean depth is estimated)
The stippled area represents material removed.
In addition, the maximum width of the scar was measured.
The curvature of the substratum is estimated by the dividend of H/L.

Figure 5.2 B

A diagramatic figure showing the disproportionate effect of an increase in the bite length on the dividend of H/L when feeding on the same substratum.

In this example, doubling the bite length (L) increases the dividend of H/L by 4.63.


A
L
H
D


B
L′
L
H
H′

U-tests were used.

In addition to the above observations, qualitative observations of bite rates and types were made on reefs around Lizard Island and on offshore reefs in the vicinity of Lizard Island, Cairns and Townsville. Representative samples of coral species eaten by scarids were collected for identification.

5.3 Results

Feeding rates

The feeding rates of large individuals of several scarid species are given in Table 5.1. To enable direct comparisons, data on *S. sordidus* and *S. frenatus* are based on equal observation times for both species in the same area of North Reef. In both species, the mean feeding rate of IP individuals was not significantly different from that of the TP individuals (Table 5.1), but the mean feeding rate of *S. sordidus* was lower than that of *S. frenatus* ($t=2.434$, $p < 0.05$, Table 5.1). The low feeding rate in *S. sordidus* and high feeding rate in *S. frenatus* were also reflected in the other species belonging to their respective groups (Tables 5.1, 5.2).

Feeding periodicity

The bites of *S. sordidus* and *S. frenatus* show a marked difference in temporal distribution (Fig. 5.3). In *S. sordidus*, the bites primarily occurred in small bursts, whilst those of *S. frenatus* frequently occurred in prolonged feeding episodes. Approximately 82% of bites by *S. sordidus* occurred in groups of 4 or

Table 5.1 The feeding rates of six *Scarus* species.

Species	Mean feeding rate (bites per min.)	95% C.I.	Number of obs.	Mean observation time (min.)
S. sordidus IP	13.9 †	3.1	10	5.4
S. sordidus TP	19.4 †	8.7	7	5.9
S. frenatus IP	22.2 ‡	5.8	12	5.4
S. frenatus TP	25.1 ‡	12.8	5	6.2
S. sordidus IP + TP	16.1 +	3.7	17	5.6
S. frenatus IP + TP	22.5 +	4.8	17	5.6
S. gibbus	10.1	1.1	12	4.0
S. rubroviolaceus	9.3	2.8	5	6.2
Cetoscarus bicolor	7.3	8.6	2	3.0

IP = Initial Phase, TP = Terminal Phase

† - No significant difference - $t = 1.644$, $p > 0.5$.

‡ - No significant difference - $t = 0.5724$, $p > 0.5$.

\+ - Both colour phases have been pooled so that data are available for each species as a whole for use in conjunction with data from species surveys.
The feeding rates of the two species are significantly different, $t = 2.434$, $p < 0.05$.

Table 5.2 Observations of the feeding rates and the extent of scarring of the substratum by scarids.

Species	Feeding rate†	Substratum scarring
Calotomus carolinus *	low	No scarring
Cetoscarus bicolor	low	Frequent - deep scars
Bolbometopon muricatum	very low	Always - deep scars
Hipposcarus longiceps *	moderately low	Large individuals produce occasional shallow scars
'sordidus' group:		
S. bleekeri	low	Frequent scarring
S. frontalis *	low	Frequent scarring
S. gibbus	low	Frequent - deep scars
S. japanensis *	low	Frequent scarring
S. sordidus	low	Frequent scarring
'frenatus' group:		
S. brevifilis	moderately high	Large individuals produce occasional shallow scars
S. dimidiatus	high	No scarring
S. flavipectoralis	moderately high	No scarring
S. frenatus	high	No scarring +
S. ghobban *	moderately high	Large individuals produce occasional shallow scars
S. globiceps	high	No scarring
S. longipinnis *	?	No scarring observed
S. niger	high	No scarring
S. oviceps	high	No scarring +
S. psittacus	high	No scarring
S. rivulatus	high	No scarring +
S. rubroviolaceus	moderate to low	Large individuals produce occasional scars
S. schlegeli	high	No scarring
S. spinus	high	No scarring
S. tricolor *	moderately high	No scarring observed
S. sp.	high	No scarring

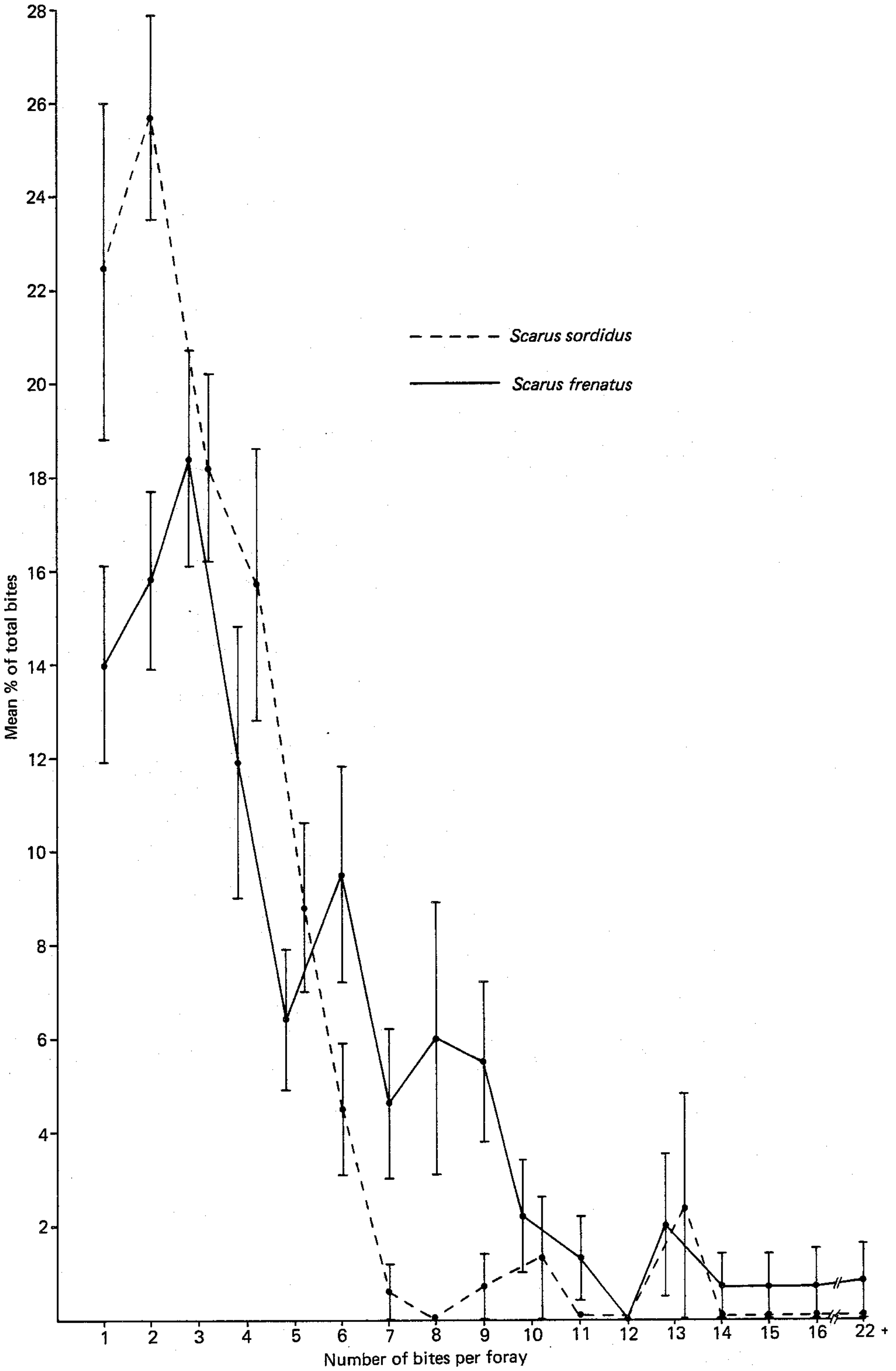
† - Feeding rates: low <15 bites/min., high >20 bites/min.
* - Limited observations were made of these species
\+ - These species may occasionally leave some scar marks in soft, internally eroded dead coral or on the surface of live corals.

Figure 5.3

The foray sizes of two *Scarus* species, expressed as the relative number of bites per foray.

S. sordidus - No. individuals = 10
No. bites = 1009
S. frenatus - No. individuals = 10
No. bites = 1297

Vertical bars ± one standard error of the mean.


Mean % of total bites
28
26
24
22
20
18
16
14
12
10
8
6
4
2
Scarus sordidus
Scarus frenatus
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
22 +
Number of bites per foray

less, compared with 60% in *S. frenatus*. Conversely, only 9% of bites by *S. sordidus* were in groups of 6 or more, compared with 33% in *S. frenatus*. The number of bites in each bite group differ in the two species ($\chi^2 = 53.6$, df. = 11, $p < 0.001$; based on the total number of forays in each species), with *S. sordidus* having a larger proportion of small forays (MWU-test, n1/n2 = 492/461, z = 2.21, $p < 0.05$; based on the frequency of each foray size). The mean number of bites per foray in *S. sordidus* was 2.12 and in *S. frenatus*, 2.75.

Bite types

The main differences between bites of the various species are their size and shape, and in the extent of substratum scarring. These differences are not discrete, as they are dependent upon the size and species of the scarid and the hardness and location of the substratum. Soft, internally bioeroded substrata were more deeply scarred than live or newly dead corals or coralline algae, particularly on exposed convex surfaces. The extent of substratum scarring as a result of feeding by various scarid species is summarized in Table 5.2 and an analysis of scar sizes of some species is given in Table 5.3. It can be seen from these tables that scarring of the substrata was primarily a result of grazing by 'sordidus' group species, *Cetoscarus bicolor* and *Bolbometopon muricatum*.

The shape of the bite scar or scrape varied between species, although similarities between groups of species were found. In 'frenatus' group species, bites typically produced scrapes marked by dislodged algae and sediment. Each bite produced two narrow,

Table 5.3 The size of substratum scars which result from the grazing activity of scarids.

Species	Approx. S.L. (mm)	Number of individuals	Approx. No. of bites examined	No. of bites/ scars measured †	Mean Length (mm)	Mean Width (mm)	Mean Depth (mm)	Mean scar volume (cm^3) *
S. sordidus	220	10	200	30	10.9	4.3	0.20	9.4×10^{-3}
S. frenatus	280	12	200	30	12.6	1.8 ††	0	0
S. gibbus	440	6	140	27	26.3	10.9	0.79	2.8×10^{-1}
S. gibbus	250	2	28	7	23.7	8.4	0.60	5.6×10^{-2}
S. rubroviolaceus	380	3 †	180	3	9.9	2.7 †	0.10	1.3×10^{-3}
C. bicolor	440	3	4 †0	4	12.5	8.2	1.00	9.6×10^{-2}
B. muricatum	550	2	4	4	40.0	16.0	1.50	5.3×10^{-1} ‡
B. muricatum	880	8	50	26	44.5	27.0	2.80	2.77 ‡

† - Bites were measured at random, with the exception of *S. rubroviolaceus* and *C. bicolor* where only those bites producing scars were measured.

†† - Each bite produces a pair of narrow scrapes, the value given is the sum of the two scrape widths.

* - Calculated from individual scar volumes.

‡ - Including scars on algal covered substrata, coralline algae and live corals.

parallel scrapes, often broken midway along their length. Larger 'frenatus' group species (*e.g.* *S. rubroviolaceus*) may produce broader scrapes with slight scarring of the substratum especially in softer substrata.

In species of the 'sordidus' group and in *C. bicolor* and *B. muricatum*, bites frequently produced scars. These were relatively wide, being approximately half as wide as long, and usually possessed 4-6 deep grooves along the length of the scar, corresponding to the protruding teeth of the uneven or crenate cutting edge.

In two 'sordidus' group species (*S. gibbus* and *S. sordidus*), two basic types of bite were observed, designated nips and crunches. A nip is a small quick bite, producing only a shallow scar. It was used on all substratum types and was the most frequently observed bite type in *S. sordidus*, comprising approximately 55% of all bites (*cf.* 24% in *S. gibbus*). Crunching bites were primarily restricted to convex substrata and invariably produced deep scars. In these bites, the pressure was applied to the substratum relatively slowly and occasionally required several bouts of muscular contraction to fracture or dislodge pieces of the substratum. Crunching bites were less frequent than nips in *S. sordidus* and comprised approximately 45% of total bites (*cf.* 76% in *S. gibbus*). A third type of bite rarely used by *S. sordidus* and *S. gibbus* utilizes the side of the jaws. This bite was of intermediate strength and produced small scars. It was most often seen in individuals feeding on narrow projections such as the tips of dead *Acropora* branches.

Bite locations/microhabitat utilization during grazing

Initial observations of microhabitat utilization when grazing revealed a marked difference between *S. sordidus* and *S. frenatus*, with *S. sordidus* utilizing convex substrata more frequently than *S. frenatus* (Table 5.4). These observations were limited by their subjectivity and were therefore quantified using the height of the substratum above the bite site (h) divided by the bite length (l) as an estimate of substratum curvature. When compared, *S. sordidus* had a significantly greater mean h/l value than *S. frenatus* (MWU-test, $z = 7.85$, $p < 0.001$, Table 5.5 A).

There are two possible explanations for this difference: either a) *S. sordidus* fed upon more convex surfaces than *S. frenatus*, or b) both species fed upon similar surfaces, but *S. sordidus* disproportionately increases the relative height of the substratum above the bite site as a result of a longer bite length (Fig. 5.2 B). However, the bite lengths of *S. sordidus* were significantly shorter than those of *S. frenatus* ($t = 6.579$, $df = 219$, $p < 0.001$, Table 5.5 B). One can therefore conclude that on average, *S. sordidus* fed upon more convex substrata than *S. frenatus*. As an equal number of bites were recorded for each species in each observation area, the above result suggests a degree of feeding microhabitat preference by one or both of the species. The restricted distribution of deep scars on edges and convex protrusions, in comparison to the ubiquitous presence of small scrapes characteristic of *S. frenatus* and other 'frenatus' group species (pers. obs.) and the relative frequency of bites by *S. sordidus* on convex surfaces (Table 5.4), strongly suggest that

Table 5.4 Patterns of substratum utilization by *S. sordidus* and *S. frenatus*

	Substratum topography			
	Convex	Plane	Concave	Site unclear
S. sordidus (n = 8)				
Total numbers of bites observed	396.0	94.0	35.0	120
Mean % of clearly observed bites †	77.6	16.4	5.7	-
Standard error of above	8.8	7.6	4.6	-
S. frenatus (n = 8)				
Total numbers of bites observed	289.0	398.0	275.0	209
Mean % of clearly observed bites †	29.6	42.7	28.0	-
Standard error of above	8.8	12.8	6.6	-

† - Each figure is based on the mean of eight individuals. Individual *S. sordidus* and *S. frenatus* were observed for approximately equal times (5-6 min. = 80-150 bites) in an area shared by the individuals of the two species.

Table 5.5 A An analysis of the curvature of the substrata grazed by *S. sordidus* and *S. frenatus* by comparing the height/length (H/L) values of the bite marks left by each species.

Species	Number of individuals	Number of bites	Mean H/L (x 100)	S.E. (x 100)	95% C.I. (x 100)
S. sordidus	15	107	22.7 *	1.3	±2.8
S. frenatus	15	107	10.7 *	0.6	±1.3

For arcsin transformed data, the variance F-ratio test (Zar, 1974 p. 101), ratio = 1.67 (*i.e.* unequal variances).
* = Significantly different, Mann-Whitney U test, $z = 7.85$, $\alpha(2)$, $p < 0.001$.

Table 5.5 B A comparison of the bite-scar lengths of *S. sordidus* and *S. frenatus*.

Species	Number of bites	Mean bite length (mm)	S.E.	95% C.I.
S. sordidus	108	12.3 *	0.41	±0.81
S. frenatus	113	15.9 *	0.37	±0.73

Variance ratio = 1.28, d.f. = 219, $t = -6.576$
* - Significantly different $\alpha(2)$, $p < 0.001$

S. sordidus was the more selective of the two species with a preference for exposed convex surfaces.

In addition to algal covered calcareous surfaces, several other food resources were utilized by scarids.

1) Live corals.

In this study, only one species was observed to regularly feed upon live corals, *viz. Bolbometopon muricatum*. In this species, approximately 57% of the bites were upon live corals. A list of the coral species eaten is given in Table 5.6. Observations on feeding were primarily restricted to the North Reef study site. Feeding upon *Porites cylindrica* was recorded from a single observation in the lagoon. When feeding upon live corals, *B. muricatum* removed whole branches or pieces. Often all branches from an arborescent *Acropora* colony were removed or broken off and on several occasions, whole plate coral colonies were dislodged. Other species which occasionally fed on live corals included *S. gibbus*, *S. rivulatus* and *C. bicolor* (Table 5.6). Grazing upon live corals by *S. gibbus* resulted in scrapes on the surface up to 3 mm deep, whilst grazing on live corals by *S. rivulatus* only removed the surface tissue to a depth of less than 1 mm.

Coral feeding by *B. muricatum* was observed on four occasions at Lizard Island (a mid-continental shelf reef) and on four occasions on four outer continental shelf reefs (Myrmidon Reef, Yonge Reef, Carter Reef and Euston Reef). Coral feeding by *C. bicolor* was observed only on two occasions at Lizard Island. Coral feeding by *S. gibbus* and *S. rivulatus* was recorded only on inshore reefs, twice

Table 5.6 Coral species eaten by scarids.

Species	Coral species	Number of colonies
Bolbometopon muricatum		
	Acropora cytherea (Dana)	1
	Acropora divaricata (Dana)	1
	Acropora hyacinthus (Dana)	5
	Acropora latistella (Brook)	1
	Acropora listeri (Brook)	2
	Acropora millepora (Ehrenberg)	4
	Acropora nasuta (Dana)	4
	Acropora secale (Studer)	1
	Pocillopora verrucosa Ellis & Solander	1
	Montipora spp.	3
	Anamastrea sp. ?	1
	Porites cylindrica Dana	1
	Favites sp.	1
Cetoscarus bicolor		
	Montipora sp.	1
	Platygyra sp.	1
	Encrusting species	1
Scarus gibbus		
	Porites lobata Dana	4
	Porites lutea Edwards & Haime	2
	Porites australiensis Vaughan	3
Scarus rivulatus		
	Porites spp.	3

Acropora species identified by Dr C. Wallace
Porites species identified by Prof. M. Pichon

by *S. gibbus* at the Palm Islands (NE. of Townsville) and three times by *S. rivulatus* at Magnetic Island (Townsville).

2) Coprophagy.

At the North Reef study site at Lizard Island, coprophagic behaviour was observed in nine *Scarus* species; *S. frenatus*, *S. gibbus*, *S. globiceps* *S. niger*, *S. oviceps*, *S. psittacus*, *S. rivulatus*, *S. sordidus* and *S. spinus*. The faeces of caesionids (especially *Caesio cuning* and *Pterocaesio chrysozona*) and pomacentrids (especially *Abudefduf whitleyi* and *Acanthochromis polyacanthus*) were frequently collected and invariably eaten. Labrid faeces, when available, were likewise rapidly collected and eaten. The faeces of *Acanthurus lineatus* and *Zebrasoma scopas*, however, were infrequently collected and eaten. The faeces of *Ctenochaetus striatus* were rarely collected and in all of the observed cases were rejected (twice by *S. sordidus* and once by *S. niger*). The faeces of other scarids were ignored.

3) Sand.

Sand ingestion was recorded in four species: *S. schlegeli*, *S. flavipectoralis*, *S. psittacus*, and *Scarus* sp. (*cf. lunula*), although only occasionally in the latter two species. *S. ghobban* was frequently observed over sandy areas, often accompanying large schools of *A. mata* and *A. dussumieri*, but sand ingestion by this species was not recorded.

5.4 Discussion

From the functional interpretations of their morphology in Chapter 1, species in the 'sordidus' group were proposed as functional 'biters', capable of delivering a strong 'cracking' bite which can dislodge pieces of the substratum. Field observations confirmed this proposal and revealed a range of behavioural traits characteristic of those species sharing the morphological features which defined the 'sordidus' group. These traits include: low feeding rates, small feeding bouts, a high utilization rate of convex surfaces and interspecific aggression directed predominantly towards other 'sordidus' group species (Section 5.7).

From functional interpretations of the morphology of 'frenatus' group species in Chapter 1, these species were described as 'scrapers', capable only of delivering a weak bite which scrapes rather than cracks the substratum. As with the 'sordidus' group, field observations confirmed this proposal and revealed a range of behavioural traits characteristic of those species sharing the morphological features which distinguish the 'frenatus' group. These include: a high feeding rate, large feeding bouts, no marked microhabitat preference and interspecific aggression directed primarily towards other 'frenatus' group species (Section 5.7). The morphological and behavioural differences between the two groups are summarized in Table 5.7.

These results reflect what is believed to be a major difference in the feeding strategies of the two groups. The 'biting' 'sordidus' group have a strategy based on a few large powerful bites, whilst the 'scraping' 'frenatus' group have a strategy based

Table 5.7 A summary of the morphological and behavioural characteristics of 'sordidus' and 'frenatus' group species.

	'Sordidus' group species (biters)	'Frenatus' group species (scrapers)
Morphological features:		
Osteology	Strong	Weak
Suspensorium (adductor fossa)	Deep	Shallow
In:out lever ratio of dentary-articular joint	Large	Small
Palatine-maxillary articulation	Simple	Complex
Cutting edge of jaws	Uneven	Even
Musculature	Well developed	Reduced
Pinnation of muscles	Strong	Weak
Anterior maxillary-premaxillary ligament	Binding	Enclosing synovial joint
Behavioural features:		
Area of bite	Large	Small
Feeding rate (bites/min.)	Low	High
Number of bites per foray	Few	Numerous
Substrate form most frequently bitten	Convex	All types
Extent of scarring	Deep scars	Usually none
Interspecific aggression directed towards	'sordidus' group species	'frenatus' group species

on numerous small weak bites. Compared to the bites of the 'frenatus' group species, the large bites of 'sordidus' group species may require relatively more energy and processing time (to grind ingested material) but are likely to contain a higher nutritive value per bite. The utilization of convex or protruding surfaces is likely to enhance the biting efficiency of 'sordidus' group species, as pieces of the substratum are more easily cracked and dislodged, carrying with them a relatively large volume of algae. Suitable convex or protruding surfaces, however, are not ubiquitous at the microhabitat scale, and once bitten, are of reduced value, because of the almost total lack of algae from the bite site and its decreased convexity. Feeding bouts are therefore, limited to a few bites in each area. The low feeding rates (in bites/min.) of 'sordidus' group species may be accounted for by the high yield per bite (in *S. sordidus* each bite removed 2.1 times the area of algae removed by an *S. frenatus* bite, Table 5.3) and/or the long time spent searching for suitable bite sites. Alternatively, the low feeding rate may be the result of a relatively long processing time necessary to grind the large volumes of algae and carbonate ingested per bite by 'sordidus' group species.

The small bites of 'frenatus' group species may have small energetic costs but are also likely to be of limited nutritional value when compared to bites of the 'sordidus' group species. The 'scraping' bites appear to be equally effective on all algal covered substratum types as all forms were readily grazed (Table 5.4). Since each 'scraping' bite removes only a relatively small area of algae, many bites are required to deplete an area of its grazing potential. Feeding bouts are, therefore, relatively large (*i.e.*

with numerous bites) as there is little benefit in switching from one feeding area to another. The high feeding rate (in bites/min.) of 'frenatus' group species may be accounted for by the low algal yield per bite, the minimal time required to find suitable feeding sites and possibly a reduced processing time, as 'frenatus' group species ingest only small volumes of algae and carbonate per bite. Overall, 'frenatus' group species appear to rely on a large number of small, non-selective bites, whereas 'sordidus' group species rely on a few large bites from specific substratum types.

Similar differences have been reported in the feeding strategies of Caribbean scarids. Caribbean *Scarus* species have high feeding rates and large feeding bouts (forays), with little evidence of searching behaviour between bites or bouts. In comparison, *Sparisoma* species have low feeding rates and small feeding bouts (forays), and carefully search the substratum between bites (Itzakowitz, 1977, 1980). It is interesting to note that these differences correlate with morphological differences comparable to those found in the 'frenatus' and 'sordidus' groups (Chapter 3). All Caribbean *Scarus* species are probably all members of the 'frenatus' group (Section 1.3.4), whilst *Sparisoma* species are closely related to the 'proto-biters' *C. bicolor* and *B. muricatum*, and possess many features associated with a 'biting' feeding strategy (Chapter 3). It appears, therefore, that the 'biting' strategy that is utilized in the Indo-Pacific by 'sordidus' group species is used by *Sparisoma* species in the Caribbean, especially *S. viride*, which has a strong bite and a low bite rate (Gygi, 1975).

In the analyses of scarid feeding by Choat and Robertson (1975), Bruce (1979) and Hatcher (1981), bites have been used as unit feeding events to compare grazing substratum utilization and feeding rates. However, bites *per se* are of limited use for comparative analyses of feeding methods and rates as they differ markedly between species (Tables 5.2, 5.3).

Scarid feeding strategies have been studied in a few Caribbean species (Ogden & Buckman, 1973, Buckman & Ogden, 1973, Itzakowitz, 1977, 1980, Lobel & Ogden, 1981 and Hanley, 1984) but for most species, they are poorly understood and require more detailed analyses. The importance of morphology in the understanding of foraging behaviour has been demonstrated in butterflies by Kingsolver & Daniel (1979) and as outlined above, it is probably of a similar importance in the analysis of the feeding strategies of scarids. In addition, it is important to consider the nature of the environment in relation to the feeding methods of species in the two groups. From this study, it appears that in terms of food availability, for 'sordidus' group species, the reef substratum is patchy (*i.e.* areas of small convexities), whilst for 'frenatus' group species, the same area is relatively uniform, with numerous turf covered areas. This disparity will strongly influence their behavioural patterns. This type of difference in food resource availability has been associated with differences in the feeding strategies of individual *S. iserti* (Ogden & Buckman, 1973 and Buckman & Ogden, 1973) and between several Caribbean scarid species (Itzakowitz, 1977, 1980).

The terms 'specialist' and 'generalist' (*sensu* Schoener, 1971) are not totally applicable to the two groups. 'Sordidus' group species are specialists in the sense that they specialize by feeding predominantly on a restricted substratum type (*i.e.* convex algal covered surfaces), in comparison to generalist 'frenatus' group species which feed on all available algal covered substrata. However, 'frenatus' group species are restricted to epilithic algae whilst 'sordidus' group species may use both epi- and endolithic material. In effect, the species forming both groups are specialists but in different ways.

The morphological specializations of scarids were interpreted in Chapter 1 in an adaptive context. However, as these interpretations were based solely on morphological observations, they could only infer an adaptive function. The combined results of this chapter and those of Chapter 1, fulfil the basic requirements of the 'synthetic method' of Bock (1980), who describes it as the only valid method for assessing biological adaptation. These results show a consistent and strong correlation between the functional morphology and behavioural ecology of adult scarids. It is therefore proposed that a large proportion of the morphological specializations of the feeding apparatus described in Chapter 1 are adapted to the scarids' present ecological role as grazing herbivores and that in adult scarids, at least, morphology and behaviour are closely related.

Part B - General Biology

5.5 Introduction

Many aspects of the biology of scarids have been examined, both in the Indo-Pacific and the Caribbean. These studies have revealed numerous differences between species, although few of these differences correspond with the morphological differences described in Chapters 1 and 3. (It should be noted, however, that the 'sordidus' group is probably not represented in the Caribbean, Section 1.3.4).

The demographic studies of Hobson (1974), Choat and Robertson (1975), Bruce (1979), Bouchon-Navaro and Harmelin-Vivien (1981), Williams (1982) and Russ (1984 a, b) have shown no group-related differences in the distribution of the 'frenatus' group and the two most abundant 'sordidus' group species: *S. sordidus* and *S. gibbus*. *S. sordidus* is a ubiquitous species, and occupies a broad range of reef types and habitats, all of which are shared by 'frenatus' group species (Williams, 1982 and Russ, 1984 a, b). *S. gibbus* has a more restricted distribution and is most numerous in shallow water, especially on the reef crest (Russ, 1984 b). This is not unusual, however, since the reef crest and shallow waters are also occupied by large numbers of scarid species, including several 'frenatus' group species (Russ, 1984 b).

The reproductive strategies of scarids have been extensively studied (Winn & Bardach, 1960, Randall& Randall, 1963, Choat, 1966, 1969, Buckmam & Ogden, 1973, Choat & Robertson, 1975, Warner & Downes, 1977, Bruce, 1978, 1979, 1980, Colin, 1978, Robertson &

Warner, 1978, Hoffman & Stouder, 1980, Yogo *et al.*, 1980, Dubin, 1981, Robertson *et al.*, 1982 and Clavijo, 1983). These studies have revealed a considerable degree of variability within and between species. Despite this, only one reproductive character corresponds with the morphological differences between scarids, described in Chapters 1 and 3, namely the formation of spherical eggs in the Sparisomatinae and spindle shaped eggs in the Scarinae (Winn & Bardach, 1960 and Randall & Randall, 1963).

Within the Scaridae, there is a wide range of social systems. These vary within and between species. Individuals may be site attached or roving, solitary or schooling (in monospecific or multispecific schools) with intraspecific and/or interspecific aggressive interactions (Choat, 1966, 1969, Ogden & Buckman, 1973, Buckman & Ogden, 1973, Barlow, 1975, Choat & Robertson, 1975, Robertson *et al.*, 1976 and Bruce, 1978, 1979). Social organization includes leks and harems (Robertson & Warner, 1978), with less well defined intermediate systems (Bruce, 1978). The only aspects of social behaviour that show signs of a relationship with the morphological groups described in Chapters 1 and 3 are those aspects which relate to feeding biology, rather than reproductive biology. Of these, two are particularly noteworthy.

Firstly, the foraging methods of some Caribbean species show genera-related differences. *Sparisoma* species are typically solitary, slow feeding and site attached, whilst *Scarus* species (only 'frenatus' group species, section 1.3.4) are frequently gregarious, fast feeding and highly mobile (Ogden & Buckman, 1973, Buckman & Ogden, 1973, Itzakowitz, 1974, 1977, 1980 and Barlow, 1975). Secondly, aggressive interactions may indicate some of the factors influencing territorial or social behaviour. Most aggression by scarids is intraspecific and indicates a probable reproductive function (Ogden & Buckman, 1973, Buckman & Ogden, 1973, Choat & Robertson, 1975, Bruce, 1978, 1979 and Robertson & Warner, 1978). Interspecific aggression by scarids has been reported in both Caribbean and Indo-Pacific species. In the Caribbean, Barlow (1975) noted that interspecific aggression towards other scarids was greater than that towards pomacentrids, and that both were considerably less than intraspecific aggression. Buckman and Ogden (1973) reported aggresssion by scarids towards *Abudefduf saxatilis*, although no consistent aggression was noted towards potential competitors for food (*Acanthurus chirurgus*) or space (*Stegastes (Eupomacentrus) fuscus*). Interspecific aggression has been noted in several Indo-Pacific species (Choat & Robertson, 1975 and Bruce, 1979). The reasons for such behaviour are largely unknown (Bruce, 1979), although in *S. niger*, interspecific aggression towards other herbivorous species (especially scarids) apparently served to defend permanent grazing sites near to cover (Choat & Robertson, 1975).

In other studies of scarid behaviour, some genera-related differences have been found. For example, in the Caribbean, the nocturnal behaviour of *Spartsoma* species differs from that of *Scarus* species. The former sleeps in open areas with no mucous cocoon, whilst the latter sleep near cover and is enveloped by a mucous cocoon (Winn, 1955, Winn & Bardach, 1959, 1960, Bardach *et al.*, 1960 and Dubin & Baker, 1982). However, several other studies have failed to reveal any consistent genus-related or morphological group-related differences in behaviour. These studies include analyses of sun compass orientation (Winn *et al.*, 1964), schooling (Choat, 1966, 1969), the frequency of non-scarid interspecific aggression (Barlow, 1975, Robertson *et al.*, 1976, Robertson *et al.*, 1979 and Robertson & Polunin, 1981) and diurnal variability in abundance (Colton & Alevizon, 1981).

In considering the studies outlined above, the detailed analyses of distribution and reproductive strategies strongly suggest that further studies in these areas are unlikely to reveal consistent differences between morphological groups. The only areas that show evidence of morphology-related differences in behaviour are those related to feeding, namely, foraging methods and interspecific aggression. The former has been considered with respect to the feeding mechanism (above) although the general behavioural aspects require further analysis. Foraging methods and interspecific aggression have been studied in several Indo-Pacific species (Choat, 1969, Choat & Robertson, 1975 and Bruce, 1978, 1979) although the results were variable and inconclusive. The behavioural analyses of adult scarids were therefore concentrated in these two areas.

5.6 Materials and Methods

Field observations were made at the North Reef study site at Lizard Island (Fig. 5.1) between November 1981 and January 1984. All observations were made using SCUBA, with notes recorded on PVC sheets. The study site was mapped by triangulation using prominent underwater features. Individual fish were identified using colour patterns, physical anomalies and parasitic scars. The positions of these fish were recorded over several days (during 10+ hours of direct observations or as a result of 50+ sight records) and plotted on the map of the area. The sizes of the home ranges or territories were then estimated from these plots, by connecting the outermost points and measuring the area enclosed. The duration of such home ranges and territories were noted both for known individuals and for harems of a particular species in a known area. Throughout the study period, aggressive interactions and general behaviour patterns were noted.

5.7 Results

I) Site attachment - an estimate of territory/home range size and duration

The territory/home range sizes and maximum known duration of recognizable site attached individuals are given in Table 5.8 A, and of harems of particular species (though not necessarily the same individuals) in Table 5.8 B. Site attachment for short periods (1-30 days) was recorded in several other species. Reproductive territories of TP *S. globiceps* (>3 days) and *S. spinus* (1 & >2 days) were recorded during the summer months (November to February). (On Lizard Island, reproduction is probably seasonal. Spawning and courtship behaviour was only recorded between the months of November and February). Site attachment was also noted for limited periods in IP *Calotomus carolinus* (14 days), IP *S. gibbus (6-23 days) and IP S. frontalis* (30 days), and in IP and TP *S. dimidiatus* (10-27 days). Transient species or those with relatively large home ranges include IP *S. brevifilis*, IP and TP *S. psittacus*, *Hipposcarus longiceps*,

Table 5.8 A Duration and size of home ranges/territories of scarids:
A – known individuals, at North Reef.

Species		Number of individuals	Duration of site attachment (days)	Estimated home range/ territory size (m^2)
S. bleekeri	TP	2	100 – 120	300 – 500+
	IP	2	110 – 152	300 – 500+
S. gibbus	TP	1	120	1000+
S. japanensis	IP	1	380	500+
S. flavipectoralis	IP	1	148	100+
S. frenatus	TP	6	230 – 626	224 – 300*
	IP	5	154 – 703	180 – 240*
S. niger	IP	1	166	250
S. oviceps	TP	2	120 – 403	300
	IP	2	90 – 682	300
S. rubroviolaceus	TP	2	120 – 626	500 – 700
	IP	4	120 – 626	500 – 700

TP = Terminal phase, IP = Initial phase
* – Lagoon home ranges = 1800+ m^2, occupied by one IP and one TP.

Table 5.8 B Duration and size of home ranges/territories of scarids:
B – permanent sites, unknown individuals, at North Reef.

Species	Number of sites	Number of individuals per site	Duration of site utilization (days)	Area (m^2)
S. frenatus (TP+IP)	6	2 – 3	583 – 687	240 – 300
S. niger	4	3 – 5	579 – 687	260 – 320
S. sordidus (TP)	2	1	626	200 – 260
S. gibbus	1	4 – 6	687	1000+
C. bicolor (TP+IP)	1	3	610	3000+

Bolbometopon muricatum and some IP *S. sordidus*.

Site attachment may be territorial or home ranging. This is primarily dependent upon the nature and frequency of aggressive interactions, as described in section II below. These interactions are both complex and variable. The typical forms of site attachment in several scarid species at North Reef are summarized below:

1) Permanent territories defended intra- and interspecifically: *S. frenatus*.
2) Permanent territories defended primarily intraspecifically: *S. niger*, *S. oviceps*, *S. rubroviolaceus* and some *S. sordidus* TPs.
3) Permanent home ranges with little aggression: *S. bleekeri*, *S. gibbus*, *S. japanensis*, *S. dimidiatus*, *S. flavipectoralis* and *S. spinus*.
4) Large home ranges or roving, often in schools: *Cetoscarus bicolor*, *Bolbometopon muricatum*, *Hipposcarus longiceps*, some *S. sordidus*, *S. brevifilis*, *S. ghobban*, *S. globiceps*, *S. psittacus*, *S. schlegeli* and *S.* sp. (*cf. lunula*).
5) Seasonal reproductive territories: *S. globiceps* and *S. spinus*.

II) Aggression

1) Intraspecific aggression

In many species, intraspecific aggression was the most frequent form of scarid-scarid interaction (Table 5.9). Although these interactions were not observed in detail, two main types were observed: a) intraspecific territorial behaviour with TP-TP and occasionally, IP-IP interactions and b) hierarchial aggression between TP-IP individuals and between large and small IP

Table 5.9 Aggressive interactions between scarids.

Recipient species:	Total number of interactions recorded															
Aggressor:	*C. bicolor*	*S. bleekeri*	*S. gibbus*	*S. japanensis*	*S. sordidus*	*S. brevifilis*	*S. frenatus*	*S. ghobban*	*S. globiceps*	*S. niger*	*S. oviceps*	*S. rivulatus*	*S. rubroviolaceus*	*S. schlegeli*	*S. spinus*	*S. sp.*
Cetoscarus bicolor													1			
Scarus bleekeri					1											
Scarus gibbus			1		6		1						2			
Scarus japanensis					1											
Scarus sordidus		1	1		14					1						
Scarus brevifilis										1						
Scarus frenatus							26				4					
Scarus ghobban							1									
Scarus globiceps							12		6		1					
Scarus niger							10			5	1					
Scarus oviceps							6				2					
Scarus rivulatus							6									
Scarus rubroviolaceus					1		1						2			
Scarus schlegeli							3							2		
Scarus spinus							4								4	
Scarus sp.							1									2
Relative abundance *	4	+	6	+	25	+	41	+	6	44	10	2	4	8	4	10

* = Total number of fish recorded in ten 5 x 50 m transects.

\+ = Species present but not recorded in above transects.

The abundance of scarids in the reef crest region of the study area are as follows (based on five 5 x 50 m replicate transects; mean number per 250 m^2 ± 95 % C.I.):

C. bicolor	0.6 ± 1.02	*S. rivulatus*	0.2 ± 0.52
S. gibbus	0.6 ± 0.63	*S. rubrovilaceus*	0.4 ± 0.63
S. sordidus	1.2 ± 1.49	*S. schlegeli*	0.2 ± 0.52
S. frenatus	3.2 ± 0.97	*S. spinus*	0.2 ± 0.52
S. globiceps	1.0 ± 1.40	*Scarus* sp.	0.6 ± 1.02
S. oviceps	1.0 ± 0.82		

The aggressive interactions were recorded during approximately 100 hrs of observations in the reef crest and reef slope regions of the North Reef study site. Most interactions were observed in the reef crest region. Only violent interactions are tabulated here, mild hierarchical displacements are not included.

individuals.

Intraspecific territorial interactions were usually vigorous involving long chases and/or lateral displays. Such aggression was observed seasonally in some species (*e.g. S. globiceps* and *S. spinus* and once in *S. rivulatus*) and year-round in others (*e.g. S. frenatus*, *S. niger*, *S. rubroviolaceus* and *S. sordidus*). Hierarchial aggression, however, was usually mild with short chases or displacements. It was most frequently observed in *S. frenatus* and *S. niger* (both species having relatively stable haremic social systems), and occasionally in *S. gibbus*, although this may have been reproductive activity.

Other forms of intraspecific aggression included violent displacement of territorial TPs by other TPs (seen in *S. frenatus*) and chasing of IPs by TPs prior to spawning (in *S. frenatus*, *S. globiceps* and *S. sordidus*).

2) Interspecific aggression

Non-scarid interspecific aggression primarily consisted of attacks upon scarids by *Plagiotremus* species, pomacentrids and *Acanthurus lineatus* (L.). *Plagiotremus rhynorhynchos* (Bleeker) and *P. tapeinosoma* (Bleeker) regularly fed upon scarids, whilst pomacentrids excluded scarids from their territories. At the North Reef site, *Plectroglyphidodon lacrymatus* (Quoy & Gaimard) was the most frequent aggressor. In the lagoon, attacks were most frequently recorded from *Stegastes nigricans* (Lacepède), *S. apicais* (De Vi), *Pomacentrus flavicuada* (Whitley), *P. wardi* (Whitley) and *P. grammorhynchus* (Fowler). (Identifications based on Allen [1975] and Russell [1983]). *A. lineatus*-scarid interactions were complex.

A. lineatus aggression was directed to all species of scarid, irrespective of morphological group or feeding type. However, large individuals of *S. gibbus*, *S. brevifilis*, *S. rubroviolaceus*, *Cetoscarus bicolor* and *Bolbometopon muricatum* were not attacked suggesting a size-related aggressive threshold (Choat & Bellwood, in press).

Interspecific aggression between scarids was rare. However, two exceptions were observed: *S. sordidus* and *S. frenatus* (Table 5.9). In both species, interspecifc aggression was of a territorial nature. In *S. sordidus*, interspecific aggression was observed only in TP individuals. In *S. frenatus*, interspecific aggression was observed in both IP and TP individuals. In the reef slope area of North Reef, *S. frenatus* formed harems of 2-3 individuals with a single TP. These individuals held territories throughout the year, with those of the IP's being completely within that of the TP. Territory patrolling behaviour (as noted by Bruce, 1978) was only observed in TPs and was restricted to the reef crest region, even though the boundaries of the territories sometimes extended to the base of the reef (at 8 m depth). *S. frenatus* territories were defended against conspecifics and most other scarid species, with the exception of *S. gibbus* and *S. sordidus*, some individuals of which held territories that overlapped those of several *S. frenatus*. Some 'frenatus' group species were tolerated, but only if they remained in the water column. *S. frenatus* in the back reef area of North Reef and in the lagoon were home ranging. They showed no signs of interspecific aggression and occasionally joined multispecific schools.

The tolerance of *S. sordidus* and *S. gibbus* (the most abundant 'sordidus' group species on North Reef) by territorial *S. frenatus* is of particular interest. Both *S. frenatus* and 'frenatus' group species attacked species of the 'frenatus' group more often than one would expect from their relative abundances if attacks were nonselective (for *S. frenatus*, $\chi^2 = 12.4$, $p < 0.001$, and for 'frenatus' group species as a whole, $\chi^2 = 8.9$, $p < 0.005$, df for both = 1, data from Table 5.9). (Comparing the observed number of attacks towards each group, vs. the expected number of attacks towards each group, based on their relative abundances). Likewise, 'sordidus' group species attacked more 'sordidus' species than expected if attacks were nonselective ($\chi^2 = 25.7$, $p < 0.001$, df = 1, based on data in Table 5.9). These results strongly suggest that 'sordidus' and 'frenatus' group species are selectively aggressive towards species of their own respective morphological groups.

Within *S. frenatus*, interspecific aggression was not equally divided between colour phases (χ^2=7.913, df=1, $p< 0.005$; Table 5.10). Although TPs represented only 45% of *S. frenatus* present in the reef slope area of North Reef, they were responsible for 67% of the recorded interspecific attacks in this area (Table 5.10). Of these, most were directed towards other TPs, in contrast to IP *S. frenatus*, where interspecific aggression was almost exclusively directed towards other IPs (Table 5.10).

Throughout the study, no attacks by scarids towards non-scarid herbivores were recorded.

Table 5.10 Differences in the extent of interspecific aggression by terminal phase (TP) and initial phase (IP) *S. frenatus* occupying common territories in the reef crest region of North Reef.

	No. of attacks	% of total attacks per colour phase	% of total attacks
Terminal phase:			
Attacks on TPs by TP *S. frenatus*	18	64	43
Attacks on IPs by TP *S. frenatus*	10	36	24
Total attacks by TP *S. frenatus* *	28	100	67
Initial phase:			
Attacks on TPs by IP *S. frenatus*	1	7	2
Attacks on IPs by IP *S. frenatus*	13	93	31
Total attacks by IP *S. frenatus*	14	100	33

* – In the study area TPs = 45% (=10) of the total *S. frenatus* count (=22). TPs therefore attack other scarids more often than IPs when their relative abundances are considered; $\chi^2 = 7.913$, $p < 0.005$.

5.8 Discussion

The nature of the site attachment of species in this study was similar to that of other scarid species. Territories/home ranges ranged from 180 to 1000 m^2 and are similar to those of several Indo-Pacific species at Aldabra, which vary from 40 - 1000 m^2 (Bruce, 1978). Comparable ranges have been recorded in one Caribbean species, *i.e.* 120 - 500 m^2 in *Scarus taeniopterus* Desmarest (Dubin, 1981), although others have notably smaller territories, for example, 10 to 12 m^2 in *Scarus iserti* (Ogden & Buckman, 1973 and Buckman & Ogden, 1973) and 25 - 50 m^2 in *Scarus vetula* Bloch & Schneider (Clavijo, 1983). In the present study and in that of Bruce (1978) considerable variation between species was apparent in both the size and duration of site attachment. The maximum recorded duration of site attachment varied with both the nature of the site attachment and the extent of the study period. Temporary reproductive territories may be held only for a few days (Clavijo, 1983 and this study) whilst territorial or home ranging species may remain in one area for at least 703 days (Table 5.8 A; *cf.* 143 days observed by Bruce, 1978).

In addition to the variability in size and duration of site attachment, there was a large degree of variability between species in the nature of site attachment. A broad spectrum of types of site attachment was apparent from home ranges to permanent territories, with individuals defending one or more of a range of resources related to reproduction, food or shelter (Buckman & Ogden, 1973 and Choat & Robertson, 1975). In at least two species (*i.e.* *S. niger*, *S. frenatus* and possibly *S. sordidus*), territorial behaviour appears to be related to the defense of more than one type of resource (Choat & Robertson, 1975 and this section). The form of site attachment is not necessarily species-specific and although many species have specific behavioural traits, a great deal of within-species variability is apparent.

This is most clearly demonstrated in *S. frenatus*. At Heron Island, Great Barrier Reef, *S. frenatus* was described by Choat (1969) as a solitary species that occasionally joins mixed species schools. At Aldabra, Indian Ocean, Bruce (1978) described *S. frenatus* as a site attached species, with solitary TPs (in respect to other TPs) and IPs in groups of 2 to 3. The ranges of these TPs and IPs overlapped partially. Violent aggression was recorded between TPs, from TPs to IPs and between IPs, although within the groups of IPs, aggression was limited to displacements (*i.e.* one fish moving another but without giving chase). No patrolling of TPs was noted and the only interspecific aggression was towards IP and TP *S. scaber* and *S. tricolor* (as *S. cyagnathos*). At other Aldabran localities, however, Bruce (1979) observed transient groups of non-site attached IP and TP individuals.

At Lizard Island, some individuals showed comparable behaviour to that described by Choat (1969) and Bruce (1978) but others showed a much stronger degree of territoriality. In the back reef area of North Reef and in the lagoon, *S. frenatus* were home ranging and occasionally joined multispecific schools of scarids. No violent aggression was recorded inter- or intraspecifically. On the reef crest of North Reef, however, *S. frenatus* were haremic and strongly territorial with IP territories being within that of the TP.

Patrolling by the TP was observed as well as violent interactions between TPs, from TPs to IPs, between IPs and from both TPs and IPs to a large range of other scarid species (Table 5.9). Similar observations were made at other localities around Lizard Island and on the back reef of outer reefs. However, on the reef crest of outer reefs, *S. frenatus* TPs appeared to hold only temporary reproductive territories, with IPs holding small solitary home ranges, although on one occasion, IPs were seen to form a large (40+) monospecific school.

These differences in the behaviour of a single species underline the need for caution when interpreting behaviour of scarids, particularly when based on observations during limited period or at a restricted number of study sites. It is particularly interesting to note that the variability in behaviour over short distances (*i.e.* 100 m from the reef crest to the back reef area of North Reef) is comparable to that found between populations in different geographic regions.

The between species variability in the nature of site attachment, as described above, is strongly reflected in the analyses of aggressive behaviour (Table 5.9). These analyses provide an indication of some of the factors inluencing site attachment and the importance of morphology in such considerations.

At Lizard Island, intraspecific aggression in many species was most apparent during the spawning months, and as in other studies (Randall & Randall, 1963, Choat & Robertson, 1975, Bruce, 1978 and Clavijo, 1983), it is believed to be primarily oriented towards reproduction. Interspecific aggression, however, was not observed in as many species as intraspecific aggression but was observed throughout the year. Interspecific aggression may have some reproductive advantages by decreasing the chances of cross-fertilization. However, the year-round aggression specifically directed towards morphologically (and ecologically) similar species strongly suggests that such attacks are non-reproductively oriented, and that these aggressive individuals are defending another type of resource.

In this study, interspecific aggression was primarily restricted to site attached *S. frenatus* in the reef crest region, although some interspecific aggression was noted in the few permanently site attached TP *S. sordidus* in the same region (Table 5.9). The aggressive interactions of *S. frenatus* were studied in most detail and revealed several interesting facets. Firstly, non-scarid interspecific aggression was always directed towards *S. frenatus*, with pomacentrids, *Acanthurus lineatus* and *Plagiotremus* species regularly attacking *S. frenatus*. No aggression by *S. frenatus* towards non-scarid herbivores was observed. Secondly, only those individuals of *S. frenatus* in the reef crest region displayed interspecific aggression towards other scarids; individuals in the back reef region of North Reef and in the lagoon were not interspecifically aggressive and occasionally joined mixed species schools. Finally, *S. frenatus* - scarid aggression was selectively directed towards 'frenatus' group species.

These observations raise two questions: firstly, why is aggression by *S. frenatus* predominantly directed towards other 'frenatus' group species and secondly, why was this behaviour only observed in the reef crest region at Lizard Island ? It appears that *S. frenatus* in the reef crest region of North Reef are actively defending a non-reproductive resource against morphologically and ecologically similar species (*i.e.* 'frenatus' group species). This type of differential aggression towards ecologically similar species has been recorded in other reef fishes, including herbivorous pomacentrids and acanthurids (Low, 1971, Myreberg & Thresher, 1974, Thresher, 1976, Ebersole, 1977, Robertson *et al.*, 1979, Gronell, 1980, Robertson & Polunin, 1981 and Choat & Bellwood, in press), and chaetodontids (Reese, 1975).

The ecological dissimilarity between 'sordidus' and 'frenatus' group species has been outlined above. Analysis of their morphology and behavioural ecology indicate a degree of resource partitioning between species in the two groups with respect to the depth and type of substratum utilized. Such partitioning would decrease potential competition between the groups and may account for the observed differences in the degree of antagonism exhibited by *S. frenatus* towards species in the two functional groups (Table 5.9). The mechanism which enables *S. frenatus* to recognise ecologically similar species is not known, although the studies of Losey (1982) suggest that some territorial herbivorous fishes may selectively attack other species in response to their feeding habits.

Resource partitioning is frequently interpreted as a result of competitive interactions (*e.g.* MacArthur & Levins, 1967, Schoener, 1968, Pianka, 1969, Emery, 1973, Fraser, 1976, Werner, 1977, Gatz, 1979 and Leviten, 1979), a hypothesis that is supported by experimental and theoretical analyses (*e.g.* Connell, 1961, Jaeger, 1971 and Werner & Hall, 1977, 1979). Competition need not, however, be the sole mechanism behind resource partitioning. Several other hypotheses have been proposed, based on non-competitive mechanisms. In these studies, partitioning has been linked with environmental gradients (Whittaker, 1967 and Harris, 1972), predation (Connell, 1970), food and predation (Dunham, *et al.*, 1978) and under-exploited resources (Ebersole, 1985). An additional potential mechanism of non-competitive resource partitioning is the specialization of a species to maximise net energy accumulation (Emlen, 1968, Mitchell, 1969 and Bloom, 1981). In Bloom (1981), two guilds of nudibranchs were shown to partition food as a result of morphological and behavioural specializations which enabled the two guilds to maximise net energy accumulation from their respective mutually exclusive feeding niches. In scarids, the two guilds (*i.e.* 'biters' and 'scrapers') do not have mutually exclusive feeding niches, however, similar energetic considerations may play an important part in maintaining the observed resource partitioning.

The lack of aggression by *S. frenatus* towards acanthurids suggests that there may be a significant difference between the diets of *S. frenatus* and acanthurids. *Acanthurus lineatus* regularly chases scarids (including *S. frenatus*) from its territories (Robertson *et al.*, 1979, Robertson & Polunin, 1981 and Choat & Bellwood, in press), yet *S. frenatus* shows no aggression towards *A. lineatus* or any other acanthurid species. This disparity may be a result of the ability of *S. frenatus* to utilize all food resources used by the browsing *A. lineatus* (see Robertson *et al.*, 1979 and Robertson & Polunin, 1981 for an account of *A. lineatus* feeding habits; browsing is as defined for acanthurids by Jones, 1968).

A. lineatus and other acanthurids, however, are capable of utilizing only a proportion of the food utilized by *S. frenatus* as a result of their morphology (acanthurid morphology is described by Jones, 1968). The energetic gains of exclusion of other herbivorous groups may therefore, differ between *S. frenatus* and *A. lineatus*.

In addition to the direct morphological limitations of the feeding apparatus of scarids and acanthurids, algal toxins may play an important role in herbivorous feeding strategies as comparable compounds have in terrestrial systems (Ehrlich & Raven, 1964, Feeny, 1970 and Freeland & Janzen, 1974). Many species of marine algae have been found to contain toxins (Ogino, 1962, Doty & Aguilar-Santos, 1966, 1970, Hashimoto *et al.*, 1972 and Norris & Fenical, 1982), some of which may influence grazing patterns of tropical marine fishes (Lobel & Ogden, 1981). Acanthurids and pomacentrids ingest large quantities of algae but have limited digestive capabilities which result in some algal species passing through the digestive tract intact (Randall, 1961 and Lobel, 1980, 1981). In scarids, the ingested material contains less algae and it is all finely triturated, irrespective of the algae species (pers. obs.). Scarids and acanthurids may therefore differ in their exposure or susceptibility to toxins in various algal species which may in turn, influence their feeding behaviour.

Another factor which potentially differentiates the feeding abilities of scarids and acanthurids is intestinal pH. Scarids typically have alkaline intestines (Gohar & Latif, 1961 b and Smith & Paulson, 1974), whilst those of acanthurids may either be acid or alkaline (Lobel, 1981). The potential ability of alkaline intestinal conditions to destroy some algal toxins has been noted by Lobel (1981). In addition, the buffering effects of carbonate may limit the ability of acid secreting species to eat algae containing carbonate, or graze in areas that result in high rates of carbonate ingestion. In conclusion, it appears that scarids and acanthurids possess several features that limit the algal resources that each family is able to utilize as a result of both morphological and physiological constraints.

It is therefore proposed that the lack of aggression by *S. frenatus* towards 'sordidus' group species and acanthurids is a result of differences in their feeding biology. These differences decrease the potential competition between species, and are likely to make exclusion of 'sordidus' group species and acanthurids by *S. frenatus* energetically less profitable than the exclusion of 'frenatus' group species. These morphologically and behaviourally similar species are potential competitors and are vigorously excluded. The benefits of this behaviour presumably outweigh the cost of exclusion.

The above interpretations assist in answering the second question: why is the year-round territorial behaviour in *S. frenatus* limited to individuals in the reef crest region at Lizard Island? From the previous discussion, it appears that territorial *S. frenatus* are defending a resource shared by species with a similar jaw morphology and feeding behaviour. This shared resource is therefore, probably food. If so, the question can then be more specific: Is the reef crest region at Lizard Island, a preferred feeding area, and if so, why? This question cannot be answered from the data collected in this study and requires manipulative experimentation. However, several lines of evidence suggest that the reef crest region is a preferred feeding area for scarids. Some indications of this condition are given below.

Scarids are diurnally active grazing herbivores which feed almost continuously on turf algae (*i.e.* epilithic algae [Hatcher, 1981]). The large number of scarids found in the reef crest area (or comparable zone) in a number of studies (Choat & Robertson, 1975, Bruce, 1979, Bouchon-Navaro & Harmelin-Vivien, 1981 and Russ, 1984 a, b) suggests that this area is a suitable, though not necessarily preferred, feeding area. The high standing crop and yield of turf (epilithic) algae (Hatcher, 1981; Hatcher & Larkum, 1983), however, strongly suggest that this area would be preferable to other areas (*e.g.* lagoon or deep reef slope) for grazing scarids.

It is interesting to compare the experimental analyses of territorial behaviour in the medaka, *Oryzias latipes* (Temminck & Schlegel), a freshwater cyprinodont fish (Magnuson, 1962), with the observed field behaviour of *S. frenatus*. Magnuson (1962) found that with excess food and space, *O. latipes* showed no aggressive behaviour, as the food supply was decreased, hierarchical systems were formed and when the food was spatially restricted, territoriality occurred. The advantages of territoriality in the latter situation were decreased at high population densities as dominant individuals were unable to defend the food from all subordinates. These observations were limited to intraspecific aggression but show a striking similarity to both intra- and interspecific aggression in *S. frenatus*.

At One Tree Reef (Great Barrier Reef), the reef crest region has a higher standing crop and yield of turf algae than the lagoon or reef slope sites (Hatcher, 1981 and Hatcher & Larkum, 1983). At Heron Island (Great Barrier Reef), the largest proportion of scarid grazed substratum was recorded in the reef crest region (Choat & Robertson, 1975). At Lizard Island, the area available for grazing by scarids in the reef crest region of North Reef was limited by a precipitous reef slope on the seaward side and interspecifically territorial *A. lineatus* on the landward side (Choat & Bellwood, in press). If algal availability at Lizard Island was comparable to other Great Barrier Reef locations, the reef crest region at the North Reef study site would have had a localized, and therefore defendable, rich algal food resource.

The advantages of defending such a resource would theoretically be decreased at high population densities of *S. frenatus* and other 'frenatus' group species. The density of *S. frenatus* in the reef crest area of the North Reef study site was relatively high with 3.2 ± 0.97 individuals per 250 m^2 (± 95% C.I.) (Table 5.9), compared to 0.4 per 250 m^2 (Table 5.8 A) in the lagoon at Lizard Island, 1.8 ± 1.7 per 250 m^2 in the reef crest region of Heron Island and 0.0 to 0.7 ± 0.6 per 250 m^2 in other Heron Island locations (Choat & Robertson, 1975). The densities of 'frenatus' group species as a whole in the reef crest region of the North Reef study site at Lizard Island were approximately 6.8 per 250 m^2 (Table 5.9) compared to 78.1 per 250 m^2 in the reef crest region of Heron Island (Choat & Robertson, 1975).

At Lizard Island therefore, *S. frenatus* appears to comply with the theoretical expectations of territoriality (discussed in Magnuson, 1962), in that permanent territorial behaviour (both intra- and interspecifically) was only observed in areas with spatially restricted, and probably rich, food resources. The low population densities of potential competitors (*i.e.* 'frenatus' group species) in the North Reef reef crest region also complies with theoretical expectations, although the densities of these species may merely reflect the efficiency of scarid exclusion in this region by territorial *S. frenatus* and *A. lineatus*. The relatively high densities of territorial *S. frenatus* in the North Reef reef crest region at Lizard Island (approximately twice that of Heron Island reef crests) are less likely to decrease the efficiency of territorial defense than the 11-fold larger density of potentially competing 'frenatus' group species at Heron Island. The high *S. frenatus* densities may even facilitate territorial defense by discouraging scarids from nearby areas and providing neighbouring territorial *S. frenatus* with a relatively scarid-free boundary area.

In the Caribbean, the lack of territorial behaviour by *S. iserti* in areas with low population densities has been discussed in terms of a response to population size, with large populations being conducive to territoriality (Buckman & Ogden, 1973). These differences may, however, be a result of food abundance and distribution rather than population size *per se*. In the present study, the lack of territorial behaviour in *S. frenatus* observed in the lagoon and the back reef areas of North Reef is interpreted as a response to the lack of localized rich food resources. At Heron Island, however, it may be due to the high scarid densities which appear to suppress rather than encourage territoriality in *S. frenatus*.

The observations in this study strongly suggest that year-round territorial individuals of *S. frenatus* are defending a food resource that is utilized by 'frenatus' group species to an extent greater than 'sordidus' group species or acanthurids, and that this resource is present or particularly abundant in the North Reef reef crest region at Lizard Island. This food resource is likely to be epilithic turf algae.

Although epilithic algae is seen as the major resource being defended by *S. frenatus* in the reef crest region at North Reef (Lizard Island), several other factors may make this region energetically profitable to defend. These include:

a) Coprophagy.

In the reef slope/crest region at North Reef, large schools of caesionids and pomacentrids were present (as noted on other reefs by Goldman & Talbot, 1976 and Williams & Hatcher, 1983). The faeces of these fishes were readily eaten by *S. frenatus* and other *Scarus* species. The high nutritional value of faeces from planktivorous species when compared to the diet of scarids has been demonstrated by Bailey and Robertson (1982). Faeces are utilized as a food source by both 'frenatus' and 'sordidus' group species (Section 5.3). However, only 'frenatus' group species are excluded by territorial *S. frenatus* in the reef crest region. This suggests that coprophagy is only a minor food resource for territorial *S. frenatus*.

b) Cover.

The defense of grazing substrata adjacent to cover has been suggested by Choat and Robertson (1975) to account for interspecific aggression by *S. niger* towards other herbivores (mainly scarids). In the present study, however, the presence of grazing substrata near to cover does not appear to be an important factor in *S. frenatus* territoriality. Cover seeking by adult territorial *S. frenatus* was not observed during the day, and at night no adult sleeping sites were recorded in the reef crest region (pers. obs.; *cf.* Winn *et al.*, 1964, Ogden & Buckman, 1973 and Dubin & Baker, 1982).

c) Food close to low tide feeding refuges.

At North Reef, the reef crest and reef slope region were traversed by a series of deep gullies. These gullies and the upper part of the reef slope region were included in the territories of *S. frenatus* and were used as feeding areas, especially at low tide when the reef crest and reef flat were inaccessible. The possession of such feeding areas at low tide may be an additional benefit of territoriality as other feeding areas available at low tide are either less valuable in terms of algal yield and standing crop (Hatcher & Larkum, 1983), or already support large populations of herbivorous reef fishes which have been forced off the reef flat by the low tide (Choat & Robertson, 1975).

d) Ease of defense.

All *S. frenatus* territories at North Reef were adjacent to *A. lineatus* territories. The exclusion of scarids from the territories of *A. lineatus* (Robertson *et al.*, 1979, Robertson & Polunin, 1981 and Choat & Bellwood, in press) may decrease the defensive costs on one border of the *S. frenatus* territories, thus increasing the net energetic gains of territoriality by *S. frenatus* in this region.

In addition to the above factors, permanent territoriality may have reproductive advantages during the spawning season by giving the resident individuals a competitive advantage over trespassers when establishing temporary reproductive territories.

The observations in this study strongly suggest that year-round territorial individuals of *S. frenatus* are defending algal resources. However, further studies are required to establish if algae is the primary resource, and if so, to what extent does algae and other parameters influence territorial behaviour in *S. frenatus*. In particular, manipulative experiments are required to elucidate the effects of scarid population densities and food (*i.e.* algae) availability upon the territorial behaviour of *S. frenatus*. Hopefully, the observations in this study will assist in designing such experiments. The observations in this study, however, advise caution in the experimental approach, in view of the degree of variability in *S. frenatus* behaviour between sites (*cf.* Choat & Bellwood, in press).

Ecological Implications: A - For scarids

Within the Scarinae, there are two main morphological species groups, each with a distinct feeding strategy. These groups are designated as the 'biting' 'sordidus' group and the 'scraping' 'frenatus' group. The species in each group are given in Section 1.3.4. The numerous differences between the two groups have important ramifications in the biology of the species in each group. Some of the ecological implications of the morphology and feeding strategies of these groups are outlined below.

From the results of this study, biting species, *i.e.* the 'sordidus' group species, *C. bicolor* and *B. muricatum*, appear to have a marked advantage over other herbivores, including other scarids, in that they are able to utilize a unique range of food resources. Biting scarids are able to utilize epilithic algae, in common with other scarids, but because of their strong deep bites, they are also able to utilize coralline algae and organisms living in the top few millimetres of the substratum. These organisms include bacteria (Di Salvo, 1969), fungi (Kohlmeyer, 1969) and algae (Golubic, 1969). Biting species, especially *B. muricatum*, are also capable of utilizing large pieces of living coral, although this resource is shared with some tetraodontids (Glynn *et al.*, 1972).

The ability of biting species to use these resources will reduce potential competition with other scarids and herbivores, and may give 'biting' species a competitive advantage over 'scraping' species in areas of high scarid density or during periods of algal shortage. Such competitive advantages resulting from variations in the feeding abilities of juvenile cichlids during times of shortage have been described by Fryer & Isles (1972) and have been discussed by Schoener (1982).

Although 'biting' species appear to have many advantages over 'scraping' species, this feeding strategy also has its disadvantages. It is expensive in terms of the muscle and bones needed for bite strength and the energy needed to maintain and transport these structures. The advantages are also limited to adults. Juveniles are incapable of powerful deep bites and are functionally scrapers (Chapter 2). Biting species therefore, undergo a modification of both structure and behaviour during ontogeny (Chapters 2 and 6) and may, as a result, have a relatively inefficient intermediate form. There is also evidence to suggest that the resources available to biting species may be limited in some areas of the reef. The overall densities of 'biting' species are typically less than those of 'scraping' species, although each group predominates in different areas, with 'biting' species being particularly numerous in reef crest regions (Choat & Robertson, 1975, Bruce, 1979, Buochon-Navaro & Harmelin-Vivien, 1981, Brock, 1982, Williams, 1982 and Russ, 1984 a, b). In the present study, *S. sordidus* was abundant in the lagoon as a juvenile (it was the only biting species present) but no adults were recorded (Chapter 6, part B). The absence of adult 'biters' from these areas may be correlated with the availability of small convex algal covered surfaces which is the predominant substratum type utilized by 'biting' species (Table 5.4). Detailed analyses of scarid population structures and substratum complexity are needed.

The 'scraping' strategy as with the 'biting' strategy also has several distinct advantages. The feeding apparatus of 'scraping' species is relatively small and weak and is, therefore, less expensive to maintain and transport. As the same strategy is utilized throughout ontogeny (Chapter 6), no marked morphological or behavioural changes are required. In addition, 'scraping' species feed on all types of algal covered substratum (Section 5.3). This ability may account for the relative abundance of 'scraping' species in all reef habitats (*cf*. distributions in Russ, 1984 a, b). The wide range of habitats occupied by 'scrapers' may also be facilitated by the ability of some species to utilize the upper layers of sand as food. This resource is not used by 'biting' species (possibly due to inadequate returns per bite when compared to the energetic costs of biting using large jaws) but is shared by several *Acanthurus* species (Russ, 1984 a, b).

It is interesting to note that the *Scarus* species observed feeding on sand particles (*i.e*. *S*. *flavipectoralis*, *S*. *psittacus*, *S*. *schlegeli* and *Scarus* sp. [*cf*. *lunula*]) comprise the 'frenatus' subgroup 'a', and that all possess relatively weak osteological structures and a type I intestine (Sections 1.3.4.2 & 1.5).

A factor which may favour 'scraping' species at high population densities is the recovery time of grazed surfaces. 'Biting' species remove all epilithic algae from the bite area, leaving a relatively large area free of algal filaments. 'Scraping' species, however, remove only a small area of algae and leave short algal fragments at the bases of the scrapes. The time to return to a pregrazed condition is therefore, likely to be shorter after a 'scraping' bite than after a 'biting' bite, as the latter requires more extensive algal growth or invasion. 'Scraping' species also have little effect upon the shape of the grazed substratum, unlike 'biting' species which often remove part of the substratum when feeding (see below). Convex surfaces therefore, become less convex when repeatedly grazed by 'biters'. As convex surfaces form the predominant substratum type grazed by 'biting' species (pers. obs. and Table 5.4), repeated grazing by these species in a limited area may decrease its suitability for further grazing by 'biters', as a result of reduced algal cover on convex surfaces and decreased convexity. (The role of algal-covered convex surfaces as a limiting resource for adult 'biting' species is discussed in Section 6.8). In contrast, the impact of grazing by 'scraping' species appears to be limited and may, therefore enhance their ability to survive at relatively high population densities.

Although the 'scraping' strategy has numerous advantages, it has one major problem, that is, potential competition. 'Scrapers' feed primarily upon epilithic algae. However, this resource is also used by 'sordidus' group species and a range of non-scarid herbivores, including acanthurids, siganids, blennies and some pomacentrids (Al Hussaini, 1947, Jones, 1968, Emery, 1973, Westernhagen, 1973, Lundberg & Lipkin, 1979, Lobel, 1980 and Robertson & Polunin, 1981). Sand scraping scarids are not exempt from this problem as this food resource is also utilized by several acanthurid species (Russ, 1984 a) and a range of invertebrates, including holothurians (Hammond, 1982 and Massin, 1982). Reef associated sand is abundant but is likely to be of limited nutritional value (Sournia, 1976, Borowitzka *et al.*, 1983 and Larkum, 1983). 'Scraping' species are therefore, unable to utilize a unique food resource and, as such, are more likely to be subjected to competition for food during times of algal shortage or at high herbivore population densities than 'biting' species would be.

It is interesting to note that examples of strong interspecific territoriality (*e.g.* *S. niger* [Choat & Robertson, 1975]) and *S. frenatus* [Section 5.7]) and differential habitat utilization (*e.g.* *S. brevifilis*, *S. flavipectoralis*, *S. frenatus*, *S. niger*, *S. oviceps* and *S. schlegeli* [Russ, 1984 b]) are prominent in the 'scraping' group. This may reflect the influence of potential interspecific competition within the group and between this group and other groups or families of herbivorous reef fishes. The role of differential habitat utilization in facilitating the coexistence of several closely related and therefore, potentially competing damselfishes has been suggested by Waldner and Robertson (1980) and Robertson and Lassig (1980).

Ecological Implications: B - For the reef ecosystem

The differences between the two scarid feeding strategies are important, not only in the way in which they influence the ecology of the scarids, but also in the way they influence the interactions between scarids and the reef ecosystem.

Scarids form a large proportion of the herbivorous reef fish community (Williams, 1982 and Russ, 1984 a, b). As grazing herbivores (as defined by Hiatt & Strasburg, 1960), they have been implicated in a wide range of ecological interactions. These include the modification of: algal and seagrass standing crops (Stephenson & Searles, 1960, Randall, 1961, 1965, Van den Hoek, 1969, Adey & Vassar, 1975, Day, 1977, Wanders, 1977, Van den Hoek, *et.al.*, 1978, Hay, 1981, Hatcher, 1982, Miller, 1982, Hatcher & Larkum, 1983 and Littler, *et.al.*, 1983); algal species diversity (Day, 1977 and Hixon & Brostoff, 1981, 1983); nitrogen fixation rates (Wilkinson & Sammarco, 1982 and Wilkinson *et al.*, 1983, 1984); the density of the mobile invertebrate epifauna (Miller, 1982); benthic invertebrate distributions (Bakus, 1964, 1967 and Vine, 1974); topographic relief (Miller, 1982); bioerosion (Risk & Sammarco, 1982) and the success of recently settled corals and coralline algae (Birkeland, 1977, Wanders, 1977, Van den Hoek *et al.*, 1978, Brock, 1979 and Sammarco & Carleton, 1981).

Studies of the ecological implications of scarids *per se* have been primarily restricted to two areas: a) coral predation and b) bioerosion. Scarids have been noted as coral predators (Hiatt & Strasburg, 1960, Bakus, 1964, Glynn *et al.*, 1972, Glynn, 1973, Randall, 1974 and Frydl, 1979) and, as such, have been implicated as important factors influencing coral distributions (Motoda, 1941, Bok & Engel, 1979 and Wellington, 1979).

The only scarid species that frequently feeds upon live corals is *Bolbometopon muricatum* (Randall & Bruce, 1983 and Section 5.3). Despite this, it has received little attention as a coral predator. A large proportion of the diet of this species consists of live corals which includes a wide range of coral species. Five species were recorded by Bruce (1979): three *Acropora* species, one *Porites* species and one *Leptoria* species. In the present study, at least 13 coral species were observed being eaten by *B. muricatum* (Table 5.6). In both studies, the dominant coral species eaten were *Acropora* species, and in the present study, all the *Acropora* species observed being eaten by *B. muricatum* were of a relatively delicate form even on the reef slope and reef crest of the outer barrier reefs, where most colonies are of a robust form. Feeding by *B. muricatum* often broke all the branches off arborescent species and on several occasions, dislodged whole colonies. These observations suggest that *B. muricatum* may significantly alter the survival rates of some of the more easily damaged species, or at least, change their morphology.

The abundance of low, compact coral species in the upper reef slope and reef crest regions of outer shelf reefs are often associated with the harsh physical conditions found in these regions (Done, 1983). However, the abundance of a delicate *Acropora* species (*A. latistella*; T. Done pers. comm.) in the surf zone of the outer reefs of the Great Barrier Reef (Done, 1983) suggests that factors other than physical conditions may also be important in regulating the distribution of coral species and their various morphological types.

As a large, coral predator, *B. muricatum* may influence the distribution or morphology of coral species and thereby modify the species or morphological composition of corals within its main feeding areas. The location of these feeding areas is, however, unclear, although in this study, *B. muricatum* was most often recorded as large schools on the upper reef slopes, reef crest and reef flats, with occasional small groups or individuals around backreef bommies. At Aldabra (Indian Ocean), *B. muricatum* is reported to be abundant in the lagoon, in drainage channels and on reef flats (Bruce, 1979 and Randall & Bruce, 1983).

The regulation of coral distribution by coral predators including scarids has been described previously (Glynn, 1976, Bak & Engel, 1979 and Wellington, 1982). Similarly, changes in colony morphology as a result of predation by fishes (Randall, R.H., 1967), especially scarids (Frydl, 1979) have been reported. The importance of *B. muricatum* in these roles, however, has not been considered previously.

The significance of *B. muricatum* as a coral predator can be assessed. Coral from sheltered areas not frequented by *B. muricatum*, transplanted to more frequently grazed areas (*e.g.* the reef crest of outer barrier reefs) may, with suitably caged treatments to exclude *B. muricatum*, give an indication of the extent of coral predation by this species.

The second area in which scarids have been noted as having ecological implications is in bioerosion, and it is in this area that the differences between species previously included in a single genus and guild are most apparent.

Since the first note of bioerosion by scarids by Darwin (1842, 1845), considerable attention has been paid to their grazing and sediment producing activities. Records of scarid bioerosion based on observations and analyses of intestinal contents are widespread, with studies from the Red Sea (Al Hussaini, 1945, 1947 and Gohar & Latif, 1959), Indo-Pacific (Cloud, 1959, Hiatt & Strasburg, 1960, Bakus, 1964, 1967, Choat, 1969, Glynn *et al.*, 1972, Glynn, 1973, Hobson, 1974 and Bruce, 1979) and Caribbean (Randall & Bishop, 1967). Quantitative analyses of scarid bioerosion are, however, primarily restricted to the Caribbean (Bardach, 1961, Gygi, 1969, 1975, Ogden, 1977, Stearn & Scoffin, 1977, Frydl & Stearn, 1978 and Scoffin *et al.*, 1980).

At present, there are no quantitative estimates of scarid bioerosion based on Indo-Pacific reefs. (The sediment production estimates of Cloud [1959] do not distinguish between reworked sediment and newly bioeroded sediment). However, from the data collected in this study, estimates of scarid bioerosion can be made. The multiplication of feeding rates (bites/min.), feeding hours per year, mean volume of substratum removed per bite (by each species), scarid densities (number/ha) and substratum density (g/cm^3) will give an estimate of the rate of bioerosion by each scarid species per m^2 per year. Estimates of the rate of bioerosion by several scarid species in the reef crest region of North Reef, Lizard Island are given in Table 5.11 A. Table 5.12 A gives a list of estimated rates of bioerosion by scarids at other locations.

The method of estimating scarid bioerosion given above is simple and direct. It avoids errors as a result of inaccuracies or variability in the estimated turnover rate of ingested material (Gygi, 1975) which vary from once per day (Bardach, 1961) to 15 times per day (Ogden, 1977). It also eliminates the need for detailed sediment and intestinal content analyses to estimate the proportion of reworked sediment in the intestine. Analyses of these parameters are both time consuming and a source of considerable variability (Frydl & Stearn, 1978 and Scoffin *et al.*, 1980).

Despite these advantages, several sources of error in the estimates of scarid bioerosion remain. One of these is the restriction of the quantitative observations to a single study site (*i.e.* North Reef). For more accurate estimates, more extensive observations are necessary. Although no marked variation in the diurnal feeding rate was apparent, nor was there any evidence of satiation, these aspects require further observatins. The estimated feeding rates in this study (Table 5.1), however, differed little

Table 5.11 A Estimated scarid bioerosion rates at North Reef, Lizard Island

Species	Bite volume (cm^3)*	Bite rate† (bites/min.)	Density†† (No./hectare)	Erosion rates (Kg/ha/yr.)‡
S. sordidus	9.4×10^{-3}	16.1	48.00	2.59×10^3
S. gibbus	1.7×10^{-1}	10.1	24.00	1.47×10^4
C. bicolor	9.6×10^{-2}	7.3	16.00	4.0×10^2
B. muricatum	2.77	7	0.33 ‡‡	2.28×10^3
			Total	2.00×10^4

* - From Table 5.3.

* - From table 5.3, using a mean value for *S. gibbus* bite volumes and allowing for the 10% scar rate in *C. bicolor*.

† - From Table 5.1.

†† - Based on five 5 x 50 m transects, a hectare (ha) = 10,000 m^2.

‡ - Calculations based on a 10 hour feeding day and a substratum density of 1.63 g/cm^3 (estimated by water displacement, n = 8, S.E. = 0.07 g). It is provisionally assumed that the material removed is 100% $CaCO_3$.

‡‡ - Two schools of approx. 25 individuals each sighted simultaneously on the reefs around Lizard Island; estimated area of fringing reef around Lizard Island = 1.5×10^6 m^2 (Fig. 5.1); all @ 880 mm S.L.

Table 5.11 B Scarid abundances: a comparison between Caribbean and Indo-Pacific reefs.

Location	Scarids/ha	Reference
Caribbean:		
Bermuda	46 - 50	Gygi (1975)
Barbados	245 - 650	Frydl & Stearn (1978)
Bahamas	356 - 379	Colton & Alevizon (1981)
Belize	625 - 2825	Lewis & Wainwright (1985)
Indo-Pacific:		
Heron Island	750 - 4330	Choat & Robertson (1975)
Red Sea	95 - 930	Bouchon-Navaro & Harmelin-Vivien (1981)
Hawaii	1340	Brock (1982)
Lizard Island	233 - 957	Choat & Bellwood (in press)

Table 5.12 A Estimates of bioerosion by scarids: a comparison between the Caribbean and the Great Barrier Reef.

Species	Rate $Kg/m^2/yr$	Location	Reference
Sparisoma viride	0.034	Barbados, Caribbean	Scoffin *et al.* (1980)
S. viride	0.035	Bermuda, Caribbean	Gygi (1969)
S. viride	0.036	Barbados, Caribbean	Stearn & Scoffin (1977)
S. viride	0.04 - 0.168	Barbados, Caribbean	Frydl & Stearn (1978)
S. viride	0.209	Bermuda, Caribbean	Gygi (1975)
Scarus croicensis	0.490	Panama, Caribbean	Ogden (1977)
[A]	0.00 - 2.00	Lizard Island, G.B.R.	present study
[B]	1.40 - 8.74	Heron Island, G.B.R.	present study

[A] - Species breakdown given in Table 5.11. The 0 value was derived from observations at the lagoon study site, where no adult bioeroding species were recorded in ten 5 x 50 m transects.

[B] - Based on the abundances of the two bioeroding species *S. sordidus* and *S. gibbus* recorded by Choat & Robertson (1975), using the estimated erosion rates of these species in Table 5.11 A.

Table 5.12 B Rates of bioerosion: a summary.

	Rate $Kg/m^2/yr$	Location	Source or Reference
Grazers:			
Parrotfishes	0.034 - 0.49	Caribbean	Table 5.12 A
Parrotfishes	2.00 - 8.74	G.B.R.	Table 5.12 A
Diadema [A]	4.6	Caribbean	Ogden (1977)
	9.0	Caribbean	Scoffin *et al.* (1980)
	8.400 - 15.1	Caribbean	Stearn & Scoffin (1977)
Echinometra	0.008 - 0.257	Enewetak	Russo (1980)
	3.9	Caribbean	Ogden (1977)
Echinostrephus	0.036 - 0.073	Enewetak	Russo (1980)
Borers:			
All borers	2.31	Caribbean	Stearn & Scoffin (1977)
All borers	2.31	Caribbean	Scoffin *et al.* (1980)
Sponges	20.00 [B]	Caribbean	Neumann (1966)
Sponges	0.190 - 3.29	Caribbean	Moore & Shedd (1977)
Sponges	0.250 - 0.30	Caribbean	Rutzler (1975)
Polychaetes	0.690 - 1.79	G.B.R.	Davies & Hutchings (1983)
Tridacna crocea	0.16 [C]	G.B.R.	Hamner & Jones (1967)

[A] - These rates may be excessive due to unusually high *Diadema* populations (see Hay, 1984 a,b).

[B] - This rate may be too high as it is based on initial erosion rates which are higher than yearly rates (see Rützler, 1975).

[C] - Estimated using rock density as 1.63 g $CaCO_3/cm^3$, Table 5.11 A.

from the extensive quantitative observations of Bruce (1979).

Several factors may result in an overestimate of scarid bioerosion, including seasonal variability in feeding rates and differences in the size of individuals analysed during feeding observations and those recorded during population surveys. Seasonal variability in the grazing rates (in bites/min.) of herbivorous fishes at One Tree Reef (southern Great Barrier Reef) have been described by Hatcher (1981). These results are, however, questionable as they are based on pooled data from several families. The size and species of the fishes studied were not stated, and in scarids, at least, feeding rates vary markedly between sizes and species (Bruce, 1979, Hatcher, 1981, Tables 5.1, 5.2 and Chapter 6). In the present study, adult feeding rates were recorded between October and February, the warmest period of the year, thus, seasonal variation in feeding rates were not monitored. In this study, estimates of bite sizes and grazing rates were based on relatively large individuals (*S. sordidus* approx. 220 mm S.L. and *S. gibbus* 250–440 mm S.L.; Table 5.3) and an overestimation of bioerosion will therefore result if the proportion of small individuals recorded in abundance surveys is particularly large.

There are also two factors which may result in underestimates of scarid bioerosion rates. Firstly, the calculations were based on a 10 hour feeding day. This allows for seasonal variations in day length and lower feeding rates at dawn and dusk (Dubin & Baker, 1982 and pers.obs.), although it is probably a slight underestimate (Gygi [1975], for example, estimated an 11.5 hour feeding day). Secondly, only scar producing species were considered. Scraping species

(Tables 5.2, 5.3) may not remove a measurable volume of substratum, as estimated by the techniques used in this study, but even if they remove a fraction of a mm^3 per bite, the large number of bites by the numerous individuals of this group will produce significant bioerosion. This is thought to be the largest potential source of error in the estimates of scarid bioerosion in this study. Total scarid bioerosion rates are therefore, probably underestimated, whilst bioerosion rates of individual scarid species are probably slightly overestimated. It should be noted that all these potential sources of error apply equally to previous estimates.

Despite the potential errors in the present estimates of scarid bioerosion on the Great Barrier Reef, these estimates may be more accurate than previous estimates of scarid bioerosion, both in the Caribbean and Indo-Pacific, as the major sources of error (*e.g.* gut turnover rates) and assumptions (*e.g.* the proportion of reworked sediment) made in previous estimates are avoided. The estimated rates are striking. The maximum value estimated at Heron Island is between 18 and 257 times greater than estimates of scarid bioerosion in the Caribbean (Table 5.12 A). This difference is not unexpected, as there is only one major bioeroding scarid species in the Caribbean, *S. viride* (Frydl & Stearn, 1978). The estimated rates of bioerosion by *S. iserti* (Ogden, 1977; Table 5.12 A) are probably inaccurate due to an underestimate of the rate of sediment reworking in this species (Frydl and Stearn, 1978). Other species (*e.g.* *S. guacamaia*) are capable of scarring the substratum, but do so only occasionally (Gygi, 1975). In comparison, on the Great Barrier Reef, there are three major bioeroding species: *S. sordidus*, *S. gibbus* and *B. muricatum*, and a range of less important species including *C. bicolor*, *S. bleekeri*, *S. japanensis* and *S. rubroviolaceus* (Table 5.2). In addition, scarid abundances are often higher in Indo-Pacific regions (Table 5.11 B). Low abundances of scarids in the Caribbean may be the result of high fishing pressure (Hay, 1984 a, b and Scoffin *et al.*, 1980), but estimates of scarid bioerosion rates which allow for this (Scoffin *et al.*, 1980) are still considerably lower than the estimated scarid bioerosion rates in this study. The magnitude and potential importance of the scarid bioerosion rates estimated in the present study (*i.e.* 0–8.7 Kg/m^2/yr) are perhaps best appreciated when compared with the estimated mean calcification rates of reefs, which vary from 0.5 to 1.8 Kg $CaCO_3$/m^2/yr (Kinsey, 1983). The maximum recorded calcification rate of an area of a reef is 12 Kg/m^2/yr (Smith, 1983). In some areas therefore, scarids may remove a volume of carbonate which is equivalent to a substantial proportion, if not all, of the calcified material produced in that area.

In the Caribbean, scarids are of only minor significance in terms of total bioerosion (Hunter, 1977, Ogden, 1977, Stearn & Scoffin, 1977, Frydl & Stearn, 1978, Scoffin *et al.*, 1980 and Wilkinson, 1983). The importance of scarid bioerosion in the Indo-Pacific, however, can only be inferred by comparing it with Caribbean non-scarid bioerosion rates. Despite this, there is some evidence to suggest that scarids may play a more important role as bioeroders in the Indo-Pacific than in the Caribbean. In the Caribbean, the major bioeroding group are the grazing echinoids, especially *Diadema* (Table 5.12 B). A comparison of urchin densities in the Indo-Pacific, where *Diadema* is present at denstities of 0.01 – 0.53 individuals per m^2 and *Echinostrephus* and *Echinometra* up to 6.5 individuals per m^2 (Randall, R.H., 1978, Randall, R.H. *et al.*, 1978, Birkeland *et al.*, 1976, Russo, 1980 and C. Birkeland, pers.comm) and in the Caribbean, where *Diadema* is present at densities of 5-100 individuals per m^2 (Ogden *et al.*, 1973, Sammarco, 1980, Lawrence & Sammarco, 1981 and Williams, A.H., 1981) strongly suggest that urchins play a much smaller role in the Indo-Pacific than in the Caribbean. However, the rates of echinoid bioerosion in the Caribbean may be overestimated, as unusually large standing crops of urchins have been reported in heavily fished areas by Hay (1984 a, b) who suggested that many of the studies of Caribbean urchins have been based on reefs with abnormally high urchin densities.

Quantitative estimates of bioerosion by boring organisms are primarily restricted to the Caribbean (Wilkinson, 1983). Of all boring groups, sponges are generally regarded as the most important (Hein & Risk, 1975, Scoffin *et al.*, 1980, Highsmith, 1981 and Wilkinson, 1983), although the estimated yearly bioerosion rates of sponges by Neumann (1966) are inaccurate as they are extrapolated from relatively high initial erosion rates (Rützler, 1975). With the exception of the estimates of Neumann (1966), total erosion rates of boring organisms in the Caribbean are approximately equal to or less than the estimated scarid bioerosion rates in the Indo-Pacific. These estimates and the low urchin densities in the Indo-Pacific strongly suggest that scarids are one of the most important bioeroding agents in the Indo-Pacific.

However, there are probably marked regional variations in the form of bioerosion, with borers and grazers being dominant in different areas. Rützler (1975) reported considerable variation in sponge populations between reefs and between zones on the same reef. Variability in the abundances of scarids have also been reported (Russ, 1984 a, b). On the Great Barrier Reef, scarids may be the major bioeroding agents in the reef crest, and possibly, upper reef slope regions of mid- and outer reefs, whereas on inshore reefs and in other zones of the mid- and outer reefs erosion is primarily by other groups, probably borers. The reef crest regions are likely to be the primary areas of scarid bioerosion as these areas have a relatively high standing crop of bioeroding scarid species (*e.g. S. sordidus*, *S. gibbus* and *B. muricatum*), and of scarids and acanthurids as a whole (Choat & Robertson, 1975, Bouchon-Navaro & Harmelin-Vivien, 1981, Russ, 1984 a, b). The presence of high standing crops of both scarids and acanthurids may be important as the grazing effects of these groups may decrease internal bioerosion rates (Risk & Sammarco, 1982 and Sammarco *et al.* ms.).

Bioerosion is important, both as a form of sediment production and as a factor which modifies the topography of the reef. The impact of 'scrapers' on the topography is likely to be minimal in comparison to the 'biting' species, as 'scrapers' remove relatively little material during grazing (Tables 5.2, 5.3, 5.7) and feed on a wide range of algal covered microhabitat types (Tables 5.4, 5.7). 'Biting' species, however, remove relatively large volumes of substratum with each bite (Tables 5.2, 5.3, 5.7), particularly from convex protruding surfaces (Tables 5.4, 5.7). Grazing by these species is therefore likely to decrease the topographic relief as a result of the erosion of convex surfaces. The low topographic relief in areas of high grazing pressure at Enewetak Atoll has been interpreted by Miller (1982) as a result of surface bioerosion by grazers. This effect may be experimentally assessed using algal covered coral blocks placed in areas with known abundances of 'biting' and 'scraping' scarid species.

Conclusion

This chapter has demonstrated that there is a strong correlation between the functional morphology and behavioural ecology of scarids. The two morphological and functional groups (the 'biting' 'sordidus' group and 'scraping' 'frenatus' group) described in Chapter 1 have been shown to have markedly different feeding strategies in the field. These differences influence both the ecology of the species in each group and the impact of these species upon the reef, particularly in their role as bioeroders.

Summary

1) Two distinct feeding groups are described within the genus Scarus. These groups correspond with the morphological groups described in Section 1.3 and are consistent with the functional interpretations in Section 1.4. 'Biting' 'sordidus' group species have a feeding strategy characterized by infrequent, large bites which leave distinctive scars in the substratum. These species frequently feed upon convex substrata, and interspecific aggression, if displayed, is predominantly directed towards other 'sordidus' group species. In contrast, 'scraping' 'frenatus' group species have a

feeding strategy characterized by numerous small bites which produce no scars in the substratum, only a characteristic pair of scrapes marked by dislodged algae. These species feed upon a range of substrata, and interspecific aggression, if displayed, is predominantly directed towards other 'frenatus' group species.

2) Similar differences were noted between species described in Chapter 1 as 'proto-biters' (*i.e. C. bicolor* and *B. muricatum*) and a species described as a 'proto-scraper' (*i.e. H. longiceps*). The former had a low feeding rate and invariably scarred the substratum whilst the latter had a higher feeding rate and only rarely scarred the substratum.

3) In addition to feeding upon turf algae, several other food sources were utilized by scarids. Live coral formed a large proportion of the diet of only one species, *B. muricatum*. It is therefore proposed that *B. muricatum* may play an important role as a coral predator. Coprophagy was recorded in nine species: *S. frenatus*, *S. gibbus*, *S. globiceps*, *S. niger*, *S. oviceps*, *S. psittacus*, *S. rivulatus*, *S. sordidus* and *S. spinus*. Sand ingestion was recorded in four species: *S. schlegeli*, *S. flavipectoralis*, *S. psittacus* and *Scarus* sp. (*cf. lunula*).

4) The extent of site attachment varied greatly within and between species. Estimated home ranage/territory sizes varied from 180 to 1000+ m^2, with observed durations of up to 703 days.

5) Intraspecific aggression was observed in most site attached species. Interspecific aggression, however, was primarily

restricted to *S. frenatus* and to a lesser extent *S. sordidus*. This aggression was only observed in species with territories in the reef crest region of North Reef. In both *S. frenatus* and *S. sordidus*, interspecific aggression was directed preferentially towards species in the same morphogical group as the aggressor. These individuals may be defending a food resource (*i.e.* turf algae). Interspecific defense of shared territories by *S. frenatus* was not shared equally by both colour phases. Terminal phases (TPs) attacked more often than initial phases (IPs). Aggression by TPs was directed primarily towards other TPs whilst IP aggression was almost exclusively directed towards other IPs.

6) The ecological implications of the differences between the two morphological/feeding groups affect both the scarid and their impact upon the reef as bioeroding agents.

a) The 'biting' species are able to utilize a unique food resource, (*i.e.* endolithic growth) but their feeding activity may decrease the abundance of the principal substratum form upon which they feed (*i.e.* convex surfaces). In comparison, the 'scraping' species are unable to utilize any unique food resource but they are able to utilize a wide range of substratum types without markedly altering their form as a result of their feeding activities.

b) Bioerosion was restricted primarily to 'sordidus' group species, *C. bicolor* and *B. muricatum*, with estimated total scarid erosion rates of 2.00 $kg/m^2/yr$ at the North Reef study site, Lizard Island and from 0 to 8.74 $kg/m^2/yr$ at other Great Barrier Reef localities. The maximum rates are considerably higher than estimates of scarid bioerosion in the Caribbean and are comparable to estimates of bioerosion by other major bioeroding groups.

CHAPTER SIX

THE BEHAVIOURAL ECOLOGY OF JUVENILE SCARIDS

Introduction

All *Scarus* species undergo major morphological changes during ontogeny. These morphological changes are primarily in the form of the feeding apparatus and associated structures. The morphological analyses of juvenile scarids in Chapter 2 have revealed a high degree of morphological and functional similarity between juvenile *Scarus* species. The degree of similarity, however, decreases during ontogeny, with a divergence of species belonging to the two adult functional groups (Chapter 1) occurring during the latter stages of the juvenile phase.

In this chapter, the feeding biology of juvenile scarids will be considered in detail (Part A). Notes on the ecology of the juveniles of several *Scarus* species are also included (Part B and Appendix 2).

Part A Feeding Biology

6.1 Introduction

There are few published accounts of the feeding biology of juvenile scarids. The majority of feeding studies are restricted to adults. Robertson *et al.* (1976) demonstrated the disruptive effects of damselfish territoriality upon the feeding rates of juvenile *S. iserti*, and recorded the feeding rates of solitary, schooling and territorial individuals. Hatcher (1981) recorded the feeding rates of juvenile (<10 cm) scarids and reported that these differed little from the feeding rates of larger specimens. The feeding rates, however, were pooled from several species. In other studies, observations on juvenile and adult scarids have been pooled (*e.g.* Ogden & Buckman, 1973 and Ogden, 1977).

In Chapter 2, five morphological stages were described during the ontogeny of scarids. Functional interpretations of the morphological features of each stage indicated potential differences in the diet and feeding strategy associated with each stage. The characteristic features of each stage are outlined in Table 6.1. Stages 1-4 represent the juvenile phase, whilst stage 5 represents the adult phase which is discussed in Chapters 1 and 5.

In this section, the dietary and behavioural changes inferred by the functional interpretations in Chapter 2 will be assessed using field observations of feeding behaviour and analysis of intestinal contents.

6.2 Materials and methods

Quantitative observations on the feeding behaviour of juvenile scarids were made at the North Reef and lagoon study sites at Lizard Island (Fig 5.1) between January 1982 and December 1983. During 10 minute observation periods, a record was made of the number of bites per minute, the number of bites per foray (a foray is defined in Section 5.2), the food item ingested (if visible) and the mode of feeding. Additional qualitative observations of feeding behaviour were made at these sites and at several other locations around Lizard Island. All feeding observations were made between 10:00 a.m. and 4:00 p.m., at high or mid-tide, using S.C.U.B.A. with

Table 6.1 Functional interpretations of the morphology of juvenile scarids.

Stage	S.L. in mm	Primary morphological features	Implied diet and feeding strategy
1	7 - 10	Large eye, canniform teeth, simple intestine	Carnivorous phase: highly nutritive diet, mobile invertebrates - micro-crustacea ?
2	10 - 22	Large eye, even cutting edge on jaws, simple intestine	Intermediate, carnivorous/browsing phase: moderately nutritive diet, selected algae or occasional micro-crustacea ?
3	20 - 50	Even cutting edge on jaws, sacculated intestine	Grazing phase 1: diet low nutritive value & high inorganic content, both species functional 'scrapers'
4	50 - 90	*S. sordidus* develops features for 'biting'	Grazing phase 2: divergence. Both species ingesting quantities of algae and carbonate, *S. sordidus* may bite slightly deeper than *S. frenatus*
5	above 90	*S. sordidus* = 'biter' *S. frenatus* = 'scraper'	Grazing phase 3: 'biters' and 'scrapers'. Both species ingest algae and carbonate particles - the adult diet. *S. sordidus* has a 'biting' strategy and *S. frenatus* a 'scraping' strategy

notes recorded on PVC sheets.

The size of individual fishes was estimated by holding a pencil close to the fish, marking off the length, then drawing a line of the same length on underwater paper. The lengths of these lines were then measured in the laboratory. In order to check the accuracy of the technique, the lengths of 31 individuals were estimated and then the individuals were caught and measured. The average degree of error was 5.9 % of the T.L. with a maximum error of 12.5 %.

Analyses of intestinal contents were based on material from two sources. Part of the material (donated by Dr. P. Doherty) was collected from artificial settlement substrata (dead *Pocillopora* colonies in concrete stands) placed on reefs off Townsville. These specimens were fixed in 10% seawater formalin shortly after collection. The remainder of the material was collected around Lizard Island. These specimens were either fixed in formalin immediately upon capture or killed then fixed within an hour. Material was stored in 70% ethanol.

The following material was examined:

	Number	mm S.L.
S. sp	8	7.5 - 10.0
S. ghobban	2	13.5 - 14.5
S. psittacus	8	25.5 - 35.5
S. rubroviolaceus	1	15.5
S. sordidus	7	8.2 - 22.0
S. sp (*cf. lunula*)	2	11.7 - 15.1
S. spinus	9	8.5 - 18.0
S. globiceps/rivulatus	2	10.4 - 13.5
S. psittacus/schlegeli	11	10.6 - 20.0

Specimens were dissected and the intestine removed. The intestinal contents were then extracted for microscopic examination. Food items were identified and grouped into major taxa. Within these taxa, individuals were grouped according to size and counted. Inorganic particulate matter and algae were visually estimated as a % of the total volume of the intestinal contents.

Several methods of measuring the diet of fishes have been reviewed by Hynes (1950) and Pillay (1953), and more recently by Hyslop (1980). Recent studies (*e.g.* Lassuy, 1984) have utilized a 'comparative feeding index' following Christensen (1978). The comparative feeding index (CFI) is a product of several measures of the dietary importance of a food item, each having a particular bias. The CFI is a compromise and, although it enables direct comparisons to be made of a single measure of the dietary importance of a food item, it reduces the amount of information available on the nature of a food item in the diet. In this study, therefore, food items in the diet were quantified in two ways: a) as a percentage occurrence and b) as a mean number of individuals or mean estimated percentage of total volume of the gut contents, with 95% confidence limits. The first measure overestimates the relative importance of items which are regularly eaten but form only a small proportion of the diet. This measure indicates the frequency with which an item is included in the diet. The second measure estimates the relative abundance of a food item in the diet but not the frequency of occurrence, although the 95% confidence limits indicate the variability in the relative abundance.

6.3 Results

A. Feeding Rates

The feeding rates of several size ranges of *S. sordidus*, *S. frenatus* and *S. psittacus* are given in Table 6.2, and are expressed graphically in Fig. 6.1 A. Marked changes in the feeding rates are apparent. Between 10 and 20 mm S.L., all three species have similar feeding rates. Between 20 and 120 mm S.L., the feeding rates are relatively consistent within each species irrespective of size, with *S. sordidus* having a significantly higher feeding rate than *S. frenatus* ($t=4.881$, $p < 0.001$, Table 6.3B). (This test is based on pooled data, as markedly uneven sample sizes, Table 6.2, precluded more detailed analyses. The comparison is therefore tentative, although the differences indicated are relatively clearly demonstrated in the graphed data in Figure 6.1 A). *S. psittacus* has a feeding rate higher than that of *S. sordidus*, at least until 80 mm S.L. In addition, no significant differences between the feeding rates of *S. frenatus* in the lagoon and at North Reef were recorded (North Reef; $n = 36$, $x= 142.2$ bites/10 min., $s = 42.7$: Lagoon; $n = 12$, $x= 137.1$ bites/min., $s = 36.2$: $t = 0.3716$, 46 df., $p > 0.5$). From qualitative, and limited quantitative, observations the feeding rates of juvenile scarids in the 20–120 mm S.L. range can be roughly divided into three groups, these are summarized in Table 6.4.

B. Feeding periodicity

Size-related differences in the mean foray size of *S. sordidus*, *S. frenatus* and *S. psittacus* are given in Table 6.5 and expressed graphically in Fig. 6.1 B. In all three species, there is a

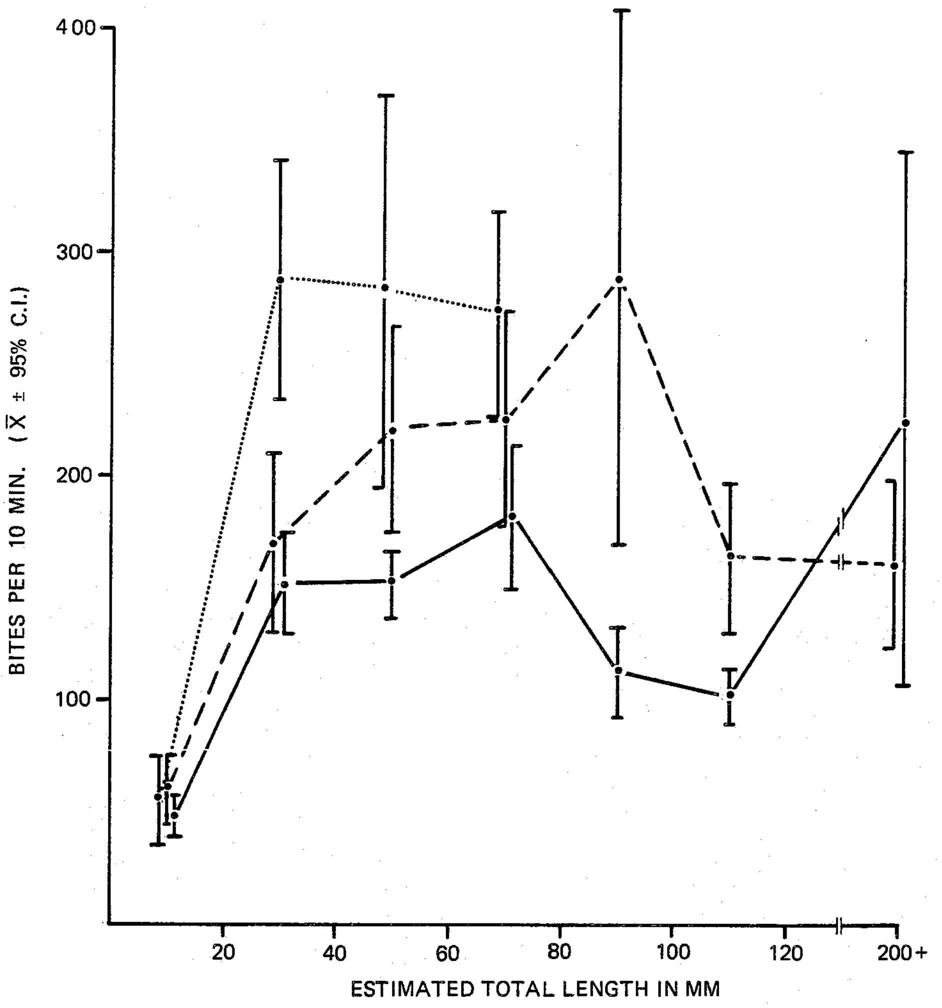
Figure 6.1 A

The mean feeding rates of three *Scarus* species between 20 and 120 mm T.L. in bites/10 minutes.

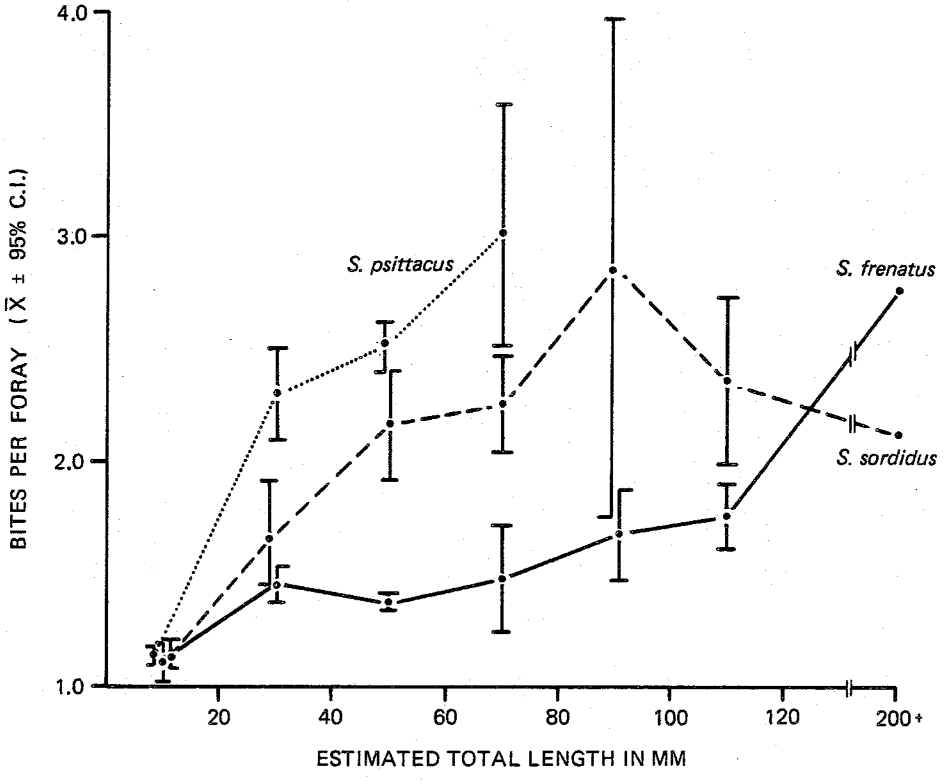
Figure 6.1 B

The mean foray size of three *Scarus* species between 20 and 120 mm T.L. in bites/foray.

The number of individuals in each size group is given in Table 6.2.



400
300
200
100
BITES PER 10 MIN. (X̄ ± 95% C.I.)
20
40
60
80
100
120
200+
ESTIMATED TOTAL LENGTH IN MM



4.0
3.0
2.0
1.0
BITES PER FORAY (X̄ ± 95% C.I.)
S. psittacus
S. frenatus
S. sordidus
20
40
60
80
100
120
200+
ESTIMATED TOTAL LENGTH IN MM

Table 6.2 Size-related differences in the feeding rates of three juvenile *Scarus* species between 20 and 120 mm T.L.

	S. sordidus				*S. frenatus*				*S. psittacus*			
Size range T.L. (mm)	No. Obs.	No. Ind.	mean bites per 10 min	95% C.I.	No. Obs.	No. Ind.	mean bites per 10 min	95% C.I.	No. Obs.	No. Ind.	mean bites per 10 min	95% C.I.
0.0 – 19.9	26	11	59	16	10	3	49	8.4	5	3	54	20
20.0 – 39.9	15	10	171	40	18	8	152	23	15	11	288	54
40.0 – 59.9	4	3	222	47	12	7	153	15	7	6	283	88
60.0 – 79.9	12	7	224	48	3	2	182	33	6	4	272	46
80.0 – 99.9	3	1	290	120	7	4	113	20	–	–	–	–
100.0 – 119.9	6	3	164	33	12	5	102	13	1	1	165	–
Adult †	17	–	161	37	17	–	225	119	–	–	–	–

Each observation period = approx. 10 min: *S. sordidus* (10.32 ± 0.490 min); *S. frenatus* (11.16 ± 1.018 min);

S. psittacus (10.32 ± 0.735 min).

† – Adult data from Table 5.1.

Table 6.3 A Changes in the bite rate and foray size of *S. sordidus* between 10 and 19.9 mm T.L.

T.L. range (mm)	No. Obs.	No. Ind.	Bites / 10 min. mean ± 95% C.I.	Bites/foray mean ± 95% C.I.
10 - 10.9	10	3	22.2 ± 8.9	1.01 ± 0.032
11 - 12.9	7	3	67.0 ± 36.0	1.19 ± 0.130
18 - 19.9	9	5	94.0 ± 11.1	1.38 ± 0.150

Each observation period was ≥ 5 minutes.

Table 6.3 B The feeding rates of *S. sordidus* and *S. frenatus* between 20 and 120 mm T.L.

Species	No. Obs.	mean bites/10 min	σ	95% C.I.
S. sordidus	45	196.6	79.74	23.94
S. frenatus	54	135.4	42.22	11.52

df=97, t=4.881, $p < 0.001$.

Table 6.3 C The mean number of bites per foray of *S. sordidus* and *S. frenatus* between 20 and 120 mm T.L.

Species	No. Obs.	$\bar{x}$ bites/foray	σ	95% C.I.
S. sordidus	45	2.04	0.56	0.167
S. frenatus	54	1.53	0.22	0.059

df=97, t=6.210, $p < 0.001$.

Table 6.4 Qualitative observations of the feeding rates of juvenile scarids between 40 and 110 mm T.L.

1) Rapid feeders	@ 250–300 bites/10 min
S. ghobban ‡	
S. globiceps ‡ *	
S. niger ‡	
S. psittacus ‡	
S. rivulatus ‡	
S. schlegeli ‡ *	
S. spinus ‡	
S. sp. (*cf. lunula*) ‡	
2) Moderately rapid–rapid feeders	@ 200–250 bites/10 min
S. bleekeri † *	
S. brevifilis ‡	
S. dimidiatus ‡ *	
S. gibbus †	
S. oviceps ‡ *	
S. sordidus †	
3) Slow feeding species	@ 100–200 bites/10 min
S. frenatus ‡	

* = Few observations.
‡ = 'Frenatus' group species.
† = 'Sordidus' group species.

Table 6.5 Size-related differenses in the mean foray size (in bites/foray) of three juvenile *Scarus* species between 20 and 120 mm T.L.

	S. sordidus		*S. frenatus*		*S. psittacus*	
Size range T.L. (mm)	Mean foray size	95% C.I.	Mean foray size	95% C.I.	Mean foray size	95% C.I.
0.0 – 19.9	1.20	0.08	1.14	0.07	1.15	0.04
20.0 – 39.9	1.67	0.24	1.45	0.08	2.29	0.21
40.0 – 59.9	2.16	0.24	1.37	0.04	2.51	0.12
60.0 – 79.9	2.25	0.22	1.48	0.23	3.03	0.56
80.0 – 99.9	2.87	1.10	1.68	0.20	–	–
100.0 – 119.9	2.35	0.37	1.76	0.14	3.57	–
Adult †	2.12		2.75			

Number of observations and individuals per species per size group as in Table 6.2.

† – Adult data from Section 5.3.

gradual increase in the mean number of bites per foray in progressively larger size groups. This trend is also present in *S. sordidus* specimens between 10 and 20 mm T.L. (Table 6.3 A). There is a significant difference between 20-120 mm T.L. *S. sordidus* and *S. frenatus* in the number of bites in each foray group (*i.e.* groups with 1,2,3 bites etc; $\chi^2 = 1413.2$, df. = 9, $p < 0.001$), with *S. sordidus* having a significantly larger mean number of bites per foray than *S. frenatus* ($t = 6.21$, df. = 7, $p < 0.001$; Table 6.3 C). The differences indicated are clearly demonstrated in the graphed data in Figure 6.1 B. The mean number of bites per foray of 20-80 mm T.L. *S.psittacus* appears to be higher than those of *S. sordidus* and *S. frenatus* at a similar size (Table 6.5, Fig. 6.1 B). Overall forays appear to be largest in *S. psittacus*, medium in *S. sordidus* and lowest in *S. frenatus*. There was no significant difference between *S. frenatus* at North Reef and in the lagoon in the mean number of bites per foray (North Reef; $n = 39$, $x= 1.523$, $s = 0.202$: Lagoon $n = 14$, $x=1.481$, $s = 0.305$: $t = 0.5754$, 51 df., $p > 0.05$).

C. Feeding behaviour

The following qualitative observations of scarid feeding behaviour are based on approximately 250 hours of observations on over 90 individuals. In all species, the feeding behaviour changed markedly throughout ontogeny. These changes occurred gradually but can be divided into five major phases. Each phase will be outlined below:

Phase 1: 9 - 10 mm T.L. (7.5-8.1 mm S.L.)

In this phase, all *Scarus* species were virtually identical in both appearance and behaviour. They were primarily translucent with faint pale dots and/or dark dashes. The main difference between species was their location on the reef. At this size, recently recruited individuals typically laid in or amongst the turf algae which grew over the coral rubble substratum, although some specimens were also observed to lie on the fronds of macroalgae (*e.g.* *Turbinaria ornata*). In this position, these individuals snapped at small objects in the turf or on the algae, although the feeding rate was low. They occasionally 'hopped' a few millimetres propelled by their pectoral fins. Movement of more than a few centimetres was rare (2-8% of the total time observed; n=2, 40 min.). When swimming, the caudal fin was curled round giving the body a characteristic 'c' shape. In this phase, most individuals were solitary and site attached, although larger individuals occasionally joined small groups of small scarids which passed through the individual's home range.

Phase 2: 10.1 - 12 mm T.L. (8.2-9.5 mm S.L.)

In this phase, small scarids began to display more pigmentation which was often species specific. They remained close to the substratum, occasionally lying on the turf algae, especially during strong wave action. Movement between sites (*i.e.* locations several centimetres apart) comprised 12-19% of the total time observed (n=3, 29 min.) and individuals continued to move with the characteristic 'c'-shaped body. When feeding, individuals typically swam at an acute angle to the substratum, apparently searching for and periodically snapping at small organisms in the turf. The bite rate remained low. Some individual algal filaments were eaten. Movement using their pectoral fins was generally slow. The caudal fin was curled round to produce the 'c'-shaped body most often when feeding. Individuals remained within small home ranges but often joined other small scarids which passed through the individual's home range. Throughout this phase, individuals remained close to the substratum and/or shelter.

Phase 3: 12.1 - 18.0 mm T.L. (9.5-14.5 mm S.L.)

Individuals in this phase possessed distinctive juvenile colour patterns (see Section 4.3). They swam in a typical scarid-like manner, propelled by their pectoral fins and no longer curled the caudal fin. When feeding, individuals in phase 3 swam at a more oblique angle to the substratum than individuals in phase 2. A large proportion (>80%) of the time was spent searching the substratum although the bite rate remained relatively low. Most bites removed algal filaments or parts of turf algae. Epiphytes on macroalgae were sometimes eaten and individuals occasionally snapped at objects in the turf. Individuals remained within restricted home ranges but, within these home ranges, they frequently travelled in pairs or in small groups of 3 to 6 individuals. At this size there was little difference in the behaviour of most *Scarus* species, the most obvious being in their location and colour patterns.

Phase 4: 18.1 - 25.1 mm T.L. (14.5 - 20.5 mm S.L.)

In this phase, individuals retained the juvenile colour patterns found in the previous phase and swam in a typical scarid manner. When feeding, most species scraped the substratum. Individual algal filaments were only occasionally ingested. *S. frenatus* appeared to select individual algal filaments or fronds more often than the other species. The bite rate in this phase was higher than that of individuals in phase 3 and there was less searching activity between bites. Although all *Scarus* species observed were home ranging at this size, the behaviour of the various species started to diverge. Some species remained solitary whilst others became increasingly gregarious and formed small schools.

Phase 5: 25.0 - 150.0 mm T.L. (20.5 - 124 mm S.L.)

In this final juvenile phase, differences between species became increasingly apparent. Most species possessed specific colour patterns and there was a wide range of behavioural types, from territorial species to species which formed large multispecific schools. Early in this phase all species fed as 'scrapers', scraping the algal covered substratum and only rarely removed individual algal filaments. They no longer snapped at objects in the turf. The bite rate was high, with little evidence of searching between bites (with the possible exception of *S. frenatus*). Approximately 14.7% of the time (± 5.57, 95% C.I., n=19, 210 min) was spent moving between sites (*cf.* 12-19% in phase 2). In the latter part of phase 5, there were marked morphological group-related differences in addition to species-related differences in feeding behaviour. 'Frenatus' group species remained 'scrapers' whilst 'sordidus' group species began to exhibit behaviour associated with a 'biting' strategy. The smallest *S. sordidus* observed utilizing 'cracking' bites was 110 mm T.L. and the smallest *S. gibbus*, 130 mm T.L.

In phases 2 to 5, two basic types of feeding behaviour were observed. The predominant type was with the head facing the substratum. This position was held throughout the searching/biting period and was maintained during wave action by facing into the wave-induced water currents. The second feeding type was only rarely observed. In this type, the fish remained in the water above the substratum and drifted with the wave-induced water movement. Small individuals feeding in this way occasionally snapped at objects in the water column, possibly crustacea. Larger individuals occasionally ate the faeces of schooling fishes in this manner.

Cessation of feeding bouts (forays) by most species at North Reef and by *S. frenatus* in the lagoon appeared to be independent of external factors. However, for other species in the lagoon, feeding bouts (forays) were often interrupted or terminated as a result of aggression from territorial pomacentrids or other scarids.

D. Analysis of the intestinal contents.

The composition of the intestinal contents of juvenile scarids, from 7.5 to 35.5 mm S.L. is listed in Table 6.6. Only three types of food item were observed: crustacea, algae and particulate inorganic matter. A breakdown of the crustacean component is given in Table 6.7. The data in Tables 6.6 and 6.7 are expressed

Table 6.6 The intestinal contents of juvenile scarids - A: Algae, sand and crustacea; mean % of gut contents and % occurrence.

S.L. size class (mm)	n	Algae †	Sand †‡	Algae + Sand	Algae + Sand % occurrence	Crustacea % occurrence
7 - 8.9	8	1.5 (1.6)	5.5 (6.7)	7.0 (8.1)	50	100
9 - 10.9	9	14.5 (16.1)	28.8 (16.9)	43.3 (28.0)	89	100
11 - 12.9	4	22.5 (26.1)	36.3 (12.5)	58.8 (32.8)	100	100
13 - 14.9	8	28.1 (22.1)	34.4 (17.7)	66.2 (20.7)	100	100
15 - 16.9	8	35.0 (16.4)	35.0 (19.1)	71.2 (21.9)	100	88
17 - 18.9	4	42.5 (10.5)	50.0 (21.4)	92.5 (11.4)	100	100
19 - above	9	21.7 (12.4)	65.6 (19.9)	100.0 (00.0)	100	44

† - Data expressed as the mean estimated % of the total volume of intestinal contents (± 95% C.I.).

‡ - The sand consisted of fine (< 1.0 mm) carbonate and silicious particles.

N.B. the intestinal contents consisted entirely of algae, sand and/or crustacea, no other food items were recorded.

Table 6.7 The intestinal contents of juvenile scarids - B: Crustacea; mean numbers per individual (± 95% C.I.).

S.L. size	n	Total	Harpacticoids			Ostracods	Copepods	Others*
class (mm)		crustacea	nauplii†	small‡	medium+		small†	
7 - 8.9	8	69.1 (36.0)	32.7 (23.1)	24.6 (10.6)	9.9 (6.0)	--- (---)	1.5 (3.0)	0.3 (0.5)
9 - 10.9	9	54.2 (48.0)	24.6 (32.1)	17.1 (13.3)	10.2 (8.6)	0.2 (0.5)	0.9 (1.4)	0.3 (0.7)
11 - 12.9	4	31.3 (30.8)	6.5 (10.3)	13.3 (11.9)	8.3 (6.7)	0.8 (1.1)	2.5 (2.2)	--- (---)
13 - 14.9	8	38.1 (31.8)	13.8 (15.7)	14.5 (10.1)	9.3 (9.9)	0.3 (0.5)	0.1 (0.2)	0.3 (0.5)
15 - 16.9	8	30.6 (23.3)	13.6 (14.7)	8.1 (3.9)	10.0 (7.4)	0.1 (0.2)	--- (---)	--- (---)
17 - 18.9	4	15.8 (17.8)	6.8 (9.7)	4.8 (3.6)	4.0 (7.5)	0.3 (0.6)	--- (---)	--- (---)
19 - 35.0	9	1.2 (2.0)	0.2 (0.5)	0.7 (0.9)	0.1 (0.2)	0.2 (0.5)	--- (---)	--- (---)

† = 0.13 mm mean diameter.
‡ = body length 0.25 - 0.30 mm.
+ = body length 0.70 - 0.75 mm.
* = includes: large harpacticoids (body length 1.3 - 1.5 mm), other large copepods (body length 0.6 - 0.7 mm) and amphipods.

Figure 6.2 A

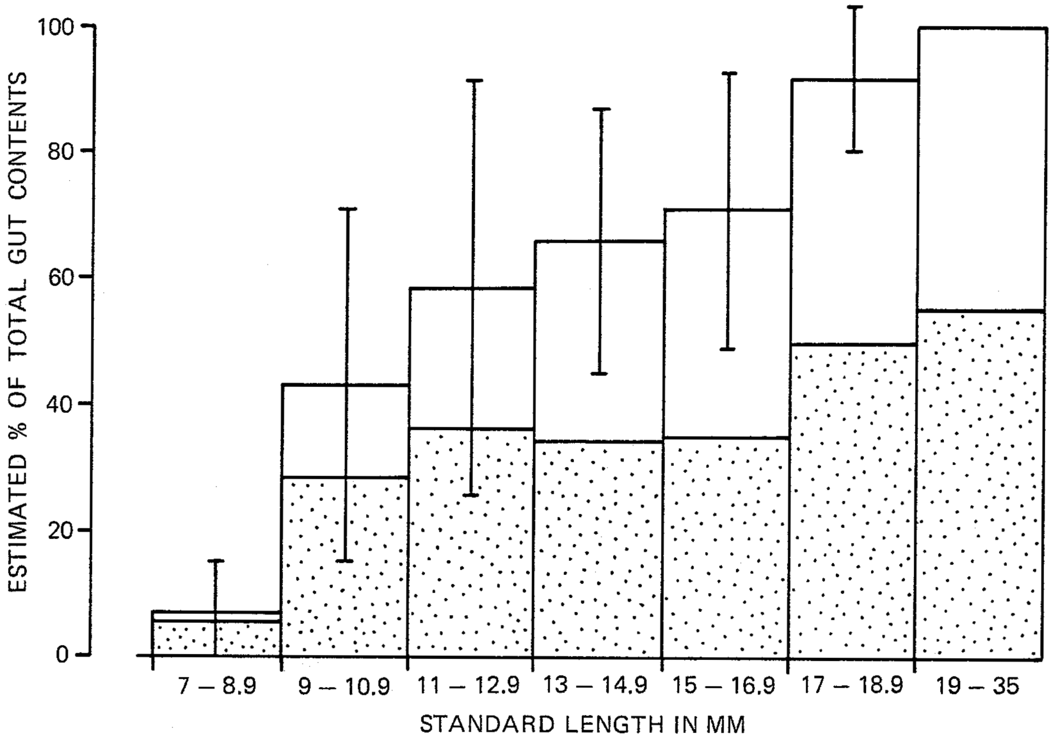
The intestinal contents of juvenile scarids; algae and sand (mean % volume ± 95% C.I.).

(Open areas = algae, stippled areas = sand).

Figure 6.2 B

The intestinal contents of juvenile scarids; crustacea (mean number per intestine ± 95% C.I.).

The number of individuals in each size group, the percent occurrence of each food item and a breakdown of the crustacean component are given in Tables 6.6 and 6.7.


ESTIMATED % OF TOTAL GUT CONTENTS
100
80
60
40
20
0
7 – 8.9
9 – 10.9
11 – 12.9
13 – 14.9
15 – 16.9
17 – 18.9
19 – 35
STANDARD LENGTH IN MM

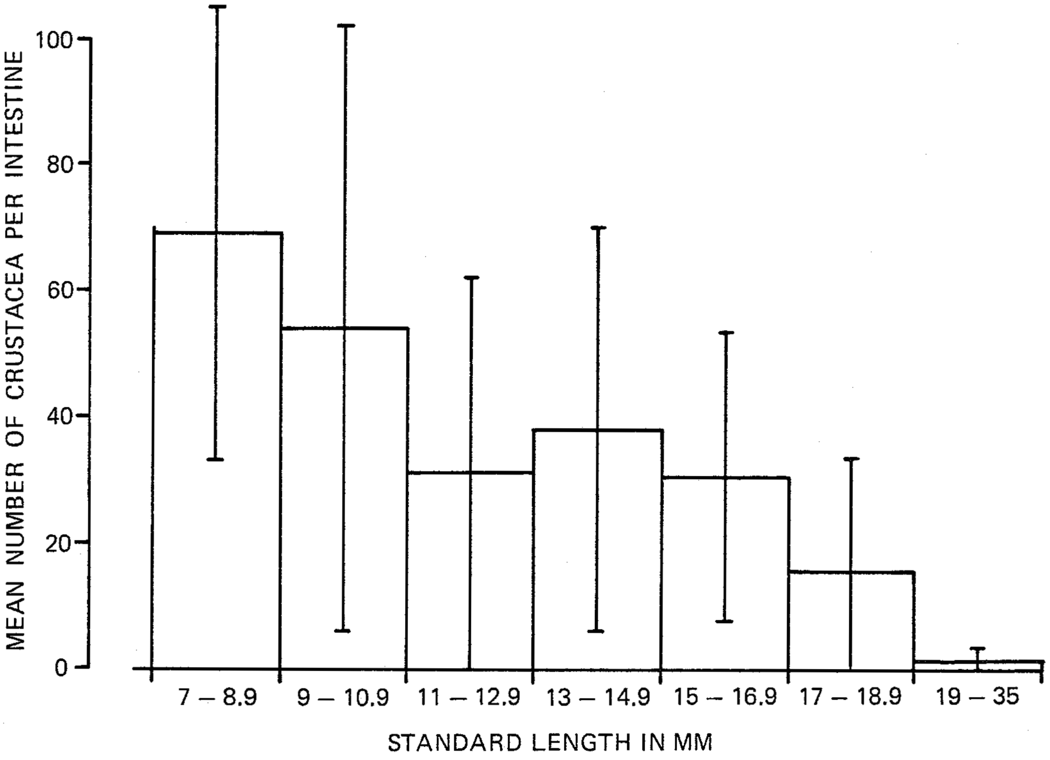

MEAN NUMBER OF CRUSTACEA PER INTESTINE
100
80
60
40
20
0
7 – 8.9
9 – 10.9
11 – 12.9
13 – 14.9
15 – 16.9
17 – 18.9
19 – 35
STANDARD LENGTH IN MM

Table 6.8 The intestinal contents of some juvenile herbivorous reef fishes other than scarids.

			ALGAL FILAMENTS		GRIT-SAND		CRUSTACEA			
Species	Number	S.L. range	% occ.	Est. % conts.	% occ.	Est. % conts.	% occ.	Est. % conts.	Mean number	
Acanthurus dussumieri	6	22.5–29.5	100	97	17	3	17	<1	0.17	a
Acanthurus olivaceus	4	28.0–30.0	100	70	50	30	25	<1	0.25	a
Zebrasoma scopas	1	30.0	100	100	0	0	100	<1	1.00	b
Zebrasoma veliferum	4	18.0–20.0	100	100	0	0	50	<1	0.75	c
Siganus spinus	4	20.5–21.5	100	100	0	0	75	<1	1.50	d
Siganus doliatus	1	26.5	100	100	0	0	100	<1	1.00	a
Centropyge bicolor	4	17.5–19.0	100	100	0	0	75	<1	1.75	e

a – small harpacticoid.
b – small copepod.
c – small harpacticoid (2) and harpacticoid nauplii (1).
d – copepod nauplii (4), small harpacticoid (2).
e – harpacticoid nauplii (3), small harpacticoid (2), ostracod (1), decapod larva(1).

graphically in Figures 6.2 A and 6.2 B. The above data represent the pooled observations of approximately eight species (listed in Section 6.2). There was no discernible difference in the composition of the intestinal contents between species nor between specimens fixed immediately upon capture or those killed upon capture and fixed shortly thereafter.

For comparative purposes, similar observations were made on a limited number of recently recruited specimens from the three other herbivorous reef fish families (Table 6.8). In these species, there was a notable lack of crustacea in the intestinal contents, even though some specimens appeared to have only recently settled, as evidenced by their lack of pigmentation.

6.4 Discussion

The results in this study indicate that there is a strong degree of correlation between the morphology, diet and feeding behaviour of juvenile scarids below 40 mm T.L. and above 110 mm T.L. The observations of scarids below 40 mm T.L., summarized in Figure 6.3, show a gradual changeover from a carnivorous, toothed, labrid-like stage which feeds close to the substratum, with a low number of bites per minute and bites per foray, to a herbivorous, typical scarid form feeding as a 'scraper'. In the last stages of the juvenile phase, above 110 mm T.L., morphology and feeding biology are also correlated as 'sordidus' group species begin to display feeding behaviour associated with a 'biting' strategy, *i.e.* strong powerful bites, fewer bites per minute, fewer bites per foray and scarring of the substratum.

Figure 6.3

A summary of the ontogenetic changes in the behaviour, diet and morphology of juvenile scarids.

(a) Feeding rates, in bites/min., based on *S. sordidus*, Tables 6.2 and 6.3 A.

(b) Mean foray size, based on *S. sordidus*, Tables 6.3 A and 6.5.

(c) Major phases in the feeding behaviour as defined in Section 6.3 C.

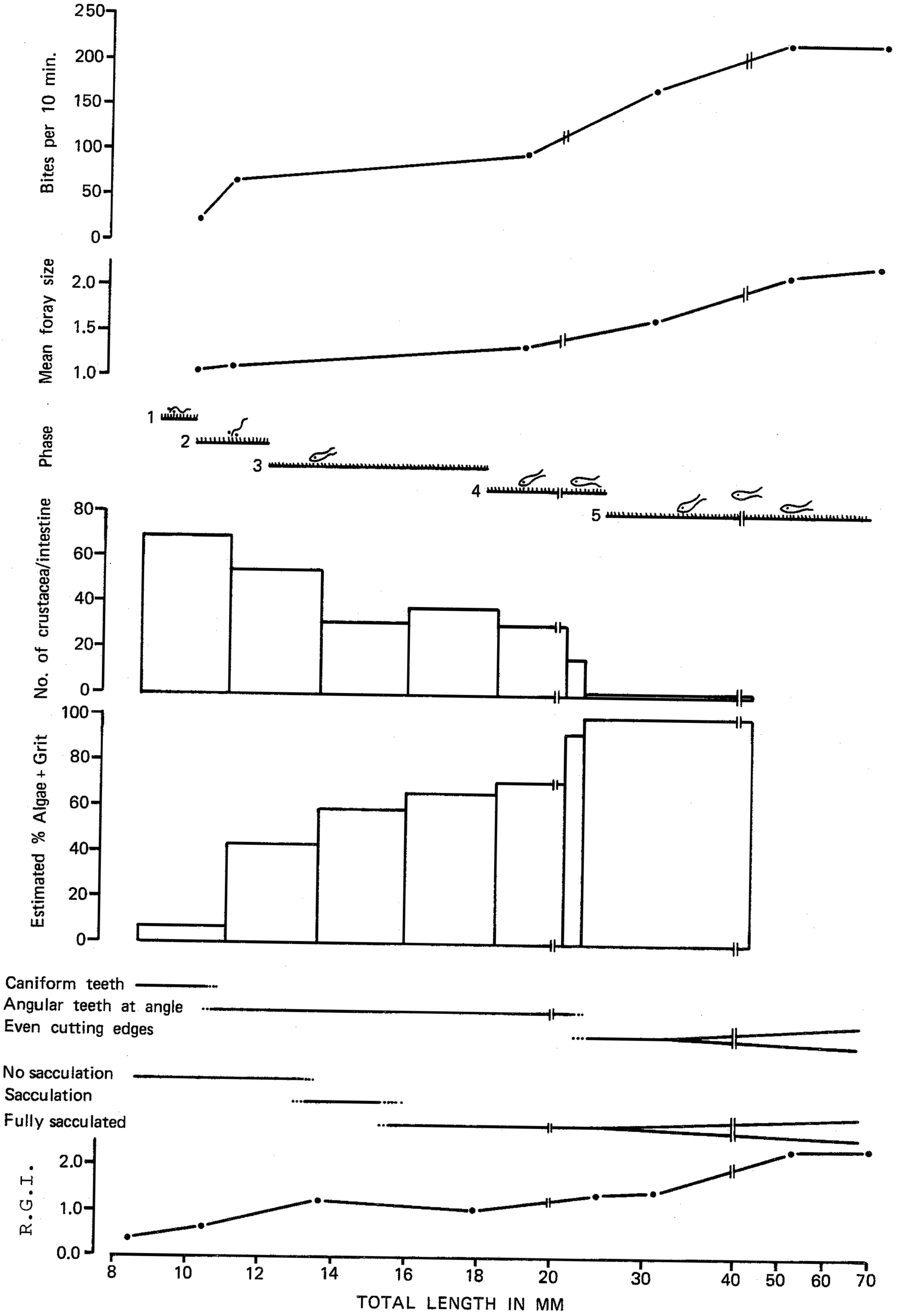
(d) Number of crustacea in the intestine, from Figure 6.2 B.

(e) Estimated volumes of algae and sand in the intestine, from Figure 6.2 A.

(f) The form of the teeth and cutting edges of the jaws, from Chapter 2.

(g) The form of the intestine, from Table 2.2.

(h) The Relative Gut Index (gut length/S.L.), from Table 2.2.


Bites per 10 min.
250
200
150
100
50
0
Mean foray size
2.0
1.5
1.0
Phase
1
2
3
4
5
No. of crustacea/intestine
80
60
40
20
0
Estimated % Algae + Grit
100
80
60
40
20
0
Caniform teeth
Angular teeth at angle
Even cutting edges
No sacculation
Sacculation
Fully sacculated
R.G.I.
2.0
1.0
0.0
8
10
12
14
16
18
20
30
40
50
60
70
TOTAL LENGTH IN MM

Between 40 mm T.L. and 110 mm T.L., however, the correlation between morphology and feeding behaviour is less consistent. In this size range, 'sordidus' and 'frenatus' group species diverge in their morphology but their behaviour remains similar. This inconsistency was most notable in *S. frenatus* which differed markedly in its feeding biology from other 'frenatus' group species. Between 40-110 mm T.L., *S. frenatus* had a bite rate and number of bites per foray which were both lower than those of *S. sordidus*. Below 80 mm T.L., these rates for *S. frenatus* were also much lower than those of *S. psittacus*, a 'frenatus' group species, which has higher rates than *S. sordidus*. The most dissimilar rates, therefore, were displayed by the most morphologically similar species. From Table 6.4, it can be seen that between 40-110 mm T.L., there is no consistent correlation between morphological groups and feeding rates, and that in this study, *S. frenatus* is an unusual species.

Numerous studies have reported a strong correlation between the morphology and feeding behaviour or diet of fishes. These include observations in freshwater (Al-Hussaini, 1949, Fryer & Isles, 1972 and Wankowski, 1979), temperate marine (Chao & Musick, 1977, Montgomery, 1977, Christensen, 1978 and Schmitt & Holbrook, 1984) and tropical marine systems (Al-Hussaini, 1947, Gohar & Latif, 1959, Jones, 1968, Emery, 1973, Bryan & Madraisau, 1977, Yamaoka, 1978, Lassuy, 1984 and Stoner & Livingston, 1984).

In the present study, a strong correlation was found between the morphology and the feeding behaviour and diet of scarids. In Chapter 5, observations of adult feeding patterns showed a marked difference between species with disparate morphologies. Likewise, in this chapter, juveniles between 10-40 mm T.L. have a diet and feeding behaviour which reflect those predicted from the morphological and functional analyses in Chapter 2.

However, in this study, there is one exception. *S. frenatus*, between 40 and 110 mm S.L., displays a behaviour which differs markedly from morphologically similar species. The functional analyses of the morphology of *S. frenatus*, at this size, in Chapter 2 indicate that it is capable of a weak scraping bite but not a strong cracking bite. It was therefore predicted to feed as a functional scraper. In this study, this was found to be true for *S. frenatus* and other 'frenatus' group species but their behaviour differed markedly. This observation underlines the observations of Bock (1980) and Lauder and Liem (1981) who emphasise the need for behavioural observations, especially in the field, before the adaptive value of a structure can be accurately assessed. *S. frenatus* shares a similar morphology with other 'frenatus' group species but has a different foraging strategy which is based on few bites per minute and few bites per foray (discussed in Chapter 6, part B). Other exceptional cases have been reported in other taxa. Schmitt and Coyer (1982), for example, found foraging behaviour, rather than morphology, to be a better indicator of diet in embiotocids. A striking example of this problem was reported by Schluter (1982) who found that two species of Galapagos finches, *Geospiza difficilis* and *G. fuliginosa*, previously thought to be strong competitors because of their morphological similarity, were, in fact, carnivorous (feeding on arthropods and gastropods) and granivorous, respectively.

Other factors which may influence the diet irrespective of the morphology must also be considered, for example, social behaviour (Coates, 1980) and predation (Grossman, 1980 and Grossman, *et al.*, 1980). The problem is further complicated by the possible effects of the diet upon the morphology (Hykes & Moravek, 1933; in Al-Hussaini, 1947 and Greenwood, 1965).

The observations outlined above suggest that the feeding behaviour and diet of an individual are limited by its morphological capabilities. However, because of behavioural plasticity, the feeding behaviour and diet of an individual may vary considerably within these morphological constraints. Morphological and functional analyses will not indicate how an individual feeds, but will indicate the limits of its feeding capabilities. How an individual feeds within its morphological constraints can only be elucidated by behavioural observations.

One of the most striking observations in the present study is the degree of difference between the feeding biology of juvenile and adult scarids. Small juveniles are carnivourous, whilst large juveniles and adults are almost exclusively herbivorous.

Ontogenetic changes in the diet are a common occurrence in fishes. Such changes are widespread in freshwater systems (*e.g.* Cadwallader, 1975, Davis, 1977, Tallman & Gee, 1982, Marrin, 1983, Magnan & Fitzgerald, 1984 and Moyle & Vondracek, 1985) and, although not ubiquitous (Helfman, 1978), they have been reported in several marine species (*e.g.* Godfriaux, 1969, Emery, 1973, Coates, 1980, Grossman *et al.*, 1980, Jones, 1984, Lassuy, 1984 and Schmitt & Holbrook, 1984).

Records of changes from omnivory/carnivory to herbivory in marine fishes are relatively common. A change from an omnivorous diet to a predominantly herbivorous diet has been reported in several pomacentrids (Ciardelli, 1967, Emery, 1973 and Lassuy, 1984) whilst a change from carnivory to herbivory has been reported in a kyphosid, *Girella nigricans* (Mitchell, 1953), a stichaeid, *Cebidicthys violaceus* (Montgomery, 1977) and three sparids, *Sarpa salpa* (Christensen, 1978), *Lagodon rhomboides* (Stoner, 1980) and *Diplodus holbrooki* (Stoner & Livingston, 1984).

In the present study, only scarids were found to change from carnivory to herbivory. Species in the other major herbivorous fish families examined, *i.e.* the Acanthuridae, Siganidae and Pomacanthidae, all fed as herbivores within a few days of recruitment to the reef (Table 6.8). These differences between the various tropical herbivorous fish families reflect what is believed to be a major difference in the early life history strategies of herbivorous coral reef fishes.

These herbivorous reef fish families may be divided based on their recruitment strategies: a) those which recruit at a small size, *i.e.* the Scaridae, and b) those which recruit at a relatively large size, *i.e.* the Acanthuridae, Pomacanthidae and Siganidae (and posssibly some members of the Blennidae). The Kyphosidae is apparently unusual as it has a pelagic juvenile phase (Mitchell, 1953 and Leis & Rennis, 1983). The advantages of the two strategies to herbivorous fishes are unclear.

It has been suggested that ontogenetic changes in the diet reduce intraspecific competition in freshwater systems (Tallman & Gee, 1982, Marrin, 1983, Magnon & Fitzgerald, 1984 and Moyle & Vondracek, 1985). However, this is unlikely to be true for scarids as the carnivorous phase persists for only a short period. In addition, small scarids have access to rich algal resources that are unavailable to large juveniles or adults, *i.e.* in pomacentrid territories (Section 6.6). A diet which is similar in both juvenile and adult phases, as in acanthurids and siganids, may ensure that settling larvae select areas which are suitable for both juveniles and adults, although there is no evidence to suggest that the algae eaten by these juveniles are a better indicator of suitable adult feeding areas than benthic copepods would be for scarids.

Differences in the size of larvae at settlement are not restricted to herbivorous reef fish families. Similar differences have been found between other reef fish families. The Labridae, Mugiloididae, Nemipteridae and Pseudochromidae, for example, settle at a relatively small size (<15 mm T.L.), whilst the Holocentridae, Lethrinidae, Lutjanidae, Serranidae and some chaetodontids settle at a relatively large size (>15 mm T.L.) (based on the size of the largest recorded planktonic larva in Leis and Rennis, 1983, and personal observations). Both groups include families with a wide range of feeding habits. This suggests that the size at settlement is related to factors other than the diet of post-recruits. It is therefore suggested that these differences reflect two distinct larval strategies in coral reef fishes. Large larvae are more likely to be strong swimmers and therefore able to move to, or remain in, favourable areas. Their larger size may also enable them to utilize food resources which are unavailable to smaller larvae and decrease predation from planktonic predators. It would be particularly rewarding to investigate the biology of the larger larval stages of other herbivorous reef fish species in comparison with smaller scarid larvae. A possible relationship between larval size and an offshore larval distribution has been suggested (Leis & Miller, 1976).

Irrespective of the possible advantages of these strategies to larval fishes, size differences at settlement do influence the feeding biology of individuals during early post-recruitment. Observations of several other herbivorous fish species have indicated that a relatively long intestine is a prerequisite for efficient digestion of algae (Bryan & Madraisau, 1977, Montgomery, 1977 and Lassuy, 1984). Newly recruited scarids are therefore likely to have a nutritional problem, as they only have a relatively short intestine. Lassuy (1984) suggested that small juvenile *Stegastes lividus* ingest a large proportion of animal matter to compensate for their relatively low algal assimilation efficiencies, probably as a result of their relatively short intestine. As newly recruited scarids have very short simple intestines, they are therefore likely to have extremely low algal assimilation efficiencies. It is probable therefore, that the carnivorous diet of recently recruited scarids is the result of nutritional limitations. This appears to be primarily a result of their intestinal morphology, which is in turn, dependent to some extent on their size at settlement, which is too small to accommodate a long complex intestine. Similar nutritional limitations appear to have resulted in carnivory in the juvenile phases of other herbivorous poikilotherms (Clark & Gibbons, 1969 and Pough, 1973). This is probably a general phenomenon and may account for the carnivorous nature of most planktonic larval fishes.

The time spent or the size attained in the planktonic stage may be the major determinant of either carnivory or herbivory in the settling recruit. The actual carnivorous period may be similar in the two types of larvae, one may be spent completely while in the planktonic stage whereas the other is spent initially in the plantonic stage but also continues after settlement.

Part B General Biology

6.5 Introduction

There have been few studies of the biology of juvenile scarids. Published accounts which include observations on juvenile scarids often pool the juveniles of several species as *Scarus* spp. or pool the juvenile and adult stages. Such studies on juvenile *Scarus* spp. include estimates of abundance (Bouchon-Navaro & Harmelin-Vivien, 1981 and Brock, 1982), diurnal variability in abundance (of *S. iserti/taeniopterus*; Colton & Alevizon, 1981) and analyses of recruitment patterns (Williams & Sale, 1981 and Shulman, 1984).

Published studies on individual juvenile *Scarus* species include observations of differential habitat utilization in *S. guacamaia* Cuvier and *S. coelestinus* Valenciennes (Randall, 1963); diurnal migration in *S. iserti* (Ogden & Buckman, 1973; juveniles and adults pooled [Ogden, 1977]), movement, feeding rates and rates of agonistic encounters in *S. iserti* (Robertson *et al.*, 1976), the effects of grazing by *S. psittacus* (as *S. taeniurus* = *S. psittacus*, Randall & Bruce, 1983) upon the benthic community structure (Brock, 1979), analyses of the recruitment patterns of *S. sordidus* (Eckert, 1984 and Sale *et al.*, 1984) and the foraging strategy of *Sparisoma viride* (Hanley, 1984).

The present study is a preliminary investigation of the biology of juvenile scarids, in an attempt to establish some basic information on their ecology and behaviour, and to assess the presence of any factors which may be correlated with the two morphological groupings proposed in Chapter 1. This study was feasible only after the taxonomic problems of juvenile identifications had been worked out (Chapter 4).

This study is primarily concerned with individuals. General trends from transects are of value but are difficult to interpret unless one has a knowledge of the behaviour of individuals. A large part of this study is therefore concentrated on individuals within restricted study areas. These data are of limited value for making generalizations about patterns of scarid behaviour on or between reefs but they do give a detailed assessment of how some individuals did behave in two specified localities. It is not an extensive study but will, hopefully, provide data which can form a basis for further detailed observations and experimental studies, across a greater number of reefs or habitat types.

6.6 Materials and Methods

Observations of juvenile scarids on reefs around Lizard Island were made during November and December, 1981; January, February, April, May, July, September, November and December 1982, and

January, February, November and December 1983. The aspects considered in this study and their respective methodology are as follows:

1) Abundance estimates

A. Examination of fixed areas

In a pilot study carried out in November/December 1981, scarids were found to be recruiting in relatively large numbers. To assess the nature of recruitment and the behaviour of post-recruits, detailed abundance estimates of juvenile scarids during the settlement season (*i.e.* November - February) were undertaken. Recruitment patterns in two such seasons were followed, in Nov - Jan 1982/83 and 1983/84.

From preliminary observations in December 1981 it was found that abundance estimates of juvenile scarids using transect methods missed many of the recently recruited individuals below 20 mm T.L. Abundance estimates of juvenile scarids up to 60 mm T.L. were therefore based on detailed examinations of 2 x 2 m areas. Each 2 x 2 m area was examined for 10 minutes, initially for large individuals, then in detail for smaller individuals by running a hand over the rubble, coral or algae to dislodge any small specimens lying on the substratum. A 10 minute observation period was chosen, as previous trials (n=6) of 20 minute observations found that all individuals which could be visually recorded in a 2 x 2 m area were located in less than 9 minutes and on average, all individuals were located within 4 minutes ($\bar{x} = 3.7$, $s = 2.7$). In each 2 x 2 m area, a record was made of the species identity and estimated total length of all juvenile scarids, and their location, behaviour and associations with other individuals. Recent recruits were defined as those individuals with incomplete juvenile pigmentation, *i.e.* only possessing pale dots, and which invariably laid on the substratum, had a phase 1 feeding behaviour (Section 6.3) and were less than 11 mm T.L.

The 2 x 2 m areas were selected as follows. Two series of transects were established within the North Reef and lagoon study sites. Each series of transects was separated by a gap of over 20 m. Each transect was 20 m long by 2 m wide and was marked by small floats every 5 m. In the lagoon, transects were laid at two depths, a) on the top of the reef (approx. = chart datum), 2 m from the edge of the reef and b) along the front edge of the reef (0-1 m below C.D.), extending from the top of the growing reef edge to the coral rubble and sand base. In this region, the reef is approximately 1 m above the lagoonal sand. At North Reef, transects were laid at three depths, a) 1-3 m below C.D., just below the reef crest, b) 3-6 m below C.D., at the base of the reef slope, covering the lower 1 m of the reef slope and 1 m of coral rubble at the base of the reef slope and c) 6-8 m below C.D., over low coral rubble and sand 2 m away from the base of the reef slope. Each transect was divided into ten 2 x 2 m areas. During each census, four such areas were examined in each transect. The areas were chosen at random (following a random number table). Each census therefore covered 16 2 x 2 m areas in the lagoon and 24 2 x 2 areas at North Reef.

B. Transects

In order to estimate abundances of individuals above 20 mm T.L. and to increase the accuracy of the abundance estimates, 20 x 2 m transects were used during the latter part of the settlement season when no juveniles <20 mm T.L. were recorded in the 2 x 2 m areas and overall numbers were low. These transects were along the 2 x 2 m transect lines described above.

Fixed 120 x 2 m transects were also used to follow changes in abundance, size and species composition of scarids in the lagoon and at North Reef. These transects were established at the depths used for the 2 x 2 m areas described above. Transects were swum slowly (≈5 m/min.) and a note was made of the number of individuals and the species identity, estimated size and behaviour of each individual.

2) Home range estimates

The study areas at North Reef and in the lagoon were mapped by triangulation of prominent underwater features. Plans of the areas were then drawn to scale (3 cm:1 m & 6 cm:1 m). Individuals were followed for 30 minute periods and their position relative to the prominent underwater features, recorded every 15 seconds. These points were then transferred to the map of the area and the outer points connected (extreme points were only connected if the individual passed between them). Clusters of points within the area were also delineated. Mapped areas were quantified using a graphic digitizer. Individuals were followed for subsequent 30-minute periods until the cumulative area occupied increased by less than 2% in a 30-minute observation period. No more than two observation periods per day were used, and these were separated by a period of at least three hours. Each individual was followed for at least four 30-minute periods, but usually required six to nine observation periods. The cumulative area occupied was then taken as an estimate of the individual's home range. Clusters of 15-second location records during the total observation time were used to produce area usage maps. A note was made of the characteristics of the areas most frequently occupied. During the observation periods, the species, location and intensity of any agonistic encounters were recorded. Individuals were identified by a combination of colour patterns or scars and size, or by subcutaneous injections of paint following the technique of Thresher and Gronell (1978).

3) Behavioural observations

A. Agonistic encounters

During the home range estimates (part 2, above) and the feeding observations (Section 6.2) described earlier, a note was made of any agonistic encounters. A record was made of the species involved, their relative sizes and the nature of the encounter.

B. General behavioural patterns.

Throughout the study period from November, 1981 to December, 1983, the sizes and locations of any known individuals were recorded. General behavioural observations on juvenile scarids at the North Reef and lagoon study sites were made throughout this period, including some observations at dawn and dusk. Additional behavioural observations were made on juvenile scarids on several inshore (4), mid (10) and outer (5) barrier reefs in the Townsville, Cairns and Lizard Island regions.

4) Algae - substratum transplantation experiments.

Six algae-covered substratum types were selected and pieces were transplanted to a lagoonal experimental area. Pieces of substratum (coral rock) about 20 x 20 cm in area were removed from various areas around Lizard Island, placed in plastic bags and transplanted to the experimental area. All pieces were treated in the same manner. The experimental area in the lagoon was on sand, near low rubble, about 2 meters from the reef edge. This area was free from territorial pomacentrids and was regularly visited by juvenile scarids. The pieces of substratum were placed at random in a triangular arrangement, 20 cm apart, with only the algae covered surfaces exposed.

The algal-covered subsratum types used in this study and the sites from which they were obtained, are as follows:

1) Within the territories of *Stegastes nigricans* in the lagoon.
2) Within *Pomacentrus flavicauda* and *P. wardi* territories in the lagoon.
3) Within *Acanthurus lineatus* territories at North Reef. Care was taken to ensure that the substratum was removed from areas where juvenile *S. frenatus* regularly fed. Raised areas which were regularly fed on by large scarids and areas near cover which were included within the territories of pomacentrids were avoided.
4) Grazed areas at the top of the reef in the lagoon, from within the home ranges of juvenile scarids.
5) Coral rubble from the base of the reef slope at North Reef.

6) Coral rubble from the base of the reef edge in the lagoon.

The algae covered pieces of substrata were left in place for two minutes, then the number of juvenile scarids feeding on each substratum type was censused every minute for the next 30 minutes. The observer was at least 1.5 m away. One minute censuses were chosen, as in previous trials the mean duration of an individual on a single substratum type was found to be 26.3 seconds (± 9.90 sec, 95% C.I., n=20; based on all six substratum types). The probability of counting the same individual without it having moved away in the meantime was therefore extremely small. The experiment was replicated eight times between April 29 to May 4, 1982. The results were expressed as the total number of individuals recorded per 30 censuses per substratum type, and were analysed using a one-way ANOVA with a Duncan's multiple comparison test.

6.7 Results

Estimates of the abundance of juvenile and newly recruited scarids during the summer settlement periods (November - January) in 1981-82 and 1982-83 are summarized in Figure 6.4. In this figure, the abundances at three transect depths at North Reef and two transect depths in the lagoon are pooled. Changes in abundance at each depth from November 1981 to January 1982 are shown in Figure 6.5. Three main features are apparent in these figures:

1) In both the 1981/82 and 1982/83 observation periods, recruitment was restricted to November/early December at North Reef and in the lagoon.
2) Recruitment rates and juvenile abundances varied considerably between years.

Figure 6.4

The relative abundance of juvenile scarids (< 40 mm T.L.) at the North Reef and lagoon study sites during the 1982-3 and 1983-4 November-January recruitment periods.

Each North Reef data point is based on 16 pooled 2 x 2 m sample areas chosen at random from transects at 1-3 m, 6-8 m and 8+ m below chart datum. The solid lines show the total number of individuals recorded and the dashed lines show the number of these that were recently settled, *i.e.* unpigmented, individuals. The data are pooled as most samples were exceptionally small.

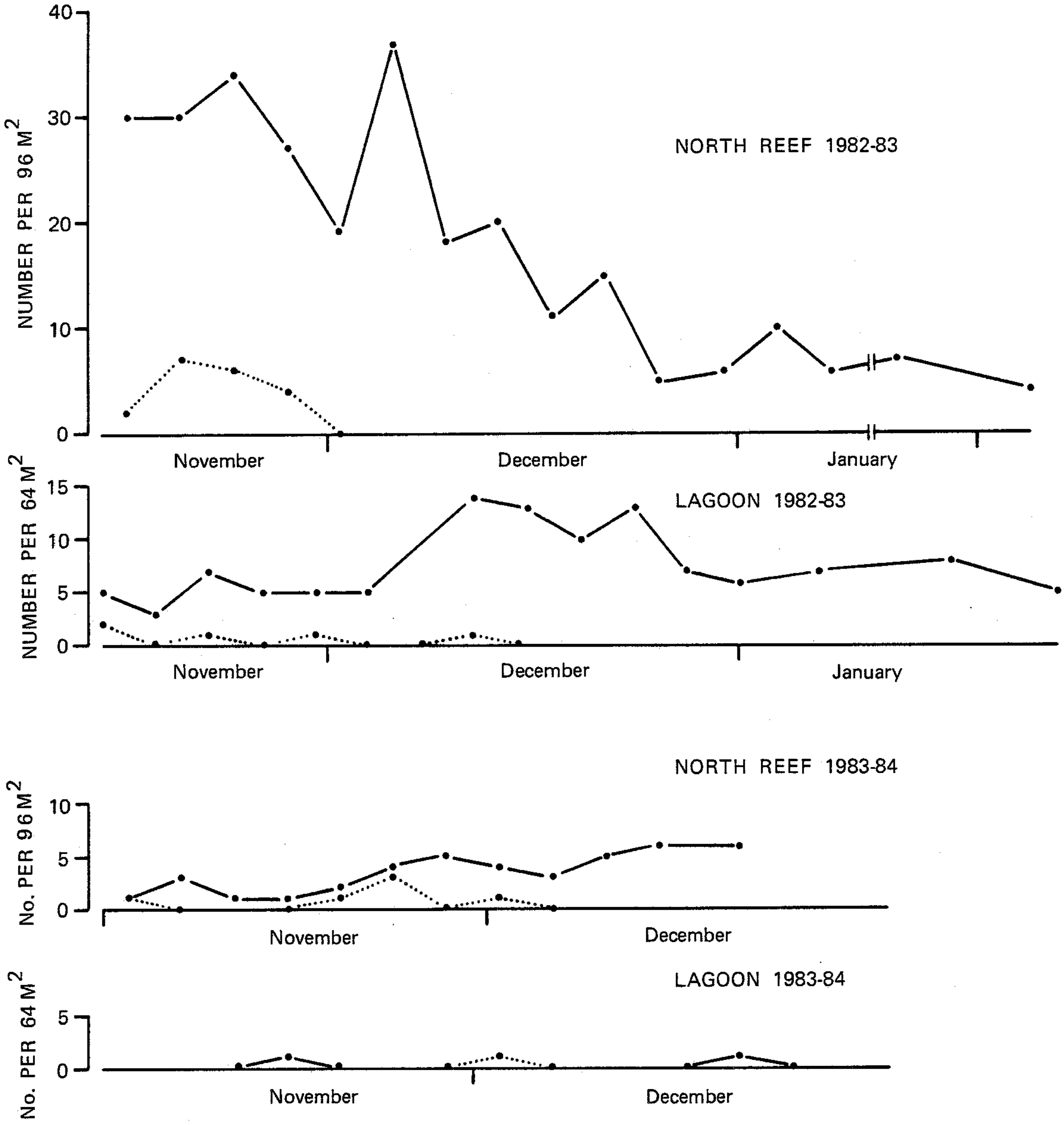
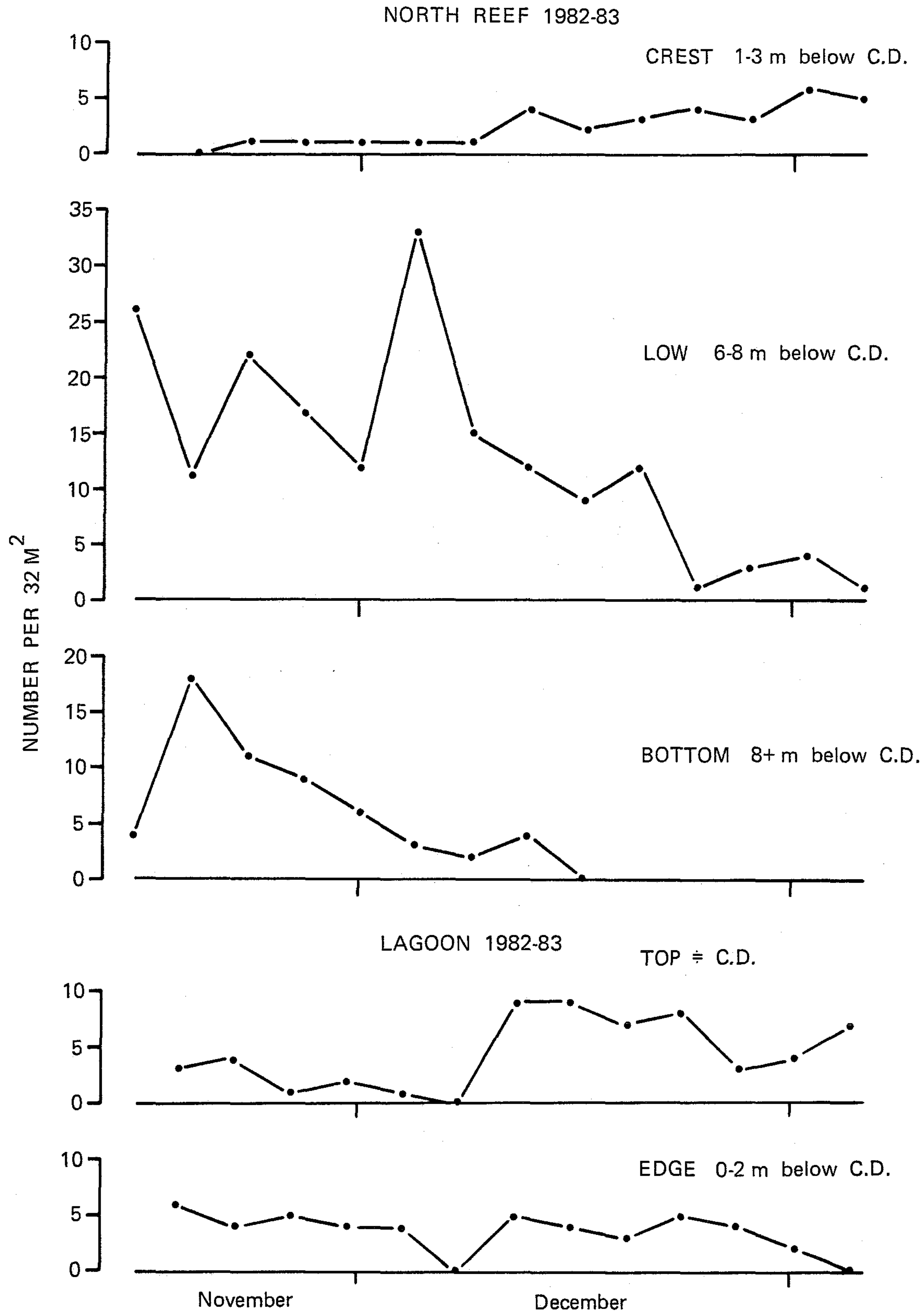

NORTH REEF 1982-83
NUMBER PER 96 M^2
40
30
20
10
0
November
December
January
LAGOON 1982-83
NUMBER PER 64 M^2
15
10
5
0
November
December
January
NORTH REEF 1983-84
No. PER 96 M^2
10
5
0
November
December
LAGOON 1983-84
No. PER 64 M^2
5
0
November
December

Figure 6.5

The relative abundance of juvenile scarids (< 40 mm T.L.) at three depths in the North Reef study site and at two depths in the lagoon study site, during the 1982-3 November-January recruitment period.

Each data point is the total number of scarids recorded in eight 2 x 2 m areas chosen at random along each depth transect. Because of consistantly low numbers the data are expressed as the total number of individuals per census.


NORTH REEF 1982-83
CREST 1-3 m below C.D.
LOW 6-8 m below C.D.
BOTTOM 8+ m below C.D.
LAGOON 1982-83
TOP ≑ C.D.
EDGE 0-2 m below C.D.
NUMBER PER 32 M²
0
5
10
15
20
25
30
35
November
December

3) The abundance of juvenile scarids at North Reef decreased rapidly during late November - December, especially in the deeper transects.

At Lizard Island, scarid recruitment appeared to be restricted to the months of November and December. Newly recruited specimens and relatively large numbers of small juveniles (< 20 mm T.L.) were only recorded during the November - December periods in 1981, 1982 and 1983. Small juveniles were observed at other times of the year, most often in the lagoon, but only occasionally and in small numbers.

Annual variation in scarid recruitment rates and juvenile abundances were recorded at the North Reef and lagoon study sites. Juvenile scarids were numerous at both sites in December 1981. The numbers were lower in November - December 1982, and in 1983, were very low (Fig. 6.4, Table 6.9). In addition, there was considerable annual variation in the species composition of juvenile and newly recruited scarids at the two study sites (Table 6.9).

Between site differences in the species composition of juvenile scarids were also apparent. Of the 16 species commonly recorded, nine occurred at both sites, four were recorded at North Reef only and three were found only in the lagoon (Table 6.10). The North Reef study site was characterized by four relatively common species: *S. sordidus*, *S. frenatus*, *S. niger* and *Scarus* sp. (*cf. lunula*). The lagoon study site was characterized by numerous individuals of two species, *S. psittacus* and *S. sordidus*, and to a lesser extent, *S. rivulatus* (Tables 6.9, 6.10). These differences were consistent between years.

Table 6.9 Relative rates of recruitment at the lagoon and North Reef study sites during three settlement seasons, expressed as a % of total juvenile scarids (<35 mm S.L.) recorded. ‡

Species	1981/82	1982/83	1983/84
North Reef:			
S. sordidus	10.6	23.1	18.2
S. spp †	27.1	34.4	6.8
S. niger	38.8	18.2	15.9
S. frenatus	22.4	4.2	20.5
S. sp. (*cf. lunula*)	–	12.9	2.3
S. rubroviolaceus	–	–	9.1
S. gibbus	–	6.1	–
S. sp. ††	–	0.4	2.3
S. psittacus/schlegeli	–	0.8	2.3
S. spinus	–	–	2.3
C. bicolor	1.2	–	–
C. carolinus	–	–	15.9
Number recorded ‡	85	264	44
Lagoon:			
S. sordids/spinus	+	31.9	–
S. spp *	+	2.6	–
S. spp **	+	62.1	33.0
S. frenatus	–	0.9	–
S. sp. (*cf. lunula*)	–	2.6	–
S. spinus	+	–	33.0
S. sordidus	+	–	33.0
Number recorded ‡	>40	116	3

‡ – 1981/82 data are based on collections of material, qualitative observations and eight 1x10 m transects at North Reef.
1982/83 data are based on 384 random 2x2 m areas in the North Reef study site and 262 random 2x2 m areas in the lagoon study site. Some specimens may therefore have been recorded on more than on occasion.
1982/83 data are based on 288 random 2x2 m areas at North Reef and 192 random 2x2 m areas in the lagoon study site.

† – Including: *S. sordidus*, *S.* sp. and *S.psittacus/schlegeli*.

†† – Unknown identity.

* – Including: *S. sordidus*, *S. rivulatus*, *S* sp., *S. psittacus* and *S. ghobban*.

** – Primarily *S. psittacus*, but may include *S. rivulatus*, *S. globiceps* and *S.* sp. (*cf. lunula*).

\+ – Present but not quantified.

Table 6.10 A list of the scarid species present as new recruits and juveniles in the vicinity of the lagoon and North Reef study sites.

	Lagoon	North Reef
Calotomus carolonus	—	*+ - rare
Cetoscarus bicolor	—	*+ - rare
S. bleekeri	+ - one specimen	+ - uncommon
S. gibbus	+ - one specimen	*+ - uncommon
S. sordidus	*+ - numerous	*+ - common
S. brevifilis	*+ - uncommon	*+ - uncommon
S. dimidiatus	+ - uncommon	—
S. flavipectoralis	—	+ - uncommon
S. frenatus	*+ - rare	*+ - common
S. ghobban	+ - uncommon	—
S. glogiceps	?	?
S. niger	+ - one specimen	*+ - common
S. oviceps	—	+ - uncommon
S. psittacus	*+ - numerous	+ - uncommon
S. rivulatus	+ - common	—
S. rubroviolaceus	—	*+ - uncommon
S. schlegeli	—	+ - common
S. spinus	*+ - common	*+ - uncommon
S. sp.	*+ - common	*+ - common

* = Newly recruited

+ = Juvenile

During November to December 1982, there was a decrease of approximately 80% in 34 days in the overall abundance of juvenile scarids, as recorded from three transect depths (Fig. 6.4). This decrease was most likely to be the result of mortality and/or migration. The increased abundance of juveniles in the 1-3 m transect in late December (Fig. 6.5) suggested that some migration had occurred as no recruitment was recorded during this period (Fig. 6.4). Migration of juvenile scarids up the reef slope was observed (see below), but no small scarids (< 30 mm T.L.) were observed to move from the lower transect areas to shallower areas, above 1 m, or into deeper water.

If one allows for migration from the two deeper transect areas up the reef slope, by assuming that: a) the initial abundance in the 3-6 m region is the same as that in the 1-3 m transect region (=an underestimate), b) that the abundance in this region after 34 days is mid-way between the abundances at the 1-3 and 6-8 m transects, and c) that the 1 m gap between the two deep transects (Fig. 6.4) is mid-way between these two, then the resultant estimated mortality rate of juvenile scarids in the early post-recruitment period in the North Reef study site is 77% within 34 days. Most predatory attempts upon juvenile scarids were by synodontids, but attacks from *Cheilinus digramma*, *Hemigymnus fasciatus* and *Thalassoma lunare* were also observed.

B) Home ranges

In this study, most juvenile scarids were found to be home ranging throughout the juvenile phase. The sizes of the home ranges of four species in the North Reef and lagoon study sites are shown

Figure 6.6

The relationship between home range/territory area and total length of juvenile scarids.

The stippled area encloses the points of 9 recently recruited individuals from North Reef and 17 recently recruited individuals from the lagoon. The curve fitted is based on the data points for *S. frenatus* at North Reef. The regression equation of the line is $\log y = 2.688 \log x - 3.1763$ ($n = 21$, $r^2 = 0.8576$).

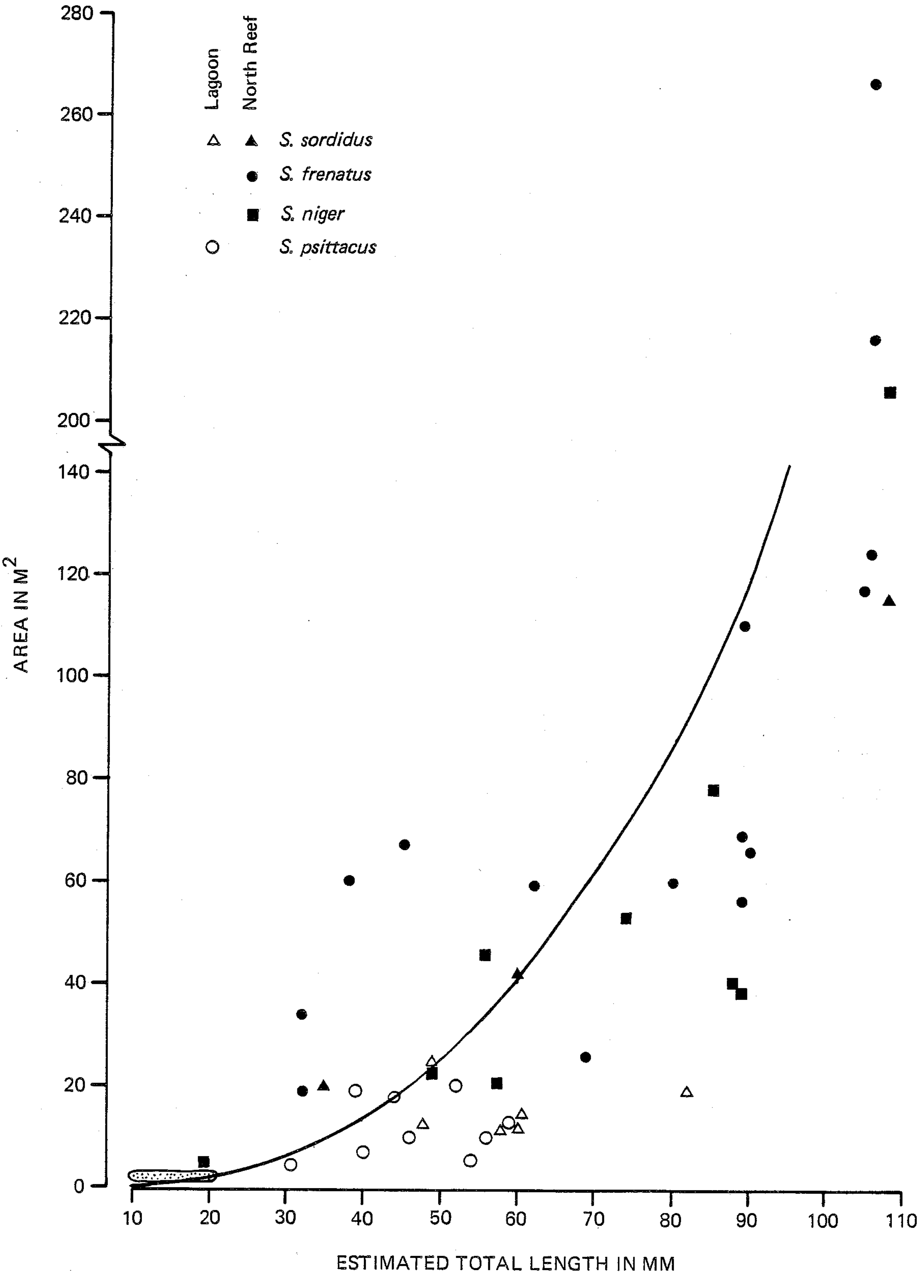

Lagoon
North Reef
△ ▲ S. sordidus
● S. frenatus
■ S. niger
○ S. psittacus
AREA IN M^2
280
260
240
220
200
140
120
100
80
60
40
20
0
10
20
30
40
50
60
70
80
90
100
110
ESTIMATED TOTAL LENGTH IN MM

Figure 6.7

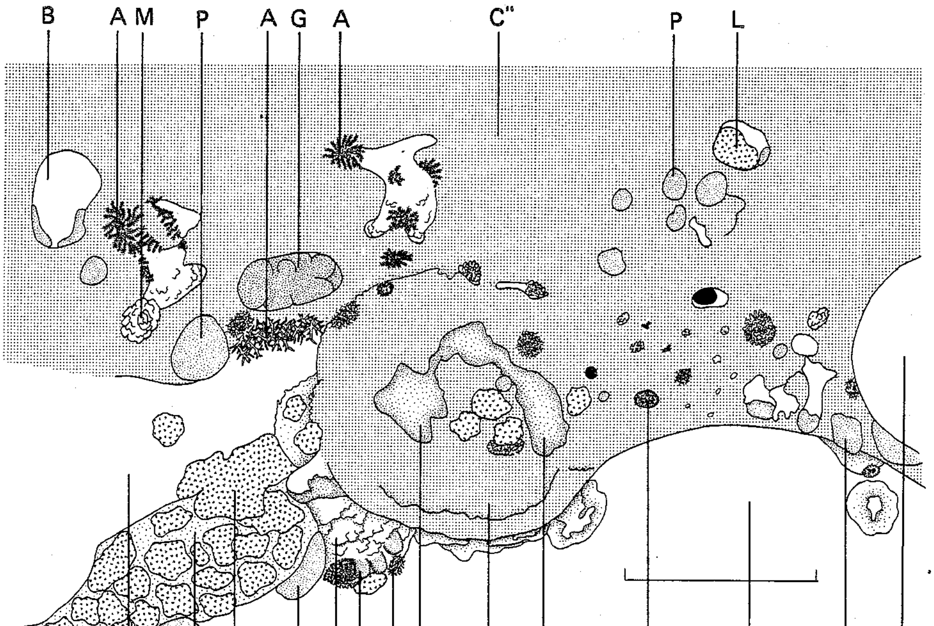
The home ranges of two juvenile *S. sordidus* in the lagoon study site.

A key to the map is given below. The upper area of the reef is at approximately chart datum. The lower sandy area is approximately 1 m below chart datum.

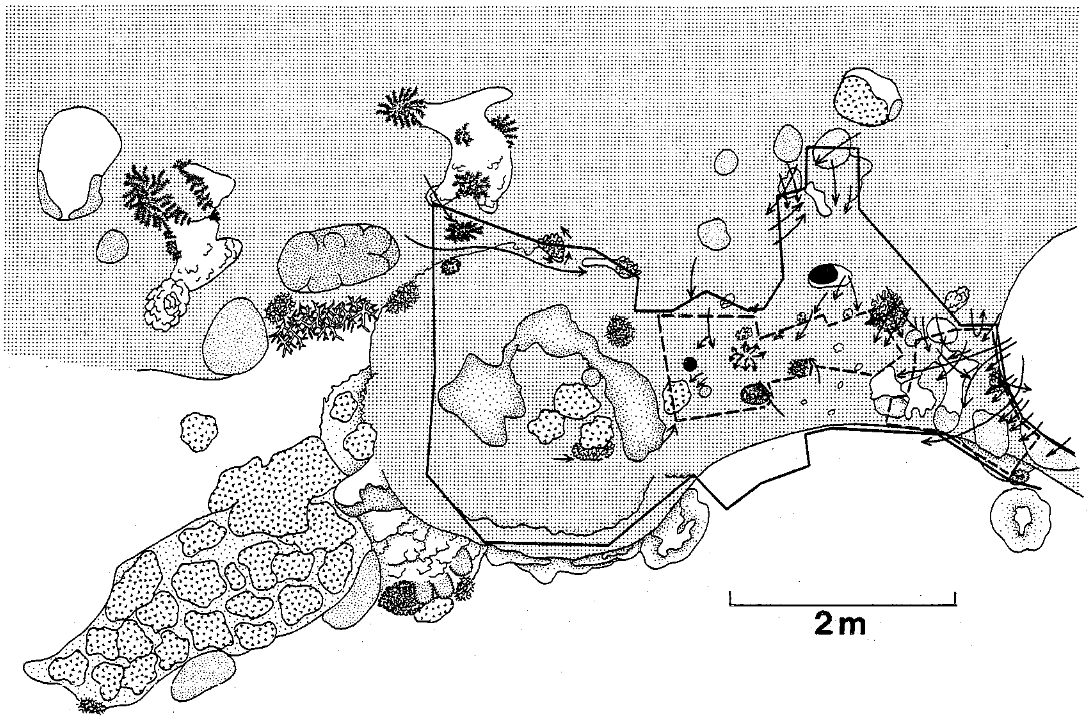
In each figure the outer solid line delineates the total home range (where the area increased by less than 2% in a 30-minute observation period). The broken lines enclose an area of high utilization. The arrows indicate the length of the chase and the direction of all attacks by pomacentrids during the total observation period.

Figure 6.7 A: A 60 mm T.L. *S. sordidus* (April - May, 1982). The total area was 14.3 m^2 and the area of high utilization 3 m^2 (= 21% of the total area). Of the total observation period (= 221 min.) 44.8% of the time was spent in the area of high utilization.

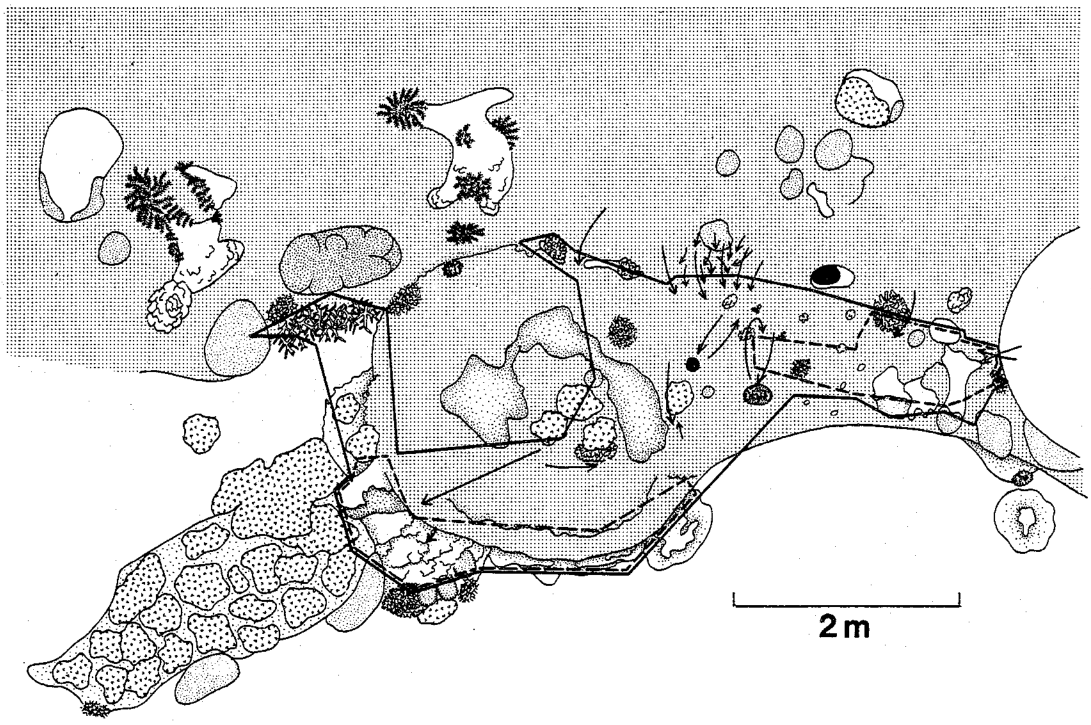
Figure 6.7 B: A 74 mm T.L. *S. sordidus* (April - May, 1982). The total area was 11.4 m^2 with a high utilization area of 3.4 m^2 (= 29.8% of the total). Of the total observation time (=158 min.) 65.8% was spent in the high utilization area.



A - *Acropora* spp.
B - Boulders; dead *Porites*
C - Coral rock
C'- Coral rock matrix 1 m above C.D.
C"- Coral rock & rubble
G - *Goniastrea* sp.
H - A hole in the reef
L - *Lobophyllia* sp. (soft coral)
M - *Montipora* sp.
P - *Porites* sp.
S - Sand
S'- *Seriatopora* sp.
T - An area occupied by territorial *Stegastes nigricans*



2 m



2 m

in Figure 6.6. Two main trends are apparent from this figure:

a) Progressively larger fish had larger home ranges.

b) Below 90 mm T.L., the home ranges of species or individuals at North Reef tended to be larger than those of species or individuals in the lagoon.

The log-log regression of *S. frenatus* home ranges/territories at North Reef versus total length is: $\log y = 2.688 \log x - 3.1763$. This is significantly greater than the standard of 2 (= a power curve, $t = 2.7376$, 19 df., $p < 0.02$; using a modified t-test, Zar, 1974). The increase in area of the home range/territory of *S. frenatus* is therefore positively allometric over this size range and from the data in Figure 6.6, appears to be similar for other species at North Reef.

The home ranges of individuals above 90 - 120 mm T.L. in the lagoon were hard to estimate as they joined highly mobile foraging schools. A few individuals were followed for short periods of time (@ 15-20 min) and in all cases, their minimum home ranges were in excess of 400 m^2 and were probably much larger.

In the lagoon, the home ranges of specimens below 90 mm T.L. appeared to be restricted primarily by the available space, as delineated by the boundaries of territorial pomacentrids and open sand. Two typical lagoonal home ranges are shown in Figures 6.7 A and 6.7 B. These figures show the close correlation between the home range boundaries and the reef-sand interface, and the direction of pomacentrid attacks which almost invariably forced the scarid back into its home range area. At North Reef , home range boundaries were occasionally limited by conspecifics, territorial juvenile *S. frenatus* or *A. lineatus* but aggression was at a much lower rate than in the lagoon (Table 6.14). At North Reef, for many individuals, there was apparently no physical or biological boundaries which delineated the home ranges. The home ranges were therefore most likely to be limited by the individual's requirements.

For most individuals, the utilization of the home range was not uniform, and discrete regularly used areas were apparent within the home ranges of individuals (as shown in Figs 6.7 A, B). This was most notable in larger individuals, above 30 mm T.L. At North Reef, *S. frenatus* (> 30 mm T.L.) were most frequently observed in open areas, within *A. lineatus* territories, characterized by a rich algal growth but close to cover. *S. niger* (> 30 mm T.L.) were most frequently recorded over flat algal covered surfaces near to cover or in small algal covered recesses in the reef slope. In the lagoon, *S. sordidus* and *S. psittacus* (> 30 mm T.L.) were most frequently recorded in open algal covered areas which were free from territorial pomacentrids and were often near to some cover. In contrast, the the home ranges of the few *S. frenatus* (> 30 m T.L.) observed in the lagoon were most frequently recorded within pomacentrid territories. Some *S. sordidus* and *S. psittacus* were regularly recorded under cover in areas near to *Stegastes nigricans* territories. These individuals regularly fed on the edge of the pomacentrids' territories before rapidly diving for cover when observed and chased by the pomacentrid.

Table 6.11 The duration and nature of site attachment in juvenile scarids.

Species	n †	approx. T.L. (mm)	Longevity (days)‡	Type *
C. carolinus	3	14–45	34–56	I?
C. bicolor	3	14–50	5–14	II? A
H. longiceps	1	60	3	I? A
S. bleekeri	5	24–79	2–121	I
S. gibbus	8	16–110	58–118	I A
S. sordidus	10	14–114	20–116	I to II (A+M?)
S. brevifilis	5	18–54	22–244	I (M)
S. dimidiatus	3	28–72	42–305	I (M)
S. flavipectoralis	2	34–44	4–16	I/II?
S. frenatus	17	12–124	44–735	I A
S. ghobban	1	36	9	I to II?
S. niger	12	16–125	33–182	I
S. oviceps	2	68–79	35–120	I to M?
S. psittacus	8	32–53	30–62	I to II
S. rivulatus	4	34–65	18–70	I to II
S. rubroviolaceus	5	18–40	21–41	I to. II? A
S. spinus	2	16–55	15–30	I to M A
S. sp. (*cf. lunula*)	1	39	44	I to II?

† – Based on observations of individuals during home range analyses and tagged, scarred or individually recogniseable individuals throughout the study.

‡ – The length of time between the first and last sighting.

* – The nature of site attachment varies considerably between species:

I = those species/individuals with a restricted home range ($<300\text{m}^2$)

II= those species/individuals with an extensive home range ($>500\text{m}^2$)

A = those species where the adult and juvenile feeding areas differed markedly.

M – those species where individuals probably migrated during or at the end of the juvenile phase. If a species is marked with an A but no M this indicates that the adult feeding areas are adjacent to the juvenile feeding areas.

The duration of home-ranging behaviour may vary between species. Some species appear to be home-ranging or territorial throughout the juvenile and adult phases (*e.g. S. frenatus* and *S. niger*, Table 6.11 and Section 5.7), whilst other species (*e.g. S. psittacus*, *S. rivulatus* and *S. sordidus*) form large mobile schools and appear to be semi-nomadic. The duration and type of home-ranging behaviour in juveniles of several species are listed in Table 6.11. The estimates of durations are observed ranges and are limited by the length of the observation periods, actual durations are likely to be considerably longer.

C) Movement

Known individuals from 10 - 110 mm T.L. were followed in the North Reef and lagoon study sites for periods of one to 24 months. At the North Reef study site, with the exception of *Calotomus carolinus* (n=4) and *Cetoscarus bicolor* (n=3), all observed juvenile scarids migrated slowly up the reef slope. This included *S. niger* (n=23), *S. frenatus* (n=12), *S. gibbus* (n=8), *S. sordidus* (n=7), *S. brevifilis* (n=3), *S. rubroviolaceus* (n=3) and *Scarus* sp. (n=8). The speed and extent of this movement varied considerably. *S. frenatus* quickly migrated up the reef slope and had established home ranges in the crest region at a size of 32 mm T.L. (Fig. 6.8). The remaining species enlarged their home ranges until they occupied a greater part of the reef slope. *S. brevifilis* and *S. rubroviolaceus* and to a lesser extent, *Scarus* sp. and *S. sordidus*, tended to occupy shallower regions whilst *S. niger* and *S. gibbus* usually remained in the deeper areas (Fig. 6.8). *S. niger* remained in this region throughout the juvenile and early

Figure 6.8

A vertical profile of the primary study area at the North Reef study site, showing the distribution of home ranges/ territories of juvenile scarids in the study area.

Figure 6.8 A

1 = The site of recruitment of 69% of the *S. frenatus* (9/13) and 89% of the *S. niger* (17/19) observed during the 1981-1984 study period.

2 = *S. niger*; 56 mm T.L.; May 1982

3 = *S. niger*; 57 mm T.L.; May 1982

4 = *S. frenatus*; 32 mm T.L.; February 1982

5 = *S. frenatus*; 62 mm T.L.; May 1982

6 = *S. frenatus*; 89 mm T.L.; September 1982

4, 5 and 6 are of the same individual.

Figure 6.8 B

1 = As in 6.8 A No. 1

2 = *S. niger*; 88 mm T.L.; September 1982

3 = *S. niger*; 49 mm T.L.; February 1982

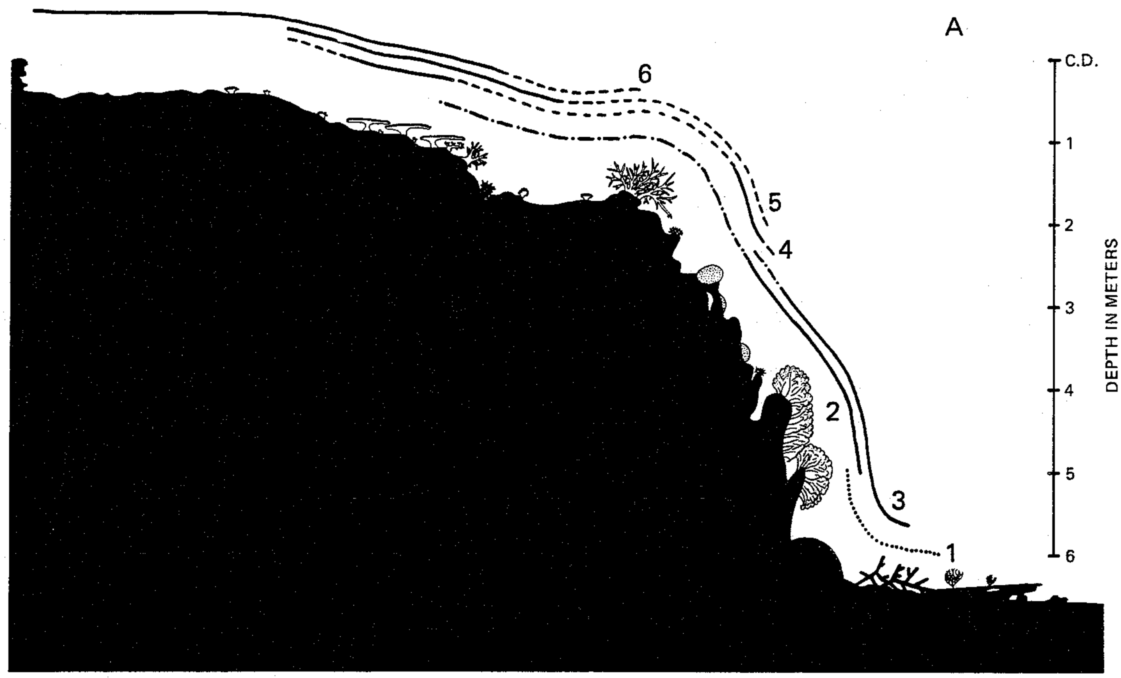
4 = *S. frenatus*; 45 mm T.L.; February 1982

5 = *S. frenatus*; 106 mm T.L.; September 1982

6 = *S. frenatus*; 90 mm T.L.; May 1982

4, 5 and 6 are of the same individual.

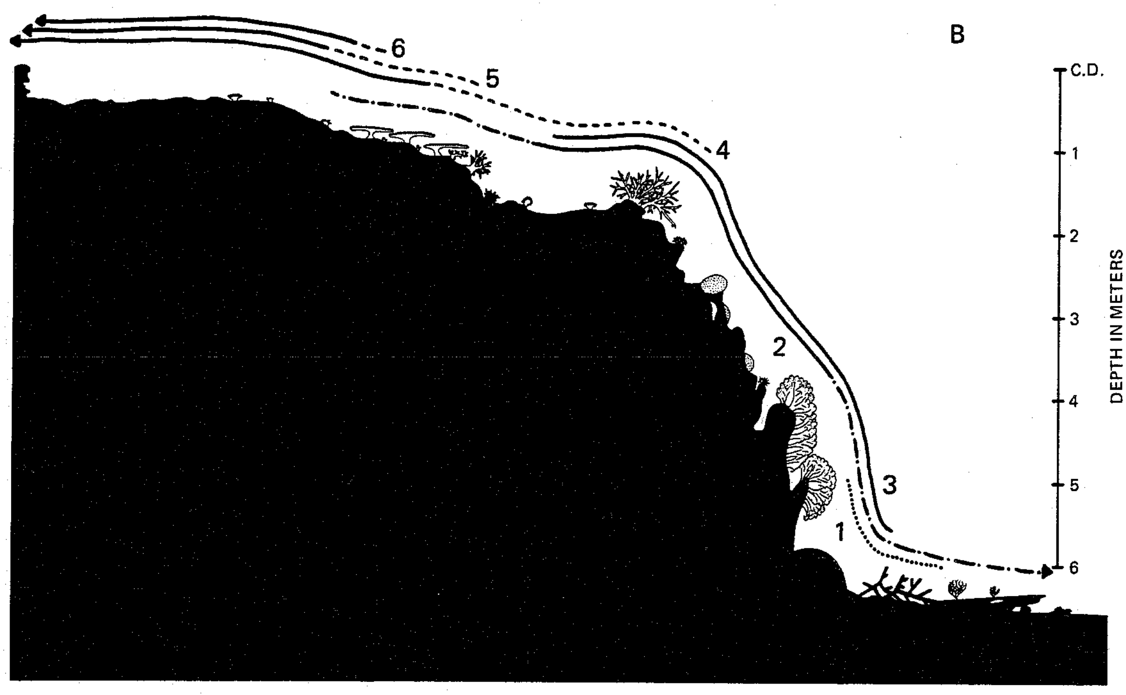
A solid line encompasses the area in which the individual spent at least 50% of the time during observations. The total extent of the home range is covered by the dashed and solid lines.



S. frenatus

S. niger

Juveniles below 15 mm T.L.



adult phases. *S. frenatus* remained in the reef crest region throughout the juvenile and early adult phases. *S. gibbus* and *S. rubroviolaceus* occupied the reef slope regions as juveniles and small adults before moving onto the reef top as large adults. *S. sordidus, S. brevifilis* and *Scarus* sp. remained in the reef slope region as juveniles but may move away as adults. (The movements of juvenile scarids are described in more detail in Appendix 2).

The observations described above were concentrated in one part of the North Reef study site with a gently sloping reef slope (@ 60°). Limited observations in nearby areas with precipitous reef slopes (@ 85°) or with slopes devoid of coral cover, however, did not show any evidence of similar patterns of vertical movement. In these areas, the reef slope region was devoid of juvenile scarids although numerous individuals were found at the base of the reef slope.

In the lagoon site, movement of small juveniles was limited. A few individuals moved from their initial recruitment sites to their early juvenile home ranges in response to attacks from pomacentrids. In all cases, the distance moved was less than two meters. Although these observations were concentrated on *S. psittacus* (n=14), *S. sordidus* (n=12) and *S. rivulatus* (n=5) this observed behaviour appeared to be consistent for other species, including *S. brevifilis* (n=3), *S. oviceps* (n=2) and *S. spinus* (n=3).

There was, however, a marked change in the behaviour of the individuals with increasing size. There is evidence to suggest that once juvenile *S. psittacus*, *S. sordidus* and *S. rivulatus* reach a minimum size of approximately 80 mm S.L., they abandon their small home ranges and join large, highly mobile schools. Firstly, relatively large *S. psittacus*, *S. sordidus* and *S. rivulatus* (above 70 to 90 mm S.L.) were no longer observed in their previously occupied home ranges. Secondly, the largest recorded home ranging individuals were 84 mm T.L. in *S. psittacus* and 102 mm T.L. in *S. sordidus* and finally, large mobile schools of juvenile scarids were present in the immediate vicinity, but only included individuals above 74 mm T.L.

Although juvenile *S. sordidus* were recorded recruiting to the lagoon during all three summer periods examined, and were present in the previous two years (H. Sweatman and G. Anderson, pers. comm.), the largest *S. sordidus* recorded in the lagoon study site (and in nearby areas) was 113 mm T.L. Other species which were present in the lagoon study site as juveniles but absent as adults include *S. spinus*, *S. dimidiatus*, *S. oviceps* and *S. gibbus*. This disparity suggests that these species migrate from the area during the late juvenile phase.

The observed movement of small juvenile scarids is reflected in the range of substrata over which various size specimens were found (Table 6.12). From these observations, three main trends are apparent:

a) At the North Reef and lagoon study sites, smaller individuals were frequently associated with complex substrata, whilst larger individuals were found more often in open areas.
b) Some individuals were found in or near pomacentrid territories at both study sites, but only those below 22 mm T.L.

Table 6.12 The size of early post-recruit scarids over various substratum types in the North Reef and lagoon study sites.

Location	n †	Mean T.L. in mm	s	Range in mm
North Reef:				
Open coral rubble	81	19.7	6.8	11-46
Open coral rock	47	29.2	5.8	16-34
Dead arborescent coral	18	22.1	5.4	16-34
Coral rubble on sand	20	16.5	3.9	11-25
In *Liagora* sp. algae	21	14.4	2.9	10-20
Algae over dead coral	11	13.6	2.0	11-17
Amongst coral rubble	9	12.0	0.7	11-13
In *P. lacrymatus* territories	6	13.4	2.9	11-17
Laying on *Liagora*	8	10.4	0.6	10-11.5
Laying on turf algae	4	10.8	0.7	10-11.5
Lagoon:				
Live coral	34	21.5	5.9	12-33
Open coral rubble	32	23.8	5.8	15-38
Algae over dead coral	19	20.5	5.7	10-33
Halimeda	13	23.1	3.5	17-27
Open coral rock	9	23.4	5.5	17-33
Coral rubble on sand	9	26.6	7.4	15-39
Soft corals	1	28.0	0.0	28
In *E. nigricans* territories	7	16.3	3.5	10-22
Bordering *E. nigricans* terr's	7	17.9	1.1	17-19
In *S. apicalis* territories	4	14.4	1.1	13-16
Bordering *S. apicalis* terr's	4	17.8	1.3	16-19

† - These observations are the pooled observations of juvenile scarids recorded during random samples in the lagoon and North Reef study sites from Nov. 1982 to Feb. 1983. Some individuals may therefore, have been recorded on more than one occasion.

c) A close association with algae or algal covered substrata was only noted in individuals below 11.5 mm T.L. (at the North Reef study site).

D) Aggression

Aggression to and from three juvenile scarid species at the North Reef and lagoon study sites are summarized in Tables 6.13 and 6.14, and Figures 6.9 A and 6.9 B. Because of a large degree of variation in the observation periods, from four to 30 minutes, these data are based on pooled, total observation periods. The interpretation of these data are therefore tentative, although major trends are still apparent. The relative frequency, nature and species of pomacentrids attacking juvenile scarids at the two study sites are given in Table 6.15. It is apparent from these data that:

a) Pomacentrids were the predominant aggressors towards juvenile scarids.

b) Pomacentrids were more frequently aggressive towards *S. sordidus* and *S. frenatus* in the lagoon than at North Reef.

c) A larger proportion (82%) of the pomacentrid attacks in the lagoon are of a high intensity when compared with the proportion (30%) at North Reef.

d) In the lagoon, *S. frenatus* was attacked less frequently than *S. sordidus* by pomacentrids.

e) Pomacentrids did not attack very small scarids.

f) At North Reef, *Acanthurus lineatus* only consistently attacked *S. frenatus* above 70 mm T.L.

Table 6.13 Aggressive interactions of three *Scarus* species.

	S. sordidus			*S. psittacus*			*S. frenatus*				
	Lagoon			Lagoon			North Reef				
T.L. (mm)	nI	O	P	nI	O	P	nI	O	P	A	S
0–10	2	40	0.0	–	–	–	6	64	0.0	0.0	0.0
10–20	6	140	9.0	2	20	0.0	2	213	0.28	0.0	0.0
20–30	6	100	12.0	–	–	–	2	70	2.25	0.0	10.5
30–40	–	–	–	10	658	22.8	4	307	0.78	0.20	0.0
40–50	3	297	6.9	5	437	12.6	3	288	0.21	0.0	0.63
50–60	4	367	19.6	5	823	11.1	–	–	–	–	–
60–70	1	221	19.5	–	–	–	1	145	1.24	0.0	3.31
70–80	3	60	42.0	3	48	25.0	2	154	1.17	2.34	0.0
80–90	2	115	6.3	–	–	–	3	628	0.86	0.29	1.43
90–100	–	–	–	–	–	–	2	204	1.18	3.82	0.29
100–110	2	26	46.2	2	6	60	5	705	1.11	3.15	0.09

nI = Number of individuals.
O = Total observation times in minutes.
P = Number of attacks from pomacentrids per hour.
A = Number of attacks from *Acanthurus lineatus* per hour.
S = Number of attacks upon other scarids per hour.

In all cases, *S. sordidus* were in schools of 2 to 10 individuals, *S. psittacus* in schools of 4 to 26, and *S. frenatus*, solitary, but observations were based on individuals.

Table 6.14 Aggressive interactions of juvenile scarids.

	S. psittacus		*S. frenatus*		*S. sordidus*	
Location	N.Reef	Lagoon	N.Reef	Lagoon	N.Reef	Lagoon
Observation time in min. (total, mean)	757,12.6	1359,22.6	2880,48	356,5.9	2054,34.2	2011,33.5
Number of observations	14	29	45	13	28	29
Number of individuals	5	14	17	5	8	9
S.L.: range	10–116	9.5–105	14.5–114	18.5–106	11.3–108	19–104
S.L.: mean ± s	55.1±42.4	43.8±28.6	61.6±34.3	53.9±38.6	48.7±32.4	50.3±21.0
Aggressive interactions per hour:						
Intraspecific	3.25	3.40	2.98	0.16	1.75	4.71
from scarids	0.08	0.09	0.0	0.0	0.32	0.42
to scarids	0.08	0.09	–	–	0.32	0.42
From pomacentrids *	1.27	14.97	0.96	2.87	2.16	15.8
To pomacentrids	–	–	0.21	–	–	–
From:						
Acanthurus lineatus	–	–	1.42	–	–	–
Ctenochaetus striatus	0.40	0.49	0.08	–	0.20	0.01
Acanthurus nigrofuscus	–	–	0.02	–	–	–
Zebrasoma veliferum	–	0.04	–	–	–	–
Zebrasoma scopas	–	0.04	–	–	–	–
Goby	0.08	0.04	–	–	0.02	–
Blenny	–	0.09	–	–	–	0.01
Labrids	–	0.09	0.08	0.68	0.58	+
Centropyge spp	0.24	–	–	–	–	–
Pseudochromis spp	–	0.22	–	–	–	0.21
Siganus sp.	–	–	–	0.17	–	–
Scolopsis bilineatus	–	–	–	–	–	0.01
To:						
Labrids	–	–	0.21	–	–	–

* – Pomacentrid attack rates:

S. frenatus – lagoon rate > N. Reef rate; $\chi^2 = 9.55$, $p<0.005$

S. sordidus – lagoon rate > N. Reef rate; $\chi^2 = 115.6$, $p<0.001$

Figure 6.9 A

The relative rates of aggression by pomacentrids towards juvenile scarids at the lagoon study site.

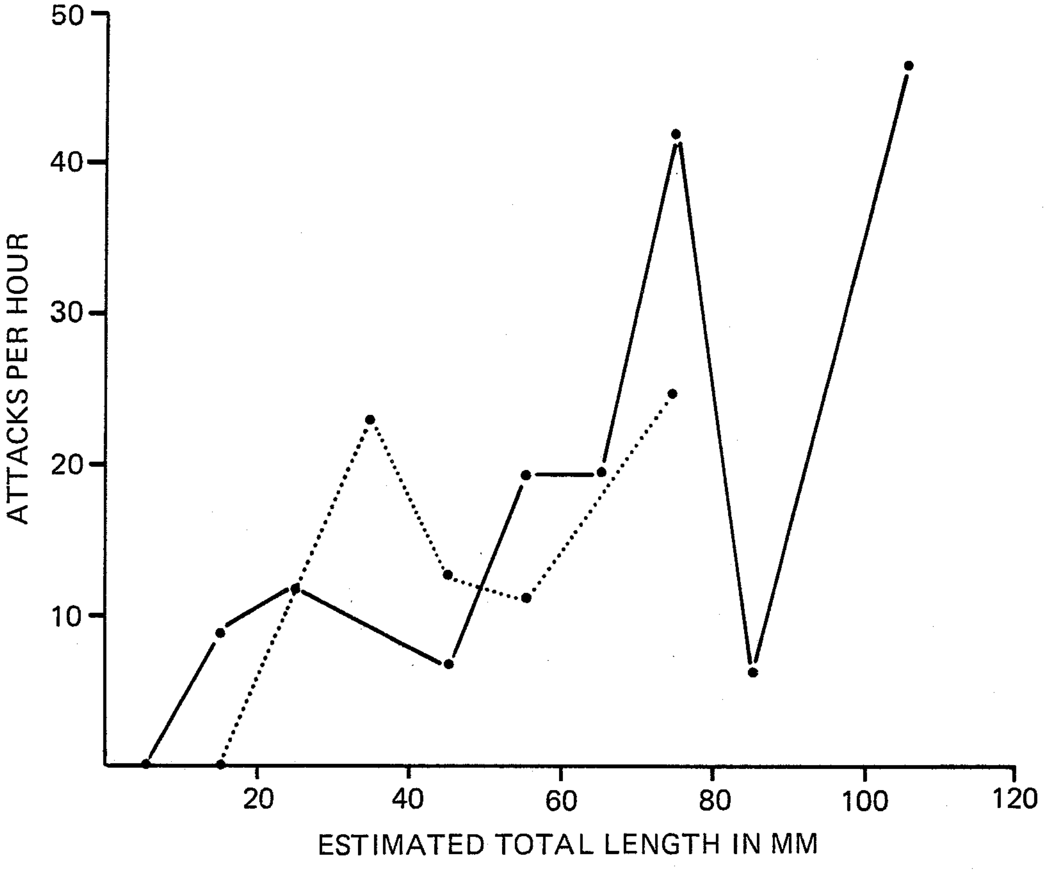
(Solid line = *S. sordidus*; dotted line = *S. psittacus*).

Figure 6.9 B

The relative rates of aggression by pomacentrids and *Acanthurus lineatus* towards juvenile *S. frenatus* at the North Reef study site.

(Solid line = by pomacentrids; dotted line by *A. lineatus*).

These graphs are based on the data summarized in Table 6.13.


ATTACKS PER HOUR
50
40
30
20
10
20
40
60
80
100
120
ESTIMATED TOTAL LENGTH IN MM

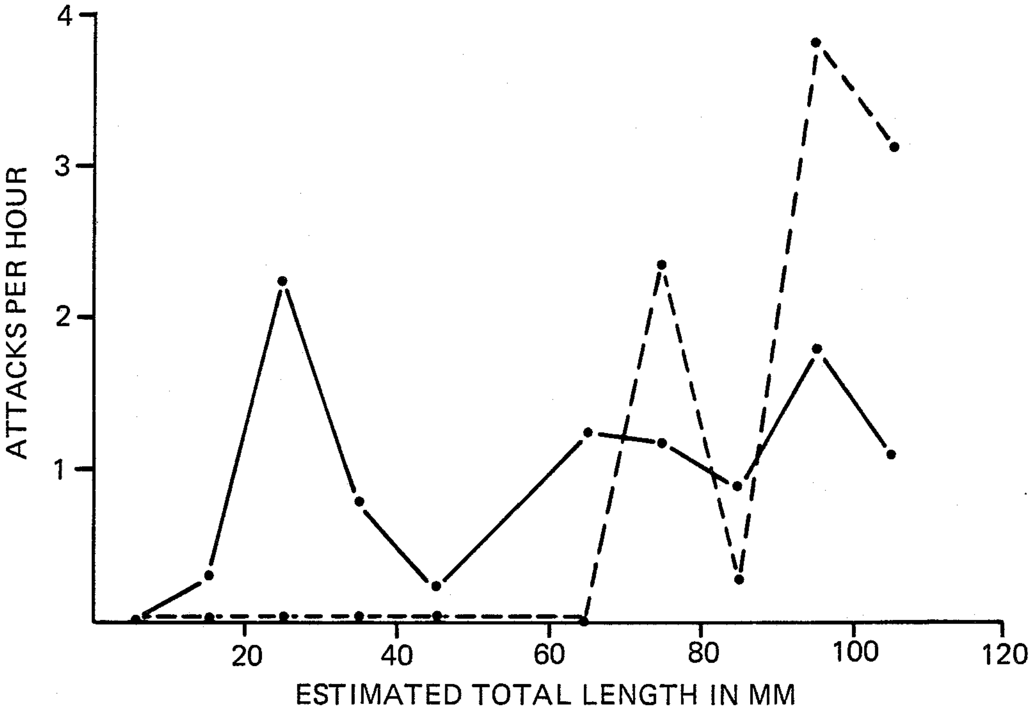

ATTACKS PER HOUR
4
3
2
1
20
40
60
80
100
120
ESTIMATED TOTAL LENGTH IN MM

Table 6.15 The relative frequency of attacks upon juvenile scarids by various damselfish species at the North Reef and lagoon study sites.

Species †	Number of attacks ‡	% of total attacks	Relative intensity
North Reef:			
Chrysiptera rex	30	42	Low
Pomacentrus amboinensis	18	25	Low
Plectroglyphidodon lacrymatus	8	11	High
Pomacentrus wardi	5	7	High
Pomacentrus bankanensis	3	4	High
Plectroglyphidodon dickii	3	4	High
Pomacentrus grammorhynchus	2	3	High
Abudefduf behni	2	3	Low
Stegastes apicalis	1	1	High
Lagoon:			
Pomacentrus flavicauda	65	30	High
Pomacentrus grammorhynchus	48	22	High
Pomacentrus wardi	33	15	High
Stegastes nigricans	28	13	High
Pomacentrus popei	24	11	Low
Pomacentrus amboinensis	12	6	Low
Plectroglyphidodon lacrymatus	4	2	High
Chrysiptera cyaneus	3	1	Low

† - Identifications follow Allen (1975) and Russell (1983).
‡ - Recorded during home range estimates. Relative attack rates per hour are given in Tables 6.13 and 6.14.

From observations of the location of aggressive interactions during home range estimates, it appears that pomacentrid aggression does restrict movement along some boundaries and may result in feeding within pomacentrid-free areas (Figs 6.7 A, B). Home ranges were not, however, strictly delineated by pomacentrid aggression, although it would be interesting to compare home ranges of juvenile scarids with those of adjacent pomacentrids. The mean % of total pomacentrid attacks in the home range border region is only 36.7% (± 15.2; 95% C.I.) at North Reef and 44.4% (± 15.8) in the lagoon (North Reef n=20: [10] *S. frenatus*, [8] *S. niger*, [2] *S. sordidus*; lagoon n=14: [8] *S. sordidus*, [6] *S. psittacus*).

E) Algal transplantation experiment

The mean numbers (± 95% C.I.) of juvenile scarids per 30 censuses, feeding on each algal substratum type are shown in Figure 6.10. Scarid abundances for each of the six substratum types, from:

A *S. nigricans* territories

B *P. flavicauda/P. wardi* territories

C *A. lineatus* territories

D Grazed lagoonal rubble from juvenile *S. sordidus* and *S. psittacus* home ranges

E Algal covered rubble from the base of the reef slope at North Reef

F Algal covered rubble from the base of the lagoon reef edge,

were as follows: A > B > C > D, E and F (ANOVA, F = 29.037, df = 5,42, p< 0.05). The results of this study, therefore, show that given a choice of the six substratum types, (ANOVA, F = 29.037,

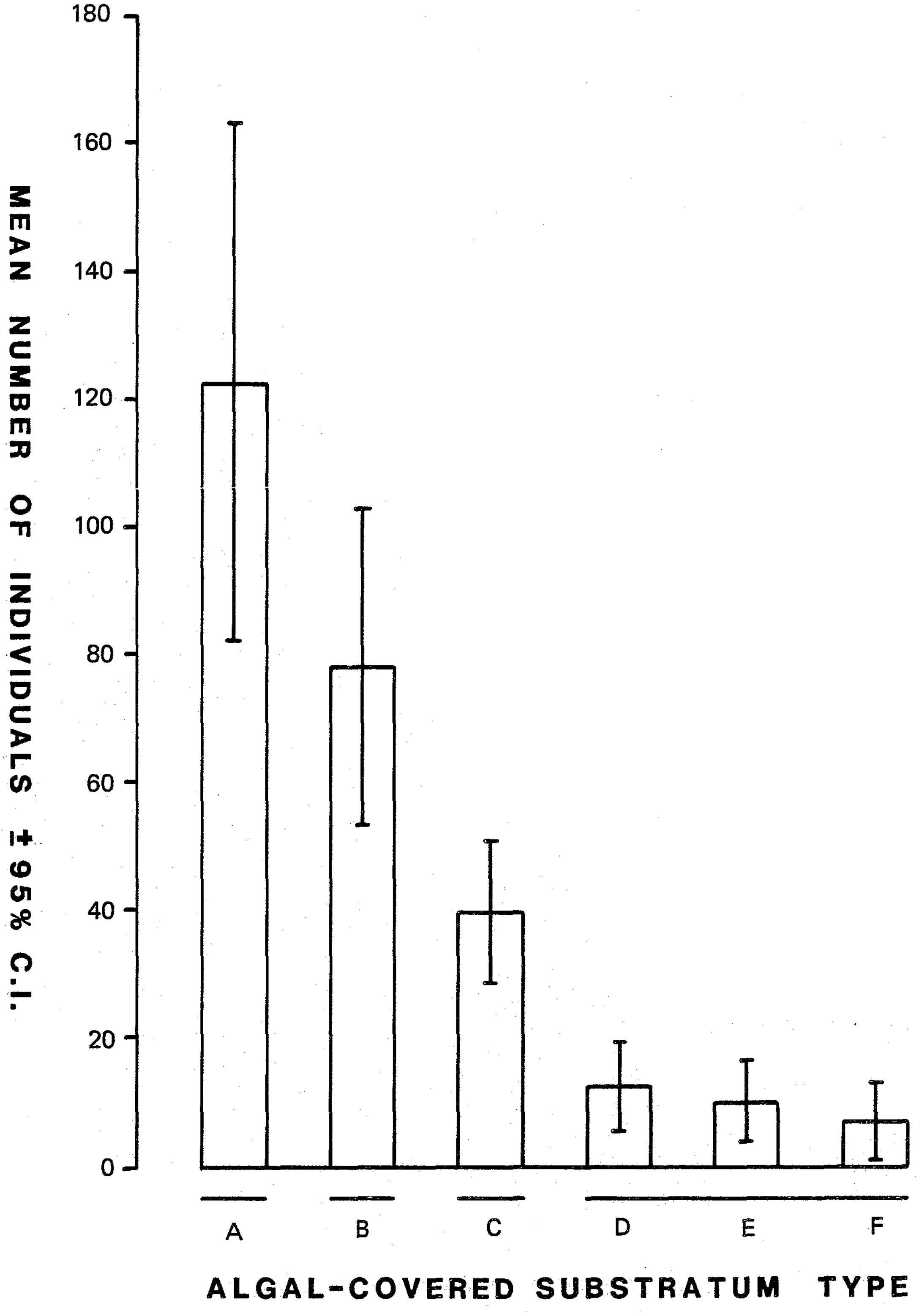
Figure 6.10

The feeding preferences of juvenile scarids: The mean number of juvenile scarids feeding on six experimental algal-covered substratum types.

The sites from which the algal-covered substratum types were removed were:

A - From *Stegastes nigricans* territories in the lagoon.
B - From *Pomacentrus flavicauda* and or *P. wardi* territories in the lagoon.
C - From *Acanthurus lineatus* territories at North Reef.
D - Grazed coral fragments from within scarid home ranges, near the reef edge in the lagoon.
E - Coral rubble from the base of the reef slope at North Reef.
F - Coral rubble from the base of the reef edge in the lagoon.

The mean number of juvenile scarids feeding on each algal-covered substratum type, is the mean of eight replicates. In each replicate the total number of individuals observed feeding on each substratum type during 30 censuses was recorded. The vertical lines indicate the 95% confidence limits.
The horizontal lines connect those substratum types which did not differ significantly in the mean number of scarids observed feeding upon them (1-way ANOVA, $F = 29.037$, df. $= 5,42$, $p < 0.05$).


MEAN NUMBER OF INDIVIDUALS ± 95% C.I.
180
160
140
120
100
80
60
40
20
0
A
B
C
D
E
F
ALGAL-COVERED SUBSTRATUM TYPE

df = 5,42, $p < 0.05$). This indicates that given a choice of the six substratum types, juvenile scarids in the lagoon exhibit a preference for substratum type A > B > C > D, E or F. Thus when compared to observed distributions (described in section B, above), only *S. frenatus* and juveniles below 22 mm T.L. fed on preferred substrata, whilst most individuals fed on the three least preferable substrata.

Notes on the biology of juveniles of several scarid species.

Because of the within-species and between-location variability in the behaviour of juvenile scarids, and the large between-species differences in their biology, the results will be partially summarized as accounts of the biology of each species in a given location (Appendix 2).

6.8 Discussion

In many respects, the biology of juvenile scarids is similar to that of many other reef fish species. In the present study, scarid recruitment was highly seasonal, with relative abundances and species composition varying markedly between years. Similar trends have been reported in numerous other non-scarid species (*e.g.* Russell *et al.*, 1977, Talbot *et al.*, 1978, Williams & Sale, 1981, Lassig, 1983, Williams, 1983 and Sale *et al.*, 1984 a). The species composition of recruits at the two study sites showed consistent differences. Similar habitat-related differences have been noted in several non-scarid species (*e.g.* Sale *et al.*, 1984 a and Williams, 1980). More specific micro-habitat differences (as in Lassig, 1977 and Sweatman, 1983), however, were not noted. Juvenile scarids recruited most often to areas of relatively high topographical complexity and, although some species-specific preferences were indicated, a large degree of overlap between species was observed. This has been reported in other studies (*e.g.* Sale *et al.*, 1980, Williams & Sale, 1981, Sale *et al.*, 1984 b and Shulman, 1984). In the present study, the high estimated mortality rate of early post-recruit scarids at North Reef is higher than most published estimates for other species, although in these studies, the highest mortality rates were also recorded during the early post-recruitment period (*e.g.* Williams, 1980, Doherty, 1983 and Sale *et al.*, 1984 a).

However, the large number of similarities between juvenile scarids and other reef fish species, as outlined above, were primarily restricted to recruitment and early post recruitment events. The biology of juveniles of these species during the succeeding year(s) have received relatively little attention, although it is during this period that many important differences between scarid species, and between scarids and other reef fish species become apparent.

In this study, one of the most distinctive features of juvenile scarids was the degree of between-species variation in the biology of individuals above 20 mm T.L. Differences associated with the 'sordidus' and 'frenatus' groupings were not detectable. Morphology therefore, appears to have a limited role in determining the biology of juvenile scarids above 20 mm T.L. The observed differences were primarily a result of behavioural patterns. The two main areas of their behaviour are considered below, these are: a) individual movement and b) interactions and social behaviour.

a) Individual movement

In scarids, there is limited movement during the first few days after recruitment and as in pomacentrids (Sale *et al.*, 1984 a), the site occupied at this time probably represents the site chosen at settlement. However, unlike pomacentrids and other species in patch reef environments (*e.g.* Williams, 1980 and Sale *et al.* 1984 a), many scarid species do not remain in the immediate vicinity of their recruitment site for extended periods of time. The extent of movement by juvenile scarids varied considerably and appeared to depend upon both the species considered and the habitat studied (Appendix 2). Some species (*e.g.* *S. frenatus* and *S. niger*) at North Reef, joined adult harems in the region where they recruited. Their home ranges may include their recruitment site and total movement was probably less than 30 m away from this point (with the possible exception of reproductive migrations).

Many species joined mobile schools (*e.g.* *S. psittacus*, *S. rivulatus* and *Scarus* sp.) which moved over considerable distances (>50 m) whilst feeding. Some species (*e.g.* *S. sordidus*, and possibly, *S. dimidiatus* and *S. oviceps*) in the lagoon, appeared to migrate large distances during the juvenile phase. The lack of large juvenile (>110 mm T.L.) or adult *S. sordidus* in the lagoon at Lizard Island, despite large numbers of small juveniles, suggests that this species migrates considerable distances, in excess of 250-500 m, away from its recruitment site. This movement is a permanent migration not a diurnal migration as reported in some Caribbean species (*e.g.* Winn *et al.*, 1964 and Ogden & Buckman, 1973).

These differences will have important implications in reef fish management and in the interpretation of observations of reef fishes based on comparisons between the abundances of juveniles and adults within restricted study areas.

It is interesting to note that the loss of *S. sordidus* from the lagoon which occurred at a size of about 110 mm T.L., corresponds with the smallest size at which *S. sordidus* possesses a full complement of 'biting' morphological features (Chapter 2) and at which it first begins to feed as a 'biter'. This supports the suggestion in Section 5.8 that the absence of adult *S. sordidus* in the lagoon is correlated with the relative availability of small convex surfaces in this area.

Interactions and social behaviour

Juvenile scarids are subject to numerous intra- and interspecific interactions that vary in both nature and intensity throughout the juvenile phase. There are, however, three areas of particular interest and potential importance. These are considered separately below:

1) In the early juvenile phase, some scarid species appear to have an association with the territories of some pomacentrid species. In the present study, it was not possible to determine whether juvenile scarids preferred to settle or live in pomacentrid territories during the early post-recruitment period. Some species were frequently found in pomacnetrid territories, whilst others were not (Appendix 2). These differences may have been the result of variations in the abundance of territorial pomacentrids in the areas

in which various scarid species recruited, in addition to species-specific differences in the selection of recruitment sites. Of those species commonly associated with pomacentrid territories (*i.e.* *S. sordidus*, *S. frenatus* and to a lesser extent, *S. psittacus*, *S. spinus* and *Scarus* sp.), an association appears to be favoured by the scarid as the scarid home range often remained entirely within the pomacentrid territory, despite the availability of comparable areas of substratum nearby. This suggests that the scarids selected areas within pomacentrid territories rather than a particular substratum type which is also selected for by some pomacentrids. The pomacentrids with which scarids are apparently associated are typified by highly territorial behaviour, territories in areas of topographical complexity and the formation of a rich algal 'lawn' within their territories. These species include *Stegastes nigricans*, *S. apicalis* and *Plectroglyphidodon lacrymatus*.

The potential advantages for scarids living within the territories of such species are quite clear:

A) Pomacentrid territories with associated algal lawns have an increased abundance of benthic crustacea (Lobel, 1980) which form the major food items of recently recruited scarids (Section 6.3).

B) Pomacentrid territories with associated algal lawns have an increased availability of benthic turf algae (Lobel, 1980) which form the major food item of juvenile scarids above 18 mm T.L. (Section 6.3) and form a preferred feeding substratum for many juvenile *Scarus* species (Section 6.7).

C) Some territorial herbivorous pomacentrid species are aggressive towards piscivorous species (Thresher, 1976 and

Donaldson, 1984) and may therefore reduce potential predation to small scarids living within a pomacentrid's territory.

Recently recruited scarids probably remain in the pomacentrid territories as 'parasites' as they are vigorously excluded above 15-18 mm T.L. A similar situation has been described involving blennies in *Acanthurus sohal* territories (Roberts, 1985). This association between scarids and pomacentrids may greatly enhance the survival of juvenile scarids during the short but highly vulnerable early post-recruitment phase. This relationship between pomacentrids and early post-recruitment scarids would be a particularly rewarding area for future studies.

2) In larger juveniles, distinct site-related differences in behaviour were apparent. At the North Reef study site, there was a large area available for grazing by juvenile scarids, with relatively abundant cover and low numbers of aggressive pomacentrids. In this area, juvenile scarids were typically solitary, occupied relatively large home ranges and experienced few agonistic encounters with other species. This behaviour was observed in many species, including those which often formed schools in other areas (*e.g. S. sordidus* and *Scarus* sp.). In contrast, in the lagoon study site, small juveniles were primarily restricted to small home ranges in a narrow pomacentrid-free area on the edge of the reef. Nearby areas were relatively free of pomacentrids but had low cover, whilst on the reef edge where cover was more abundant, aggressive pomacentrids were numerous. Larger juveniles apparently left their small home ranges and moved over extensive areas in large schools. Throughout the juvenile phase, most species were in groups

and were subject to consistent attacks from territorial pomacentrids.

The differences in the behaviour of juveniles at the two sites appeared to be primarily a result of different species compositions at these sites. At North Reef, most species were solitary, whilst those in the lagoon were primarily schooling. Schooling in this area presumably decreases predation in areas of low cover (Chapter 4) and may also enable these individuals to swamp pomacentrid territories. It must be noted, however, that in this study, pomacentrid aggression was less than that noted in the Caribbean by Robertson *et al.* (1976).

Despite these species related differences, similar differences in behaviour were noted in some species that occurred at both study sites. *S. sordidus* and *Scarus* sp., for example, were typically solitary or in small (1-3) groups at North Reef, but joined larger groups in the lagoon. This suggests that the behavioural pattern observed at the 2 sites may be, in part, the result of local conditions, possibly associated with available cover and pomacentrid concentrations.

Overall, juvenile scarid behaviour and social interactions are complex, and are probably site-, species- and density-dependent. It is difficult to make generalizations and observed differences underline the need for caution in interpreting behavioural observations made on a species in a single habitat type.

3) Of all the types of interactions and social behaviour of juvenile scarids, those of *S. frenatus* stand out as being particularly unusual. Firstly, they were the only territorial juvenile scarids observed. Secondly, they had relatively low feeding rates and few bites per foray and thirdly, they were able to feed within pomacentrid and *Acanthurus lineatus* territories without eliciting aggressive behaviour, whilst other similarly sized *Scarus* species were vigorously excluded.

It is suggested that, at North Reef, *S. frenatus* behaves as a mimic. It does not, however, appear to mimic any specific species, but rather a generalized, *i.e.* carnivorous, labrid. This represents a form of antergic-defensive mimicry (*sensu* Vane-Wright, 1976) but differs from the typical Batesian mimicry in that the models are not necessarily repellent. This suggestion is supported by the following observations:

A) The colour patterns of juvenile *S. frenatus* are distinctive and differ markedly from the 'typical' uniform or striped scarid pattern. The longitudinal stripes on the head, in particular, give the snout a more pointed labrid-like appearance (Chapter 4).

B) The feeding rate (bites/min.) and number of bites per foray of *S. frenatus* were both markedly lower than those of other *Scarus* species (Section 6.3), and bore a stronger resemblance to the feeding behaviour of small labrids (pers. obs.).

It is thought that the mimetic behaviour of *S. frenatus* enables it to feed in the territories of territorial herbivores. There are two behavioural characteristics of *S. frenatus* which would potentially enhance such a mimetic strategy: a) the maintenance of a relatively large home range/territory, which decreases its exposure to any single territorial herbivore and thereby decreases the benefits to be gained by the individual territorial herbivore in excluding juvenile *S. frenatus*, and b) territorial behaviour, which decreases the abundance of other juvenile scarids within the *S. frenatus* territory.

Although it is possible that the territorial behaviour of *S. frenatus* may benefit local territorial herbivores (*cf.* Robertson & Polunin, 1981, who describe such relationships as symbiotic), the function of the behavioural patterns of *S. frenatus* outlined above are thought to be of a simple nature which enables *S. frenatus* to parasitize the food resources of local territorial herbivores. In laboratory experiments, Losey (1982) has shown that a decrease in the exposure of a territorial pomacentrid to grazing herbivores also decreases the agonistic response of that individual towards individuals grazing within its territory. It is therefore possible that by excluding small scarids from its territory, and by its own mobile behaviour, juvenile *S. frenatus* confers upon itself a similar advantage.

The potential advantages to juvenile *S. frenatus* are clear. By looking and feeding like a labrid and possibly decreasing agonistic levels of local territorial herbivores towards juvenile scarids, juvenile *S. frenatus* are able to feed in pomacentrid and *A. lineatus* territories at sizes greater than that at which other juvenile scarids are vigorously excluded. Pomacentrid and *A. lineatus* territories both contain preferred feeding substrata for juvenile scarids (Fig. 6.10), probably as these both contain relatively large standing crops of algae (Robertson *et al.*, 1979 and Lobel, 1980), which in pomacentrid territories, include relatively easily digested algal species (Lassuy, 1980).

In addition to rich food resources, the territories of herbivores may also be desirable feeding areas as a result of decreased potential predation, as some piscivorous predators are attacked or excluded by the territory holders. This behaviour has been reported in several pomacentrid species (Thresher, 1976, Ebersole, 1977 and Donaldson, 1984) and was observed in *A. lineatus*. (In the present study *A. lineatus* were observed to exclude *Plectropomus leopardus* from their territories on two occasions [= 1.2 % of observed attacks by *A. lineatus*]).

In conclusion, therefore, it appears that *S. frenatus* is able to mimic labrids and that it utilizes this mimicry to deceive territorial herbivores, enabling it to feed within their territories.

The present study has revealed many interesting facets of the biology of juvenile scarids. However, the study has two main limitations. Firstly, only a limited number of observations were undertaken of each species at each size, these often being of a qualitative nature, and secondly, the observations were primarily restricted to two locations, *i.e.* the North Reef and lagoon study sites, in a single reef system, *i.e.* Lizard Island.

Despite these problems, the observations in this study are of value especially as a basis for further observations and in assisting the interpretation of other studies. The three main advantages of the present study are:

a) As a result of the taxonomic descriptions of juvenile scarids in this study, most species could be identified in the field, and in some species individuals could be accurately identified shortly after recruitment.

b) Many known individuals were followed so actual movement, growth and behavioural changes *etc.*, could be observed, rather than being inferred from transects or censuses.

c) All observations were on a natural reef. Artificial substrata were not used and disturbance to the environment was minimal. The observations in this study therefore, probably represent natural events.

CONCLUDING DISCUSSION

In this last section, the results of the previous sections will be discussed in four parts: namely,

1) The relationship between the functional morphology and the behavioural ecology of scarids,
2) The role of adult scarids in the coral reef fish community,
3) A comparison of the biology of juvenile and adult scarids, and
4) Scarid zoogeography and speciation.

The suggested directions for future studies are also outlined.

1) The relationship between the functional morphology and behavioural ecology of scarids.

In this study, a strong correlation was found between the functional morphology and behavioural ecology of scarids. This correlation was observed in five genera/groups of adult scarids: *Cetoscarus*, *Bolbometopon*, *Hipposcarus*, the 'sordidus' group and the 'frenatus' group, and throughout the ontogeny of juveniles in the 'sordidus' and 'frenatus' groups. Similar correlations have been recorded from a wide range of fish groups (*e.g.* Jones, 1968, De Martini, 1969, Emery, 1973, Christensen, 1978, Motta, 1980 and Stoner & Livingston, 1984) and there appears to be a relatively consistent relationship between the functional morphology and behavioural ecology of a species.

There are, however, limits to the extent of this relationship, that is, in the predictive value of functional morphology in determining the behavioural ecology. In the present study, for example, the behaviour of juvenile *S. frenatus* differed markedly from that of a species with a similar morphology and was more similar to that of a species with a different morphology.

From this study, it is concluded that analyses of the functional morphology of a structure can determine its functional capabilities, although the application of the structure remains dependent upon the behaviour of the organism within these functional constraints. The ecological significance of a structure is therefore dependent upon both the functional capabilities of the structure and the behaviour of the animal in relation to that structure.

There are currently two hypotheses concerning the role of morphology in the regulation of the diet of fishes. Chao and Musick (1977) suggested that differences in the food habits of fishes are the result of different morphological constraints, and not the result of selective feeding. Conversely, Liem (1980) suggested that feeding repertoires are extremely flexible and relatively independent of jaw morphology, a suggestion which is, in part, supported by Stoner and Livingston (1984).

The observations in the present study suggest that a compromise between the two hypotheses is probably most applicable. Behavioural flexibility may determine the diet, but only within certain morphological constraints.

In scarids, the relationship between the functional morphology and the behavioural ecology of juveniles appears to differ slightly from that of adults. In adults, the functional morphology and behavioural ecology are strongly correlated, presumably, as efficient feeding is of primary importance, in order to maximise the energy and/or time available for reproduction. In juveniles above 20 mm T.L., the correlation between morphology and behaviour was limited and a large degree of between-species variation in behaviour was observed. In almost all cases, however, the behavioural traits appeared to be related to predation-avoidance (Chapter 4). This suggests that in juveniles, predation-avoidance is of primary importance. As similar studies of other reef fish families are lacking, comparisons between juvenile and adult phases of other species in terms of their functional morphology and behavioural ecology are therefore recommended.

2) The role of scarids in the coral reef fish community.

There are four major herbivorous fish families on coral reefs, the Scaridae, Acanthuridae, Siganidae and Kyphosidae. Other families with some herbivorous species include the Pomacentridae, Blenniidae and Pomacanthidae. Scarids are one of the most abundant groups of herbivorous reef fishes in the central Great Barrier Reef region (Williams, 1982, Williams & Hatcher, 1983 and Russ 1984 a, b). Scarids are also one of the most numerically dominant groups of herbivorous reef fishes at other geographic localities, including the southern Great Barrier Reef (Choat & Robertson, 1975), the Indian Ocean (Robertson & Polunin, 1981), the Red Sea (Bouchon-Navaro & Harmelin-Vivien, 1981), Hawaii (Brock, 1982) and the Caribbean (Lewis & Wainwright, 1985). It is, therefore, no surprise that the scarids have often been reported as an important group of grazers on coral reefs.

In recent years, herbivory and herbivore-algal interactions on coral reefs have received increasing attention. Several studies have examined herbivory on coral reefs (*e.g.* Ogden & Lobel, 1978, Hatcher, 1981, Littler *et al.*, 1983, Hay, 1981, Hay *et al.*, 1983 and Lewis & Wainwright, 1985). In almost all cases, however, scarids have been grouped together and their effects judged as a whole, often along with acanthurids.

One of the most important conclusions that can be drawn from the present study is that the scarids can not be considered as a uniform group, as previously believed (*e.g.* Goldman & Talbot, 1976 and Sale, 1977). Scarid species may be taxonomically similar, but they differ markedly in their functional abilities and their behaviour. The species composition of a group of scarids, therefore, will markedly influence the role of that group in the reef fish community. Bites, for example, (as in Hatcher 1981 and Steneck, 1983) are not uniform units between species.

Scarids display a wide range of feeding strategies. These include: coral predation, seagrass and algal browsing, algal grazing (biting and scraping) and sand ingestion. Some of these strategies overlap with those of species in other families including the Tetraodontidae, Acanthuridae, Siganidae and Kyphosidae. The results of the present study enable the feeding strategies of many scarid species to be assessed, although further analyses in other geographic locations are required. A similar study of the Acanthuridae by Jones (1968) enables some comparisons to be made between these two major groups.

In studies of herbivory on coral reefs, it is important that a suitable scale is chosen to answer the questions asked or that the scale used is taken into account when interpeting the results. These include not only spatial and temporal scales but also the taxonomic scale. In terms of the herbivorous reef fish population structure, for example, large differences have been reported at all spatial scales examined, from geographic scales to localities within reef zones (Williams, 1982, Williams & Hatcher, 1983, Russ, 1984 a, b, Lewis & Wainwright, 1985, and Choat & Bellwood, in press). Herbivorous grazing rates also vary greatly between areas and within locations (Hay, 1981, Hay *et al.*, 1983 and Lewis & Wainwright, 1985).

In terms of herbivory and the behaviour of herbivorous reef fishes, important differences also occur at a much smaller spatial scale, *i.e.* bite sized. The importance of these differences and the need for observations which are based, taxonomocally, at the species level is exemplified in the present study of scarid bioerosion. Scarid bioerosion rates are dependent upon the species present in the scarid community, their sizes, abundances and their bite form. The latter parameter can only be assessed when feeding behaviour is analysed at a small (cm^2) scale. A knowledge of species-related differences in these small scale events enables enables estimates of scarid bioerosion to be made over wide geographic ranges. In addition, it may be able to explain the apparent species specific nature of some aggressive interactions. As a consequence, it enables the scarid community to be more accurately divided into functional guilds or groups for more generalized comparisons.

It is therefore recommended that the choice of the relevant scales be considered carefully in future studies of herbivorous reef fishes. Studies of herbivory by reef fishes must consider feeding events at a bite-sized scale in addition to broader scale observations. At the taxonomic scale, the only observations which can give an accurate estimate of the herbivorous reef fish community are those at the species level. Some subdivision of the herbivorous fish community may be desirable, but in this case, feeding guilds rather than taxonomic groupings are most useful.

Subdivisions based on feeding guilds require a knowledge of the species composition and the feeding biology of each species, including its functional morphology, feeding behaviour and digestive physiology. There is, however, a need for more detailed studies of the feeding biology of herbivorous reef fish species. If major ontogenetic trends in the feeding biology of herbivorous reef fishes are found, then analyses of herbivorous reef fish communities must include some indication of species size class compositions.

From the observations of adult scarids in this study, two areas of particular interest for future studies are apparent. Firstly, what is the relationship between the major herbivorous groups on coral reefs? This includes both fish and invertebrates. A correlation between the absence of herbivorous fishes and the abundance of*Diadema* on Caribbean reefs, for example, has been suggested (Hay & Taylor, 1985). A comparison of the feeding biology and ecology of species from different fish families within major herbivorous feeding guilds may therefore be particularly rewarding.

Secondly, what influences the distribution and abundance of adult scarids? Although recruitment patterns and early post-recruitment mortality rates are probably of primary importance, especially in sedentary species, what inflences the distribution and abundance of the more mobile species? Observations in the present study, for example, suggest that some species may be influenced by the form of the substratum (Chapters 5, 6 B).

Overall, one can conclude that scarids have a wide range of roles in the coral reef fish community. Some roles are species-specific, other are more general. The major roles of scarids in the Great Barrier Reef region are outlined below, with a note of the species specificity:

1) As a major prey item for many piscivorous fishes: this encompasses most *Scarus* species.
2) As coral predators: this is restricted almost exclusively to *B. muricatum*.
3) As herbivores feeding primarily upon turf algae. This includes:
    a) Browsers, primarily *Calotomus carolinus* and probably *Leptoscarus vaigiensis*, feeding predominantly on marine angiosperms and/or macroalgae,
    b) Biting grazers, including *B. muricatum*, *C. bicolor* and 'sordidus' group species, feeding on turf algae and possibly endolithic growths,
    c) Scraping grazers, *i.e.* 'frenatus' subgroup 'b' species, feeding predominantly on turf algae,
    d) Sand-ingesting scraping grazers, *i.e.* species in the

'frenatus' subgroup 'a', feeding upon turf algae and the surface of open sand.

4) As bioeroding agents. Bioerosion is primarily a result of feeding by *C. bicolor*, *B. muricatum* and 'sordidus' group species.

5) As predators or indirect agents which modify the standing crop and species composition of algae and benthic invertebrate communities.

3) A comparison of the biology of juvenile and adult scarids.

The present investigation of the biology of juvenile scarids was of a preliminary nature. However, it has revealed several interesting trends, the most important of these being the marked differences between the strategies of juvenile, IP and TP stages. In juveniles, the colour patterns, social behaviour and feeding behaviour all appear to function primarily as predation-avoidance mechanisms. In IP individuals, some similarities in the non-reproductive colour patterns, social behaviour and feeding behaviour suggest that predation-avoidance may continue to be of major importance, although the correlation between feeding behaviour and morphology at this stage suggests that feeding efficiency is of increasing importance. In TP individuals, feeding efficiency continues to be of importance although at this stage, reproductive success appears to be of primary importance. The typically gaudy colour patterns and solitary or territorial behaviour of TPs probably have a reproductive function (Choat & Robertson, 1975). Predation-avoidance therefore appears to be of secondary importance to TP individuals.

The reasons for these differences are relatively clear. Scarids are eaten by a wide range of piscivorous fishes including muraenids (Winn & Bardach, 1959), scorpaenids (Hiatt & Strasburg, 1960), serranids (Choat, 1968), carangids (Popova & S'erra, 1983), sharks (Stevens, 1984) and synodontids (Chapter 4). In addition, the estimated 77% mortality of juvenile scarids in 34 days at North Reef suggests that juvenile mortality rates may be particularly high. The high potential predation pressure upon smaller prey on reefs was also noted by Choat & Robertson (1975). In addition, from the theoretical analyses of Meats (1971), it is apparent that predation events are not all of equal importance. Pre-reproductive mortality is more important to an individual than post-reproductive mortality, in terms of its reproductive output. The most important factor influencing the biology of scarids therefore changes from survival at small sizes to reproduction at large sizes. The various factors influencing the biology of scarids during the three post-larval life stages are summarized in Table 7.1.

In the present study, as in other studies, the importance of the juvenile phase in the biology of a species is apparent. In the past, most studies of the biology of reef fishes were restricted to the adult phase. In the last decade, however, the importance of recruitment and early post-recruitment events have become increasingly apparent. The spatial and temporal variability in the recruitment of coral reef fishes are both well established (Talbot *et al.*, 1978, Williams, 1980, 1983 and Sale *et al.*, 1984 a). These factors, acting in concert with selectivity of recruitment sites by settling larvae and post-recruitment mortality will markedly alter the composition of reef fish assemblages. The biology of juveniles

Table 7.1 A summary of the biological factors influencing the three post-larval life stages of scarids.

Stage:	Juvenile phase	Initial phase	Terminal phase
Mortality rates †	High	Low	Low
Significance of mortality ‡	High	High->Low *	Low
Function of the:			
Colour pattern ††	Decrease predation	Decrease predation	Increase reproductive success
Feeding behaviour ‡‡	Decrease predation?	Increase feeding efficiency	Increase feeding efficiency
Social behaviour	Decrease predation	Decrease predation	Increase reproductive success
Individual energy requirements for:			
Growth	High	High->Low	Nil
Reproduction	Nil	High	Low-High **

† - Section 6.8 and pers. obs.
‡ - Meats (1971)
†† - Chapter 4, Randall & Choat (1980) and pers. obs.
‡‡ - Chapters 4, 5 and 6
* - Depending on the individuals age/size
** - Depending on the season

therefore, encompasses several major stages in the biology of the species as a whole. In scarids, these include a change-over from carnivory to herbivory and marked morphological differentiation. These events at recruitment and during the juvenile phase can influence the distribution and abundance of adults, which may in turn determine the behavioural patterns of the adults, including territoriality (Buckman & Ogden, 1973, Chapter 5) and reproductive strategies (Warner, 1984).

Although the biology of juvenile reef fishes has received considerable attention in recent years, many of the studies have been restricted to pomacentrids, particularly in lagoonal habitats. Comparable studies of species in other families and in other reef zones are necessary. In particular, observations of the distribution and abundance of recruits, early post-recruits, juveniles and adults of large herbivorous species would be interesting as a contrast to previous studies which concentrated on smaller species. The present study has shown marked differences in the biology of early post-recruit, juvenile and adult scarids. Although juvenile scarids resemble other reef species in many ways, some important differences between scarids and other species in factors such as movement patterns during ontogeny, their relationship with territorial herbivorous reef fishes and mortality rates are potentially of considerable significance and require further analysis.

4) Scarid zoogeography and speciation.

Studies on the zoogeography of the Scaridae have been restricted as a result of the lack of adequate systematic studies (Bruce, 1979). The importance of cladistic studies in particular, has been emphasised by Springer (1982). The systematic and cladistic analyses in Chapter 3 have therefore provided a means of analyzing the factors influencing scarid zoogeography at the generic or group level. The genera considered are listed below in order of increasing specialization (based on Schultz, 1958, and Chapter 3):

Sparisomatinae:
- *Cryptotomus*
- *Nicholsina*
- *Calotomus*
- *Scaridea*
- *Leptoscarus*
- *Sparisoma* (including *Euscarus*)

Scarinae:
- *Cetocarus*
- *Bolbometopon*
- 'sordidus' group (genus *Scarus*)
- *Hipposcarus*
- 'frenatus' group (genus *Scarus*)

Their geographic distribution (based on Schultz, 1958, 1969, Bohlke & Chaplin, 1968, Randall, 1968, 1985, Rosenblatt & Hobson, 1969 and Randall & Bruce, 1983) is as follows:

Caribbean and West Atlantic : *Cryptotomus*, *Nicholsina*, *Sparisoma* and the 'frenatus' group.
Mid- and East Atlantic : *Nicholsina* and *Sparisoma* (*as Euscarus*) and the 'frenatus' group.
Mediterranean : *Sparisoma* (as *Euscarus*)
Red Sea : *Leptoscarus*, *Calotomus*, *Cetoscarus*, *Bolbometopon*, the 'sordidus' group, *Hipposcarus* and the 'frenatus' group.
Indian Ocean and West Pacific : *Leptoscarus*, *Calotomus*, *Cetoscarus*, *Bolbometopon*, the 'sordidus' group, *Hipposcarus* and the 'frenatus' group.

Mid Pacific and Tahiti : *Leptoscarus*, *Calotomus*, *Cetoscarus*, *Bolbometopon*, the 'sordidus' group, *Hipposcarus* and the 'frenatus' group.
Hawaii : *Leptoscarus*, *Calotomus*, *Scaridea* and the 'sordidus' and 'frenatus' groups.
Eastern Pacific : *Nicholsina*, *Calotomus* and the 'frenatus' group.

The earliest fossil records of scarid-like fishes are from the Eocene (38-54 million years ago) (Romer, 1966). During this period, there was a great deal of interconection between tropical seas, with tropical marine species being restricted to a single large body of water called the Tethys Sea (Vermeij, 1978). This interconnection was severed by the formation of a land bridge between the Mediterranean and the Red Sea approximately 16 million years ago (Por, 1971, 1975) and the Isthmus of Panama at least 3.5 million years ago, in the late Pliocene (Woodring, 1966) (Fig. 7.1). In addition, a large area of open ocean described by Ekman (1953) as the Eastern Pacific barrier further hindered movement of tropical marine species (Vermeij, 1978).

The present distribution of scarid genera has several unusual or distinctive features. These are:

1) *Sparisoma* is present in the Caribbean, mid-Atlantic and Mediterranean, but absent from the Indo-Pacific. In the Indo-Pacific, however, two closely related genera, *Cetoscarus* and *Bolbometopon*, are present.
2) All sparisomatine genera present in the Caribbean have ranges that extend no further than the Atlantic, Mediterranean and Eastern Pacific.
3) In the Caribbean, three sparisomatine genera are present but

only one scarine genus, *Scarus*, which is represented by the 'frenatus' group.

4) In the Indo-Pacific, all scarine genera are present but only three sparisomatine genera. The genera in the two subfamilies are not closely related, both being more closely related to the Caribbean genus *Sparisoma* (including *Euscarus*).
5) The only Indo-Pacific genera or groups with ranges that extend to the Eastern Pacific are *Calotomus* and the 'frenatus' group.

The following hypothesis is proposed to account for these discontinuities in the distributions of scarid genera and groups (summarized in Figure 7.1).

After their appearance in the Eocene, the scarids proliferated during the Oligocene and by the early Miocene, were probably widespread throughout the tropical seas. At the time of the formation of the Mediterranean - Red Sea land bridge (approximately 16 m.y. ago), the most advanced scarid form is believed to have been a common ancestor of *Sparisoma* and the Scarinae. The Mediterranean - Red Sea land bridge resulted in two geographically distinct scarid populations, separated from each other by the land bridge and the East Pacific barrier (Fig. 7.1). The East Pacific barrier refers to the large expanse of deep oceanic water in the eastern Pacific, which appears to be a barrier to the dispersal of many marine organisms (Briggs, 1974).

The western population probably extended throughout the Mediterranean, Atlantic, Caribbean and Eastern Pacific (the latter two being connected throughout the Miocene and early Pliocene), whilst the eastern population occupied extensive areas of the

Figure 7.1 A

The proposed distribution of early scarids during the

late Eocene period (approx. 50 m. y. ago).

The distribution of the scarids approximates that of the Tethys Sea. The location of the major land masses are drawn following Tarling (1980). The formation of the Red Sea land bridge (c. 15 m. y. ago) across the points marked A and B essentially bisected the existing scarid population.

Figure 7.1 B

The proposed distribution of the major scarid groups

approximately 4 million years ago.

This is prior to the formation of the isthmus of Panama, which isolated the Atlantic and Indo-Pacific scarid populations.

Dark stipple = *Sparisoma* and *Nicholsina*.

Pale stipple = *Leptoscarus*, *Calotomus*, *Cetoscarus*, the 'sordidus' and 'frenatus' groups and, with the exception of the Hawaiian region, *Bolbometopon* and *Hipposcarus*.

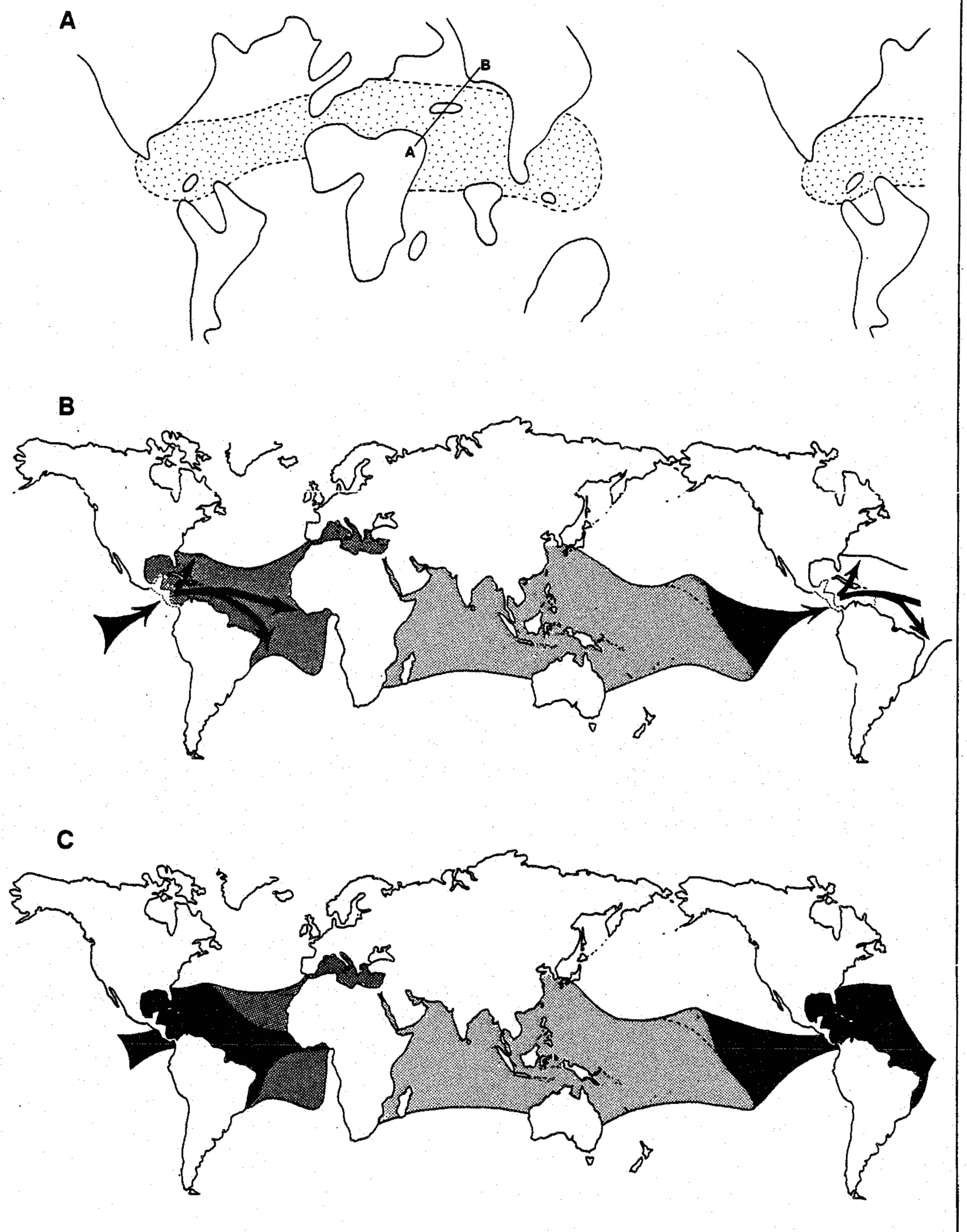
Black area = The 'frenatus' group.

Note that the 'frenatus' group had passed across the Eastern Pacific and into the Caribbean before the formation of the Isthmus of Panama. The formation of this land bridge isolated the Caribbean and Atlantic populations from those in the Indo-Pacific.

Figure 7.1 C

The present distribution of the major scarid groups.

Stippling as in 7.1 B. Note the proliferation of the 'frenatus' group in the Caribbean and Atlantic regions.


A
B
A
B
C

Indo-Pacific. The distribution of extant scarid genera strongly suggests that there was a period of speciation during the mid to late Miocene and/or early Pliocene (*i.e.* between 16 and 3.5 m.y. ago), but this was restricted to the eastern, *i.e.* Indo-Pacific, population. The new genera that arose during this period ramified throughout the Indo-Pacific, with the most 'advanced' genus (or group), the 'frenatus' group (genus *Scarus*), having crossed the Eastern Pacific barrier by the late Pliocene (Fig. 7.1). This group survived after the formation of the Panama land bridge, and presently has a distribution which includes the Eastern Pacific, Caribbean and Atlantic (*i.e.* in the western population). The only other genus which appears to have crossed the Eastern Pacific barrier is *Calotomus*, but the absence of this genus from the Caribbean and Western Atlantic suggest that this crossing occurred after the formation of the Panama land bridge (Rosenblatt, 1967).

There are several lines of evidence that support the above hypothesis. Firstly, it is the most parsimonious explanation that can account for the present distribution of scarid genera. Secondly, it is consistent with a) present distributions, b) major geological events (the sites and sequence of these events correspond with the sites of deliniations between the distributions of extant scarid genera and the phylogenetic status of those genera involved) and c) the limited fossil record (scarids have been recorded from Eocene European sites and Miocene South Asian sites [Romer, 1966]). Finally, it reflects similar trends in other families of marine fishes and other marine phyla. Similar geographic distributional patterns in relation to the phylogeny of the species or genera within the family have been recorded in the Branchiostegidae (Marino

& Dooley, 1982), Acanthuridae (Tyler, 1970), Chaetodontidae and Pomacanthidae (Steene, 1978 and Allen, 1981). Springer (1982) described the geographic distribution of several fish families which are consistent with the above hypothesis. The role of the Isthmus of Panama as an important vicariance factor in marine fish populations has been discussed by Rosenblatt (1967). Geographic distributional patterns of genera and species in other marine phyla which are consistent with the above hypothesis have been recorded in corals (Rosen, 1981), echinoderms, crustcea and molluscs (Briggs, 1974 and Vermeij, 1978).

Two other observations are consistent with the above hypothesis. Firstly, of the four East Pacific *Scarus* species, only two are represented in the Western Pacific, *S. ghobban* and *S. rubroviolaceus*. Both species have extensive ranges throughout the Indo-Pacific, and are of particular interest as they sometimes occur in deeper water, away from reefs. *S. ghobban* is occasionally caught by trawls in inter-reef areas off Townsville (pers. obs.), whilst both species have been caught in trawls in deep waters (below 90 m) off the north-west shelf of Australia (K. Sainsbury, pers. comm.). This ability to survive in non-reef areas may have been instrumental in their passage across the Eastern Pacific barrier and in their survival in the Eastern Pacific (as this area lacks extensive reef formations [Glynn *et al.*, 1972]). Rosenblatt and Hobson (1969) suggested that these species are recent immigrants from the Western Pacific. Secondly, in the Caribbean, only the 'scraping' *Scarus* species appear to be present. The niche occupied by the 'biting' 'sordidus' group species in the Indo-Pacific is occupied in the Caribbean by a single species, *Sparisoma viride*

(Section 5.4). The lack of specialized 'sordidus' group species in an area where their 'typical' niche is occupied by a relatively primitive *Sparisoma* species suggests that the 'sordidus' group was never present in this area.

The differential development of the western (Atlantic, Caribbean) and eastern (Indo-Pacific) scarid populations may have been influenced by their disparate geographic ranges and the climatic histories of these ranges. The Indo-Pacific includes a large area which is inhabitable by scarids because of its extensive reef formations and as such, has a high probability of containing more species than a smaller area such as the Caribbean, which has fewer reefs (Rosen, 1981). This effect has been described as the 'area effect' (Briggs, 1974). The large area of the Indo-Pacific also decreases the probability of the whole area being fully occupied by all species present, and as a large area, it is more likely to undergo changes (locally or extensively) in conditions that defer an equilibrium (Rosen, 1981). Studies of ecological succession suggest that a deferred equilibrium may help maintain a high species diversity (Connell, 1978 and Talbot *et al.*, 1978). The rate that an equilibrium is reached is dependent upon the relative stability of the area and the dispersal abilities of the inhabitants (MacArthur & Wilson, 1967). Differences in species dispersal abilities may result in a large area being 'perceived' by a species as differentiated, and therefore, enhance species diversity (Rosen, 1981). Speciation is also likely to be enhanced by dispersal barriers in areas of geographic complexity. Such a zone of geographic complexity is apparently present in the archipelagic region of Indonesia and the Western Pacific (Rosen, 1981). In the

Indo-Pacific therefore, several factors may have favoured speciation.

The Caribbean, Atlantic and Mediterranean, however, appear to have been exposed to less favourable conditions. The cooling trend throughout the Cenozoic era, culminating in the glacial episodes of the Pleistocene may have had more severe effects in the Atlantic than in other oceans, partly as a result of its relatively small size (Vermeij, 1978). A detrimental effect of these cooling periods upon the scarids, chaetodontids and acanthurids in the Eastern Pacific has been suggested by Rosenblatt and Hobson (1969). The Mediterranean has experienced large scale extinctions since the Miocene (Vermeij, 1978), whilst interruption of coral reef construction in the Eastern Pacific and Caribbean has been suggested (Glynn *et al.*, 1972). These differences between the Indo-Pacific and Atlantic may, in part, account for the present differences in the number and type of scarid genera in the two areas.

The proposed hypothesis is tentative. It requires further analyses, but will hopefully form a basis for such studies. Two aspects, in particular, require attention. Firstly, comparisons between fossil and extant scarid genera are essential in the understanding of their evolutionary history. Secondly, detailed analyses of sparisomatine genera are required to elucidate their phylogenetic relationships and their relationships with scarine genera. The above considerations are limited to relationships at the generic level. However, the increasing stability of scarid nomenclature at the species level may result in a more detailed understanding of the factors and/or events that have led to their present distributions.