

Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef.

II. Patterns of zonation of mid-shelf and outershelf reefs*

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ABSTRACT: This study describes the patterns of species richness and abundance of herbivorous grazing fishes (Acanthuridae, Scaridae, Siganidae) in 5 zones (reef slope, reef crest, reef flat, lagoon, back reef) of 3 reefs on the mid-continental shelf and of 3 reefs on the outer continental shelf in the central region of the Great Barrier Reef. Herbivorous fishes (all 3 families considered together) occur in assemblages which are characteristic of several major zones and this pattern of zonation is consistent on the 6 reefs. Assemblages in deep, outer-slope zones are distinctive from those in shallow zones. There are distinctive assemblages of herbivorous fishes on reef flats, reef crests and over sandy areas in both lagoon and back reef zones. Similarity in these patterns of zonation between reefs suggests that they will be maintained through time. Families display distinctive patterns of zonation also, but patterns differ between families. Acanthurids and scarids generally have higher numbers of species and individuals on reef crests and in lagoons than on reef flats or reef slopes; siganids have higher numbers of species and individuals in lagoons and back reefs than in the other 3 zones studied. Variation in species richness and abundance of individual families between zones was, however, not consistent among reefs at the same shelf location. Different guilds of herbivorous fishes were distributed differently between zones. Suckers feeding on fine sediments were most abundant near windward and leeward edges of reefs; suckers feeding over sand were most abundant in back reefs and lagoons; large and small croppers and scrapers were more abundant in shallow zones (reef crest, reef flat, lagoon) than in deep zones (reef slope, back reef).

INTRODUCTION

Russ (1984) demonstrated that there is distinct within-reef variation in the composition of assemblages of herbivorous grazing fishes (Acanthuridae, Scaridae, Siganidae) across reefs on the central Great Barrier Reef (GBR). Distinct assemblages are associated with different reef zones. Wells (1954) defined a zone on a coral reef as 'an area where local ecological differences are reflected in the species association and signalized by one or more dominant species'. Done (1983) pointed out that the 'ecological differences' referred to by Wells are largely physical, e.g. light, wave motion and sediment load. The 'species associations' of Wells refer essentially to corals. Done (1982) described the patterns of zonation of corals on the reefs

of the central GBR and recently has provided a comprehensive review of coral zonation (Done, 1983).

It has long been recognized that species of fishes are associated characteristically with particular zones and habitats within coral reefs. This has been documented in various parts of the Pacific such as Hawaii (Gosline, 1965; Jones, 1968; Hobson, 1974), the Johnston Islands (Jones, 1968), the Marshall Islands (Hiatt and Strasburg, 1960), the Tuamotu Archipelago (Harry, 1953), Guam (Jones and Chase, 1975), the Line Islands (Chave and Eckert, 1974), and the Great Barrier Reef (Talbot and Goldman, 1972; Goldman and Talbot, 1976; Hatcher, 1982). It has been described also in the Indian Ocean (Talbot, 1965; Harmelin-Vivien and Bouchon, 1976; Harmelin-Vivien, 1977; Robertson and Polunin, 1981), Red Sea (Bouchon-Navaro, 1980; Bouchon-Navaro and Harmelin-Vivien, 1981) and Caribbean (Clarke, 1977; Gladfelter and Gladfelter, 1978). Patterns of zonation of coral reef fishes have

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been reviewed briefly by Sale (1980). The descriptions of zonation in many of these studies are often not quantitatively rigorous. None that the author is aware of has compared patterns of zonation of coral reef fishes between a number of reefs within a region in order to characterize the range of spatial variability in such patterns. This study describes the patterns of species richness and abundance of herbivorous grazing fishes in 5 zones (reef slope, reef crest, reef flat, lagoon, back reef) of 3 mid-shelf reefs and 3 outershelf reefs in the central GBR.

MATERIALS AND METHODS

Study sites. The study was conducted on 6 reefs on the continental shelf in the central region of the GBR. Three reefs were located on the mid-shelf, approximately 50 km offshore (Rib, John Brewer, Lodestone) and 3 on the outershelf, approximately 100 km offshore (Myrmidon, Dip, Bowl). The locations of these reefs are shown in Fig. 1 of Russ (1984). Five zones were studied within each of these 6 reefs: windward reef slope, windward reef crest, reef flat, lagoon and back reef. Areas studied within reefs, together with a description of the characteristics of each zone are given in Russ (1984). A schematic representation of the 5 zones is given in Fig. 3 of this paper.

Methods. The species of fishes studied, together with a description of the visual census technique are given in Russ (1984). A brief outline of these methods is provided here.

Three families, constituting the vast majority of species of large, herbivorous fishes on coral reefs of the Great Barrier Reef, were studied: the Acanthuridae, Scaridae and Siganidae. A total of 51 species was chosen for detailed examination and each species was assigned to a feeding guild as defined by Hatcher (1983) (see Table 1 of Russ, 1984).

The assemblages of fishes were surveyed using a visual census technique similar to that used by Williams (1982). A census dive consisted of a 30 min swim (using SCUBA) through a zone recording the abundance of each species on a log 3 abundance scale from 1 to 7 (Table 2 of Russ, 1984). All individuals within approximately 5 m of either side of the diver were censused. The abundance of a species was recorded cumulatively throughout a census and all species were censused simultaneously.

Census dives for the reef slope, reef crest and reef flat were unidirectional and parallel to the reef crest while those for the lagoons and back reefs followed a meandering path between bombies. The distance covered by a census dive varied with conditions of wave surge and current but generally ranged between

300 and 400 m, so that the area censused varied between approximately 3,000 and 4,000 m² (300 × 10 m and 400 × 10 m, respectively). All zones on the upper part of the reef (crest, flat, lagoon) were censused within 2 h either side of high tide. This was the only constraint placed upon the time of day when censuses were taken. Censuses were carried out between July and October, 1982. Four replicate, non-overlapping censuses were made once in each zone. Five zones were censused on each of the three mid- and three outershelf reefs making a total of 120 censuses.

Analysis of data. Analysis of the within-reef patterns of abundance of all species of herbivorous fishes combined (Acanthurids, Scarids, Siganids) was carried out using the classification technique described in Russ (1984). Three-factor analyses of variance were carried out on the species richness and log 3 abundance category data for each family (Acanthuridae, Scaridae, Siganidae) and, in the case of abundance categories, for all species combined. The numbers of individual fishes contained within each abundance category are shown in Table 2 of Russ (1984). The abundance of a family in any one census was taken as the sum of the abundance categories for all species within the family. The 3 factors in the analysis were location on the continental shelf (mid-shelf, outershelf), reefs nested within locations (mid-shelf: Rib, John Brewer, Lodestone; outershelf: Myrmidon, Dip, Bowl), and zones within reefs (reef slope, reef crest, reef flat, lagoon, back reef). Throughout the following the term 'reefs nested within locations' will be referred to simply as 'reefs'. Locations and zones were treated as fixed factors and reefs as a random factor (Underwood, 1981). Zones are orthogonal to both the location and reef factors in the analysis. There were 4 replicate censuses taken within each of the combinations of the 3 factors. The total number of degrees of freedom in each 3-factor analysis of variance was 119. The use of log abundance categories summed over all species in a family in an analysis of variance is justified on the basis that it is approximately equivalent to carrying out the analysis on log-transformed actual counts of individuals in that family. Homogeneity of variance for all analyses (at a significance level of $p = 0.05$) was determined using Cochran's test (Winer, 1971). Multiple comparisons of means (at a significance level of $p = 0.05$) were carried out using the Student-Newman-Keuls (SNK) procedure (Winer, 1971). The percentage of the variability in the data accounted for by the various factors in the analyses (the variance component) was calculated according to the procedure in Sokal and Rohlf (1969, p. 263).

Patterns of abundance of 5 feeding guilds (fine sediment suckers, sand suckers, large and small croppers

and scrapers – see Table 1 of Russ, 1984, and Hatcher, 1983) and of selected species are presented graphically. In all graphical presentations the minimum number of individuals in an abundance category, was used as a conservative estimate of abundance rather than using abundance categories. The abundance of a guild or species is expressed as the mean (of 4 replicate censuses) minimum number of individuals per census.

RESULTS

The result of the classification analysis of the abundance of all species of herbivorous fishes considered

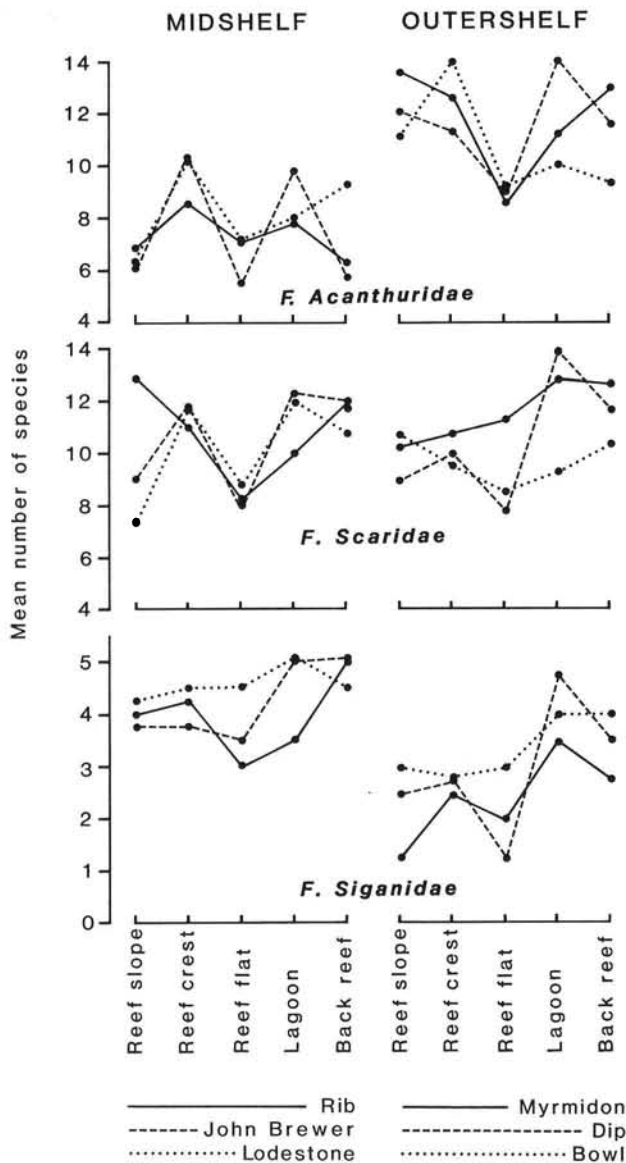


Fig. 1. Mean number of species per census of each family for each location on continental shelf, each reef within these locations, and each zone within these reefs

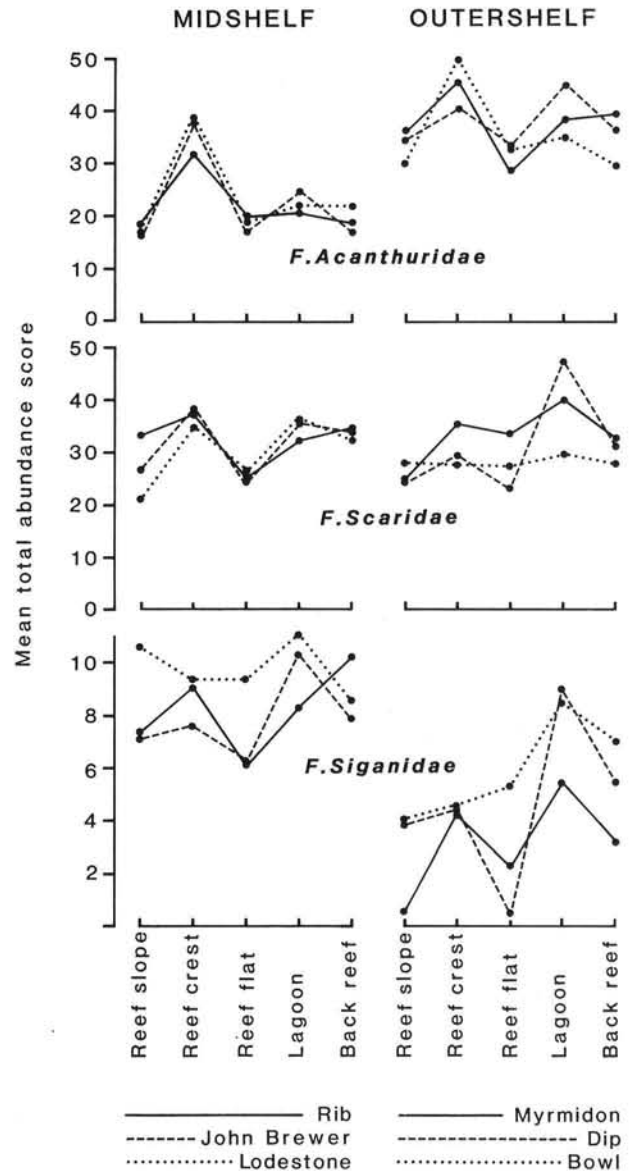


Fig. 2. Abundance of each family (expressed as mean total abundance score per census) for each location on continental shelf, each reef within these locations, and each zone within these reefs

together is given in Fig. 3 of Russ (1984). Results of 3-factor analyses of variance of number of species and of abundance of the 3 families of herbivorous fishes studied are summarized in Table 1. Mean number of species and mean total abundance score of each family for each location on the continental shelf, reef and zone are plotted in Fig. 1 and 2 and results of the Student-Newman-Keuls *a posteriori* multiple comparisons of means from the 3-factor analyses of variance are summarized in Table 2.

There were often significant differences in species richness and abundance between shelf locations and these were consistent among zones (as indicated by the

Table 1. Summary of 3-factor analyses of variance involving number of species and abundance of individuals of 3 families of herbivorous fishes (Acanthuridae, Scaridae, Siganidae) in the Central GBR. Significance of the F-value and the variance component (parentheses) expressed as percentage of the sum of variances for each analysis are given for each factor. Mean values from these analyses are plotted in Fig. 1 and 2, and analyzed by Student-Newman-Keuls procedure in Table 2

Source of variation	Degrees of freedom of F ratio	Number of Species			Abundance			All 3 families
		Acanthuridae	Scaridae	Siganidae	Acanthuridae	Scaridae	Siganidae	
Location on Shelf	1,4	** (53 %)	ns (0 %)	* (38 %)	*** (56 %)	ns (0 %)	* (46 %)	** (21 %)
Reefs (Locations)	4,90	ns (1 %)	*** (20 %)	** (5 %)	ns (0 %)	** (6 %)	*** (8 %)	ns (0 %)
Zones	4,90	*** (12 %)	*** (20 %)	*** (16 %)	*** (25 %)	*** (34 %)	*** (13 %)	*** (43 %)
Location × Zones	4,16	ns (2 %)	ns (2 %)	ns (2 %)	ns (2 %)	ns (5 %)	ns (1 %)	ns (5 %)
Reefs (Locations) × Zones	16,90	** (9 %)	*** (22 %)	ns (5 %)	*** (7 %)	*** (20 %)	ns (4 %)	*** (10 %)
Residual		(22 %)	(36 %)	(34 %)	(10 %)	(35 %)	(28 %)	(21 %)

Significance levels: * 0.05 > P > .01; ** 0.01 > P > 0.001; *** P < 0.001; ns P > 0.05

lack of any significant location by zone interactions) (Table 1). The 3 families displayed different patterns of cross-shelf change in both number of species and number of individuals. Acanthurids had a significantly higher species richness and number of individuals on the outershelf than on the mid-shelf. The number of species and individuals of the scarids did not differ significantly across the shelf. Siganids had a significantly higher number of species and individuals on the mid-shelf than on the outershelf (Tables 1 and 2; Fig. 1 and 2).

There were significant differences between zones also, as anticipated in the previous study (Russ, 1984), and between reefs within locations (Table 1). Because the zone by reef interaction was not significant in the analyses of siganids (Table 1), general statements of differences among reefs can be made by pooling mean reef values across all zones. Similarly, differences among zones can be compared by pooling mean zone values across all reefs. On the mid-shelf reefs the number of species and number of individuals of siganids was significantly higher at Lodestone than at Rib reef and the number of individuals of siganids was significantly higher at Lodestone than at John Brewer reef (Table 2). On the outershelf reefs the number of species and individuals of siganids was significantly higher at Bowl and Dip reefs than at Myrmidon Reef (Table 2). The lagoon had a significantly higher number of species of siganids than reef slope, reef crest and reef flat, whilst the back reef had a significantly higher number of species of siganids than the reef crest and reef flat (Table 2). The lagoon had a significantly higher abundance of siganids than all other zones, there was a significantly higher number of individuals

of this family in the back reef than on the reef slope and reef flat, and a significantly higher abundance of siganids on the reef crest than on the reef flat (Table 2).

Analysis of the acanthurid and scarid data, unlike that of siganids, demonstrated significant zone by reef interactions, indicating that patterns of zonation varied significantly among reefs at the same location. The SNK comparisons of means indicate the complexity of these patterns (Table 2). One general trend was, however, for a higher number of species and individuals of acanthurids and scarids on the reef crests and in the lagoons than on the reef flats and reef slopes for both mid- and outershelf reefs (Table 2; Fig. 1 and 2).

The relative contributions of the three factors (locations on shelf, reefs and zones) in the analyses, together with their appropriate interactions, varied considerably between families (Table 1). Location on the shelf provided a major contribution to the overall variance in the data sets for acanthurids and siganids but contributed virtually nothing to the data set for scarids (Table 1). The variance component for reefs was small in all analyses apart from that for the number of species of scarids (Table 1). The variance component for zones was relatively high in all but the analyses of number of species of acanthurids and number of individuals of siganids (Table 1). The location by zone interaction contributed very little to the overall variance in all analyses, as did the reef by zone interaction, with the exception of the analyses for the scarids (Table 1).

Tables 1 and 2 provide a summary of an analysis of abundance of large, herbivorous grazing fishes pooled over all 3 families. There was a significantly higher number of individuals of these fishes on the outershelf

Table 2. A. *posteriori* multiple comparisons of means from the 3-factor analyses of variance shown in Table 1. Student-Newman-Keuls procedure was used; significance level for all comparisons was $p < 0.05$. Locations: M = mid-shelf, O = outershelf. Reefs: Rib = Rib Reef, Lod = Lodestone Reef, J. B. = John Brewer Reef, Myr = Myrmidon Reef, Dip = Dip Reef, Bowl = Bowl Reef. Zones: S = reef slope, C = reef crest, F = reef flat, L = lagoon, B = back reef

FACTOR	NUMBER OF SPECIES					ABUNDANCE				All 3 families
	Acanthuridae	Scaridae	Siganidae	Acanthuridae	Scaridae	Siganidae	Scaridae	Siganidae	All 3 families	
Location	M < O	M = O	M > O	M < O	M = O	M > O	M = O	M > O	M < O	M < O
Reefs (Locations)	Mid-shelf	Lod > JB (B)	Rib > JB, Lod (S)	Lod > Rib			Rib > Lod, JB (S)	Lod > JB, Rib	No significant differences between reefs for any zones	No significant differences between reefs for any zones
	Outershelf	Bowl > Dip (C) Dip > Bowl (L) Myrs > Bowl (B)	Myr > Dip, Bowl (F) Dip, Myr > Bowl (L)	Bowl, Dip > Myr			Myr > Dip, Bowl (C) Myr > Dip (F) Dip > Bowl, Myr (L) Myr > Bowl (L)	Bowl, Dip > Myr	Dip > Myr, Bowl (L)	
Zones	Mid-shelf	C, L > S, F, B (JB) C > S, F (Lod)	S, C, B > F (Rib) C, L, B > S, F (JB) C, L > S, F (Lod)				C > F (Rib) C, L, B > S, F (JB) C, L > S, F (Lod) B > S (Lod)			C > S, F, L, B (Rib) C > S, F, L, B (JB) L > S, F, B (JB) C > S, F, L, B (Lod) L > S, F (Lod) B > S (Lod)
	Outershelf	S, C, L, B > F (Myr) L > F (Dip) C > S, F, L, B (Bowl)	L > S, C, F, B (Dip) B > F (Dip)	L > S, C, F B > C, F			C > S, F (Myr) S, L, B > F (Myr) L > S, F (Dip) C > S, F, L, B (Bowl)	C, F, L, B > S (Myr) L > S, C, F, B (Dip)		C > S, F (Myr) L > S, F (Myr) B > S, F (Myr) L > S, C, F, B (Dip) C > S, F (Dip) B > F (Dip) C > S, F, B (Bowl)

than on the mid-shelf (Tables 1 and 2). There was a significant interaction between reefs and zones (Table 1) making the comparisons of means for these 2 factors complex (Table 2). In general there was very little difference in abundance of these fishes between reefs within a location and a higher abundance on reef crests and in lagoons than on reef flats and reef slopes for both mid- and outershelf reefs (Table 2). Zones accounted for a very high proportion of the variability in this set of data, with the location on the shelf contributing a high proportion also (Table 1).

Each species was assigned to a feeding guild as defined by Hatcher (1983). Table 3 indicates the feeding guild to which each of the abundant species was assigned. A complete list of species and their modes of feeding are provided in Table 1 of Russ (1984). The patterns of abundance within reefs of 5 guilds of herbivorous fishes in the three families studied are shown in Fig. 3. The suckers feeding upon fine sediments

There appears to be a higher abundance of these suckers on the exposed side of the reef than on the sheltered side, particularly on the mid-shelf reefs. The suckers feeding over sandy substrata (many of the larger species of *Acanthurus* including 'mata', plus 2 species of scarid – see Table 1 of Russ, 1984) are far more abundant in the lagoon and back reef than in the other three zones studied and are more abundant on outershelf than mid-shelf reefs (Fig. 3). The large cropers (including all species of siganids, most species of *Naso* and *Acanthurus lineatus* – see Table 1 of Russ, 1984) have a distinct peak in abundance on the reef crest (Fig. 3). Small cropers (including *Acanthurus nigrofuscus* and *A. triostegus*) are far more abundant on outershelf than mid-shelf reefs (Fig. 3). They are more abundant in the shallow zones, particularly the reef flat and reef crest, than the deep zones. The scrapers (most species of scarids) are abundant in all zones, with a tendency toward a higher abundance in the shallow zones (reef crest, reef flat, lagoon) than the deep zones (reef slope, back reef). The patterns of abundance of the guilds of suckers and cropers often were influenced strongly by the patterns of abundance of particular species, e.g. *Acanthurus 'mata'*, *A. lineatus*, *A. nigrofuscus*, *Ctenochaetus* spp.

Patterns of abundance within reefs of 12 common species of herbivorous grazing fishes are shown in Fig. 4 to 6. These figures provide examples of the wide range of patterns of within-reef abundance observed in

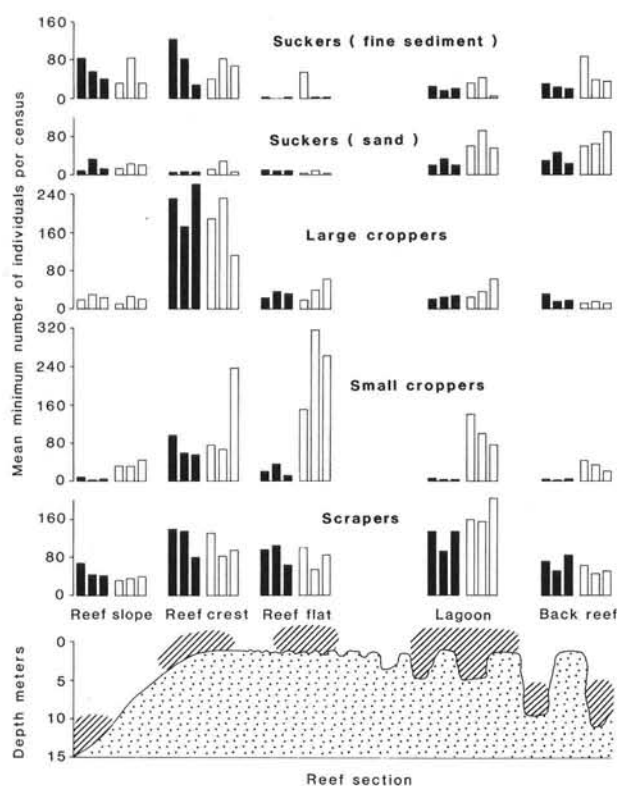


Fig. 3. Abundance of 5 guilds of herbivorous fishes in 5 zones of 6 reefs. Abundance expressed as mean minimum number of individuals per census. For each zone, mid-shelf reefs (black bars) are from left to right: Rib, John Brewer and Lodestone; outershelf reefs (white bars) are from left to right: Myrmidon, Dip and Bowl

(*Ctenochaetus striatus* and *C. binotatus*) are most abundant in the reef slope, reef crest and back reef zones and occur in very low abundance on the reef flat (with the exception of the reef flat at Myrmidon Reef).

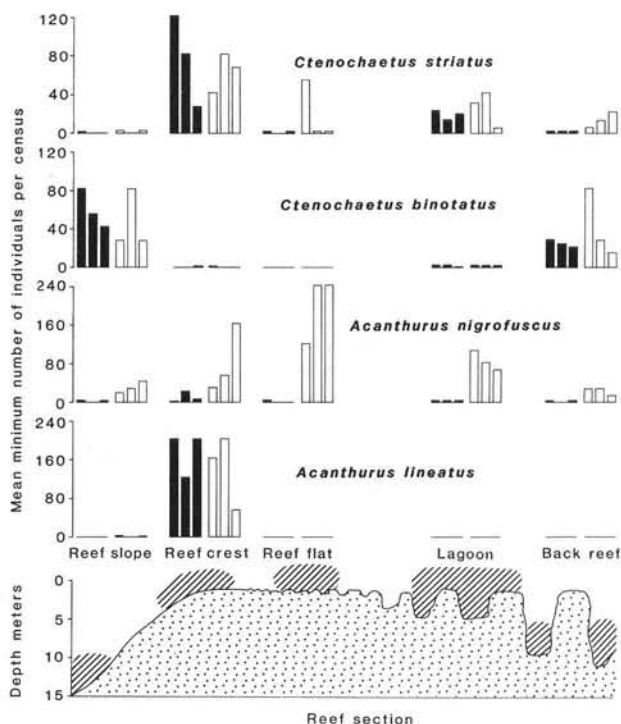


Fig. 4. Abundance of 4 species of herbivorous fishes in 5 zones of 6 reefs. For further explanation see legend to Fig. 3

Table 3. Herbivorous grazing fishes characteristic of zones and locations in central Great Barrier Reef, and feeding guild to which each species was assigned. SS = sand sucker, SFS = sucker of fine sediments, SC = small cropper, LC = large cropper, S = scraper

Inshore	Zones	Mid-shelf (M) + Outershelf (O)
No distinct patterns of zonation in the structure of the reefs	Reef slope (12–15 m)	<i>Ctenochaetus binotatus</i> (SFS) <i>Scarus sordidus</i> (S) <i>S. niger</i> (S) <i>S. schlegeli</i> (SS?) M: <i>Naso unicornis</i> (LC), <i>Siganus corallinus</i> (LC) O: <i>Acanthurus nigrofuscus</i> (SC), <i>Naso lituratus</i> (LC), <i>Acanthurus 'mata'</i> (SS)
Characteristic species: <i>Scarus rivulatus</i> (S) <i>Acanthurus 'mata'</i> (SS) <i>A. dussumieri</i> (SS) <i>Siganus doliatus</i> (LC)	Reef crest	M: – O: <i>Acanthurus nigrofuscus</i> (SC), <i>A. glaucoparietus</i> (SC), <i>Acanthurus 'mata'</i> (SS)
	Reef flat	M: <i>Scarus rivulatus</i> (S), <i>S. globiceps</i> (S) <i>Siganus doliatus</i> (LC) O: <i>Acanthurus nigrofuscus</i> (SC)
	Lagoon	M: <i>Scarus rivulatus</i> (S), <i>S. globiceps</i> (S), <i>Siganus doliatus</i> (LC) O: <i>Hipposcarus longiceps</i> (S), <i>Acanthurus 'mata'</i> (SS), <i>Scarus brevifilis</i> (S), <i>Acanthurus nigrofuscus</i> (SC), <i>Scarus oviceps</i> (S)
	Back reef (8–12 m)	M: <i>Scarus rivulatus</i> (S), <i>S. flavipectoralis</i> (SS?) O: <i>Acanthurus nigrofuscus</i> (SC), <i>A. 'mata'</i> (SS), <i>Naso lituratus</i> (LC), <i>Scarus brevifilis</i> (S)

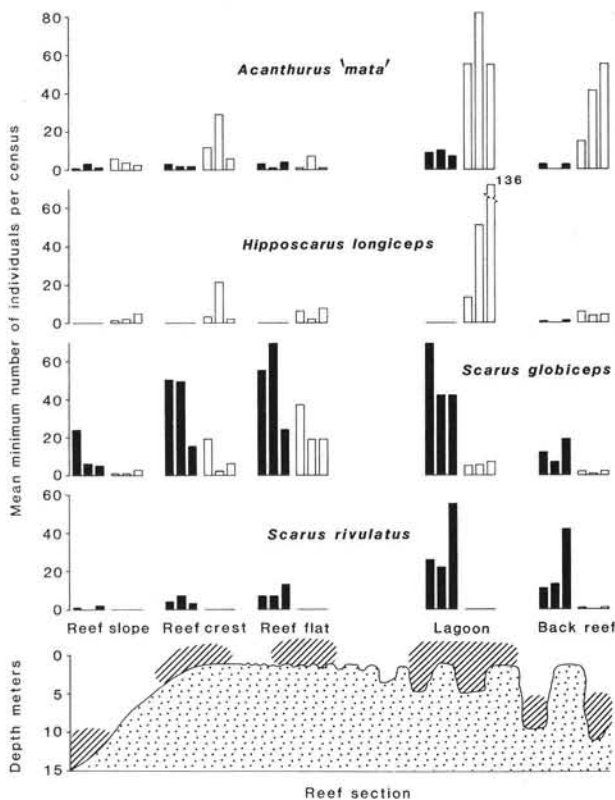


Fig. 5. Abundance of 4 species of herbivorous fishes in 5 zones of 6 reefs. See also legend to Fig. 3

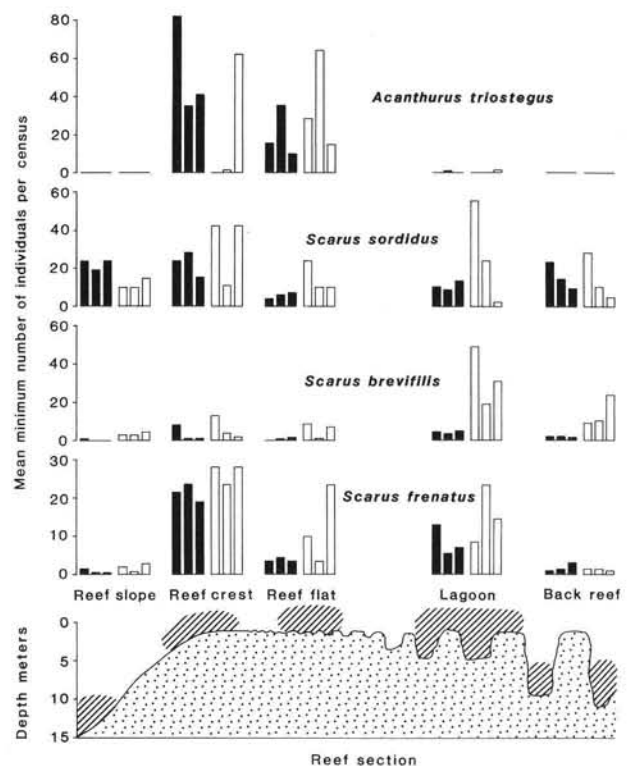


Fig. 6. Abundance of 4 species of herbivorous fishes in 5 zones of 6 reefs. See also legend to Fig. 3

this study*. The following generalizations about the patterns of abundance of species both within reefs and at different locations on the shelf are based on such data. Some species are abundant in only 1 or 2 zones: *Ctenochaetus binotatus* (reef slope, back reef), *Acanthurus lineatus* (reef crest), *Hipposcarus longiceps* (lagoon), *Acanthurus triostegus* (reef crest, reef flat), *Scarus brevifilis* (lagoon, back reef), *Scarus flavipectoralis* (back reef), *Scarus oviceps* (lagoon), *Acanthurus nigricauda* (back reef). Other species have a peak in abundance in 1 or a few zones also but are commonly present in many zones, e.g. *Acanthurus nigrofuscus*, *Acanthurus 'mata'*, *Scarus rivulatus*, *Scarus psittacus*. A few species are almost equally abundant in all zones, e.g. *Scarus sordidus*, *Naso unicornis*, *S. gibbus*. Certain species are most abundant in the shallow zones (*Ctenochaetus striatus*, *Scarus globiceps*, *S. frenatus*), the deep zones (*Ctenochaetus binotatus*, *Scarus flavipectoralis*, *S. niger*) or are frequently associated with sandy habitats (*Scarus schlegeli*, *S. flavipectoralis*, *Acanthurus nigricauda*). On the basis of their relative abundance species can be defined as characteristic of mid- or outershelf locations also. Species characteristic of mid-shelf reefs are *Scarus globiceps* (Fig. 5), *S. rivulatus* (Fig. 5), *S. flavipectoralis*, *Siganus corallinus* and *S. doliatus* (see Fig. 6 of Russ, 1984). Species which are characteristic of outershelf reefs are *Acanthurus nigrofuscus* (Fig. 4), *A. 'mata'* (Fig. 5), *Hipposcarus longiceps* (Fig. 5), *Scarus brevifilis* (Fig. 6), *S. oviceps*, *Acanthurus glaucoparietus* and *Naso lituratus*. Table 3 shows the species which are characteristically abundant in particular zones within reefs at different locations on the continental shelf based upon the generalizations above. This table includes species which are characteristic of a set of 3 inshore reefs referred to in a companion paper (Russ, 1984).

DISCUSSION

This study and that of Russ (1984) have demonstrated that herbivorous fishes occur in assemblages which are characteristic of several major zones and this pattern of zonation is consistent for 6 reefs in the central GBR. The assemblages of herbivorous fishes in the deep, outer-slope zones are very distinct from those in the shallow zones (see Fig. 3 of Russ, 1984). The assemblages of herbivorous fishes on the reef flats tend to have relatively low numbers of species and individuals (Fig. 1 and 2). There are very distinctive assemblages of herbivorous fishes on the wave exposed reef crest and over areas of sandy substratum in both the lagoon

and back reef zones (Table 3 and Fig. 3 of Russ, 1984). The similarity in the patterns of zonation of herbivorous fishes on replicate reefs (Fig. 3 of Russ, 1984) suggests that these patterns are likely to be maintained through time.

The 3 families of fishes examined (Acanthuridae, Scaridae, Siganidae) display very different patterns of both between zone and cross-shelf change in number of species and individuals (Table 2). The acanthurids and scarids generally have higher numbers of species and individuals on the crests and in the lagoons than on the reef flat or the reef slope, whereas siganids have higher numbers of species and individuals in the lagoon and back reef areas than in the other 3 zones studied (Table 2). There was a significantly higher number of species and individuals of acanthurids on outershelf than mid-shelf reefs, a significantly higher number of species and individuals of siganids on mid-shelf than on outershelf reefs and no significant cross-shelf change in either parameter was detected for scarids (Tables 1 and 2). These results are consistent with those of Williams (1982) and Williams and Hatcher (1983) who reported distinctly different patterns of cross-shelf distribution of a large number of different families of coral reef fishes.

The variation in species richness and abundance of the 3 families between zones was not consistent for all reefs nested within locations (Fig. 1 and 2). These zone by reef interactions were significant (though they did not often account for a high component of the overall variance) for the acanthurids and scarids and for the abundance of all species combined (Table 1), producing a complex set of comparisons of means (Table 2). A high degree of variation in juvenile recruitment within the same zones on different reefs may account largely for these significant zone by reef interactions recorded in Table 2. No studies have documented the differences, if any, in juvenile recruitment of coral reef fishes for the same zone on different reefs but Williams (1982) has suggested that, at this spatial scale, such variability is likely to have a major effect on differences between the assemblages of the adult fishes. Williams (1980), Doherty (1982, 1983) and Victor (1983) have all suggested that the local abundance of coral reef fishes may be a function largely of the availability of recruits from the plankton rather than the availability of a resource such as space.

A number of studies of the distribution and abundance of herbivorous fishes within coral reefs have been made. In the list of references on zonation of coral reef fishes given in the introduction, all but three (Harmelin-Vivien and Bouchon, 1976; Clarke, 1977; Bouchon-Navaro, 1980) provide information on within-reef distributions of herbivorous fishes. The descriptions of zonation in many of these studies are not

* Similar figures for other species are available from the author on request

quantitatively rigorous. Furthermore, none of the studies (with the exception of the largely descriptive ones of Hiatt and Strasburg, 1960 and of Jones, 1968) have included a comparison of the pattern of zonation of fishes with that of other reefs nearby to establish the regional consistency of the zonation pattern. All these studies document distinctive differences in the assemblages of herbivorous fishes associated with different zones on coral reefs. Most of the studies demonstrate that the assemblages of herbivorous fishes on deep outer slopes are distinctive from those on shallow, inner reef zones such as the lagoon and reef crest. Some studies show that the shallow (often intertidal) reef flat supports relatively low numbers of species and individuals of herbivorous fishes (e.g. Talbot, 1965; Talbot and Goldman, 1972; Chave and Eckert, 1974; Goldman and Talbot, 1976). Other studies have demonstrated that distinctive assemblages of fishes often are associated with areas of high wave action (e.g. Jones, 1968; Hobson, 1974; Robertson and Polunin, 1981) or areas of sandy substratum in sheltered habitats (e.g. Hiatt and Strasburg, 1960; Jones, 1968; Chave and Eckert, 1974; Jones and Chase, 1975).

Various studies have quantified rates of grazing by herbivorous fishes in various habitats of coral reefs. Hatcher (1982) and Hatcher and Larkum (1983) concluded that fishes, particularly acanthurids and scarids, were the dominant herbivorous grazers in the outer reef habitats of One Tree Reef (Southern GBR) and that the yield of the epilithic algal community to grazing organisms was of the order of 50 % of the net daily primary production. Hatcher (1982) recorded the highest yields of algae to grazers on the reef crest and reef slope and low yields in the lagoon. Using a field bioassay technique Hay (1981), Hay and Goertemiller (1983) and Hay et al. (1983) concluded that herbivorous fishes were responsible for up to 90 % of the grazing intensity on a series of reefs in the Caribbean and that grazing intensity was significantly higher in shallow (1 to 10 m) reef slopes than on deep (30 to 40 m) reef slopes or on shallow reef flats. The results of the present study suggest that rates of grazing by herbivorous fishes are likely to be higher on the reef crests and in the lagoons than on reef flats and reef slopes of reefs on the mid- and outer continental shelf in the central GBR. The high abundances of herbivorous fishes in the lagoons of these reefs compared with One Tree Reef (Hatcher, 1982) are likely to be related to the deeper and more enclosed nature of the One Tree Lagoon. The results suggest also that rates of grazing by herbivorous fishes may be higher on outershelf than mid-shelf reefs. Such contentions require experimental verification.

A great deal more research is required to elucidate the factors determining patterns of zonation in coral

reef fishes. One proximal factor determining such patterns is likely to be habitat selection by fishes at the time of or after settlement. Williams (1979, 1980) and Williams and Sale (1981) have demonstrated that fishes are particularly adept at selecting the habitat in which to settle. A variety of environmental factors such as exposure to wave action, illumination, depth, and type of substratum, could be used as cues during selection of a habitat. Differential survivorship after settlement is another factor which may be important in determining the patterns reported here but this is more likely to be an ultimate rather than a proximal determining factor. Interspecific interactions (e.g. competition for space or food) could cause the observed patterns of zonation by influencing patterns of settlement and survivorship after settlement but there is very little evidence to support this contention.

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LITERATURE CITED

- Bouchon-Navaro, Y. (1980). Quantitative distribution of the Chaetodontidae on a fringing reef of the Jordanian coast (Gulf of Aqaba, Red Sea). *Tethys* 9: 247–251
- Bouchon-Navaro, Y., Harmelin-Vivien, M. L. (1981). Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Mar. Biol.* 63: 79–86
- Chave, E. H., Eckert, D. B. (1974). Ecological aspects of the distributions of fishes at Fanning Island. *Pacif. Sci.* 28: 297–317
- Clarke, R. D. (1977). Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* 40: 277–289
- Doherty, P. J. (1982). Coral reef fishes: recruitment limited assemblages? *Proc. 4th Int. Coral Reef Symp.* 2: 465–470
- Doherty, P. J. (1983). Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176–190
- Done, T. J. (1982). Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95–107
- Done, T. J. (1983). Coral zonation: its nature and significance. In: Barnes, D. J. (ed.) *Perspectives on coral reefs*. Australian Institute of Marine Science, Townsville, Australia, p. 107–147
- Gladfelter, W. B., Gladfelter, E. H. (1978). Fish community structure as a function of habitat structure on West Indian patch reefs. *Rev. Biol. Trop.* 26 (Suppl. 1): 65–84
- Goldman, B., Talbot, F. H. (1976). Aspects of the ecology of coral reef fishes. In: Jones, O. A., Endean, R. (ed.) *Biology*

- and geology of coral reefs, Vol. III, Biology 2. Academic Press, New York, p. 125–154
- Gosline, W. A. (1965). Vertical zonation of inshore fishes in the upper layers of the Hawaiian Islands. *Ecology* 46: 823–831
- Harmelin-Vivien, L. (1977). Ecological distributions of fishes on the outer slope of Tulear Reef (Madagascar). *Proc. 3rd Coral Reef Symp.* 1: 289–296
- Harmelin-Vivien, M. L., Bouchon, C. (1976). Feeding behaviour of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). *Mar. Biol.* 37: 329–340
- Harry, R. R. (1953). Ichthyological field data of Raroia Atoll, Tuamotu Archipelago. *Atoll Res. Bull.* 18: 1–190
- Hatcher, B. G. (1982). The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. *Proc. 4th Int. Coral Reef Symp.* 2: 515–529
- Hatcher, B. G. (1983). Grazing in coral reef ecosystems. In: Barnes, D. J. (ed.) *Perspectives on coral reefs*. Australian Institute of Marine Science, Townsville, Australia, p. 164–179
- Hatcher, B. G., Larkum, A. W. D. (1983). An experimental analysis of factors controlling standing crop of the epilithic algal community on a coral reef. *J. exp. mar. Biol. Ecol.* 69: 61–84
- Hay, M. E. (1981). Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat. Bot.* 11: 97–109
- Hay, M. E., Goertemiller, T. (1983). Between habitat differences in herbivore impact on Caribbean coral reefs. In: Reake, M. L. (ed.) *The ecology of deep and shallow reefs*. Symposia Series for Undersea Research, Vol. 1. Office of Undersea Research, NOAA, Rockville, Maryland, p. 97–102
- Hay, M. E., Colburn, T., Downing, D. (1983). Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia (Berl.)* 58: 299–308
- Hiatt, R. W., Strasburg, D. W. (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30: 65–127
- Hobson, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs on Kona, Hawaii. *Fish. Bull. U. S.* 72: 915–1031
- Jones, R. S. (1968). Ecological relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes). *Micronesica* 4: 309–361
- Jones, R. S., Chase, J. H. (1975). Community structure and distribution of fishes in an enclosed high island lagoon in Guam. *Micronesica* 11: 127–148
- Robertson, D. R., Polunin, N. V. C. (1981). Co-existence: symbiotic sharing of feeding territories and algal food by some coral reef fishes from the western Indian Ocean. *Mar. Biol.* 62: 185–195
- Russ, G. R. (1984). The distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Progr. Ser.* 20: 23–34
- Sale, P. F. (1980). The ecology of fishes on coral reefs. *Oceanogr. mar. Biol. A. Rev.* 18: 367–421
- Sokal, R. R., Rohlf, F. J. (1969). *Biometry*. W. H. Freeman and Co., San Francisco
- Talbot, F. H. (1965). A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa), and its fish fauna. *Proc. Zool. Soc. Lond.* 145: 431–470
- Talbot, F. H., Goldman, B. (1972). A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef System. *Proc. Symp. Corals and Coral Reefs. Mar. Biol. Ass. India*, p. 425–443
- Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. mar. Biol. A. Rev.* 19: 513–605
- Victor, B. C. (1983). Recruitment and population dynamics of a coral reef fish. *Science, N. Y.* 219: 419–420
- Wells, J. W. (1954). Recent corals of the Marshall Islands. *U. S. Geol. Surv. Prof. Pap.* 260-I: 285–486
- Williams, D. McB. (1979). Factors influencing the distribution and abundance of pomacentrids (Pisces: Pomacentridae) on small patch reefs in the One Tree Lagoon (Great Barrier Reef). Ph. D. thesis, University of Sydney
- Williams, D. McB. (1980). Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bull. mar. Sci.* 30: 159–170
- Williams, D. McB. (1982). Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1: 35–43
- Williams, D. McB., Sale, P. F. (1981). Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within 'One Tree Lagoon', Great Barrier Reef. *Mar. Biol.* 65: 245–253
- Williams, D. McB., Hatcher, A. I. (1983). Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Progr. Ser.* 10: 239–250
- Winer, B. J. (1971). *Statistical principles in experimental design*, 2nd ed. MacGraw-Hill Kogakusha, Tokyo

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