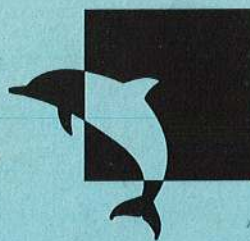


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A STUDY OF THE INTERHABITAT
DIFFERENCES WITHIN THE CORAL REEF FISH
COMMUNITY ON AND AROUND THE
BELIZEAN BARRIER REEF, BELIZE, CENTRAL
AMERICA.

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BIOLOGY DEGREE (BSc. Hons.) AT SOUTHAMPTON UNIVERSITY.

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ABSTRACT.

The degree of interhabitat differences within the coral reef community in 12 zones on the Belizean Barrier Reef, Belize was examined. The study used 69 common, visually obvious fish species, recorded by SCUBA divers using a semi-quantitative scoring scale. Patterns in the community structure of the fish species richness and total abundance were correlated to several independent variables: site, coral species richness and total abundance, depth, length and algal coverage. The stations within each habitat type were found to be sufficiently homogeneous for comparison. Significant differences in species richness were found between many of the habitats, including adjacent coralline zones, such as the inner and outer forereef.

Apart from the site variable which incorporates elements of all the independent variables, this pattern was best explained by the coral species richness variable, which was interpreted as a measure of habitat complexity. However, the remaining independent variables, and others not quantified, such as wave action, are likely to have a rôle in determining the distribution of the fish species. The differences in these univariate measures of the fish community were not manifested as highly distinct assemblages, as measured by multivariate analysis. Gross differences of assemblages were found between coralline and non-coralline habitats, but total separation of coralline zones was restricted to assemblages of the patch reefs and the inner forereef. The lack of species individual counts is likely to have caused the differences between this and other work.

Trophic structures were also examined, with significant differences found between certain habitats with respect to particular groups. Reasons for these differences were suggested on the basis of food resource differences. There was also an indication of gross ecological differences, as measured by species rank diagrams, in the more species rich inner forereef habitat. The results of the study were then interpreted in view of the debate about the mechanisms maintaining reef fish diversity. The limited degree of distinct fish assemblages, and the increased richness with habitat complexity are interpreted as being consistent with competitive hypotheses, although the data was not accurate enough to support classical or lottery ideas.

1.INTRODUCTION.

"To do science is to search for repeated patterns, not simply to accumulate facts".

MacArthur (1972).

1.1.A SUMMARY OF THE HYPOTHESES OF THE PROCESSES MAINTAINING REEF FISH DIVERSITY.

Coral reefs are well known for their bewildering diversity, complexity and productivity. This is particularly true for the coral reef fish which are the most obvious aspect of the biota to even the most casual observer. Sale (1977) reports that the Great Barrier Reef is occupied by approximately 1500 species and Smith and Tyler (1972) found 75 species on a single patch reef only three metres in diameter.

The processes maintaining this diversity have been the source of great debate for ecologists. The early work (for example Stephenson and Searles, 1960; Randall, 1961, 1965) suggested that the fish community was an equilibrial, competitively organized system. Thus the fish diversity appeared to be maintained by fine-scale partitioning of the resources which reduces niche overlap and competition, allowing coexistence. These views of the fish ecology complying with classical competition theory (*sensu* Hutchinson, 1959) fitted in well with the general ecological thoughts of the time, which was based on communities being structured by competitive interactions (MacArthur, 1972). Furthermore the work was consistent with the data obtained for the gastropod genus *Conus* (Kohn, 1968, 1971; Kohn and Nybakken,

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1975), which showed low overlaps of the feeding niches, with each species concentrating on a different prey species. There was even evidence of intraspecific partitioning in *C. ebraeus*. Indeed Goldman and Talbot (1976) stated that "Coral reefs are the epitome of mature, biologically accommodated communities.".

These views were then questioned by small scale experiments, particularly by Sale (Sale 1978, 1979; Sale and Dybdahl, 1975, 1978), who showed little temporal constancy and microhabitat partitioning. This led to the lottery hypothesis (Sale, 1977, 1982; Chesson and Warner, 1981) which argued that the coexistence of species was due to a "lottery" for living space in which the pelagic larvae are "tickets" and that the first arrival "wins" that site. This stochastic element of space allocation and the apparent decoupling of present competitive success from future recruitment by individuals of that species, means that any interspecific competition cannot lead to competitive exclusion and distinct niches of the species over time. The theory rapidly grew in importance, even though there was mathematical criticism (Abrams, 1984) and concern over the scale of the experiments used to support the hypothesis (for example, Anderson *et al*, 1981). Furthermore it sparked great research and a fruitless debate (for example, Anderson *et al.*, 1981; Sale and Williams, 1982) as to the correct hypothesis, since the two ideas, although both competitively mediated, are fundamentally different. The lottery hypothesis predicts one resource limiting the total density of several competitively equal species whilst the classical hypothesis requires n limiting resources for the coexistence of n species. Obviously there are not as many resources as fish species and so for this second theory continuously varying resources, such as food particle size, are viewed as potentially an infinite number of size classes,

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each of which can be considered as separate resources. However, since it takes a finite amount of resource to sustain a population there is a fixed maximum number of species (Clarke, 1977).

The lottery hypothesis assumes space to be the limiting factor on a reef, based on a number of lines of evidence, such as the rapid recolonization of artificial and denuded reefs (Randall, 1965; Sale and Dybdahl, 1975, 1978; Talbot *et al.*, 1978) and the constancy of numbers in specialized habitats such as anemones (Ross, 1978). However, food availability is another possible limiting resource, and although evidence is harder to obtain it can be implied from any partitioning, such as that found by Roughgarden (1974) when reanalyzing Randall's 1967 data. He found a prey-size axis between within the groupers and hamlets (Serranidae), with, for example, the large *Epinephelus itajara* taking the largest prey. A similar pattern was found in the nocturnally active, benthic-crustacean-feeding guild where the overall feeding overlap was 0.13 on average (Gladfelter and Johnson, 1983). When this evidence is combined with fine-scale spatial partitioning that has been found, especially among small, cryptic species (Greenfield, 1975; Greenfield and Greenfield, 1982) and territorial species (Robertson and Lassig, 1980), there certainly seems to be a large component of competitively mediated coexistence. It therefore seems that both theories are certainly partly correct, perhaps in different areas or species, and may even not be mutually exclusive due to the size scale that each is focusing on. Very small scale fluxes may average out across a community to give an overall picture of constancy (Brock *et al.*, 1979). The debate has now shifted to a more dynamic question of "to what degree are precise niche parameters and to what degree

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are chance events responsible for the structure of any given coral reef assemblage?" (Clarke, 1988).

The situation has been further complicated by recent ideas that competition *per se* is unimportant because of recruit limitation to the reef. Unknown processes in the plankton may limit the larval availability and thus the carrying capacity of the reef, the point where competition begins, is usually not reached (Mapstone and Fowler, 1988). Thus diversity is maintained by stochastic processes based on settlement from the plankton (Sale, 1980; Doherty, 1982, 1983; Victor, 1983). Clear evidence has yet to be collected, especially on whether recruitment and post-recruitment dynamics are truly density-independent as expected in an undersaturated environment. Furthermore all the general hypotheses must be balanced against more specific processes maintaining coexistence such as predation pressure (reviewed by Hixon, 1991), aggressiveness and size based dominance (Robertson, 1984) and "money-in-the-bank" refuge strategies (Sale, 1975; Dale, 1978).

1.2. THE SEARCH FOR EVIDENCE.

Testing unambiguously for any type of competitive processes on coral reefs is extremely difficult, and this is true in all ecological communities (Connell, 1975; Weins, 1984; Salt, 1984), often due to the statistical problems of showing that the community is different from randomly generated assemblages (Moulton and Pimm, 1987). However, it is easier to collect, or not as the case may be, consistent evidence. One method of doing this is searching for patterns across the community. Species are well known to be unevenly distributed (Williams, 1991), but if distinct

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assemblages can be found in clearly defined habitats within a community then it is possible to hypothesize about the presence of broad scale resource partitioning, which may be evidence of present day competition or the result of evolutionary adaptations, the "ghost of competition past" (*sensu* Connell, 1980). This technique has been used in terrestrial systems, especially in bird communities (for example, Diamond, 1975). Such results will be especially significant if there is habitat segregation in an area where the distributions of different species are known to overlap.

Finding such distinct habitats in the system is very easy, since physiographic zonation is a striking feature of all coral reefs (Done, 1983). Furthermore the zonation patterns of Caribbean reefs have been well described by a number of workers (Goreau, 1959; Stoddard, 1969; Glynn, 1973; Milliman, 1973). These major reef zones have also been shown to differ predictably from each other in terms of a number of factors such as topographic complexity (Risk, 1972; Talbot and Goldman, 1972; Gladfelter and Gladfelter, 1978; Luckhurst and Luckhurst, 1978), depth (Stark, 1968; Colin, 1974) and water movement and quality (Stark, 1968).

The search for broad scale patterns has mostly been conducted in the Pacific (Jones and Chase, 1975; Talbot and Goldman, 1972; Goldman and Talbot, 1976; Anderson *et al*, 1981; Fowler, 1988). These studies all described patterns at a variety of scales and taxonomic levels, but the best data is for the chaetodontids. For example Anderson *et al* (1981) studied their distribution and found conspicuous differences in the niches of most of the species that coexist locally, and geographical replacement between species from the same niche across a 50-km transect. The data was compared to the similar situations found by terrestrial vertebrate ecologists (for example

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Diamond, 1975). Fowler (1988) found the eight abundant species of butterflyfish to be widely distributed among the zones, while 11 out of 14 rarer species were highly restricted in distribution. Further patterns have been observed in the deeper waters of the outer reef slopes down to 400-m, with distinct distributions of species that can be characterized according to depth and substrate type (Mead, 1979).

Similar data for the Caribbean is more sparse, and only three studies have investigated broad-scale partitioning. Clarke (1977) studied the patterns of pomacentrids and chaetodontids off Bimini, but the area and the habitats used were not typical of the Caribbean and zonation effects were obscured. Alevizon *et al* (1985), however, visually censured fish distribution in four Bahamian zones. The zones used were named lagoonal patch reef, reef crest, *cervicornis* (area dominated by the coral *Acropora cervicornis*) and *annularis* (area dominated by *Montastrea annularis*), habitats typical throughout the Caribbean reefs. The study found community structure and population densities of all but one of the species to be significantly more similar at different sites within zones than between them. Cluster analysis showed four clearly defined, homogeneous groups with only 5% of the samples clustering with groups consisting mainly of samples from a different zone. Greenfield and Johnson (1990) studied the distribution of blennioid fish across 12 habitats in Belize and Honduras, some of which were the same as those used by Alevizon *et al* (1985), by destructive techniques. They found 11 distinct blennioid assemblages, even between adjacent habitats, using detrended correspondence analysis.

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1.3. THE ROLE OF HABITAT VARIABLES.

As already stated the physiographic zones of coral reefs have been shown to differ with regard to a number of factors. The rôle of competitive processes can be further implied if interhabitat differences of the fish assemblages can be correlated to specific variables. In a competitively mediated community it is expected that species richness will, everything else being equal, increase with the habitat heterogeneity. This should occur since a more complex environment allows a greater number of niches to exist. Again this part of competition theory has a grounding in terrestrial ecology, with evidence of a link between habitat complexity and species diversity originating with Huffaker's (1958) experiment with orange mites and spider predators. Further evidence came from MacArthur's work with birds in 1964. In contrast, if the community is maintained below the carrying capacity by recruit limitation then no such relationship should be expected. Williams (1991) emphasized this point by stating that how fish respond to spatial heterogeneity of reefs is of major concern to reef fish ecology.

This correlation has been found in a number of studies. The first definite results were from Risk (1972) who found a positive correlation between substrate topographic complexity and reef fish species diversity in the Virgin Islands. Alevizon and Brooks (1975) felt that a factor causing the increased diversity at one of their sites was the maze-like network of *Millepora* spp., sponges, gorgonians and other soft corals, combined with the greater physical relief of the underlying reefs. Other examples are relatively common (Luckhurst and Luckhurst, 1978; Molles, Jr, 1978; Gladfelter *et al*, 1980; Roberts and Ormond, 1987). Simply increasing the habitat size

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can also increase the complexity, since it allows a means for greater spatial specialization (Clarke, 1988). Due to the high levels of predation on reefs (Chave, 1978; Hixon, 1991) many of these studies have highlighted the rôle of sheltering holes as a component of habitat complexity. For example Roberts and Ormond (1987) found that the numbers of holes of three sizes taken together accounted for 77% of the variance in overall fish abundance, but was not correlated with species richness. Similarly Molles, Jr (1978) found no correlation between interspace size diversity and fish species richness on model or natural reefs.

It is also expected that strongly determined communities should exhibit taxonomic or trophic constancy (Sale, 1980, 1991). Such comparisons have received little attention, and much of the work that has been done has used artificial reefs (Russell *et al*, 1977; Talbot *et al*, 1978; Bohnsack, 1983) or before and after denuding (Brock *et al.*, 1979). Furthermore the aims of the studies have been to examine the trophic structures in different geographical areas (Gladfelter *et al*, 1980; Sale *et al*, 1991). It seems no study has examined the trophic variability within and between sites of the same area.

1.4. THE AIMS OF THIS STUDY.

The aim of this study is, therefore, to characterize, via visual, semi-quantitative censuring the fish species in specific habitats across all zones of the Belizean Barrier Reef and the associated lagoon. Further analysis will then examine whether there are significant differences between the habitats or whether no patterns of fish distribution exist across the reef in terms of species richness, total abundance and whole

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assemblages. Differences between the zones will also be examined by comparing the trophic structures. Any variation will then be related to a number of independent variables: geographical position, site, coral species richness and abundance (measures of habitat complexity), floral abundance, depth and zone length. No direct study on the link between zonal assemblages and specific habitat variables, beyond general coral zonation, exists in the Caribbean, but it is possible here because of the extensive data set that has been collected by intensive sampling over a relatively short time period. These patterns can then be discussed in the context of the paradigm of thought concerning the mechanisms maintaining the diversity and coexistence of coral reef fish.

2.METHOD.

2.1.THE STUDY AREA.

The Belizean Barrier Reef, Belize, Central America is the second largest in the world at a length of approximately 250-km (Rutzler and Macintyre, 1982). It intersects the mainland at Ambergris Cay, but otherwise lies 12.8-40.1-km offshore (Greenfield and Johnson, 1990). Oceanic conditions and rich reef development prevail on the windward side. The cays experience a mixed, semidiurnal, microtidal (mean range 15 cm) régime, but the tides are still the major cause of currents (Kjerfve *et al.*, 1982).

The data used for this study were collected as part of the Coral Cay Conservation project from May 1992 to September 1992, during the large survey being carried out by them on an area of the Belizean Barrier Reef. The author was on the project helping to collect data during September 1992. The area of the reef studied was approximately square, containing parts of the lagoon, shoreward of the barrier reef system, the reef itself and a number of sandy and mangrove cays. The study area was centred on South Water Cay, where the project was based, and stretched from 16°45' to 16°54' north and from 88°05' to 88°12' west. The study area and general location can be seen in figure [1] overleaf.

2.2.DATA COLLECTION TECHNIQUES.

Surveying of the reef itself consisted of 200 east to west transects 100 m apart. The length of the transect was surveyed by four teams of four divers due because of the safety and air limitations of SCUBA diving. Buoys were taken by each team to ensure

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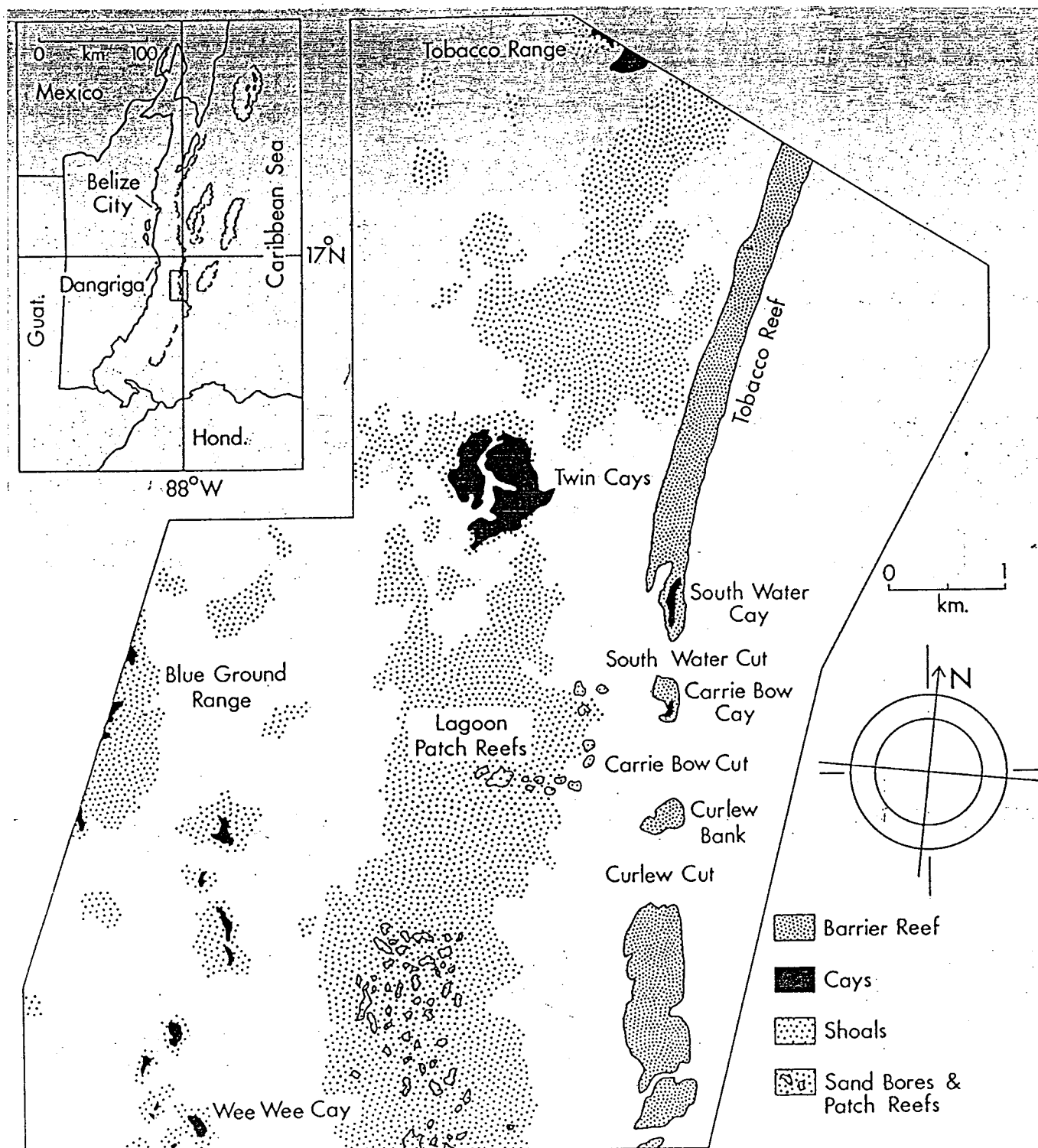


FIGURE [1]: Index map of the barrier reef complex in the vicinity of South Water Cay: area of larger map located on insert by rectangle. After Rutzler and Macintyre (1982).

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the surveys were continuous and non-overlapping, and to allow a precise geographical fix of the transect to be taken. Each team consisted of a navigator and physical profile recorder (depth was noted off a depth gauge and distances were estimated by fin-strokes), a fish recorder, a coral recorder and an algal recorder. The station depth used in this study represents the midpoint of the upper and lower extremes. All the volunteers were experienced divers and competent at recognizing the species seen after an initial weeks training. Each species seen by the biota recorders within approximately 5-m either side of the transect were scored according to the following scale:

FISH	SCORE	CORALS / ALGAE	PERCENTAGE
None	0	none seen	0
Rare	1	a little	0-5
Occasional	2	some	6-30
Frequent	3	nearly half	31-50
Common	4	more than half	51-75
Abundant	5	almost all	76-100

The scores were recorded on underwater notepads and later transferred to standardized survey forms, along with the physical data. A different form was used for each habitat, and such habitat changes were chosen on the basis of gross substrate differences or coral zonation patterns, such as from a sand plateau to a coral environment. Lagoonal surveys were carried out along similar lines, except that an east-west distance of 300-m was used for the transect length since there are no obvious boundaries as on the reef.

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In this study a representative sample of 12 reef transects from different areas along the length reef were used, along with 9 spatially separated lagoonal transects. The position of these transects can be seen in figure [2] overleaf. For the analysis not all the species listed on a recording form were used since many are only very rarely encountered and would waste computer processing time. Others were too small or cryptic to be identified accurately (Brock, 1982). The fish and coral species that were used are listed in Appendices I and II. The 69 species selected represented 18 families of commonly seen coral reef fish of the western Atlantic.

2.3. CLASSIFICATION OF THE HABITATS USED.

The habitats used in this study were categorized as follows (the number of stations of each type and the abbreviation used later in the text are shown in parentheses):

H1 - Lagoonal patch reefs (8 / P) - within the protected lagoon there are large numbers of patch reefs, consisting of extensive live coral. They are in relatively shallow water (less than 15-m), vary greatly in size and are in areas of low wave energy. There is usually a variety of corals, with species of *Montastrea*, *Acropora* and *Diploria* the dominant hard corals. Gorgonians and other epifauna are often common. The patch reefs are often in seagrass beds, from which they are separated by a grazed "halo" of several metres (Randall, 1965; Ogden *et al.*, 1973). Patch reefs are the only structures in the open lagoon environment that give shelter and protection to the fish. This habitat is the same as the patch reef habitats of Alevizon *et al.* (1985) and Greenfield and Johnson (1990).

H2 - Lagoonal with algae dominated substrate (1 / LA) - this habitat is not often

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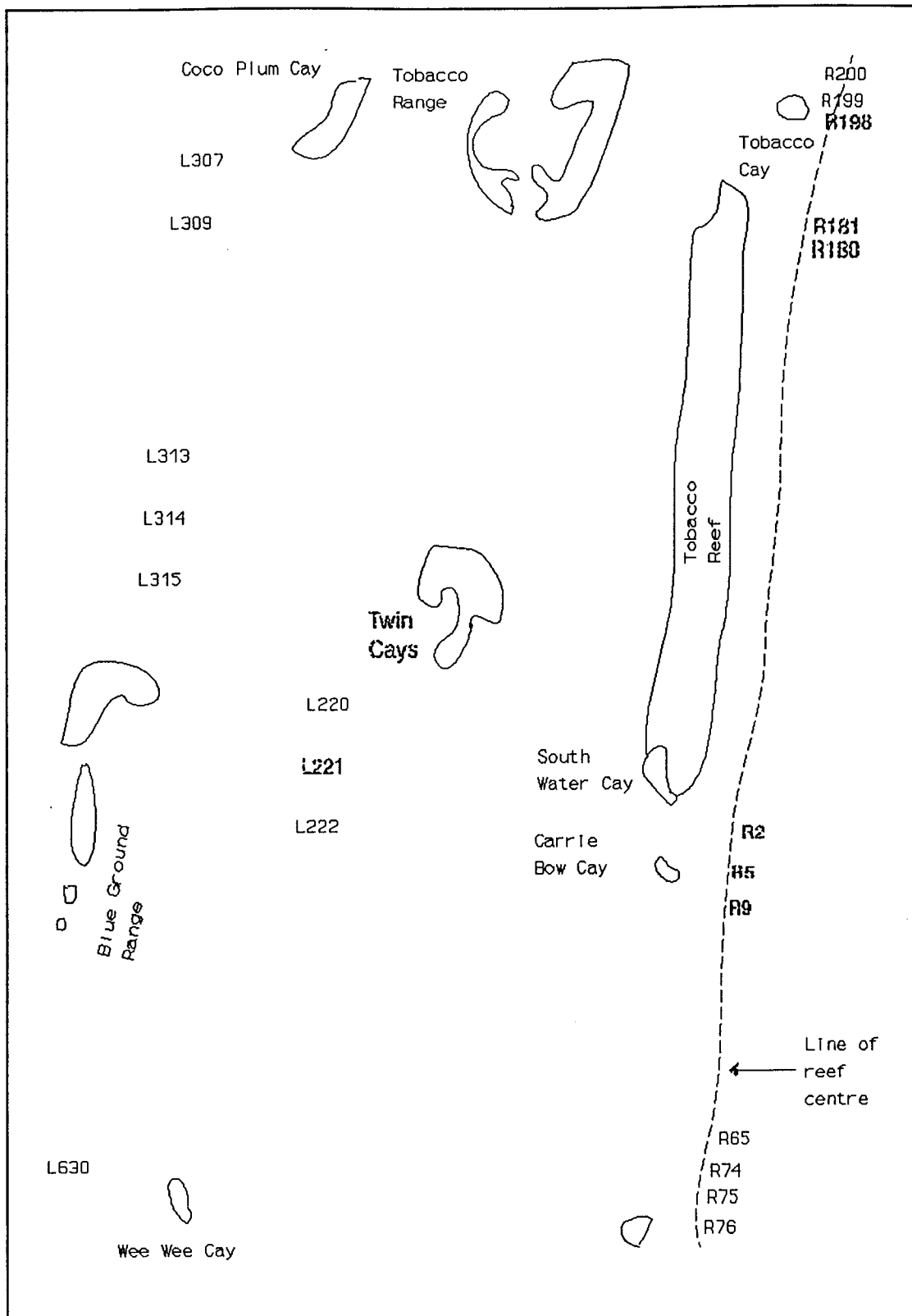


FIGURE [2]: Schematic diagram of the study area, showing the position of the transects used in the project. L = lagoon transect; R = reef transect.

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found in the lagoon and simply consists of a soft sediment almost entirely covered by algae. There are no live corals present and the habitat has none, or very few, macrofaunal species.

H3 - Lagoonal seagrass beds (6 / LSG) - areas within the lagoon with extensive marine spermatophyte development (for example *Thalassia* spp.) covering over 75% of the area. They were all found at less than 15 m depth. A limited amount of varying live coral species are often found among the seagrass. There is a greater amount of macrofauna than in H2 areas. This habitat is analogous to a combination of the shallow grass beds and deep grass beds of Greenfield and Johnson (1990).

H4 - Lagoonal with mud substrate (3 / LM) - these areas within the lagoon are predominately muddy with a limited amount of seagrasses and live coral and rubble. There is little macrofaunal presence.

The remaining seven habitats are areas of the reef itself and are best described by use of a general transect cross-section seen in figure [3].

H5 - Reef crest (1 / RC) - the reef crest represents the position where the reef system reaches the surface and most of the wave energy reaching the reef is dissipated (Alevizon *et al.*, 1985). The depth is obviously minimal (less than three metres), and the danger of diving in such shallow, turbulent areas accounts for the low number of stations. The reef crest is continual for many hundreds of metres, usually at a width of less than 50-m, although many sizeable breaks or "cuts" appear along its length. Furthermore there are many small channels (2-4-m wide and 3-4-m deep) which facilitate water exchange between the lagoon and fore reef (Rutzler and Macintyre, 1982) and result in a net oceanic flow, with water into the lagoon being pumped over

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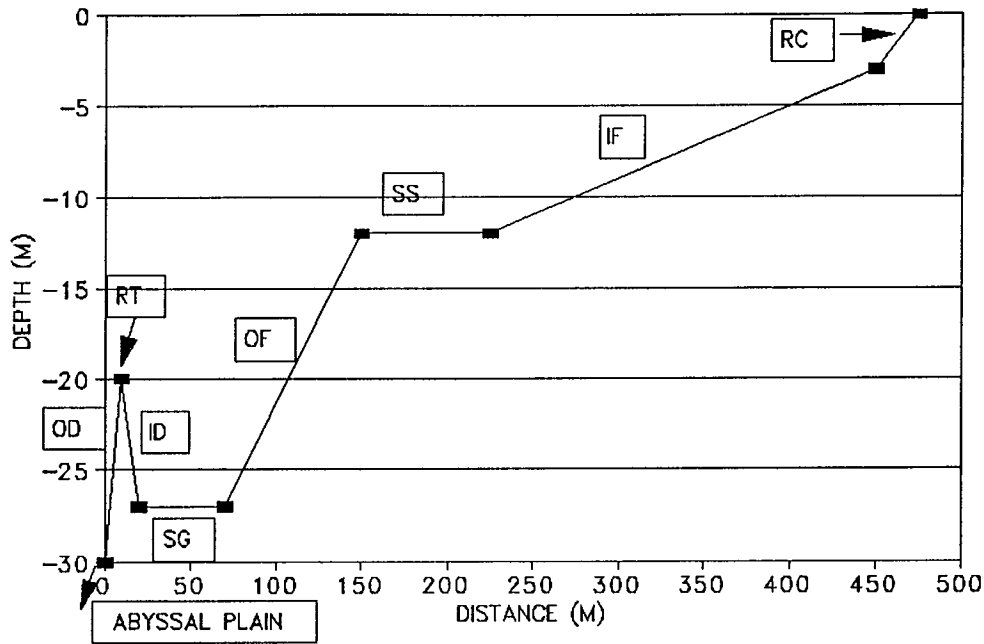


FIGURE [3]: Stylized cross-section of a reef transect. OD = outer dropoff; RT = ridge top; ID = inner dropoff; SG = sand gully; OF = outer fore; SS = shallow sand; IF = inner fore; RC = reef crest.

the crest by breaking waves (Kjerfve, 1982). There is extensive coral growth but the physical conditions mean that the diversity is low, with *Acropora palmata* the dominant species. This habitat is the same as the reef crest zone of Alevizon *et al.* (1985) and the shallow forereef of Greenfield and Johnson (1990).

H6 - Inner forereef (20 / IF) - seaward of the reef crest the reef profile begins to gradually deepen towards the dropoff area and the portion of this area down to a general depth of 12 m is the inner forereef. This depth limit is not all encompassing since it may vary slightly along the length of the reef, but in such cases the division between this and the next habitat is often highlighted by a sandy area. This habitat is the most structurally diverse and complex with most of the coral species being represented. It is dominated by *Acropora cervicornis* although species of the genera

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Montastrea, *Diploria* and *Siderastrea* are frequently found. Gorgonians are diverse and common along with many species of epifauna and green algae. The habitat sometimes contains a spur and groove relief, comprised of central sand flats separating large spurs of coral, approximately 5 m high, lying in a seaward-shoreward manner. This inner forereef is analogous to part of the spur and groove habitat (Greenfield and Johnson, 1990) and the *cervicornis* zone of Alevizon *et al.* (1985).

H7 - Outer forereef (15 / OF) - this habitat is adjacent to the inner forereef and begins at around 12 m. The boundary between the two is sometimes marked by a stretch of sand, and usually signifies a steepening of the profile gradient, as seen in figure [3]. Again there is a large diversity of corals, algae and epifauna, however the dominant coral is usually *Montastrea annularis*. Spur and groove formation is a common feature. This zone generally finishes at a depth of around 30 m. This habitat is analogous to part of the spur and groove habitat (Greenfield and Johnson, 1990) and the same as the *annularis* zone of Alevizon *et al.* (1985).

H8 - Shallow sand (8 / SS) - on the reef transects areas of predominantly sand were found within the inner and outer forereef and these were grouped in this habitat. Depths were generally less than 10-m and the length was approximately 50-m. Significant marine spermatophyte development is lacking but some isolated coral heads of varying species are seen.

H9 - Sand gully (11 / SG) - this habitat is characterized by its position between the seaward ridge formation and the outer forereef. It is simply a band of sand separating these features by around 50-m. The depth varies along the length of the reef, as does whether it deepens shoreward or seaward. The sand gully is generally deeper around

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South Water Cay (transects 2, 5, 9) than it is at the northern and southern extremes of the study area. As with the shallow sand habitat there is little marine spermatophyte development and some coral heads are often seen.

H10 - Inner dropoff (7 / ID) - this habitat is the shoreward wall of the reef ridge that runs from the ridge top to the sand gully. There is a wide diversity of corals along with many algae and epifaunal species. The horizontal width is usually small (less than 10-m) but the vertical distance can be large (up to 10-m).

H11 - Outer dropoff (7 / OD) - the outer dropoff is the wall from the ridge top to 30 m. This lower depth limit is not a biological one but is imposed by safe diving limit. This habitat has vertical or near vertical walls, along with underhangs and extensive live coral coverage. Many coral species are seen, including some exclusively deeper water species such as red sea whips. The ridge formation from transects 180, 181, 198, 199 and 200 were omitted from both the dropoff habitats because they are topographically different, with little vertical definition, were often too deep to survey properly and were surveyed as one habitat. These factors would obviously mean that these stations are not comparable. The inner and outer dropoff constitute the dropoff zone of Greenfield and Johnson (1990).

2.4. DATA ANALYSIS.

The dependent variables in this study were fish species richness and total abundance (total of all the "scores") and the independent ones were site, coral species richness and total abundance, depth, length and algal coverage. Linear and multiple regressions, ANOVA's and homogeneity tests were calculated using the Statgraphics

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computer package. The site variable represents the habitats in order of increasing fish species richness, to allow analysis of interhabitat changes of this richness. Stepwise variable selection, separate variance t-tests, dendrogram production and principle component analysis, using all the dependent and independent variables, was done using the Unistat computer package. All the combinations of dependent and independent variables were tested for simple correlations, but only the independent variables shown to be significant by stepwise selection were used in the multiple linear regression analysis, both within and between habitats. The separate variance t-test was used since they do not require the standard deviations of the two variables to be similar, which is unlikely for this data. The formula used was:

$$t = \frac{M_1 - M_2}{\sqrt{A_1 + A_2}} \quad \text{where} \quad A_1 = \frac{S_1^2}{N_1} \quad , \quad A_2 = \frac{S_2^2}{N_2}$$

where M = mean; S = standard deviation; N = number of values. (Toker, 1991).

The dendrograms were generated by using a euclidean distance matrix and grouping by the average between groups method on all the 87 stations. The euclidean distance between two points was calculated by: (Toker, 1991).

$$\text{Euclidean distance } (x_i, y_i) = \sqrt{\sum_i (x_i - y_i)^2}$$

The homogeneity of the fish species across the habitat types was tested using a G - test according to the following formula: (Sokal and Rolf, 1981).

$$G = \sum_{i=1}^h O_i * \ln O_i / E_i$$

where O = observed result; E = mean of observed result; h = number of habitats.

The observed result used was found by counting the number of times each species

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was present in six stations of each habitat type. Habitat types with less than six stations were excluded and those with more than six were reduced using random numbers.

Dominant species of fish and coral in each habitat were found by counting the number of stations where each species was present. Dominant species were considered to be present in greater than 50% of the stations of that habitat (Greenfield and Johnson, 1990). The trophic structure was analyzed by splitting the fish species into four main categories: herbivores, general invertebrate eaters, fish or crustacean eaters and planktivores, based on Humann (1989). The categories to which each species was assigned is shown in Appendix I. The second and third categories were further subdivided into daytime and nocturnal feeders. Species rank diagrams were created by ordering the species by descending proportional abundance. All computation was carried out using an IBM PS2.

3.RESULTS.

3.1.INTRAHABITAT DIFFERENCES.

Before looking at differences between the habitat types used in this study it was necessary to assess whether the habitats are homogeneous groups worthy of comparison. Regression analysis between the dependent variables fish richness and total abundance and each of the independent variables coral richness, total coral abundance, depth, length and algal coverage revealed only limited intrahabitat differences. Within the nine habitats tested (the reef crest zone and lagoonal, algal dominated habitats only have one station each) only four significant correlations were found. Thus the fish species richness within the sand gully and shallow sand habitats were negatively correlated with depth ($R = -0.6416$ and -0.7390 respectively, $P < 0.05$) along with a negative correlation between the total abundance and depth in the shallow sand zone ($R = -0.7224$, $P < 0.05$). The final correlation was a positive one ($R = 0.7730$, $P < 0.05$) between the fish total abundance and the coral total abundance in the inner dropoff habitat.

Stepwise variable selection tested for possible significant independent variables to use in a model of the dependent variables, and this analysis revealed a limited amount of significant variables. The results are shown in tables [1] and [2] overleaf. These tables show few, strong within habitat differences, with most simply being a decrease in fish richness and total abundance with increasing depth. Thus, for example, the effect of the depth variable is highest in the shallow sand zone, explaining 54.61% of the variation of fish species abundance ($P = 0.0362$). However, coral abundance was also selected as a significant contribution to the variation of both fish total

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TABLE [1]: Table showing independent variables selected by stepwise multiple regression versus fish species richness. * = significant ($P < 0.05$) addition to multiple linear regression.

INDEPENDENT VARIABLE	MULTIPLE R	MULTIPLE R-SQUARED	SIGNIFICANCE
OUTER FORE			
CORAL ABUNDANCE	0.4843	0.2345	0.0673
SAND GULLY			
DEPTH	0.6416	0.4117	0.0333*
LENGTH	0.7914	0.6263	0.0195
INNER DROPOFF			
CORAL ABUNDANCE	0.6941	0.4818	0.0836
OUTER DROPOFF			
ALGAL COVER	0.7392	0.5464	0.0576*
DEPTH	0.9167	0.8404	0.0255
SHALLOW SAND			
DEPTH	0.7390	0.5461	0.0362*

TABLE [2]: Table showing independent variables selected by stepwise multiple regression versus fish total abundance. * = significant ($P < 0.05$) addition to multiple linear regression.

INDEPENDENT VARIABLE	MULTIPLE R	MULTIPLE R-SQUARED	SIGNIFICANCE
SAND GULLY			
DEPTH	0.5996	0.3595	0.0512
LENGTH	0.7830	0.6131	0.0224
INNER DROPOFF			
CORAL ABUNDANCE	0.7730	0.5976	0.0415*
OUTER DROPOFF			
ALGAL COVER	0.7102	0.5044	0.0737
DEPTH	0.9465	0.8958	0.0109
SHALLOW SAND			
DEPTH	0.7224	0.5218	0.0430*

abundance in the inner dropoff zone (59.76%, $P = 0.0415$), along with length in

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the sand gully zone (21.46%, $P = 0.0195$). The other variables listed are not significant at the $P = 0.05$ level. The significant variables were then used in multiple linear regression and the significant additions to the models are highlighted in the table. This univariate analysis showed little intrahabitat variation, but differences were also studied by multivariate techniques. Euclidean, average between group analysis was used, and two of the dendrograms are presented in figures [4] and [5]. Also presented in figures [6] and [7] are dendrograms representing any differences in coral distributions. Only two of the stations are presented for clarity since all the results were similar, and they show it is not possible to see obvious, strong distributions within each habitat type, either within the fish or coral data. Furthermore by reference to the transect numbers there is little evidence of stations in similar geographic regions clustering together.

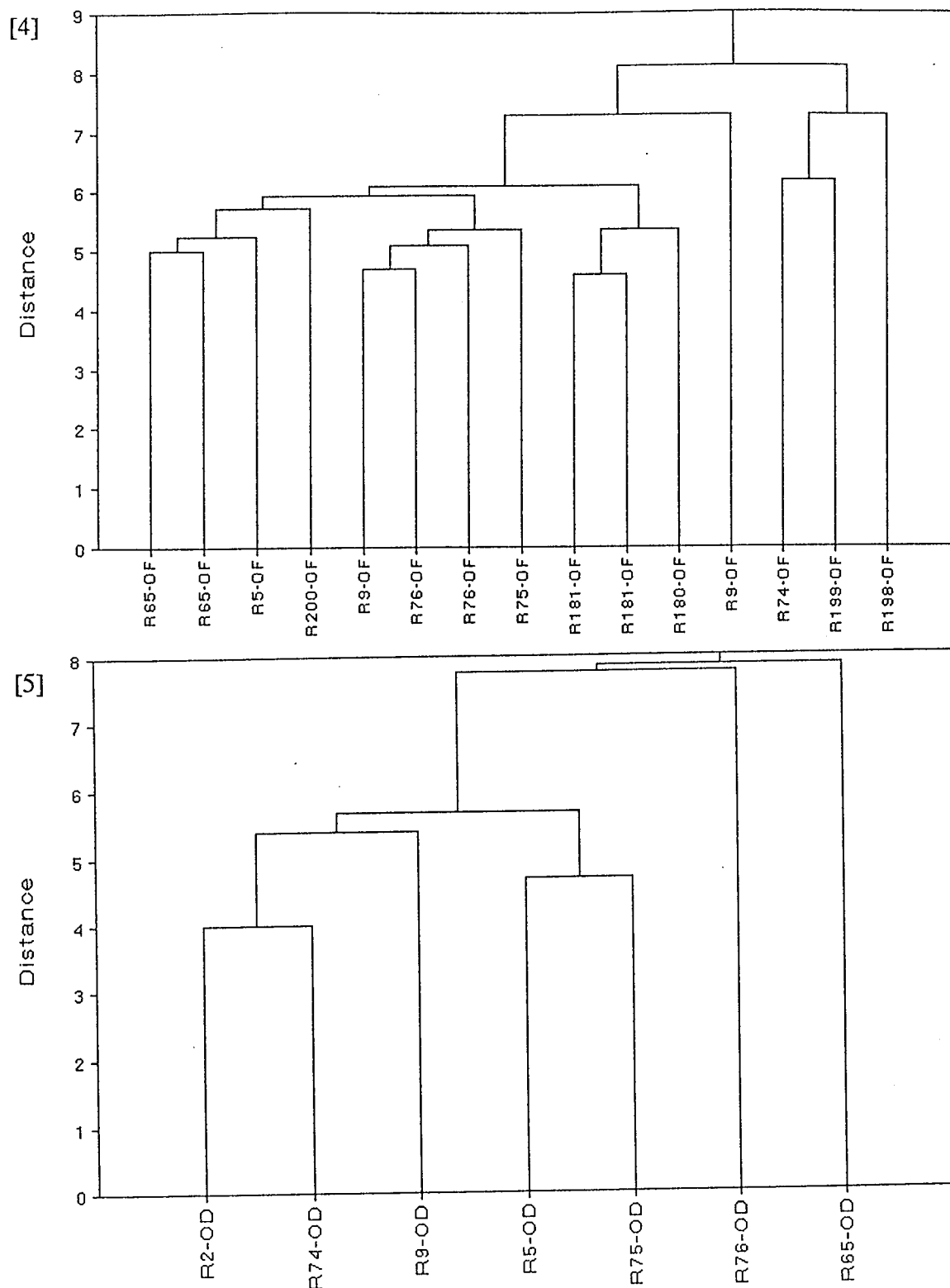
3.2. INTERHABITAT DIFFERENCES.

3.2.1. Gross trends.

One-way ANOVA's allowed a general testing of interhabitat differences between all the 87 stations in the zones on the basis of each dependent and independent variables. The results from the analysis can be seen in table [3]. The table shows that each variable is highly significantly more variable between habitats than within habitat types.

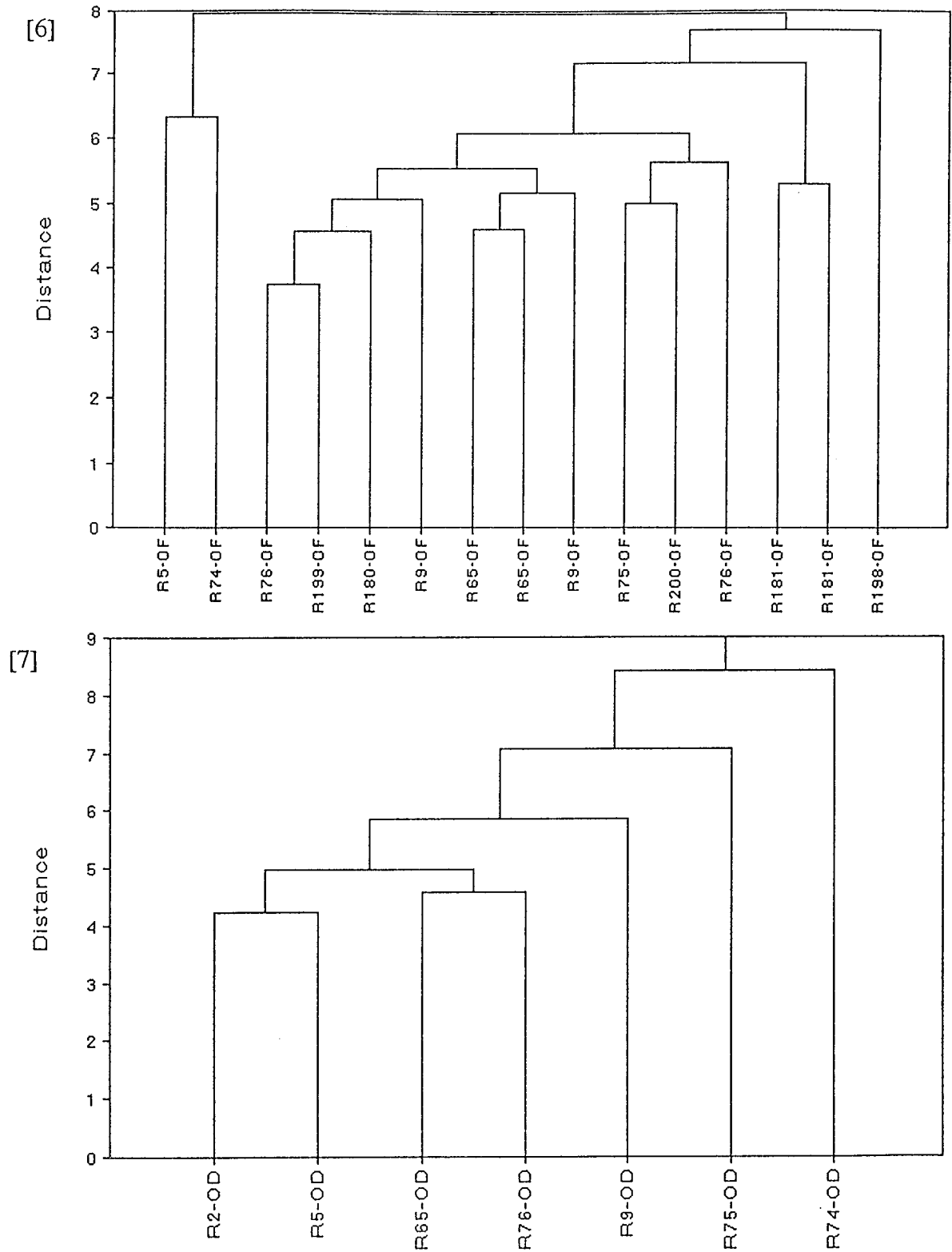
Regression analysis examined more detailed relationships between the dependent and independent variables. The results of this analysis was that both fish species richness and total abundance are significantly ($P < 0.0001$) positively correlated with the site

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FIGURES [4] AND [5]: Dendrograms of fish assemblages of two sample habitat types. [4] = outer forereef. [5] = outer dropoff. R represents transect number of that station.

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FIGURES [6] AND [7]: Dendrograms showing coral assemblages of two sample habitat types. [6] = outer forereef. [7] = outer dropoff. R represents transect number of that station.

TABLE [3]: Table showing the results of one-way ANOVA's using all the stations. 86 degrees of freedom.

INDEPENDENT VARIABLE	F-RATIO	SIGNIFICANCE LEVEL
FISH SPECIES RICHNESS	16.590	0.0000
FISH TOTAL ABUNDANCE	18.126	0.0000
CORAL SPECIES RICHNESS	9.180	0.0000
CORAL TOTAL ABUNDANCE	8.459	0.0000
DEPTH	18.381	0.0000
LENGTH	3.922	0.0003
ALGAL COVER	3.102	0.0023

($R = 0.7993$ and 0.7916 respectively), coral species richness ($R = 0.6103$ and 0.6106 respectively) and coral total abundance ($R = 0.6004$ and 0.5748 respectively). Similarly the coral species richness and coral total abundance are also correlated with the site variable ($R = 0.6439$ and 0.6200 respectively, $P < 0.0001$). The relationships between fish species richness and the variables coral species richness and site are shown graphically in figures [8] and [9].

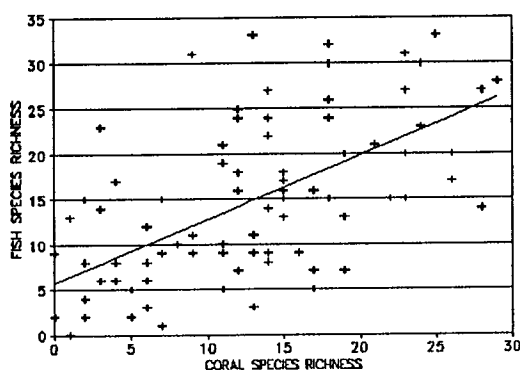


FIGURE [8]: Graph showing relationship between fish species richness and coral species richness in all the stations. $R = 0.6103$, $P < 0.0001$.

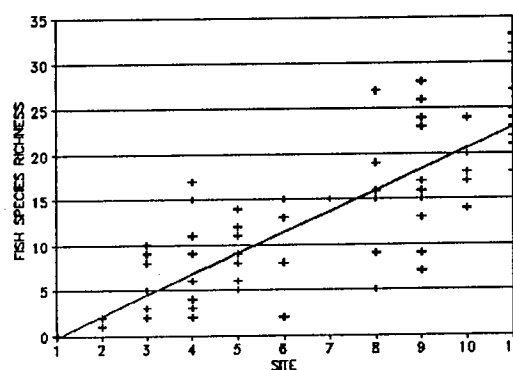


FIGURE [9]: Graph showing relationship between fish species richness and site for all the stations. $R = 0.7988$, $P < 0.0001$.

Figure [10] shows the more general trend between fish and coral species richness using totals for each habitat type. All these correlations can be seen to be stronger than the relationship between, for example, fish species richness and depth shown in figure [11]. This lack of correlation is also seen between length and algal cover and the site and dependent variables.

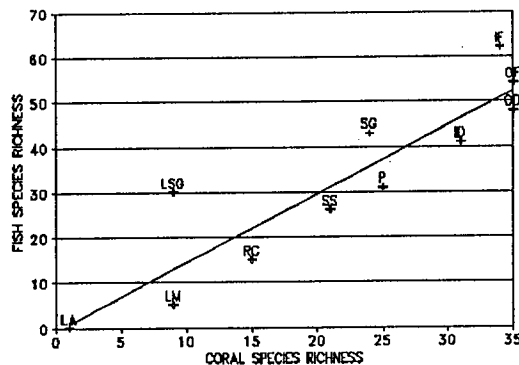


FIGURE [10]: Graph showing relationship between total fish and coral species richness in each habitat type. $R = 0.9069$, $P = 0.0012$.

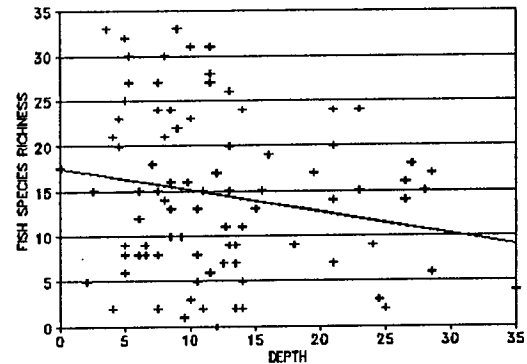


FIGURE [11]: Graph showing relationship between fish species richness and depth for all stations. $R = -0.2007$, $P = 0.0623$.

Stepwise variable selection on all the data allowed identification of the significant variables to be used in multiple linear regression, in the same way as during the intrahabitat differences analysis. The results obtained from stepwise variable selection are shown in table [4]. The table shows that, as with the regression, the site variable is dominant, accounting for 63.88% ($P < 0.0001$) of the variation in fish species richness and 62.67% ($P < 0.0001$) of the variation in fish total abundance. The coral total abundance and depth variables are less important, only explaining 1.79% and 1.72% respectively, of the variation in fish species richness but are significant ($P < 0.0001$), along with coral species richness, which accounts for 1.74% of the variation of fish total abundance. Without the site variable included each dependent

TABLE [4]: Table showing the ~~results~~ ^{RESULTS} stepwise variable selection on all the station's data using combinations of independent variables against fish species richness and total abundance.

INDEPENDENT VARIABLE	FISH SPECIES RICHNESS			FISH TOTAL ABUNDANCE		
	MULTIPLE R	MULTIPLE R-SQUARED	PROB	MULTIPLE R	MULTIPLE R-SQUARED	PROB
INCLUDING SITE VARIABLE						
SITE	0.7993	0.6388	0.00	0.7916	0.6267	0.00
CORAL RICH				0.8025	0.6440	0.00
CORAL ABUND	0.8104	0.6567	0.00			
DEPTH	0.8209	0.6739	0.00			
LENGTH						
ALGAL COVER						
WITHOUT SITE VARIABLE						
CORAL RICH	0.6103	0.3724	0.00	0.6106	0.3728	0.00
CORAL ABUND						
DEPTH	0.6398	0.4093	0.00			
LENGTH						
ALGAL COVER						

variable is obviously less well correlated with the independent ones, with coral species richness explaining the largest proportion of the variation of fish species richness and total abundance (37.24% and 37.28% respectively, $P < 0.0001$). The only other variable chosen was depth, which contributed to 3.69% of the variation of fish species richness ($P < 0.0001$). When the significant variables were used in multiple regression analysis, all were shown to be significant additions to the models of the dependent variables.

The G-tests of fish homogeneity throughout the eight zones with a minimum of six stations gave an indication of highly site specific fish species. The values, seen in Appendix I, showed that few species fell into this category to a significant degree. *Holocanthus tricolor*, *Pomacanthus arcuatus*, *Microspathodon chrysurus*, *Gramma loreto* and *Clepticus parrai* were significantly heterogeneously distributed at the $P < 0.05$ level and *Chromis cyanea* was at the $P < 0.01$ level. The significance levels

are from a chi squared distribution with seven degrees of freedom.

3.2.2. Specific differences.

The first distinction that can be made between the habitat types in this study is the difference in the dominant species of each zone. The list of dominant species, in those habitats with more than one station, can be seen in table [5].

TABLE [5]: Table showing the dominant species (greater than 50% occurrence) within each habitat type with more than one station.

FISH SPECIES	PERCENTAGE OCCURENCE
SAND GULLY	
<i>Ocyurus chrysurus</i>	72.7
<i>Chromis cyanea</i>	54.5
INNER DROPOFF	
<i>Chaetodon capistratus</i>	57.1
<i>Holocanthus tricolor</i>	57.1
<i>Acanthurus coeruleus</i>	85.7
<i>Ocyurus chrysurus</i>	57.1
<i>Haeniulon flavolineatum</i>	57.1
<i>Stegastes fuscus</i>	57.1
<i>Stegastes variabilis</i>	57.1
<i>Stegastes partitus</i>	100.0
<i>Stegastes planifrons</i>	85.7
<i>Chromis cyanea</i>	71.4
<i>Scarus taeniopterus</i>	100.0
<i>Thalassoma bifasciatum</i>	57.1
OUTER DROPOFF	
<i>Chaetodon capistratus</i>	85.7
<i>Holocanthus tricolor</i>	71.4
<i>Acanthurus coeruleus</i>	85.7
<i>Ocyurus chrysurus</i>	100.0
<i>Stegastes fuscus</i>	71.4
<i>Stegastes partitus</i>	71.4
<i>Stegastes planifrons</i>	85.7
<i>Chromis cyanea</i>	100.0
<i>Gramma loneto</i>	85.7
<i>Scarus taeniopterus</i>	100.0
<i>Halichoenes gamoti</i>	57.1
SHALLOW SAND	
<i>Acanthurus chirurgus</i>	62.5
<i>Chromis cyanea</i>	62.5

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TABLE [5] continued.

FISH SPECIES	PERCENTAGE OCCURENCE
PATCH REEF	
<i>Chaetodon capistatus</i>	50.0
<i>Pomacanthus arcuatus</i>	62.5
<i>Stegastes partitus</i>	50.0
<i>Stegastes planifrons</i>	50.0
<i>Scarus taeniopterus</i>	50.0
LAGOONAL SEA GRASS	
<i>Chaetodon capistatus</i>	66.7
<i>Pomacanthus arcuatus</i>	50.0
<i>Ocyurus chrysurus</i>	50.0
<i>Stegastes planifrons</i>	50.0
<i>Scarus taeniopterus</i>	66.7
INNER FOREREEF	
<i>Chaetodon ocellatus</i>	55.0
<i>Chaetodon capistratus</i>	90.0
<i>Chaetodon striatus</i>	55.0
<i>Holocanthus tricolor</i>	85.0
<i>Pomacanthus arcuatus</i>	60.0
<i>Acanthurus bahianus</i>	55.0
<i>Acanthurus chirurgus</i>	75.0
<i>Acanthurus coeruleus</i>	80.0
<i>Ocyurus chrysurus</i>	60.0
<i>Haeniulon flavolineatum</i>	70.0
<i>Microspathodon chrysurus</i>	75.0
<i>Stegastes fuscus</i>	50.0
<i>Stegastes partitus</i>	75.0
<i>Stegastes planifrons</i>	50.0
<i>Chromis cyanea</i>	95.0
<i>Scarus taeniopterus</i>	80.0
<i>Scarus iserti</i>	60.0
<i>Sparisoma vivide</i>	90.0
<i>Halichoenes gamoti</i>	95.0
<i>Thalassoma bifasciatum</i>	100.0
<i>Holocentrus adscensionis</i>	70.0
<i>Balistes vetula</i>	50.0
OUTER FOREREEF	
<i>Chaetodon capistratus</i>	73.3
<i>Holocanthus tricolor</i>	80.0
<i>Acanthurus chirurgus</i>	53.3
<i>Acanthurus coeruleus</i>	80.0
<i>Ocyurus chrysurus</i>	66.7
<i>Chromis cyanea</i>	73.3
<i>Sparisoma vivide</i>	53.3
<i>Thalassoma bifasciatum</i>	80.0
<i>Holocentrus adscensionis</i>	60.0

The table shows the obvious discrepancy in actual numbers of dominant species

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throughout the zones, with, for example, the inner forereef having the most (22) and the lagoonal, mud substrate areas which had none, and were therefore excluded from this table. The coral habitats generally had more dominant species than the sand, mud and seagrass zones. The paucity of dominant species in the patch reef habitat (5 species), as compared to the other coralline habitats can be seen. The only dominant species in any of the zones that are not dominant in the inner fore reef are *Stegastes variabilis* and *Gramma loreto* that are uniquely dominant in the inner and outer dropoff zones respectively.

Separate variance t-tests revealed significant differences between the fish species richnesses and total abundances of each habitat. These results are summarized in table [6].

TABLE [6]: Table showing the results of interhabitat t-tests between fish species richnesses (unshaded) and total abundances (shaded). * = $P < 0.05$, ** = $P < 0.01$.

	P	LSG	LM	IF	OF	SG	ID	OD	SS
PATCH REEF	X		**	**	**			**	
LAGOONAL SEAGRASS		X	*	**	**	**	**	**	*
LAGOONAL MUD	**	*	X	**	**	**	**	**	**
INNER FOREREEF	**	**	**	X	**	**	**	**	**
OUTER FOREREEF	**	**	**	**	X	**			**
SAND GULLY			**	**	**	X	*	**	
INNER DROPOFF	*	*	**	**		*	X		*
OUTER DROPOFF	**	**	**	*		**		X	**
SHALLOW SAND			**	**	**		**	**	X

The two halves of the table are obviously similar, but there are some differences, such as the significant difference between patch reef and inner dropoff total

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abundances as compared to the insignificant difference between their species richnesses. The general pattern of the table reflects the distinction between the species rich coralline habitats, such as the forereef and dropoffs, and the species poor mud, seagrass and sandy habitats. The patch reef habitats appear to be intermediate between the two groups, exhibiting no difference from the coralline inner dropoff zone and also the lagoonal seagrass and sandy regions ($P > 0.05$). There are, however, distinctions between coralline habitats, even between adjacent, true reef habitats, such as the inner and outer forereefs ($P < 0.01$). No differences were seen between the inner and outer dropoff zones ($P > 0.05$). Further differences between the habitats in terms of coral species richnesses and depths are shown in table [7].

TABLE [7]: Table showing the results of interhabitat t-tests between coral species richness (unshaded) and depth (shaded). * = $P < 0.05$, ** = $P < 0.01$.

	P	LSG	LM	IF	OF	SG	ID	OD	SS
PATCH REEF	X	*		**	**		*	**	
LAGOONAL SEAGRASS		X		**	**	*	**	**	*
LAGOONAL MUD			X	**	**		**	**	
INNER FOREREEF				X		**			**
OUTER FOREREEF	**	**		**	X	**			**
SAND GULLY	**	**	**	**	**	X	**	**	
INNER DROPOFF	**	**	*	**			X		*
OUTER DROPOFF	**	**	**	**	**			X	**
SHALLOW SAND		**		**	*	**	*	**	X

The results of the tests between the coral species richness is similar to that of the fish species richness tests, as would be expected from the regression analysis. The data shows that the differences between what have been termed coralline zones and

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the seagrass, mud and sand zones are significant ($P < 0.05$) in terms of coral species richness. Again the patch reef habitat appears to be intermediate, exhibiting a difference from the seagrass zone ($P < 0.05$) and also from the forereef and dropoff zones ($P < 0.05$). There is no significant difference between the sand gully and shallow sand zones ($P > 0.05$). In contrast to the fish data there is no difference between the inner and outer forereefs ($P > 0.05$) in terms of coral species richness.

The depth results show a different separation of the nine zones. The trend with this data is a difference simply between the lagoonal habitats, inner forereef and shallow sand zone and the seaward dropoff and sand gully habitats. The outer forereef is the intermediate zone, exhibiting a difference from the inner forereef ($P < 0.01$) but not from the inner dropoff zone ($P > 0.05$).

Multiple range tests allowed analysis to find any homogeneous habitat groups using the variables tested above, and all of the habitat types. The results of this analysis are shown in table [8], where the columns of "X"'s represent the groupings found. Thus two groups are totally homogeneous if they have X's in the same columns or are highly different if the columns used are totally different. Only the variables fish species richness, coral species richness and depth have been used for clarity. The fish total abundance results were similar to fish species richness and the other variables have been seen not to correlate with site.

The table shows similar patterns to those found by the t-tests. Thus, for fish species richness, there is a highly significant ($P < 0.01$) grouping of the lagoonal algal and mud habitats and the sandy zones, which is then separated from the dropoff and forereef zones by the intermediate patch reef, lagoon seagrass and reef crest regions.

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TABLE [8]: Table showing the results of tests of homogeneity using three variables and all habitat types. Habitat abbreviations used as stated in the method.

VARIABLE								
FISH SPECIES RICHNESS			CORAL SPECIES RICHNESS			DEPTH		
PROB	95%	99%	PROB	95%	99%	PROB	95%	99%
LA	X	X	LA	X	X	RC	X	X
LM	XX	X	LSG	XX	X	LSG	X	XX
SS	XXX	X	LM	XXX	X	P	X	XX
SG	XXX	X	SG	XXX	X	IF	X	XX
P	X X	XX	SS	XXX	X	SS	XX	XXX
LSG	XXX	XXX	P	XXX	X	LM	XX	XXX
RC	XX	XXXX	RC	X XX	XX	LA	XXX	XXXX
ID	XX	XXXX	IF	X	X	OF	XXX	X XXX
OF	XX	XXX	ID	X	X	ID	X X	X X
OD	XX	XX	OF	X	X	SG	XX	X X
IF	X X	X X	OD	X	X	OD	X	X

It can also be seen that the species rich zones do not form a single, homogeneous group, in concordance with the t-tests. The results using coral species richness show that at the $P < 0.01$ level there are two distinct groups containing the lagoonal and sandy regions and the dropoff and forereef habitats respectively. The reef crest zone is intermediate between the two groups. Finally the depth results demonstrated that the lagoonal, shallow sand and innerfore habitats are similarly shallow and the dropoff and sand gully region is significantly deeper. The outer forereef zone seems to be intermediate between these groups as shown by the t-tests.

Multivariate techniques were used to add detail to the apparent interhabitat differences since they allow comparison of actual assemblages by using all the data collected for each station. Cluster analysis conducted on the fish and coral data first attempted to group the coralline and non-coralline stations, and these dendrograms can be seen in figures [12] and [13]. They can be seen to be generally successful, although the clustering is not strong enough to distinguish clear groups and so overall

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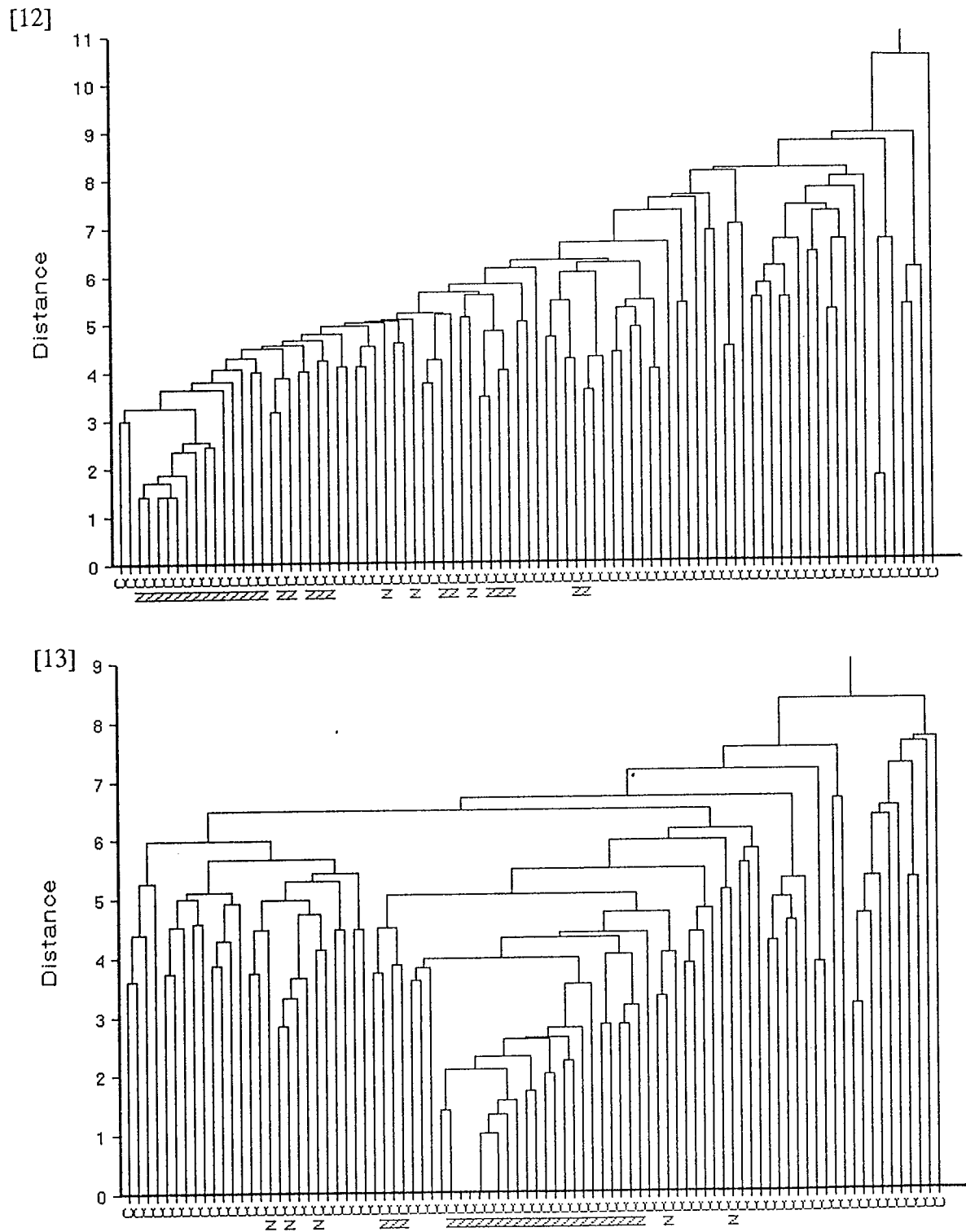
impressions must be used in the absence of any appropriate statistics.

This general dendrogram can give more detailed information if the habitat types themselves are used to label the dendrogram. This can be seen in figures [14] and [15] using the fish and coral data respectively. Within this analysis of all the stations it is possible to see specific interhabitat differences. Such a difference was seen between the patch reef and inner forereef habitats, which was also seen demonstrated using the coral data, though not as distinctly (figures [16] and [17]). However, the separation is clearer and better explained than using the depth variable, as seen in figure [18]. No clear distinctions could be seen between adjacent, coralline habitats, as demonstrated using the inner and outer forereef habitats in figure [19], in contrast to the significant differences found between their total species richnesses, although there may be a weak tendency for the innerfore stations to be found on towards the right of the dendrogram.

The final dendrogram, figure [20], was constructed using simply the presence and absence of each species in each station. This dendrogram seems not to be grossly different from the one using the semi-quantitative data, although there is no statistical test.

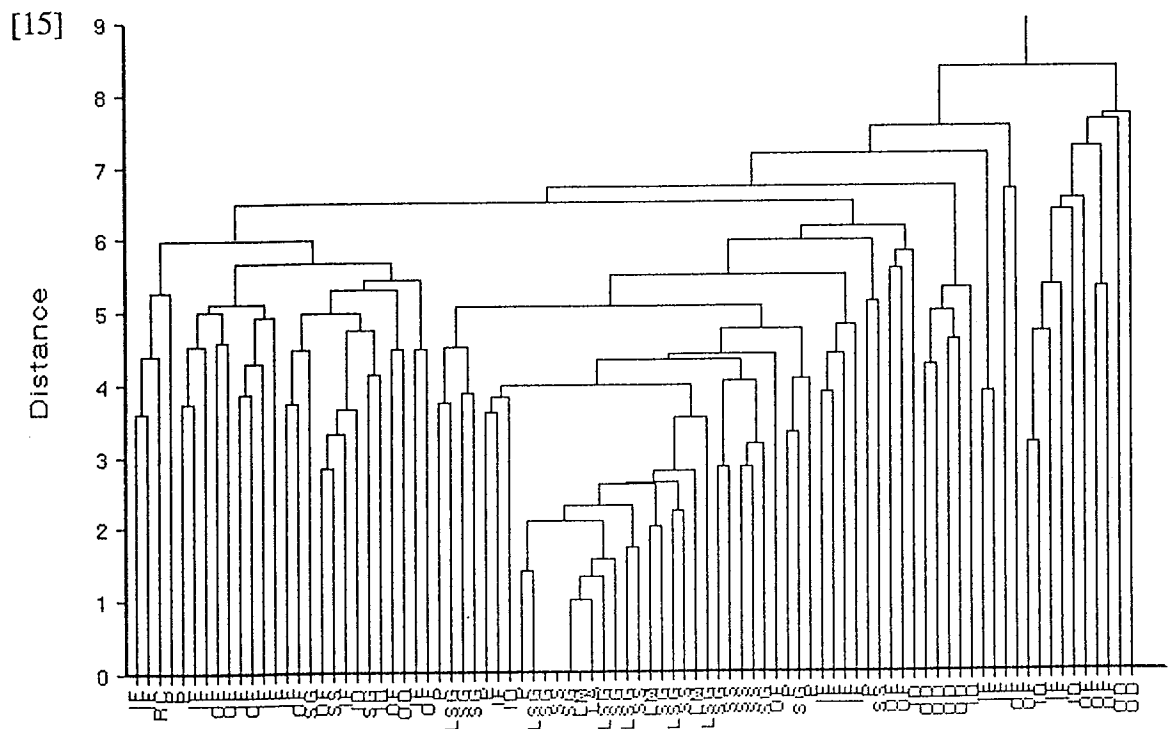
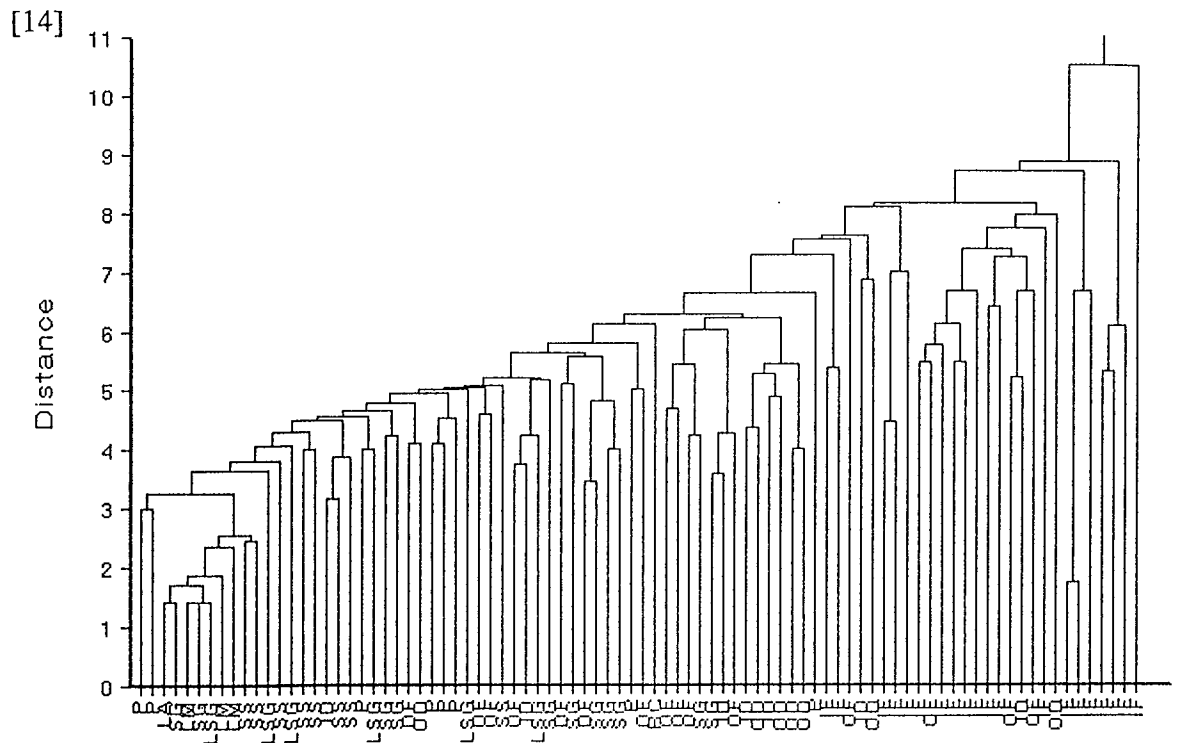
Principal component analysis was also conducted in an attempt to distinguish between the groups of stations. The analysis using all the variables, with the exception of site as stated in the method, and the result, using the two main components accounting for 64.31% of the variation, can be seen in figure [21]. The groupings are again not clear and difficult to test statistically but there is a tendency for the species rich stations to be together and distinguishable from the species poor

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FIGURES [12] AND [13]: Dendrograms showing the assemblages of coralline (c) and non-coralline (nc) stations. [12] = fish data. [13] = coral data.

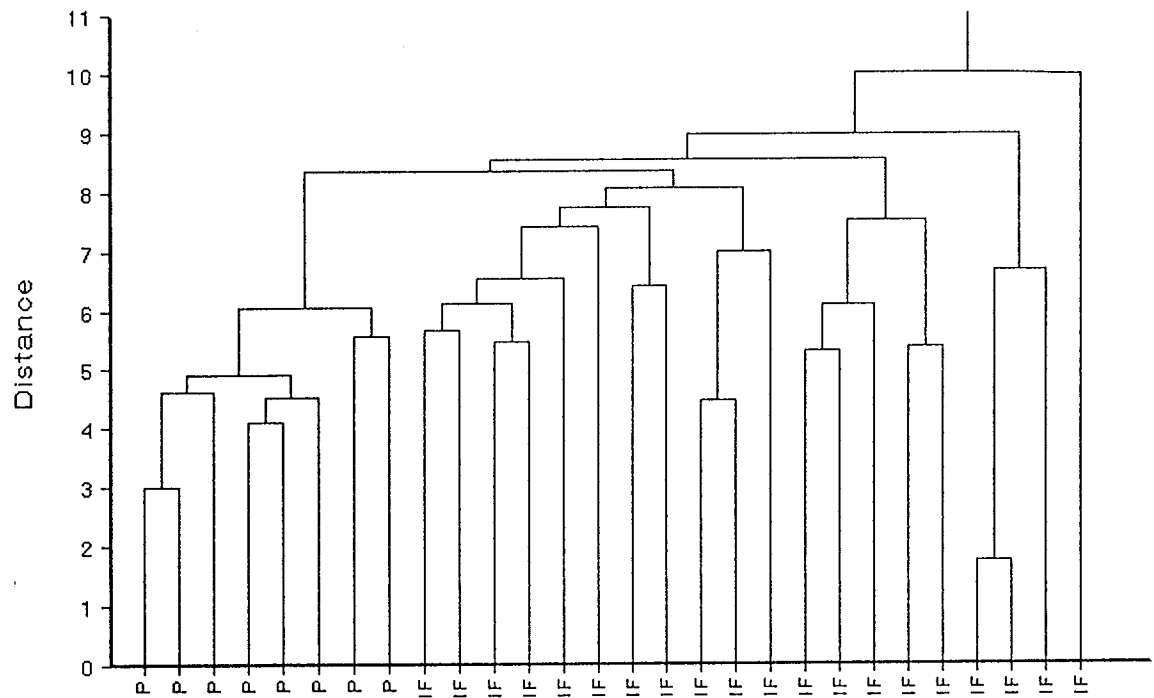
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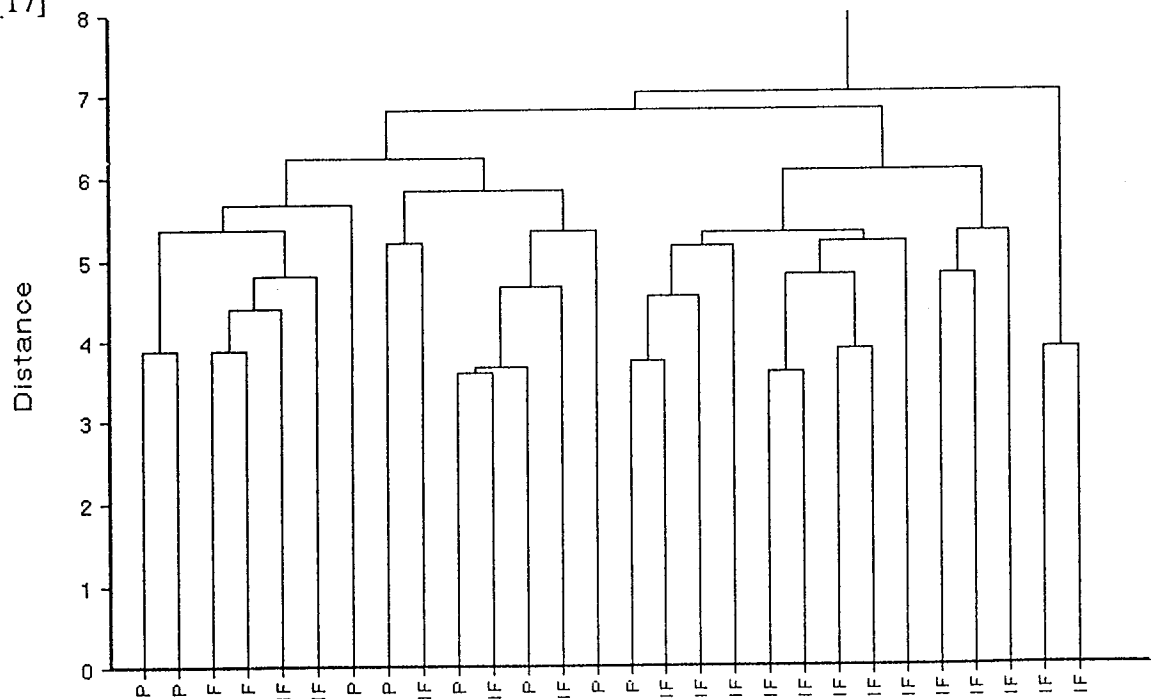
FIGURES [14] AND [15]: Dendrograms showing the assemblages of all the stations using habitat labels. [14] = fish data. [15] = coral data.

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[16]



[17]



FIGURES [16] AND [17]: Dendrograms showing the assemblages of the patch reefs and the inner forereef. [16] = fish data. [17] = coral data.

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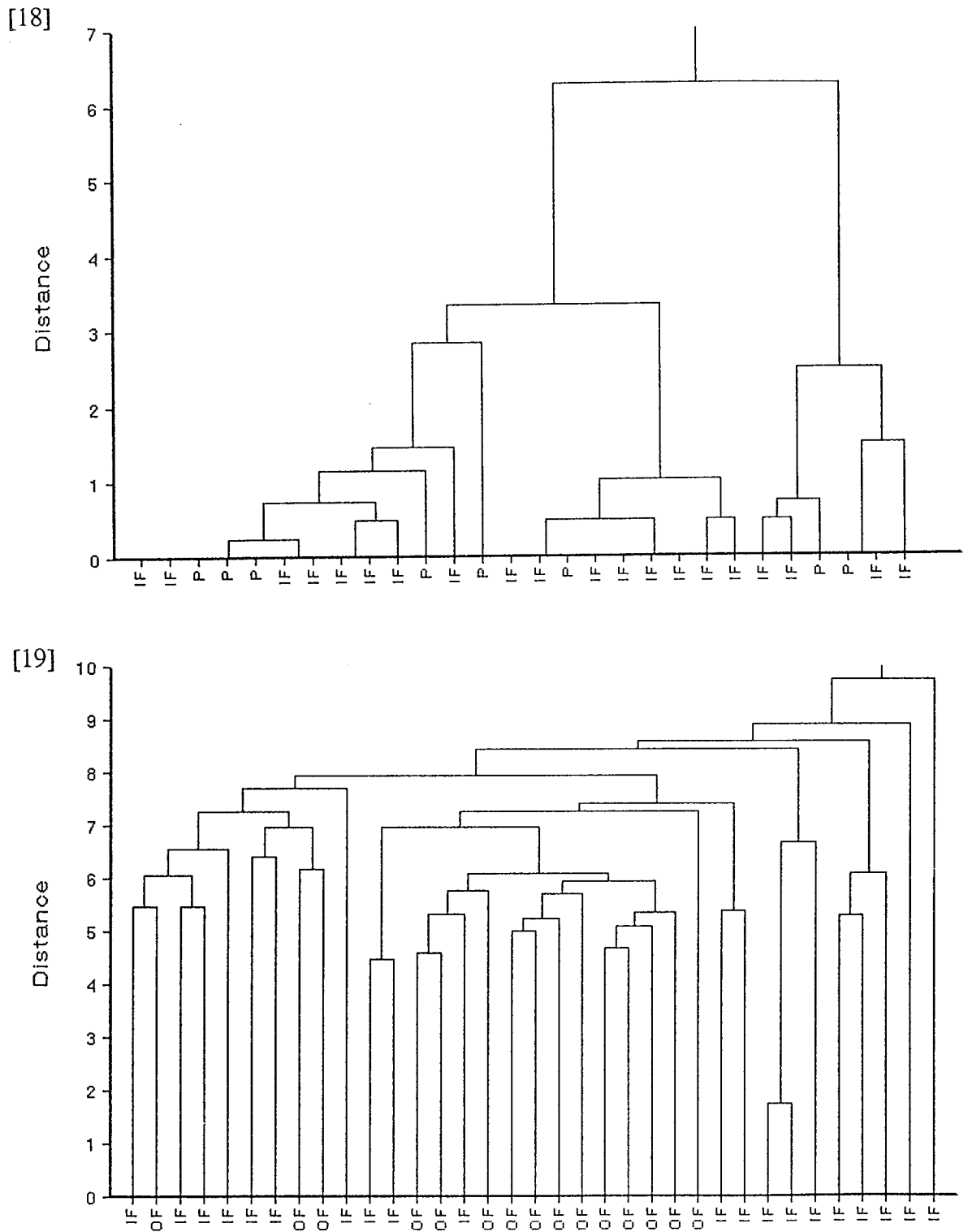


FIGURE [18] AND [19]: Dendrograms showing the assemblages of specific pairs of habitats. [18] = assemblages of patch reef and inner forereef using depth data. [19] = assemblages of inner and outer forereef using fish data.

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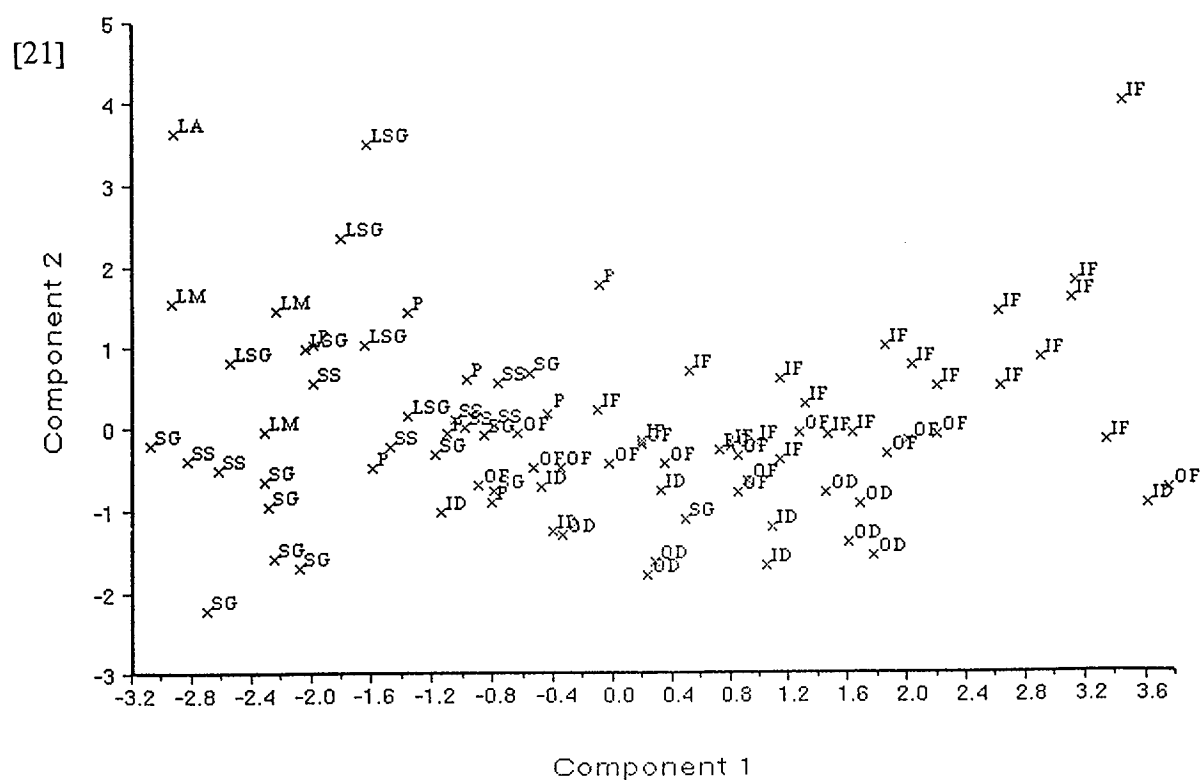
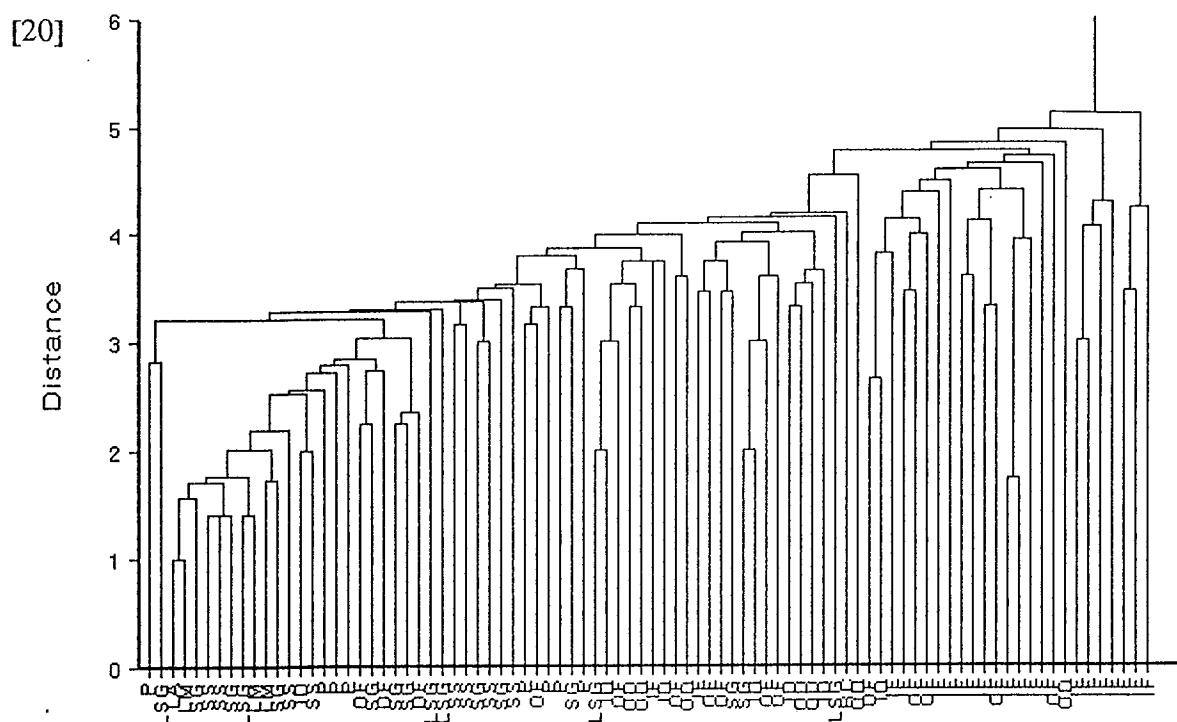


FIGURE [20]: Dendrogram showing the results of cluster analysis using presence / absence fish data.

FIGURE [21]: Results of principle component analysis using fish data of all stations.

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stations.

3.2.3. Trophic comparisons.

Interhabitat differences were also studied using analysis of the trophic structure of each habitat. The first analysis was between the carnivore and herbivore total abundance in each habitat type. A graph of the total abundances in all the stations (figure [22]) shows that there is a strong correlation between these variables ($R = 0.9930$, $P < 0.0001$). However, the actual ratio of the variables is not constant as can be seen in figure [23], which shows the ratios between the mean herbivore and carnivore proportions in each habitat. The lagoonal algal habitat was excluded since

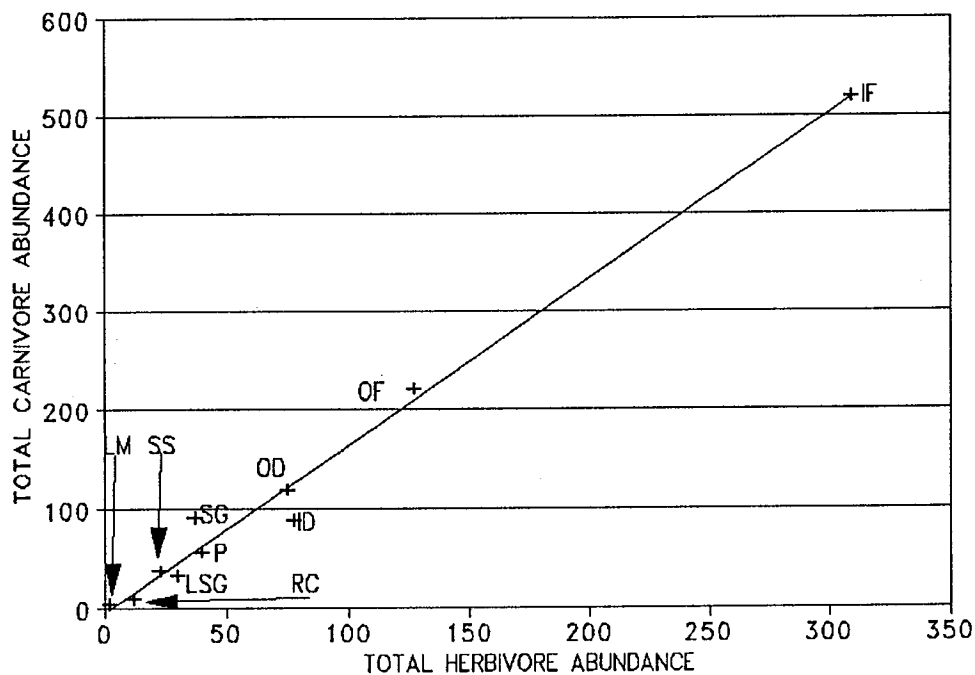


FIGURE [22]: Graph showing the relationship of herbivore and carnivore total abundances in each habitat type. Abbreviations as stated in the method. $R = 0.9930$, $P < 0.0001$.

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no fish were found there, and care must be taken with the reef crest result since there is only one station.

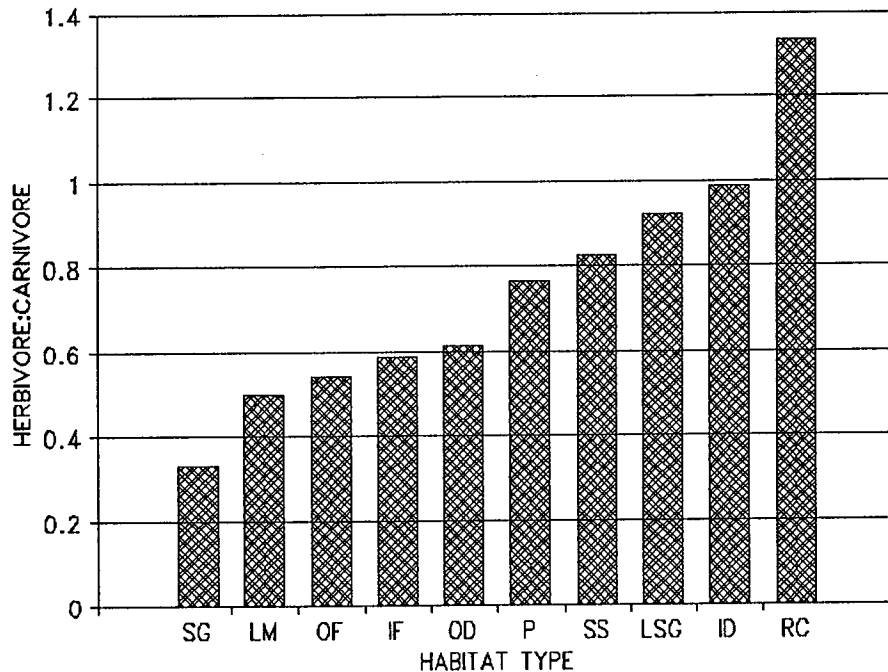
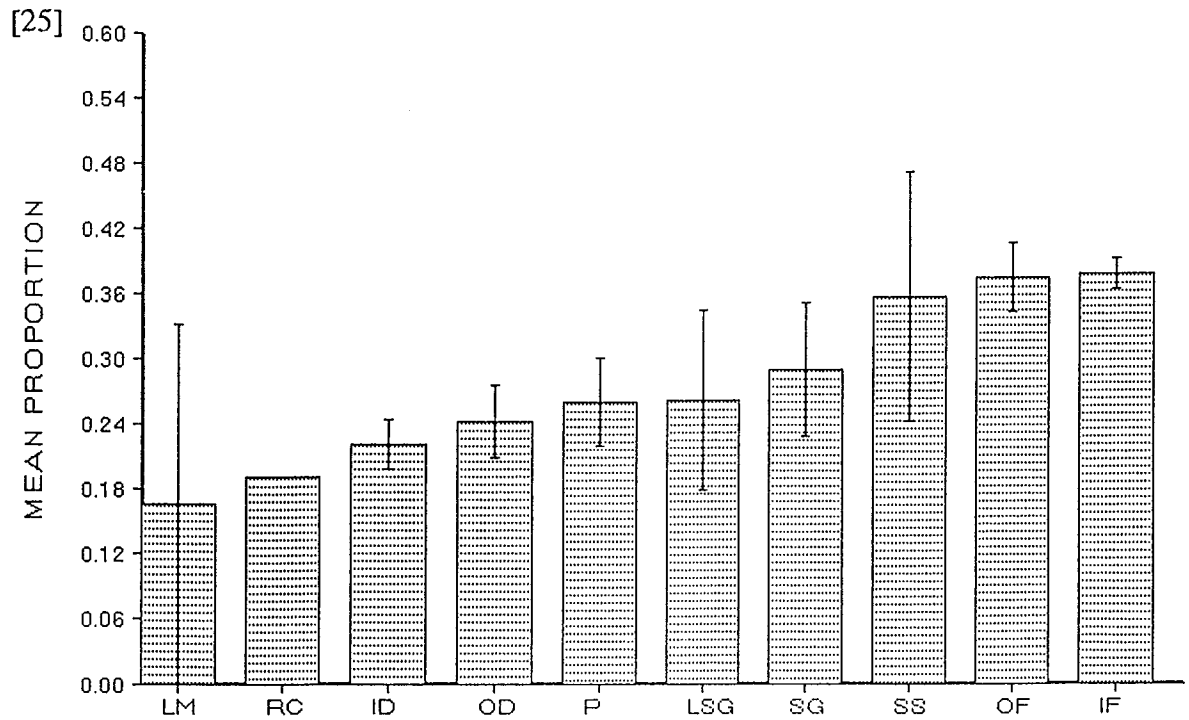
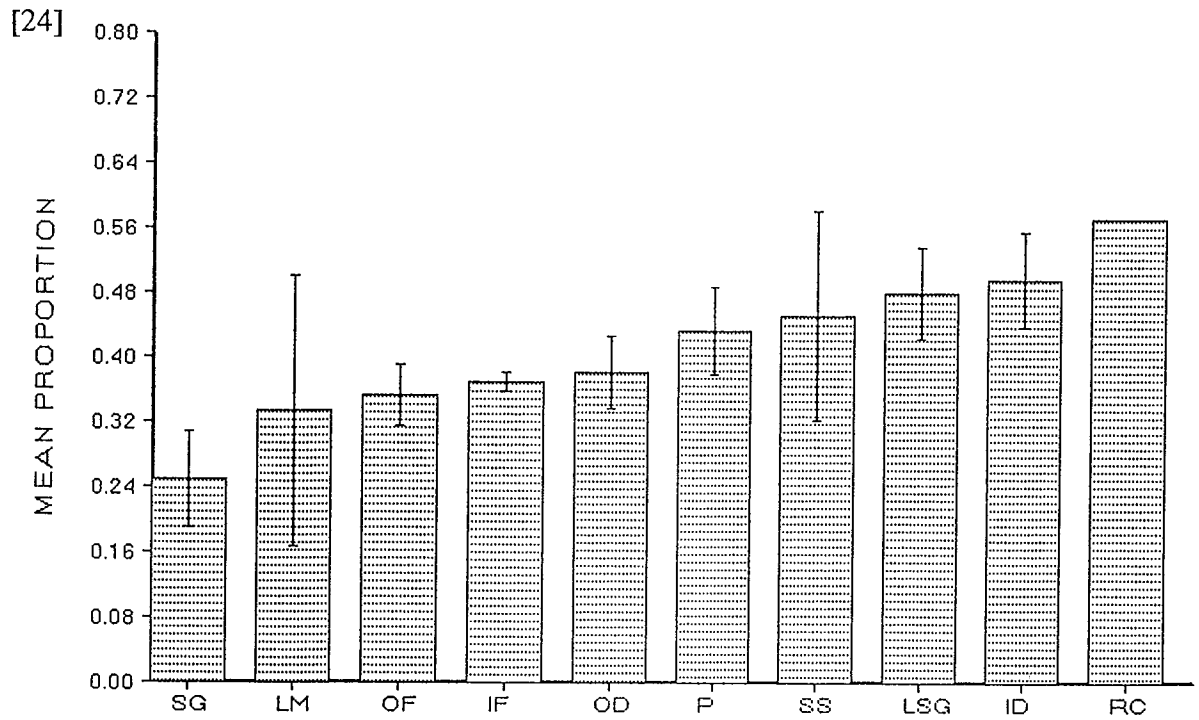


FIGURE [23]: Bar chart showing the relationship between the proportion of carnivores and herbivores in each habitat type. Abbreviations as listed in the method.

The bar chart shows that most of the habitat types have more carnivores than herbivores, with the exception of the reef crest zone with the lagoonal seagrass and inner dropoff regions also having large proportions of herbivores. The sand gully habitat has the highest proportion of carnivores. The forereef habitats have similar ratios and the shallow sand region has a distinctly higher herbivore proportion than the sand gully areas.

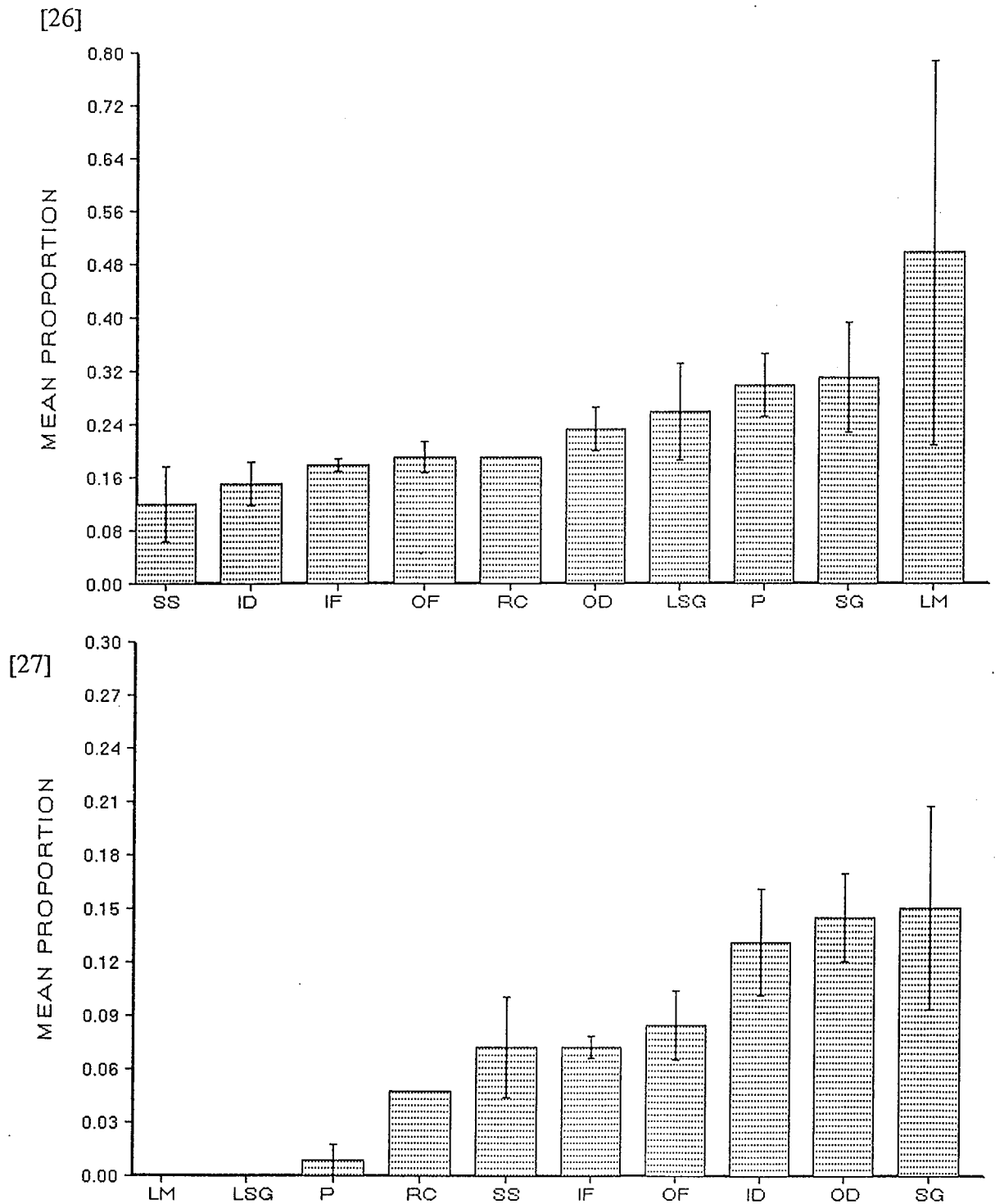
More detailed analysis was done by using the mean proportions of each trophic group in each zone, calculated from the abundance data of all the stations. This is

RESULTS



FIGURES [24] AND [25]: Bar chart showing the mean proportions of trophic feeding groups. [24] = herbivores. [25] = general invertebrate feeders. Abbreviations as method. Standard error of the mean indicated.

RESULTS



FIGURES [26] AND [27]: Bar charts showing the mean proportions of trophic feeding groups. [26] = fish / crustacea feeders. [27] = planktivores. Abbreviations as method. Standard error of the mean indicated.

RESULTS

presented in figures [24]-[27]. The lagoonal algal habitat was again excluded but the reef crest region was included simply for comparison, since with only one station no confidence limits can be generated.

The results show a number of significant differences. The lagoonal seagrass, inner dropoff and possibly, remembering the small sample size, the reef crest zones have a larger herbivore population from forereef and outer dropoff habitats ($P < 0.05$), which in turn are larger ($P < 0.05$) than the sand gully population. The patch reef data seems to be an intermediate between the first two groups and the lagoonal mud and shallow sand regions are not significantly ($P > 0.05$) different from any of the habitats due to their large confidence limits. These results are obviously consistent with the herbivore : carnivore ratio results. Differences are also seen between the general invertebrate feeders, with the the forereef habitats having larger means ($P < 0.05$) than the dropoff and patch reef zones. The fish and crustacea feeding populations seem to be more similar, however, the patch reef populations are greater ($P < 0.05$) than those of the forereef, inner dropoff and shallow zone habitats. The outer dropoff populations are larger ($P < 0.05$) than in the inner dropoff and shallow sand zones. Finally, the planktivore data shows a general distinction ($P < 0.05$) between the lagoonal and reef habitats. Within the reef habitats the outer dropoff zone has a larger population of planktivores ($P < 0.05$) than the forereef and shallow sand regions.

These trends are summarized in figure [28], comparing the proportions of each feeding group comprising each habitat type. The proportions were again the mean abundances, and again the lagoonal algal habitat was excluded. Further separation of

RESULTS

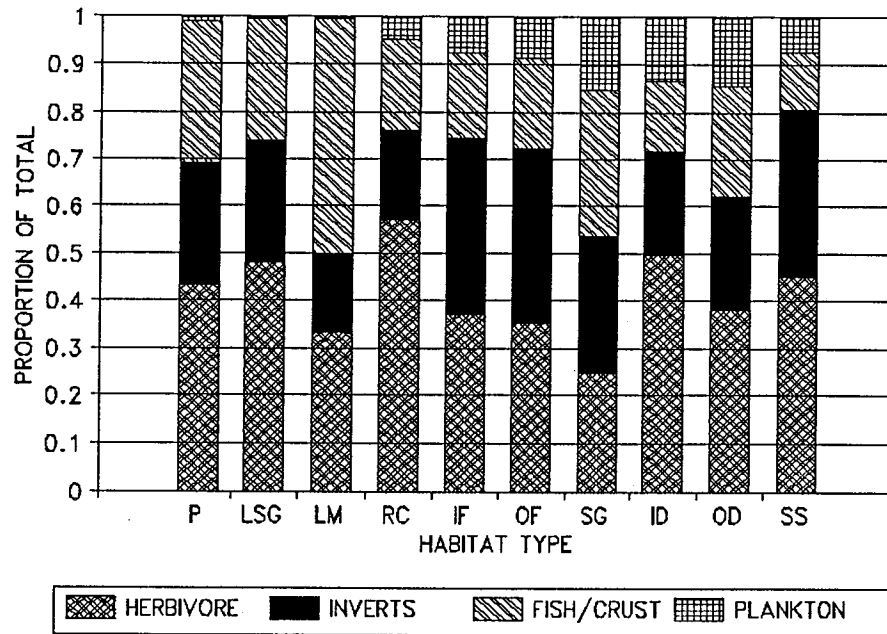


FIGURE [28]: Stacked bar chart of the mean proportions of each feeding group. Habitat abbreviation as stated in the method.

the general invertebrate and fish / crustacea trophic groups into diel and nocturnal species. This analysis is shown in figure [29].

The figure shows that the proportions of diel and nocturnal species are approximately constant throughout the habitats for both feeding groups. The mean diel proportion : nocturnal proportion ratios for each group are 10.38 (general invertebrate feeders) and 0.35 (fish / crustacea feeders).

Species rank diagrams give more general information on the ecological structure of each habitat assemblage. When plotted on a normal scale the points for each habitat were well fitted by a decreasing exponential curve ($R > 0.9$, $P < 0.01$), such as seen in figures [30] and [31]. Again not all the graphs have been included since they are all similar. When plotted on a logarithmic scale the diagrams showed a strong,

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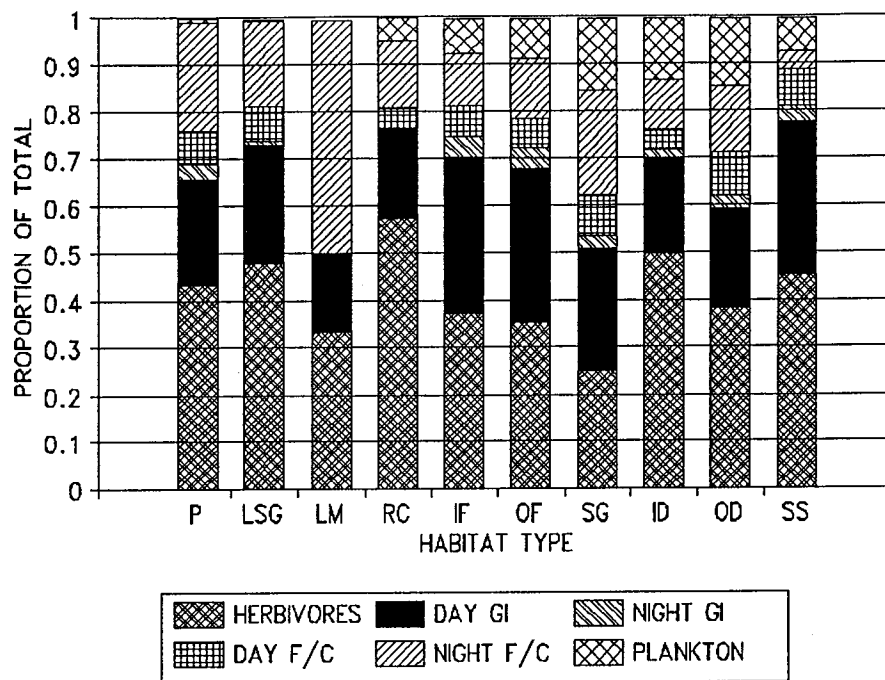
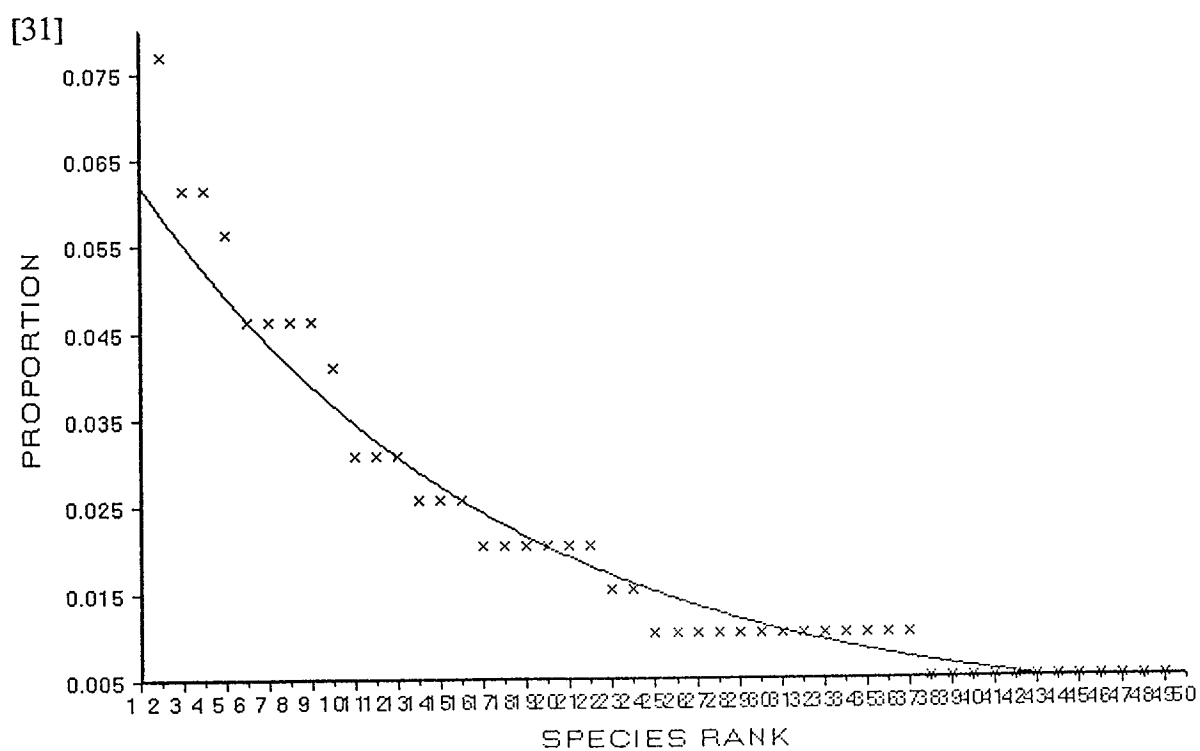
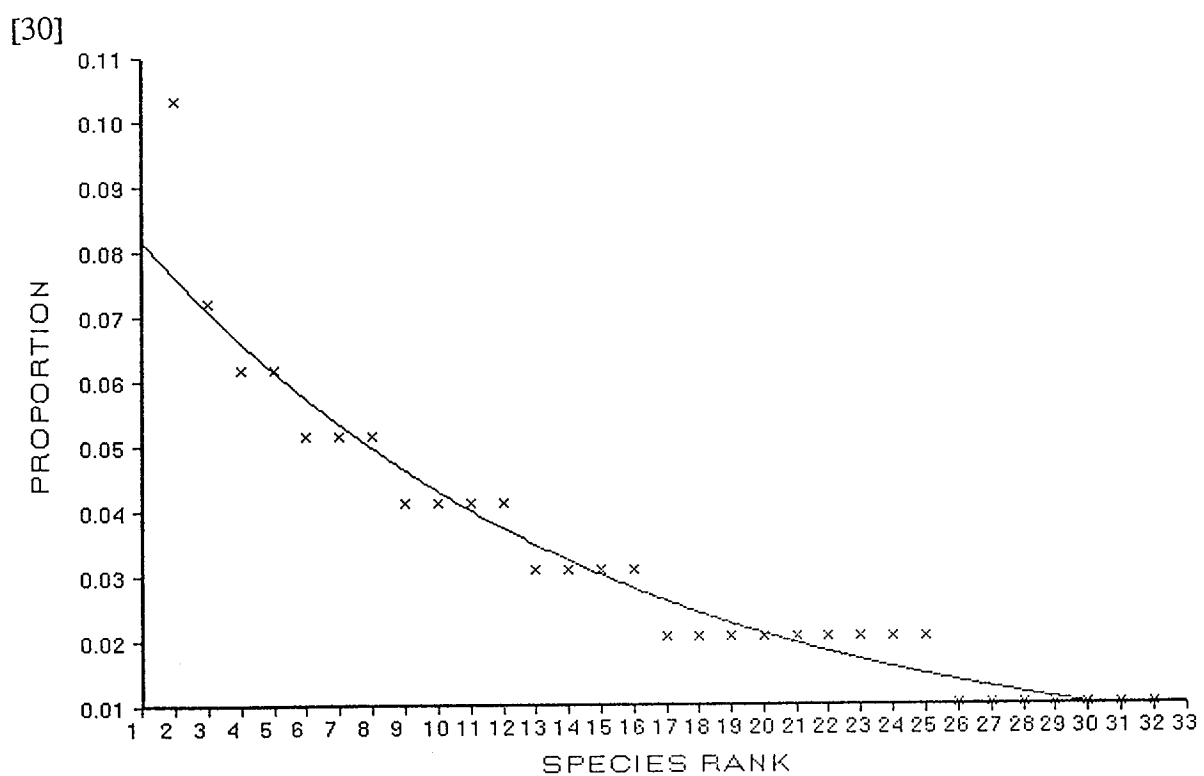


FIGURE [29]: Stacked bar chart showing the mean proportions of the four trophic groups, subdivided into diel and nocturnal species.

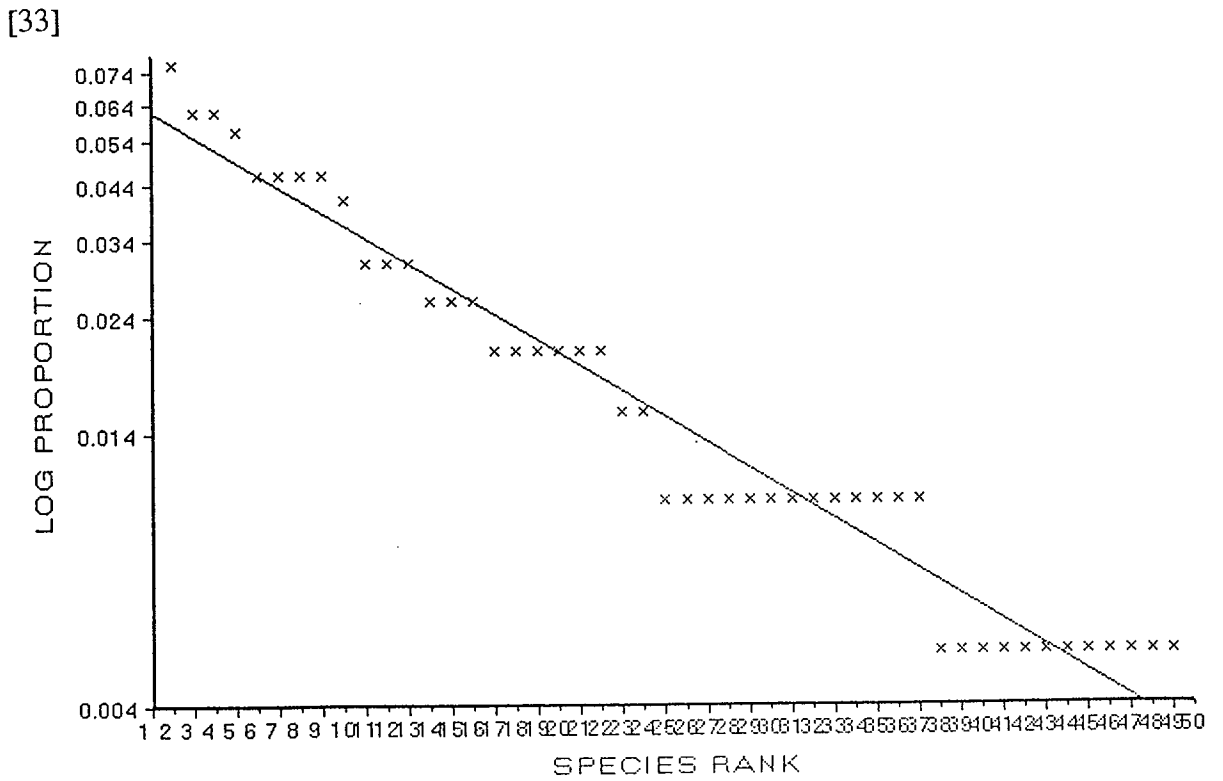
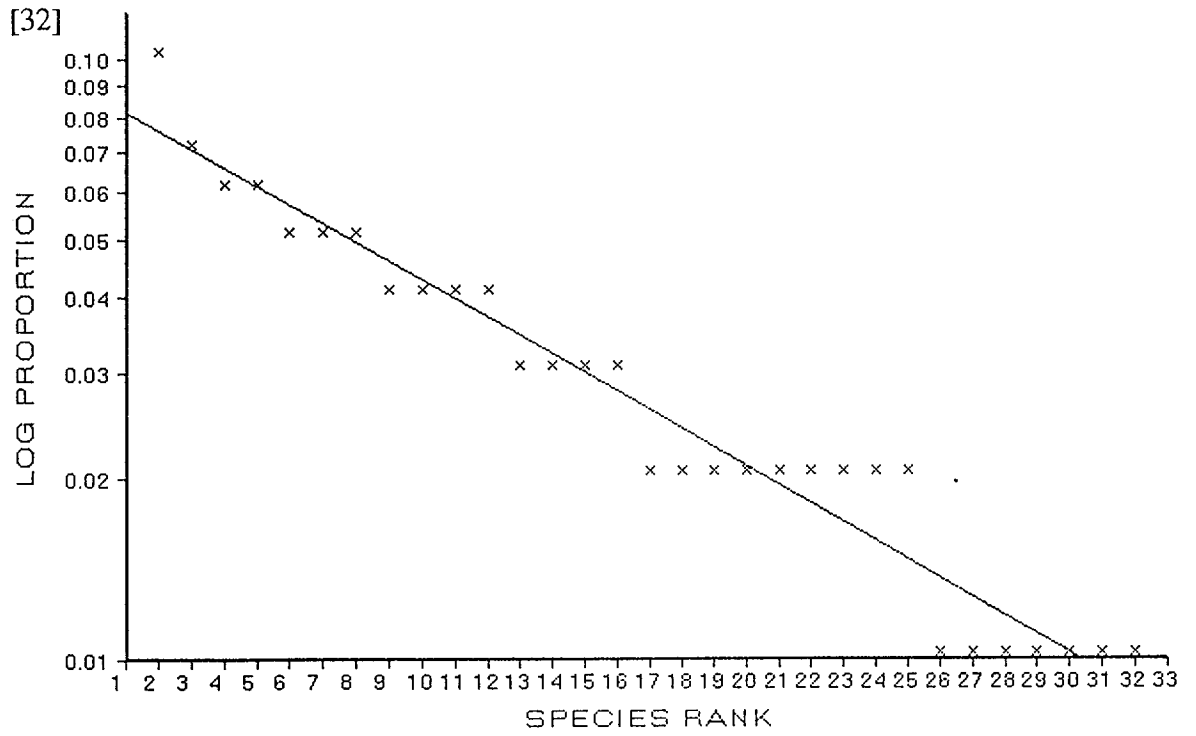
negative correlation ($R > 0.9$, $P < 0.01$), as expected from an exponential curve (figures [32] and [33] show two examples). However, the points could also be fitted by a polynomial degree seven curve, ($R > 0.9$, $P < 0.01$), but the only ecologically meaningful shape was found using the inner forereef data, and this is shown in figure [34].

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FIGURES [30] AND [31]: Graphs showing species rank diagrams as fitted by exponential curves. $R > 0.9$, $P < 0.01$. [30] = patch reef. [31] = outer dropoff.

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FIGURES [32] AND [33]: Species rank diagrams plotted on a semi-log scale and fitted by regression line. $R > 0.9$, $P < 0.01$. [32] = patch reef. [33] = outer dropoff.

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[34]

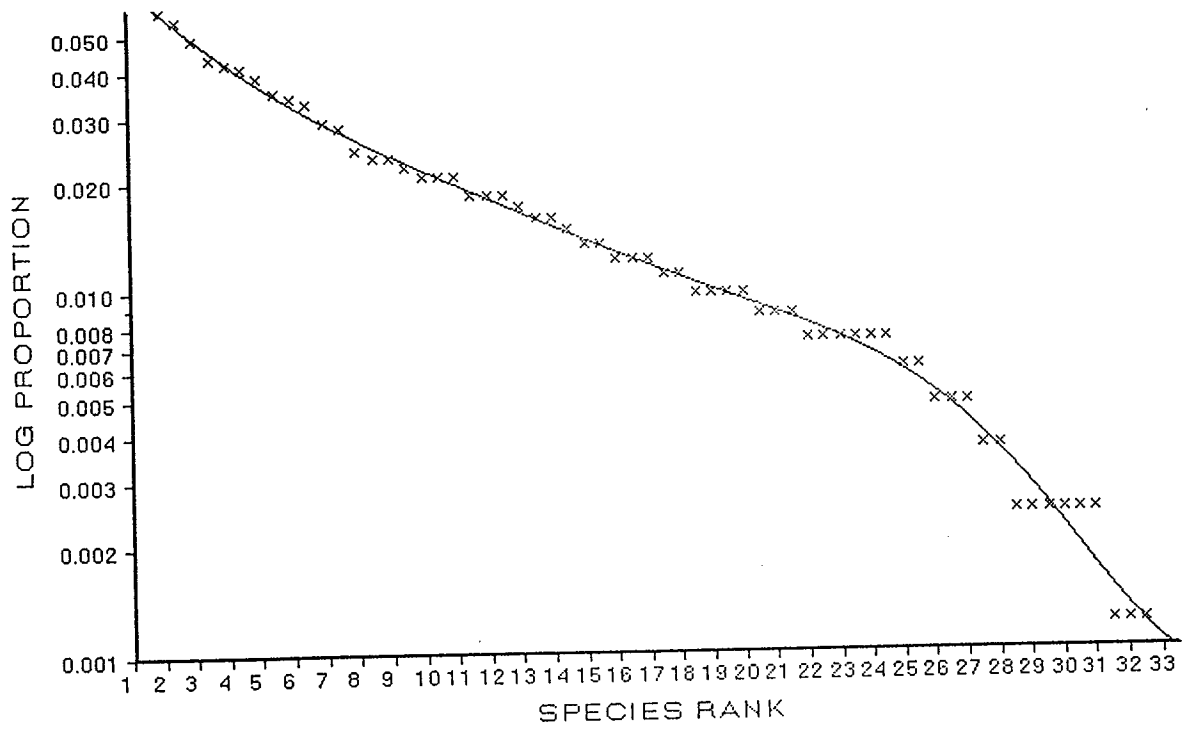


FIGURE [34]: Species rank diagram for the inner forereef plotted on a semi-log scale and fitted by a seven degree polynomial curve. $R > 0.9$, $P < 0.01$.

4.DISCUSSION.

4.1.THE INTRAHABITAT VARIATION.

The results of this study seems to show that the habitats used for the comparison of interhabitat differences consisted of relatively homogenous groups of stations. There were only four significant intrahabitat correlations with the independent variables and three of these were restricted to the species poor sand gully and shallow sand zones, meaning that the actual decrease in fish species richnesses seen with increasing depth is relatively small. The other correlation was a positive one between fish total abundance and coral total abundance in the inner dropoff habitat, which was also selected by stepwise selection. However, there were no correlations between the fish species richness and any independent variables in the coral rich zones. This is important since a comparison of the species richnesses was a main aim of the study. Stepwise variable selection also revealed little variation and using the significant variables in multiple linear regression found only four variables to be significant additions to the model of both fish species richness and total abundance in all the habitats. Again these were restricted to species poor zones or fish total abundance.

Furthermore there is no evidence of large-scale variation along the length of the reef, as measured by multivariate techniques. This seems to be true for both the fish and coral distributions, although this difficult to analyze statistically. There is no comparative study for latitudinal variation along the Belizean Reef, but it is consistent with studies in the Pacific. Anderson *et al* (1981) found a distribution of butterflyfish across the shelf at 14.5°S that was similar to that seen at 18.5°S (Williams, 1982; Sale and Williams, 1982). A fuller studies of the Vanuata island chain (Williams,

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1989) and the Great Barrier Reef (Williams and English, in prep.) suggest that the cross shelf pattern explains most of the variation in these regions, and is much greater than any north-south variation. Latitudinal variation is more apparent in the Hawaiian chain, but this seems to be due to variation in physical factors such as temperature variation and change in the gross habitats (Hobson, 1984).

4.2. THE INTERHABITAT VARIATION.

Differences between these apparently homogenous habitats have been demonstrated. There are highly significant gross trends of between site variation for all the dependent and independent variables used, but only some of the independent variables show correlations with the dependent ones. The strongest correlations, in both simple and multiple models, for both fish species richness and total abundance were with site, as might be expected since this variable encompasses intrinsic elements of all the more specific factors. It does, however, give a good measure of distinct patterns of distribution, at least at the level of simple measurements, across the reef. This is again reflected in the t-test results which show significant differences between most of the habitats and the homogenous group analysis which highlight groups of zones and differences between the habitats, especially between the coralline and non-coralline zones. The principle component analysis utilized all the variables, except site, and this picture of fish species distributions is reflected by the tendency of stations from the same habitat to cluster. The effectiveness of this technique was limited since the two principle components use only 64% of the variation within the data.

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Using all the data in multivariate clustering dendrograms reveals that this pattern is not manifested in assemblages distinctive to each habitat and repeated in each station. There is a tendency for the species rich assemblages to be located towards the right of the diagram and for coralline and non-coralline stations to be separated, but there is no strong clustering of each habitat type and there is extensive overlap of the extremes of most of the zones. Some distinct groups are discernable, particularly between the species rich forereef and dropoff zones and the lagoonal regions, but there seem to be no distinct assemblages on adjacent, or even different, reef habitats.

The multivariate results are in marked contrast to the two comparable studies in the Caribbean. Alevizon *et al* (1985) found four distinct assemblages of common, visible reef fish, which included adjacent reef habitats, and Greenfield and Johnson (1990) categorized 11 assemblages, but used only blennioids. There is a possibility that the difference between my data and that of Alevizon *et al* (1985), which is the most comparable since it utilized 41 similar species, reflects actual differences in the structuring of the fish community between the Bahamas and the Belizean Reef.

It is, however, more likely to be due to the differences in sampling techniques. Alevizon *et al* (1985) used highly quantitative data collected by counting the number of individuals of each species. The semi-quantitative data used here suffers from the same criticism levelled at presence / absence data: that it obscures habitat differences since it indicates that most of the species used most of the habitats. This is supported by the fact that the presence / absence dendrogram appears similar to the one generated using the abundance class data. Bortone *et al* (1986) quantify this problem in their comparison of several *in situ* methods. They conclude that "methods which

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produced the greatest amount of data or information with regard to number of species and abundance tended to produce less error or confusion in recognition of ecological parameters." (pp. 17).

Sale (1991) cites the variation in research designs as a major reason for the lack of a clear consensus on community structure. A survey of the literature reveals almost each study uses a different methodology, such as underwater television (Smith and Tyler, 1973), ichthyocides (Talbot and Goldman, 1972; Greenfield and Johnson, 1990), transects (for example Jones and Chase, 1975; Roberts and Ormond, 1987), quadrats (Hastings, 1979) and species-time, random counts (Jones and Thompson, 1978). Studies have also varied hugely in temporal and spatial scales and the habitats used, in both natural and artificial reef work.

The difference from the data of Greenfield and Johnson (1990) is, however, likely to be due, at least in part, to real biotic differences. Again there are sampling differences, with the blennioid study using carefully controlled rotenone poisoning which yielded individual totals for each species, but it is also expected that these small, cryptic species will exhibit greater site specificity. Intuitively it is sensible to assume that crypsis will lead to these species being more closely associated with the substrate, and hence different regions of coral zonation, than the larger bodied fish which simply use the reef itself for shelter (Shulman, 1984). In such species it would not be evolutionarily advantageous to search for a highly specific site within the reef structure. The authors themselves state that they feel blennies may be at one extreme of a graduation of habitat specificity. This idea is supported by other studies such as the segregation of two *Acanthemblemaria* species on horizontal and vertical surfaces

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of the same coral head (Greenfield and Greenfield, 1982) and the presence of *Emblemariopsis pricei* only in living *Acropora palmata* branches one metre above the reef (Greenfield, 1975). Differences in the spatial partitioning of the small and cryptic species, which constitute a sizeable segment of the reef fish fauna (Alevizon *et al*, 1985), and some of the larger, non-cryptic species therefore seems likely.

Nevertheless, there is a tendency to see distinct assemblages of the larger species, both in my study and, more explicitly, in those of (Alevizon *et al*, 1985) and others from the Pacific (for example Anderson *et al*, 1981). Large scale segregation among habitats seems to be correct (Sale, 1988) and, therefore, some spatial partitioning must be occurring. However, despite this knowledge, little is known of the processes causing the distributions (Williams, 1991). Site specialization should be particularly true for the territorial species which defend their own areas of the reef, and the site chosen must contain the correct resources. Indeed, the distribution of territorial species, such as the damselfish (Pomacentridae), is highly influenced by habitat selection (Williams, 1979) as shown by experimental evidence from the Great Barrier Reef (Allen, 1975; Eckert, 1985; Meekan, 1988). Furthermore the damselfish have also been demonstrated to partition the algae, and are important in the reef trophodynamics and regeneration (Klumpp and Polunin, 1989). Debate remains as to the mechanism of this selection, but in the damselfish there seems to be an element of chemical cues left by adult conspecifics (Sweatman, 1988). Limited evidence (Wellington, 1992) suggests that this habitat selection may be an adaptation to differential juvenile mortality between the zones. The rôle and mechanism of habitat selection by juveniles and adults of the less site specific species is largely unknown,

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but it is likely to be important, and probably due to the distribution of food (Robertson and Gaines, 1986), along with competition and predation.

The lack of species specificity in this study means that habitat selection itself is difficult to examine, however, it can be implied from some of the data. The tests of homogenous distributions and the presence in the lists of dominants for each fish species can be used to suggest habitat selection. Thus the heterogeneous distribution of the damselfish, *Microspathodon chrysurus*, that is a dominant only in the rich inner forereef, is consistent with habitat selection for spatial resources in such species and the results of Allen (1975) who found damselfish to be largely restricted to shallow reef areas. The lack of such distributions in other damselfish in this crude test is probably due to them being less common, but there is a tendency for the fish of the genus *Stegastes* to be dominant on the biotically diverse inner forereef and dropoff habitats.

In contrast the heterogeneity of the damselfish *Chromis cyanea*, the basslet *Gramma loreto* and the wrasse *Clepticus parrai* were likely to be due to food distributions. All feed, at least in part, on the plankton which is found mainly on the seaward side of the reef, due to the stronger currents that cause higher nutrient levels (Johannes *et al*, 1970; Goldman and Talbot, 1976). This hypothesis is supported by *Gramma loreto* only being dominant in the outer dropoff habitat and *Chromis cyanea* not being dominant in any of lagoonal habitats. Even though *Clepticus parrai* is classed in the general invertebrate feeder category in this study it spends a large amount of time in the water column, presumably eating plankton (personal observation). The heterogeneity of the angelfish *Holocanthus tricolor* and *Pomacanthus arcuatus* is

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harder to explain due to the few ecological studies (Lindquist and Gilligan, 1986) but since they are relatively large and conspicuous the ideas expressed above suggest it is likely to be due to the distribution of food resources.

4.3. THE ROLE OF THE INDEPENDENT VARIABLES.

This specific habitat settlement is obviously important in maintaining distinct assemblages of specific fish species in different physiographic zones and in ecological separation, but the gross trends in species richness, if the competitive paradigm is largely correct, are greatly influenced by independent factors of the region. The results of this study revealed that coral species richness varied significantly between the sites but is relatively homogeneous within them. It was then shown to be an important determinant of fish species richness and total abundance, as measured by linear and multiple regression. The differences measured by the t-tests closely matches those of the fish species richnesses and the homogeneous groups formed are also similar to those formed using this fish data, although statistical comparison is difficult. Furthermore the dendrograms using the coral data were the closest to those of the fish data.

Few studies have used coral species richness explicitly, but it acts as an, admittedly weak, measure of habitat complexity. Luckhurst and Luckhurst (1978) used the variable, in combination with two other measures of heterogeneity and found it to be correlated with fish community parameters. Many other studies have examined the link between more general complexity and species richness, and all have found a definite correlation, as stated earlier in the introduction. There is no reason to believe

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that the correlation found here between fish and coral species richness does not simply reflect this trend. However, this is only because it is the most parsimonious explanation of the data. The coral species richness variable only incorporates a limited amount of the topographic complexity, and better indices are those used by, for example, Roberts and Ormond (1987) who used biological diversity of the substratum, along with structural complexity.

Furthermore, when using coral species richness as a variable influencing the distribution of the fish community it is unlikely that it is truly independent. Williams (1991) highlights the correlation of fish distributions to that of suitable food and shelter as a potential tautology, since food and shelter may be defined to a large extent by the taxon itself. This effect has been seen to work at a variety of scales. For instance Wellington (1982) showed that the monotypic stands of pocilloporid corals in shallow water and the dominance of *Pavona gigantea* in deeper areas of the Gulf of Panama was due to differential mortality in the shallow areas from the omnivorous damselfish *Eupomacentrus acapulcoensis*. Less dramatic effects were found by Kaufman (1977), who showed that another damselfish, *Eupomacentrus planifrons*, kills living corals either directly or indirectly to produce a more favourable habitat. This problem is of real concern since the extent of such processes on the major benthic organisms is not known, however, it is likely that coral zonation is only really influenced by highly site specific fish species, but the ramifications on the distribution of food resources and larger predators remains to be discovered. Perhaps work should concentrate on the link between richness and structural diversity, as suggested by Begon *et al.* (1990).

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Although coral species richness seems to be a dominant factor causing the patterns of fish distribution found in this study, no complete conclusions can be drawn, since there are many other variables that have not been used or merely implied, that have been shown to relate to this spatial heterogeneity. No measure of current flow and water quality (Williams, 1979; Thresher, 1983), availability of hiding places (Molles, Jr, 1978; Roberts and Ormond, 1987) or live coral cover (Hourigan *et al.*, 1988) was used. The importance of wave action exposure (Talbot, 1965; Williams, 1982) is another variable that can only be implied by this study. The majority of the wave energy is dissipated in the reef crest zone (Alevizon *et al.*, 1985) and this, combined with some exposure at very low tides, must have some effect on the presence of fish species. It is certainly the reason leading to the dominance of *Acropora palmata* (Alevizon *et al.*, 1985), and this reduced complexity combined with the direct wave action is likely to be the reason for the difference of this zone from the adjacent inner forereef in the homogeneous group tests and notably in the dendrogram of assemblages. In contrast it is well known from terrestrial ecology (for example, Miller, 1982) that a limited number of disturbances can increase diversity by limiting predictability and thus reducing competitive exclusion. It is possible that this effect plays a rôle in the high diversity in the relatively shallow inner forereef and the outer most dropoff zone.

The importance of coral zonation and species richness over the other independent variables used here, however, is obvious. Thus, for instance, the two coralline habitats with the greatest overlap in depths, the patch reefs and the inner forereef, are very distinct with respect to fish species richness, total abundance and coral species

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richness. Furthermore they represent distinct assemblages in the multivariate analysis. The species paucity of the patch reefs is evident throughout the results and deserves further consideration. Patch reefs represent a useful natural experiment with the coral patches separated by large distances of lagoonal substrates (Molles, Jr, 1978; Walsh, 1985; Schroeder, 1987). Molles, Jr (1978) reviews the situation as lying at a convergence of two theories. The vagaries of recruitment of coral reef fish (for review see Mapstone and Fowler, 1988), especially in such isolated areas, mean that diversity will be a result of colonization and extinction in accordance with the theory of island biogeography (MacArthur and Wilson, 1963), whilst there should be an element of the competitive community structuring discussed earlier. His experimental work found the patterns of immigration and extinction approximated the predictions of insular zoogeography, and the results of this study seem to be consistent with this. Although no detailed data is available on isolation and patch reef size, the general paucity of species suggests that they are not as saturated, and thus highly partitioned and structured, as the main reef habitats.

In contrast the lagoonal seagrass beds have more diverse fish assemblages than expected from their low coral species richness, though the presence of many isolated coral heads (personal observation) means that a site specific damselfish, *Stegastes planifrons*, is classed as a dominant species. This is likely to be due to variety of reasons, such as their use as a food resource for herbivores. This reason is supported by the high herbivore : carnivore ratio and the high mean proportion of herbivores. In this light it would be a constructive exercise to link the number of fish on the seagrass to distance from a patch reef, which acts as shelter for the feeding fish

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(Randall, 1963). Perhaps more importantly, however, seagrass beds have been shown to act as a nursery for reef fish (Ogden and Gladfelter, 1983; Shulman, 1985). This rôle seems to be confined to the Caribbean (for example, Parrish, 1987), however, its importance in the diversity of the habitat and the feedback to the abundances on the coral reefs requires more detailed study than this one.

4.4. *THE INTERHABITAT DIFFERENCES IN TROPHIC STRUCTURE.*

The high proportion of herbivores in the lagoon seagrass beds is obviously expected, but more subtle effects were also seen in the trophic analysis. The equally high ratio in the inner dropoff zone, much higher than the adjacent outer dropoff, is more difficult to explain, but one hypothesis is that the increased shelter of this leeward slope (Goldman and Talbot, 1976) allows greater floral growth. The depth of the zone is also an important factor governing floral abundance via light attenuation, and this variable can be invoked to explain the greater proportion of herbivores in the shallow sand habitat as compared to the sand gully. At a more general level, the strong correlation between the herbivore and carnivore total abundances in each habitat hints at an intriguing element of community structure.

Within the other trophic groups there were a limited number of specific trends, but perhaps the clearest is seen in the planktivores. It has already been stated that the heterogeneous distributions of three fish species was likely to be due to the distribution of the plankton itself, and this is reflected in the very low mean proportions of the lagoonal habitats and the high levels in the seaward dropoff and sand gully zones. Other trends seen were the high levels of general invertebrate

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feeders in the forereef zones, perhaps due to the high topographic complexity allowing a larger epifaunal community, and the high mean proportion of fish / crustacean feeders in the sand gully, patch reef and lagoonal seagrass habitats. This may be due to the lack of a diverse, coralline substrate which means a predomination of more migratory, predatory species.

The relatively constant ratio of diel and nocturnal species in the two trophic groups analyzed, although the sample sizes are rather too small, also suggests an interesting feature of community structure. The striking diel migrations from resting places to feeding areas at a "changeover period" has been well documented (for example, Hobson, 1973) and is often predictable in terms of timing and routes. Again analysis of whether this changeover ratio is totally constant, and a method of temporal separation, in all the habitats, or varies between them, depending on, for example, the number and diversity of shelter holes, requires more detailed study.

All the interpretations based on trophic differences, however, must be viewed sceptically due to the difficulty of assigning the species into biologically realistic groups. This is highlighted by the rather artificial fish / crustacea feeding class. Specific trophic studies need to use precise guilds (*sensu* Root, 1967) to study the way resources are divided and utilized within the community. Furthermore no study was made of differences between stations in the same habitat type, because of the vagaries of the semi-quantitative data, but this would add information to the constancy of habitat assemblages. These types of study, however, will first rely on better documentation of species specific niches.

The problem of trophic classification does not apply to the species rank diagrams.

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They showed that the communities appeared to conform to an exponential, or logarithmic, distribution and this suggests niche pre-emption. However, the more complex curve fitted to the inner forereef data suggests that the situation may not be quite as simple. The shape of this curve is more reminiscent of a log-normal model, which means the abundant species may be more common than expected and the rarer species less abundant than expected. What the general ecological characteristics of the reef are, and whether it indeed does vary between the zones remains a tantalizing question for future research.

4.5. APPLICATION OF THIS STUDY TO THE HYPOTHESES OF THE PROCESSES MAINTAINING REEF FISH DIVERSITY.

It has been stated many times, since the distinct dichotomy between various theories was removed in favour of a more dynamic approach, that the reasons for coral reef fish diversity are complex and that each is likely only to refer to one site or species. However, as Williams (1991) states, this is rather trite and the challenge is to search for non-trivial generalizations to stimulate further work. The most obvious generalization is the degree to which the community appears to be competitively mediated and the evidence from this study can be used in this way. As stated in the introduction, there are a number of expectations of a structured community, one of which is that distinct physiographic zones should support markedly different assemblages. This study certainly demonstrated differences in characteristics such as

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species richness and total abundance, which is consistent evidence, but the multivariate analysis failed to recognize tightly clustered groups of stations from the same habitat. This may be interpreted in a number of ways, depending on the significance placed on the results, and the first of these is that they conform the lottery hypothesis. Sale (1991) states that evidence for more stochastically structured fish assemblages is that although different species are found in the zones, sampling replicate sites within a zone shows a more transient association. However, it is likely that the lack of highly quantitative data has caused a blurring of the assemblage boundaries and that counting individuals would produce more distinct groups, similar to those found by Alevizon *et al.* (1985).

Competition *per se* and interhabitat differences, however, have certainly emerged as having an important rôle in maintaining the diversity of coral reef fish, and there is no apparent need to search for theories drastically different from classical ideas. The distinct changes in species richness, correlated with changes in measures of habitat heterogeneity, the limited extent of broad-scale partitioning by assemblages and specific species, and the explainable trophic differences within an overall structure suggests that recruitment limitation is not of great importance. Again many qualifying statements must be attached to this conclusion, namely that such partitioning does not prove competitive processes are, or were, definitely acting (Sale, 1991), resource limitation cannot be dismissed without density-dependence experiments (Mapstone and Fowler, 1988) and that "snap-shot" views of any community are poor indicators of overall structuring processes and community "trajectories" (Drake, 1991) and give no idea of the expected temporal constancy

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(Sale, 1977).

Much research on coral reef ecology has focused on the problem of scale, and it is useful to briefly state how this study fits into the debate. It is likely that much of the confusion has occurred due to the variety of scales used (for example Anderson *et al.*, 1981) since the non-equilibrial view has been concerned with local coexistence and at this level the reef is highly unpredictable (Sale, 1977). Robert May highlighted the problem of research size scales determining the results found in the recent British Ecological Society conference. This data is essentially large scale, although it is likely to be smaller than the large partitioning referred to by Sale (1988) and quoted earlier, but the use of adjacent habitats removes the possibility of different species pools or passive water movement accounting for the patterns (Sale, 1980; Sale and Williams, 1991). This problem of scale, however, is still of concern, since it is difficult to know whether transect sampling encompasses a full assemblage of even these rather sedentary (Sale, 1977) organisms, since a species' perception of a zone is largely dependent on the home range of individuals (Williams, 1991).

Although coral reef fish are relatively constant at the family level (for example, Sale, 1991) it is possible that the evidence of a seemingly structured community on this reef, does not hold true for other geographical areas. There are certainly differences of total species richness between the Caribbean and, for example, the Pacific (Sale, 1980) and furthermore the western Atlantic is more saturated with species (Ross, 1986). Combined with the different results there has been speculation that the structuring processes are fundamentally different (for a review see Thresher, 1991), such as that the Caribbean communities are more "classically competitively"

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mediated. The data is still patchy, but there is a strong indication of real geographic patterns, and until these have been elucidated by well designed comparative studies, the extrapolation of results from a particular area will remain very dangerous.

Throughout this discussion I have tried to indicate the limitations of the data and possible future work. All research ends with a plaintive cry for further work, but in this area it is desperately needed. Categorization of real geographical and site specific patterns will direct research towards detailed studies of demographics, larval biology, recruitment and resource utilization. It is a far off target that this work can then be combined into a dynamic theory of coral reef fish coexistence.

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APPENDIX I.

THE FISH SPECIES USED.

SPECIES NAME	FAMILY	TROPHIC GROUP	G-TEST RESULT
<i>Chaetodon ocellatus</i>	Chaetodontidae	GI	11.743
<i>C. capistratus</i>	"	"	10.581
<i>C. striatus</i>	"	"	7.558
<i>C. sedentarius</i>	"	"	8.318
<i>C. aculeatus</i>	"	"	0.000
<i>Holacanthus tricolor</i>	Pomacanthidae	"	14.725
<i>H. ciliaris</i>	"	"	7.244
<i>Pomacanthus paru</i>	"	"	6.198
<i>P. arcuatus</i>	"	"	15.312
<i>Acanthurus bahianus</i>	Acanthuridae	H	8.318
<i>A. chirurgus</i>	"	"	6.422
<i>A. coeruleus</i>	"	"	7.448
<i>Caranx ruber</i>	Carangidae	F/C	5.131
<i>Calamus calamus</i>	Sparidae	*	5.545
<i>Sphyraena barracuda</i>	Sphyraenidae	F/C	9.364
<i>Lutjanus apodus</i>	Lutjanidae	F/C (N)	8.318
<i>L. joco</i>	"	"	5.545
<i>Ocyurus chrysurus</i>	"	"	8.891
<i>Haemulon sciurus</i>	Pomadasyidae	"	7.558
<i>H. macrostomum</i>	"	"	4.159
<i>H. chrysargyreum</i>	"	"	4.159
<i>H. striatum</i>	"	"	8.318
<i>H. plumieri</i>	"	"	14.064
<i>H. melanurum</i>	"	"	5.545
<i>H. flavolineatum</i>	"	"	4.726
<i>H. parrai</i>	"	"	0.000
<i>H. aurolineatum</i>	"	"	11.292
<i>Anisotremus virginicus</i>	"	"	4.700
<i>Microspathodon chrysurus</i>	Pomacentridae	H	17.315
<i>Stegastes fuscus</i>	"	"	11.377
<i>S. diencaeus</i>	"	"	7.473
<i>S. variabilis</i>	"	"	5.059
<i>S. leucostictus</i>	"	"	9.400
<i>S. partitus</i>	"	"	5.181
<i>S. planifrons</i>	"	"	10.581
<i>Abudefduf saxatilis</i>	"	"	10.044
<i>Chromis cyanea</i>	"	P	18.900
<i>C. multilineata</i>	"	"	8.997
<i>Hypoplectrus puella</i>	Serranidae	F/C	5.545

<i>H.indigo</i>	"	"	8.997
<i>H.gemma</i>	"	"	0.000
<i>H.gummingatta</i>	"	"	0.000
<i>Epinephelus striatus</i>	"	"	4.159
<i>Mycteroperca bonaci</i>	"	"	0.000
<i>E.guttatus</i>	"	"	5.885
<i>E.adscensionis</i>	"	"	0.000
<i>Cephalopholis cruentatus</i>	"	"	4.159
<i>C.fulvus</i>	"	"	5.545
<i>Serranus tigrinus</i>	"	"	12.816
<i>S.tabacarius</i>	"	"	11.234
<i>Gramma loreto</i>	Grammidae	P	17.177
<i>Scarus vetula</i>	Scaridae	H	5.544
<i>S.taeniopterus</i>	"	"	7.165
<i>S.iserti</i>	"	"	13.835
<i>Sparisoma viride</i>	"	"	5.124
<i>S.aurofrenatum</i>	"	"	8.318
<i>Lacholaimus maximus</i>	Labridae	GI	8.658
<i>Bodianus rufus</i>	"	"	6.225
<i>Clepticus parrai</i>	"	"	14.543
<i>Halichoeres gamoti</i>	"	"	4.726
<i>Thalassoma bifasciatum</i>	"	"	3.713
<i>Holocentrus ascensionis</i>	Holocentridae	"(N)	9.373
<i>H.marianus</i>	"	"(N)	11.090
<i>H.rufus</i>	"	"(N)	10.017
<i>Malacanthus plumieri</i>	Malacanthidae	"	11.292
<i>Aulostomis maculatus</i>	Aulostomidae	F/C	4.159
<i>Balistes vetula</i>	Balistidae	GI	8.318
<i>Melichthys niger</i>	"	"	12.173
<i>Pseudupensis maculatus</i>	Mullidae	"	4.642

H = herbivores, GI = general invertebrate feeders, F/C = fish or crustacea feeders, P = planktivores. N = nocturnal species.

* = no information on feeding behaviour.

APPENDIX II.

CORAL SPECIES USED.

Acropora palmata
A.cervicornis
A.prolifera
Porites porites
P.furcata
P.astreoides
Madracis mirabilis
Montastrea annularis
M.cavernosa
Siderastrea radians
S.siderea
Dichocoenia stokesii
Favia fragum
Solenastrea hyades
Agaricia lamarcki
A.agaricites var. *agaricites*
A.agaricites var. *danai*
A.tenuifolia
A.undata
Helioseris cucullata
Colpophyllia natans
Diploria labyrinthiformis
D.strigosa
D.clivosa
Meandrina meandrites
Mycetophyllia lamarckiana
M.danaana
M.aliciae
Isophyllastrea rigida
Dendrogyra cylindrus
Gorgonia ventalina
G.flabellum
Plexaura flexuosa
P.pluma
Flagellia rougum
F.panka

APPENDIX III.

MEAN VALUES OF THE DEPENDENT VARIABLES.

ZONE	FISH SPECIES RICHNESS	FISH TOTAL ABUNDANCE
P	8.875	12.125
LA	0.000	0.000
LSG	9.000	10.500
LM	1.667	2.000
RC	15.000	21.000
IF	25.350	41.500
OF	15.733	23.200
SG	7.909	11.909
ID	15.142	23.857
OD	18.714	28.000
SS	6.125	8.250

MEAN VALUES OF THE INDEPENDENT VARIABLES.

ZONE	CORAL SPECIES RICHNESS	CORAL TOTAL ABUNDANCE	DEPTH	LENGTH	ALGAL COVER
P	8.125	15.250	7.063	57.500	1.625
LA	1.000	1.000	12.000	300.000	4.000
LSG	2.500	3.833	6.417	100.000	2.833
LM	4.000	4.333	10.333	67.667	3.667
RC	15.000	33.000	2.500	20.000	0.000
IF	16.500	27.250	7.175	82.750	1.700
OF	17.600	31.533	13.050	33.333	1.933
SG	6.545	9.636	21.291	45.000	1.455
ID	17.143	29.143	18.857	12.714	1.857
OD	18.143	30.571	24.000	10.857	2.429

