

Testing the Intermediate Disturbance Hypothesis
Around Turneffe atoll,
Belize, Central America.

Abstract: Four sites were chosen on reefs around Turneffe atoll, in order to establish a gradient of wind exposure. 20 replicate transects were taken at each site from 30m to the surface identifying all species present. The sites were analysed in their entirety and in habitat types. Hard coral (Scleractinia and Milleporina) diversity (Simpson's index) was found to be highest within habitat types and sites as a whole at an intermediately wind-exposed site. Coral cover was also highest at this site. These results do not support intermediate disturbance as a factor promoting diversity. Herbivory was found to have no effect on algal diversity. The fish and invertebrate (other than coral) assemblages did not reflect the benthic resources available (food and shelter), supporting a recruit-limited model for fish and invertebrate assemblages.

To CCC,

Thanks for the help.

Colin J. J. J.

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INTRODUCTION

Coral reefs are one of the most diverse ecosystems on earth. They are oases in an oligotrophic sea (Nybakken, 1993). This is due to the endosymbiosis between the corals and the dinoflagellate zooxanthellae which they house. The zooxanthellae are dinoflagellate primary producers and facilitate nutrient cycling which approaches 100% efficiency with the corals (Wellington, 1982). The diversity shown in coral reef ecosystems has been the subject of much research. Understanding the processes that regulate and control coral reef diversity is essential in order to manage this precious natural resource as sustainably as possible. This is particularly important in the light of the increasing stress which man exerts upon coral reefs. This stress comes from fishing, recreational activity such as SCUBA diving, the capture of reef animals for aquaria, and coastal development. Human population rises in tropical coastal countries compound this stress. Without sensible and sustainable use of the world's coral reefs irreversible damage will ensue. This management can only be effective if it is undertaken with comprehensive knowledge of the ecological processes that regulate and maintain coral reef diversity.

The maintenance of species diversity in any ecosystem is important not just from an academic or aesthetic view point, but because the health of the ecosystem concerned is dependent upon the richness of species of which it consists. The loss of a few species may not alter an ecosystem significantly, but its ability to adapt over evolutionary time to climate change or stochastic events such as catastrophes will be reduced (Simberloff, 1986). The greater the reduction in diversity is, the more unstable the ecosystem will be under these threats.

This is particularly poignant for coral reef ecosystems from an anthropogenic view point because globally coral reefs serve as an enormous source of food and income upon which many people are dependent.

THE ROLE OF DISTURBANCE

(The Intermediate Disturbance Hypothesis)

The aim of this study is to investigate the influence of wave and swell exposure on coral reef communities. Waves and swell act as a disturbance which is believed to be a structuring force acting on the coral reef benthos. Coral reefs are subjected to many forms of disturbance. These disturbances differ in intensity and act on a wide range of temporal and spatial scales.

Disturbance is believed to be an important factor in promoting diversity on coral reefs. The intermediate disturbance hypothesis (Connell, 1978) states that when disturbance is at an intermediate level then diversity will be maintained at its highest level for the ecosystem concerned. This is because disturbance prevents succession from reaching a climax community where dominant species outcompete inferior competitors. Disturbance causes compensatory mortality and effectively retards the growth and spread of the faster growing species which are, however, more vulnerable to disturbance than the slower growing species. Disturbance, therefore, allows species to co-exist, never allowing any species to become dominant and thus prevents competitive exclusion. Diversity should be low at both low and high levels of disturbance: at low levels of disturbance there is little compensatory mortality and so the dominant species will be able to outcompete others, and at high levels many species will not be able to survive. Diversity, therefore, will be highest at intermediate levels of disturbance preventing competitive exclusion but not eliminating most

species (Paine & Vadas, 1969; Richardsen *et al.*, 1970; Grassle & Sanders, 1973; Grime, 1973; Grigg & Maragos, 1974; Osman, 1977; Connell, 1978; Lubencho, 1978; Huston, 1979, 1994).

Disturbance affects not only coral but also the algal diversity (Hixon and Brostoff, 1983). This disturbance is in the form of herbivory. There is a link between the intensity of herbivory and the wave and swell intensity: herbivores are prevented from grazing efficiently during periods of high wave and swell. Therefore, the type of disturbance may not have a uniform effect on the benthos as a whole. A disturbance promoting coral diversity such as waves and swell may reduce algal diversity.

SCALE

The intermediate disturbance hypothesis arose in the climate of belief that coral reef and tropical rain forest ecosystems were stable. Connell (1973) studied fixed one-metre-square quadrats on a coral reef. He noticed that the benthos changed greatly during his yearly observations. This lead him to believe that the coral communities were not stable but dynamic. However, at the scale of the one-metre-square quadrat the coral communities are unpredictable (Jackson, 1991). Testing the intermediate disturbance hypothesis on coral reefs has been met with little success. This is largely due to the small scale of these studies (Jackson, 1991) which is inappropriate when one colony can easily fill one quadrat. It is only when large scale studies are undertaken that trends are observed rather than simply unpredictability. Aronson and Precht (1995) tested the hypothesis on an area of $>10^4 \text{ m}^2$. They concluded that their observations support the intermediate disturbance hypothesis. However, their conclusions are questionable and will be discussed later. The scale of

this investigation is large in order to combat problems of unpredictability, with sites of $>1000 \text{ m}^2$ and areas of 500 m^2 of habitat being compared.

HISTORICAL DISTURBANCE

Unfortunately, in the absence of a detailed knowledge of past major disturbance events such as hurricanes or boats running aground, it is not possible to account for historical events that still influence the reef communities. The importance of the history of corals reefs in determining their structure and their susceptibility to future disturbances was outlined by Witman (1992). His study of exposed and protected reefs in the U.S. Virgin Islands revealed that the exposed reef was less damaged by hurricane Hugo (1989) than the sheltered reef. This is surprising until it is looked at in the context of the history of the reef. A year earlier the exposed reef was severely damaged by hurricane Gilbert, and the fragile corals had been damaged then so when hurricane Hugo came there was little damage that could be done. The sheltered reef, however, had not been damaged by hurricane Gilbert and was highly susceptible to damage by hurricane Hugo, the most severe hurricane of the past century (Witman, 1992).

In this study historical disturbance events are ignored and it is assumed that the atoll has been either equally affected by these events or that the atoll has been affected by these events in accordance with the exposure gradient investigated.

FISH ASSEMBLAGES

Fish assemblages on coral reefs should be dictated to some extent by the benthos present. It is logical to assume that on sites where there is more algae there will be more herbivorous fish, and on sites where there is more coral there will be more coralivores. This assumption is likely to be valid up to a point. Coral reef fish assemblages are recruitment limited and for this reason coral reef habitats never reach carrying capacity (Sale, 1980). This has been demonstrated by the translocation of fish to increase the demand on a particular resource without a loss of fitness to any fish concerned (Robertson *et al.*, 1981). The species composition of fish assemblages are therefore unpredictable, but the trophic groups within these assemblages should be more predictable. The number of herbivores and corallivores within the same habitat type should be similar, but there should be significant differences between habitats types, and possibly within habitat types if disturbance plays a role.

BELIZEAN CORAL REEFS

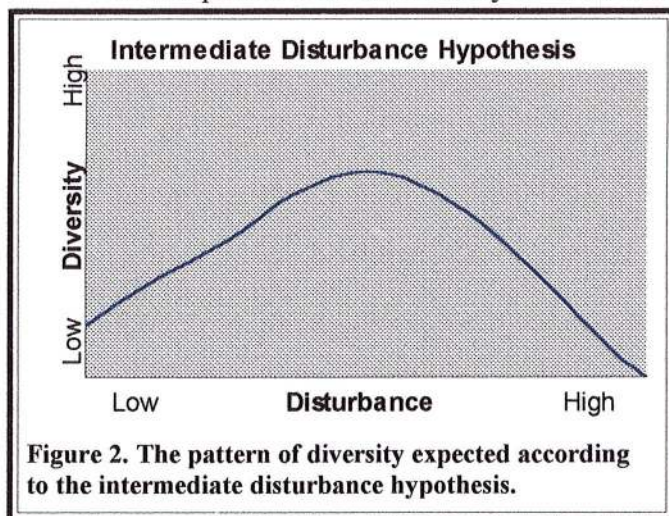


A Caribbean coral reef system was chosen as a study area because they are easier to study than Indopacific ones due to the former housing less species (Nybakken, 1993) and therefore conclusions can be drawn more

easily. The coral reefs around the coast of Belize (see figs. 1 and 3) are very important for both ecological and economic reasons. In 1996 the Belizean barrier reef was declared a world heritage site. With this declaration carries a responsibility to protect the reef from overexploitation and thus development on and around the reef should be monitored and controlled so as to be as sustainable as possible. The study sites were chosen from coral reefs around a Belizean atoll. The sites around the atoll were chosen in order to establish an exposure gradient driven by wind (see fig. 3). These reefs are considered to be pristine, with little fishing or recreational activity around the atoll, and therefore the structuring influence of man should not manifest itself in the results.

EXPECTED RESULTS

It is expected that the diversity of coral will reflect the regime of disturbance



to which each site is subjected in accordance with the intermediate disturbance hypothesis. The sites should lie on the graph in fig. 2 in their order along the gradient.

As it is unknown where along the exposure gradient the disturbance

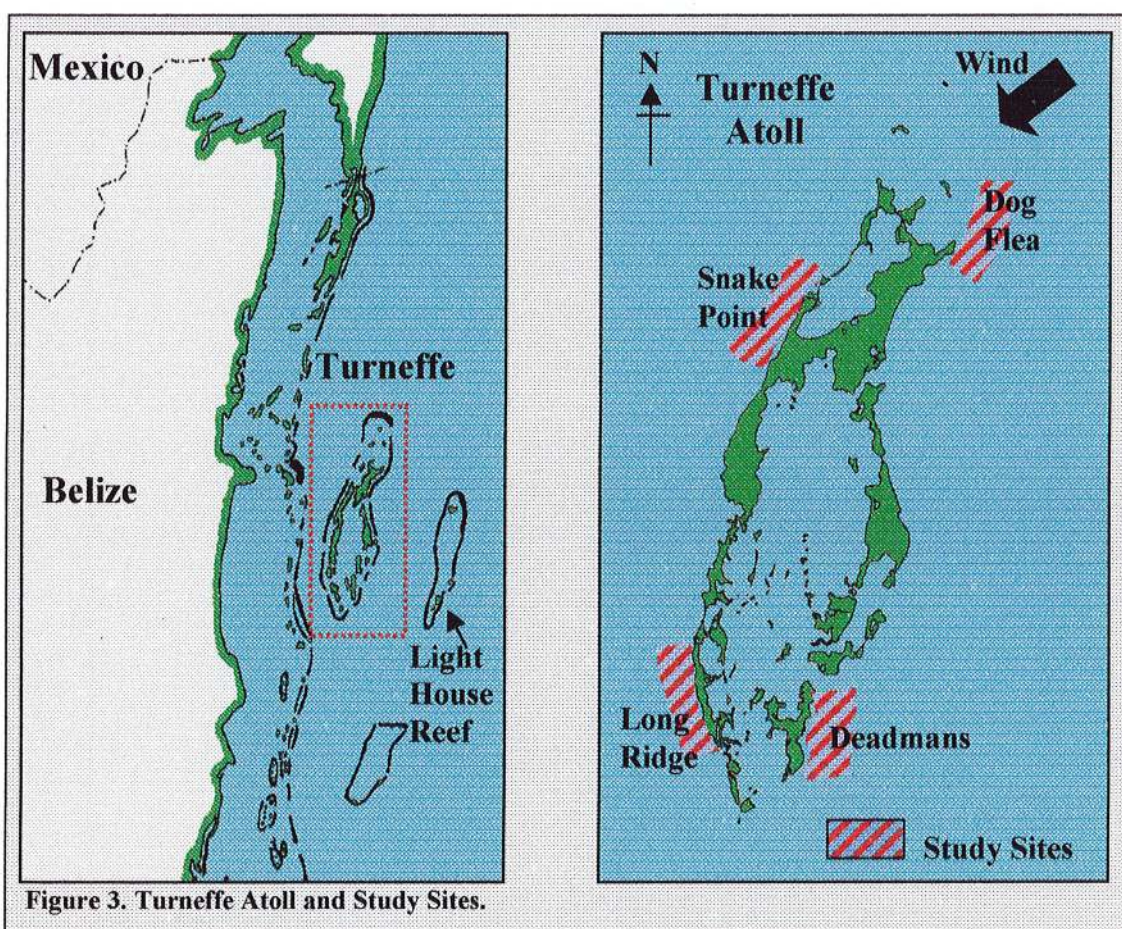
regime is "intermediate", *in sensu* Connell (1978), the position of the exposure gradient on this graph cannot be predicted, but the sites should lie in their order along the exposure gradient.

The percent coverage of coral is expected to decline with increasing exposure, but the percent algae cover is expected to increase with exposure as the pressures from grazing are reduced with exposure. The diversity of algae should reflect grazing intensity as a disturbance in accordance with the intermediate disturbance hypothesis. The assemblages of fish are expected to show a loose correlation with the food and shelter resources available.

METHODS

ESTABLISHING AN EXPOSURE GRADIENT

The locations of the four sites were chosen in order to establish an exposure gradient (see fig. 3). Dog Flea at the north east tip of the atoll is most directly exposed to the predominant north-easterly winds and subsequent wave crash and swell.



Deadmans at the south east of the atoll is more sheltered than Dog Flea because Light House reef to the east protects it, but is more exposed than the two sites on the west, leeward side, of the atoll. Snake Point on the north west is moderately sheltered, and Long Ridge on the south west is the most sheltered as it is on the leeward side of the atoll and like Deadmans is protected by Light House reef.

In order to have a measure of disturbance the study sites were chosen along the exposure gradient described. This measure is not quantifiable, but due to the

predominate north-westerly winds (Aronson and Precht, 1995, and personal observations) a gradient of exposure to waves and swell should exist. Thus the influence of wind generated disturbance can be tested. By visual censuses of the animal component of the reef it is possible to estimate the disturbance caused biotically from grazing by herbivores as a function of the density of herbivores present. In this study large scale historical disturbance events were ignored and it is assumed that the atoll has been either equally affected by these events or that the atoll has been affected by these events in accordance with the exposure gradient investigated. The latter assumption should hold true to large scale disturbance events generated by wind (storms and hurricanes).

TRANSECT SURVEY TECHNIQUE

The data were collected in teams of four scuba divers who were allocated different tasks: physical, fish, coral, and invertebrates (divers 1 to 4 respectively). Transects were taken perpendicular to the shore from a depth of 30m to 3m (or to a depth at which surveying is no longer viable). Each transect was started by descending to a depth of 30m and finding substratum at this depth. The first pair, divers 1 and 2, swam along a bearing determined at the surface for 10m whilst the other pair wait. This distance was measured by a positively buoyant 10m rope held at one end by diver 1 and at the other by diver 3. Once the rope was taught the second pair swam 10m to the now stationary first pair. Whilst swimming this 10m, data were collected relevant to the task assigned each diver:

Diver No.1 - Physical:

Responsible for the bearing
 Held the rope
 Measured depth every 10m
 Sketched a lay out of the substratum
 Determined whether there was a change in habitat

Diver No. 2 - Fish

Holds the SMB (surface marker buoy)
 Identified all fish

Diver No. 3 - Coral

Held the other end of the rope
 Identified corals and sponges

Diver No. 4 – Invertebrates and Algae

Identified algae, and the invertebrates not covered by any other diver
 Small samples of any unknown alga are removed for identification on land.

These data were taken 1m either side of the transect line for coral, algae, sponge and invertebrates but 2.5m either side for fish so that a transect constitutes a 2m band and a 5m band respectively from 30m to 3m (see fig.4) A change of habitat was determined by diver 1 if the substratum changed significantly over a distance of 10m or more along the transect line. Data were collected separately for each habitat identified along the transect. The possible habitat types identified were sand, sand and coral matrix, gorgonian plain, spurs and grooves, seagrass bed, seagrass patches, patch reef, sandy algal canopy, reef crest, hard coral reef, matrix drop off, sandy drop off, and coral drop off. These habitat types are distinguishable according to the descriptions in table 1.

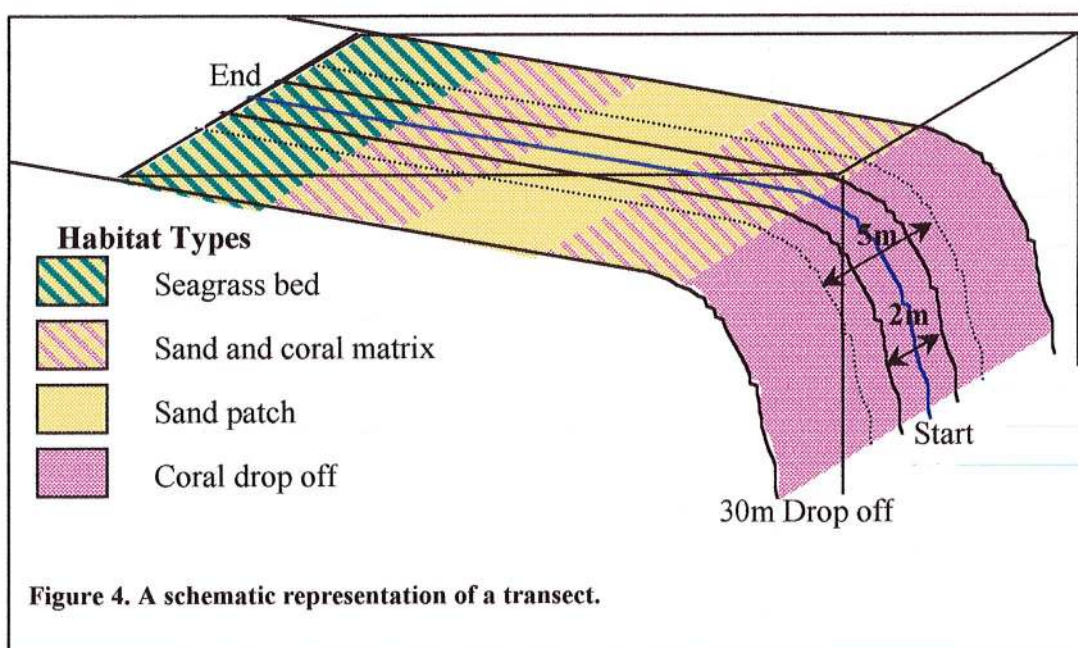
Table 1. Habitat Description.

Habitat Type	Description
Sand	Substratum is predominantly sand.
Sand and coral matrix	Substratum is coral interspersed with sand.

Table 1. (continued)

Gorgonian plain	Substratum largely devoid of coral or algae, but gorgonians predominant.
Spurs and grooves	Spurs are parallel mounds covered with coral and algae, separated by surge channels of sand or coral rubble, characteristic of exposed reefs.
Seagrass bed	Seagrass predominant.
Seagrass patches	Patches of seagrass on a substratum otherwise dominated by sand
Patch reef	A concentration of coral colonies with surrounding substratum largely devoid of coral.
Sandy algal canopy	Algae growing on a sandy substratum
Reef crest	Coral or algal reef close to the surface and characterized by area of breaking waves.
Hard coral reef	Coral predominates the substratum.
Matrix drop-off	Drop off substratum mixed assemblage of coral and algae, sand and bedrock.
Sandy drop-off	Drop off substratum predominantly sand.
Coral drop-off	Drop-off substratum limited in sand and bedrock, but predominantly coral.

If the transect was not completed (3m depth has not been reached) during the dive time allocated then the buoy held by diver 2 was tied off on the nearest piece of suitable substratum to where the team finished. The next team then descended along

**Figure 4. A schematic representation of a transect.**

This survey technique was based on methods recommended by the Marine Nature Conservation Review team of the Joint Nature Conservation Council to Coral Cay Conservation Ltd.. The techniques was modified to suit a tropical environment considering the methods advocated by the South Pacific Commission/United Nations Environment Programme (SPC/UNEP, 1984). The data were collected by volunteers working for Coral Cay Conservation Ltd. All volunteers are rigorously trained in species identification before surveying and a validation of the technique and use of volunteers has been executed (Mumby *et al.*, 1995). The surveying was carried out for the purposes of Coral Cay Conservation Ltd. and was not designed for the purposes of this study.

IDENTIFICATION OF SPECIES

The data were collected by identifying every organism and substratum type allocating them abundance ratings of 0-5 for each habitat encountered during the dive. This abundance rating is outlined in table 2.

Table 2. Abundance ratings for all organisms and substratum identified.

Rating	Coral / Substratum / Algae		Fish / invertebrates(# individuals)
0	None	None	0
1	Rare	Little	1-5
2	Occasional	Some	6-20
3	Frequent	Nearly half	21-50
4	Abundant	More than half	51-250
5	Dominant	Almost all	250+

20 replicate transects were taken at each of the four sites around Turneffe Atoll (see fig. 3).

TRANSFORMING DATA FOR STATISTICS

The data were transformed from the ordinal abundance rating so as to reflect actual numbers of fish present and actual percent coverage of coral and algae. This was done in the following fashion. For the benthos (algae and coral) the abundance rating is replaced by a percentage:

Rating	Percentage
0	0
1	1
2	10
3	40
4	60
5	90

This percentage was then multiplied by the length of the transect to which the data belong. A similar method is used for the fish data. The abundance rating is replaced by the following numbers:

Rating	Number of Individuals
0	0
1	3
2	13
3	36
4	150
5	300

This may seem convoluted and unnecessary, but due to the time constrictions whilst diving it is more efficient, albeit less accurate, to use the abundance rating than to attempt to estimate the numbers of fish and percent coverage of the benthos whilst under water.

RESULTS

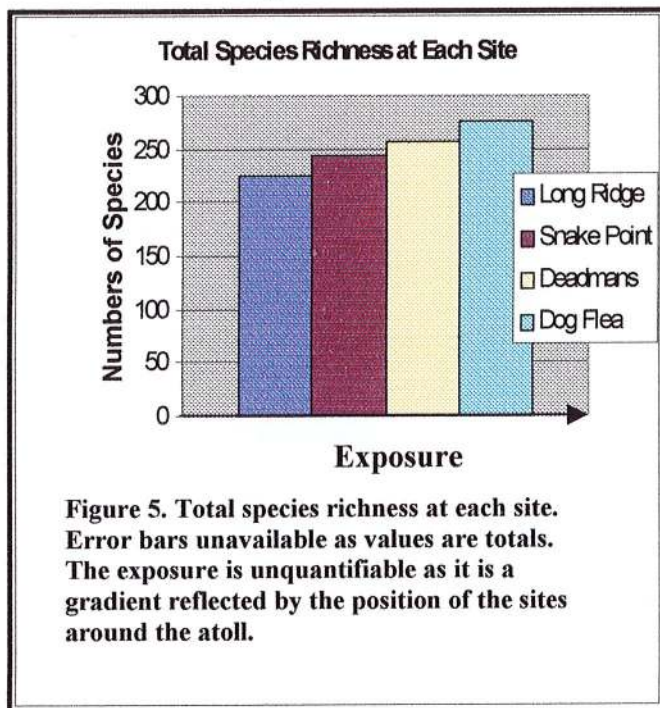
For the purposes of data analyses the species identified are placed into taxonomic groups. These groups are algae, hard corals, soft corals, fish, and invertebrates. Hard corals include Scleractinia, and Milleporina. Soft corals include Gorgonacea, Telestacea, and Alcyonacea. Invertebrates includes all invertebrate species not included within hard and soft corals. Data collected on sponges (Porifera) were ignored as species identification is impossible without *ex situ* investigation into their spicules.

The results are divided into three main sections. The first deals with the sites in their entirety, the second deals with the different habitat types within each site, and the third deals with correlations between fish/invertebrate data and the benthos. Totals for sites and habitats are used as values rather than the means of their constituent transects, or constituent habitat data. This is because the differences in species composition of the constituent transects/habitat data would be lost in a mean, but are not lost in a total value for each site/habitat type. The constituent parts were used, however, to calculate the one-way analyses of variance between sites and between habitat types within sites.

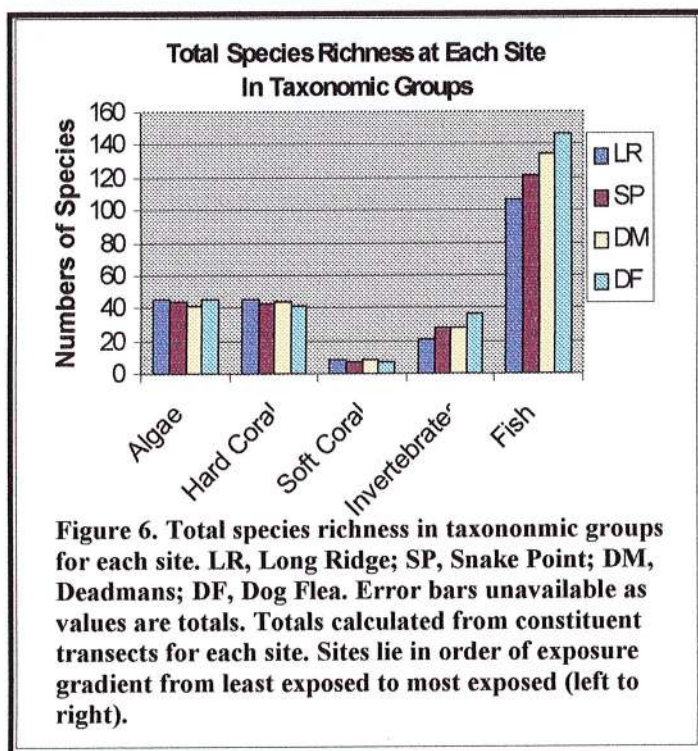
ANALYSIS OF SITES

Species Richness Between Sites

The total species richness of each site was calculated in order to obtain a crude



measure of diversity for each site (see fig. 5). The mean species richness of each site, calculated from its constituent transects, was not used because the mean would not represent species richness of a site as a whole, as explained earlier. There is an increase in species presence along the



exposure gradient (see fig. 5). This increase in species richness is largely attributable to the increase in fish species richness along the gradient (see fig. 6). However, a one-way analysis of variance on the fish species richness of the replicate transects within sites shows that there is no significant difference between the fish species richness of each site ($F_{3,77}=14.09$,

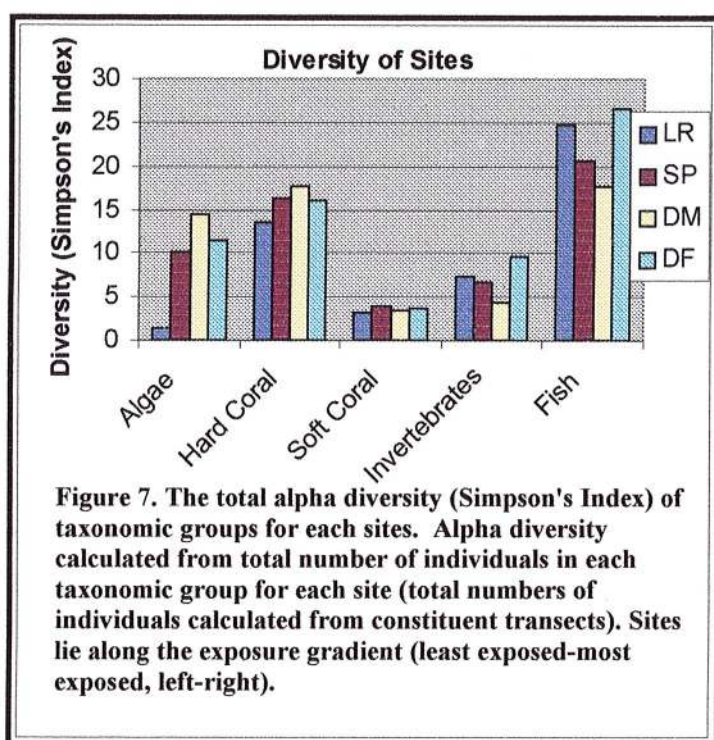
$p>0.05$, see appendix for ANOVA table). A one-way analysis of variance of the

replicate transects for each site shows there to be no significant difference between

the species richness of algae along the exposure gradient ($F_{3,77}=1.04$, $p>0.05$), nor is there a significant difference between the soft coral species richness between sites ($F_{3,77}=0.86$, $p>0.05$), but there is a significant difference between the species richness for hard corals between sites ($F_{3,77}=3.29$, $p<0.05$). The difference between coral species richness follows a downward trend with exposure which could be explained by the intermediate disturbance hypothesis: the “intermediate” disturbance regime (*In sensu* Connell, 1978), that which promotes the most diversity according to the hypothesis, is closest to the disturbance regime which is found at the least exposed site along the gradient.

Diversity of Sites

The alpha diversity (Simpson's Index) of each taxonomic group in each site reveals a



trend of increasing diversity at the intermediate sites along the exposure gradient for algae and hard coral. One-way analyses of variance show that there are significant differences between sites for both algal diversity and hard coral ($F_{3,77}=6.14$, $p<0.005$, and $F_{3,77}=5.22$, $p<0.005$ respectively). The

pattern of alpha diversity for hard corals shows a different trend to that which is shown by the species richness of each site for hard coral (see figs. 7 and 6). Hard coral alpha diversity is highest at Deadmans, and decreases at more and less exposed

sites. A contrast in patterns of species richness and alpha diversity along the exposure gradient does not nullify the results, but is explainable by the factor of evenness.

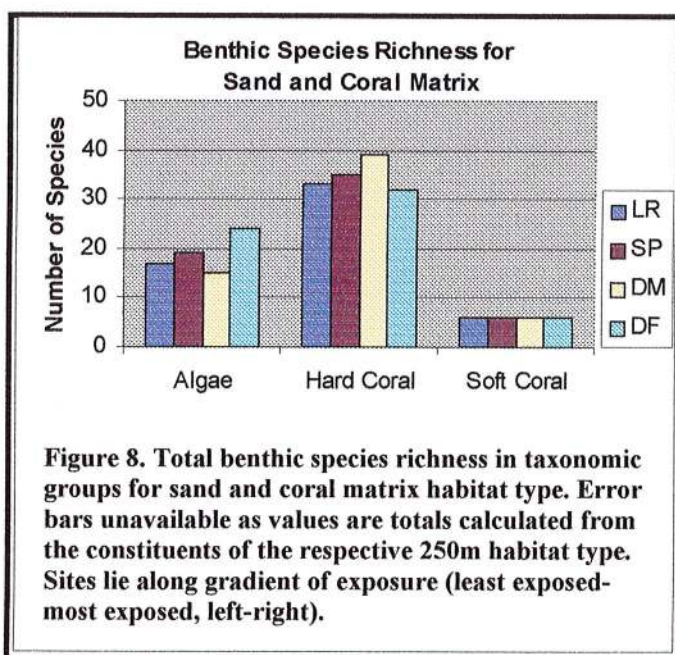
ANALYSIS OF HABITATS

250m of data transect representing each habitat were taken (where available) at random from the available data for each site. For each habitat type data were taken within a similar depth range: sand and coral matrix were taken at 5-15m, and matrix drop-off and spurs and grooves were taken at 18-30m. This allows identical sized areas of identical habitat to be compared between sites eliminating other variables such as depth and associated light availability from affecting the results as far as possible.

Sand and Coral Matrix

Benthic Species Richness for Sand and Coral Matrix

The sand and coral matrix habitat type is characterised by colonies of coral,



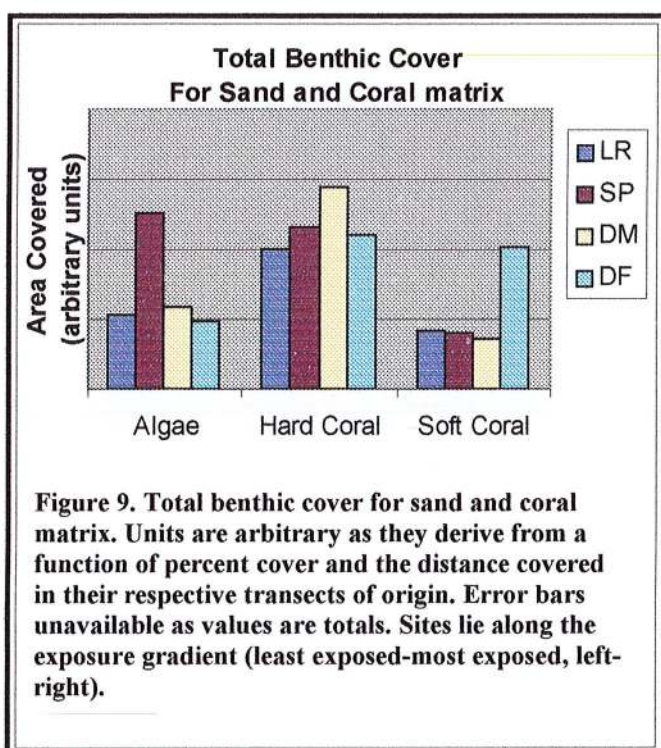
large or small, interspersed with a sandy substratum. The sand and coral matrix habitat is the only habitat type represented by all four sites. A one-way analysis of variance on the constituent habitat data for hard coral shows that there is no significant difference between

site hard coral species richness ($F_{3,65}=2.58$, $p>0.05$). The trend shown in fig. 8 for hard coral species richness follows that which is expected according to the

intermediate disturbance hypothesis, albeit insignificant. A one-way analysis of variance for algal species richness, calculated from constituent habitat data, shows significant differences between sites ($F_{3,65}=3.11$, $p<0.05$).

Benthic Cover for Sand and Coral Matrix

If the intermediate disturbance hypothesis accounts for the trend observable for hard coral species richness in fig. 8, then it is expected that at the sites where coral species presence is highest coral benthic cover will be intermediate. Fig. 9 shows this



not to be the case. A one-way analysis of variance for benthic cover, calculated from constituent habitat data show significant differences between sites for hard coral cover ($F_{3,65}=3.77$, $p<0.05$).

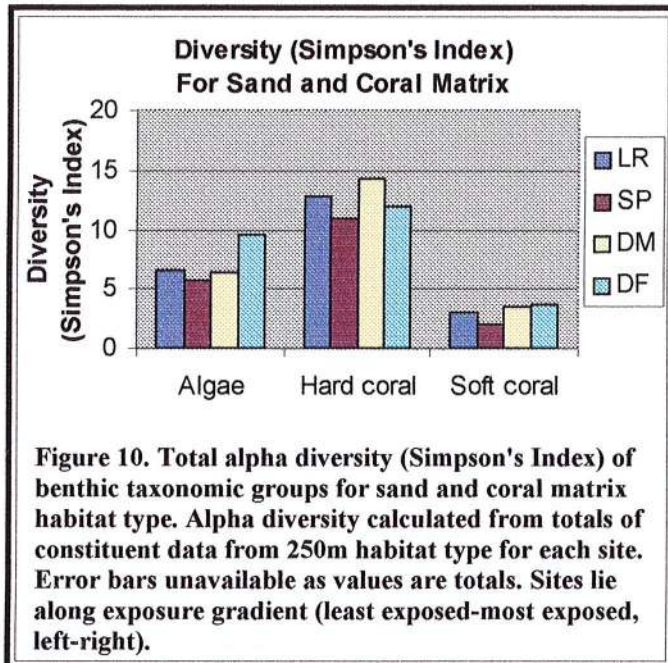
The trend shown in fig. 9 is surprising, and not in accordance with the intermediate hypothesis.

One-way analyses of variance

show that the algal cover is not significantly different between sites ($F_{3,65}=1.93$, $p>0.05$), but that the soft coral cover is significantly different between sites ($F_{3,65}=3.77$, $p<0.05$). The latter result is unexpected.

Diversity of Sand and Coral Matrix Benthos

The alpha diversity (Simpson's Index) of the benthic species for sand and coral matrix habitats reflects a similar trend to that of species presence, except for the fact that Long Ridge has a higher diversity of hard coral than Snake Point (see fig.



10). One-way analyses of variance, calculated from constituent habitat data, show that the differences between hard coral diversity are significant between sites ($F_{3,65}=7.90$, $p<0.001$), and the trend shown in fig. 10 loosely follows that which is predicted by the

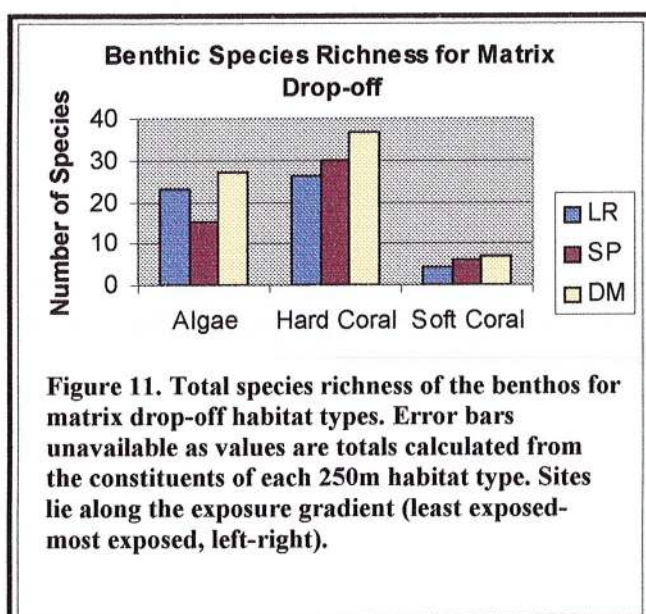
intermediate disturbance hypothesis.

Matrix Drop-Off

The matrix drop-off habitat type is similar to sand and coral matrix, coral colonies interspersed with sand, but on the outer, steep slope of the reef (drop-off) from 18-30m. Data were sufficient only for three of the four sites for 250m matrix drop-off habitats, Long Ridge, Snake Point and Deadmans.

Benthic Species Richness for Matrix-Drop-off

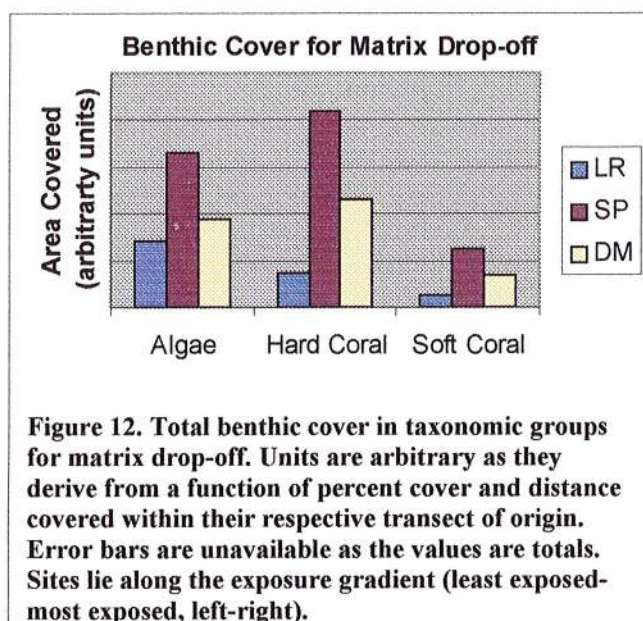
Fig. 11 shows that species richness increases with exposure for hard corals and



soft corals (the sites are significantly different, one-way analysis of variance, $F_{2,15}=5.11$, $p<0.05$), but algae species richness reveals no pattern, and there is no significant difference between sites (one-way analysis of variance, $F_{2,16}=0.01$, $p>0.5$).

Benthic Cover for Matrix Drop-off

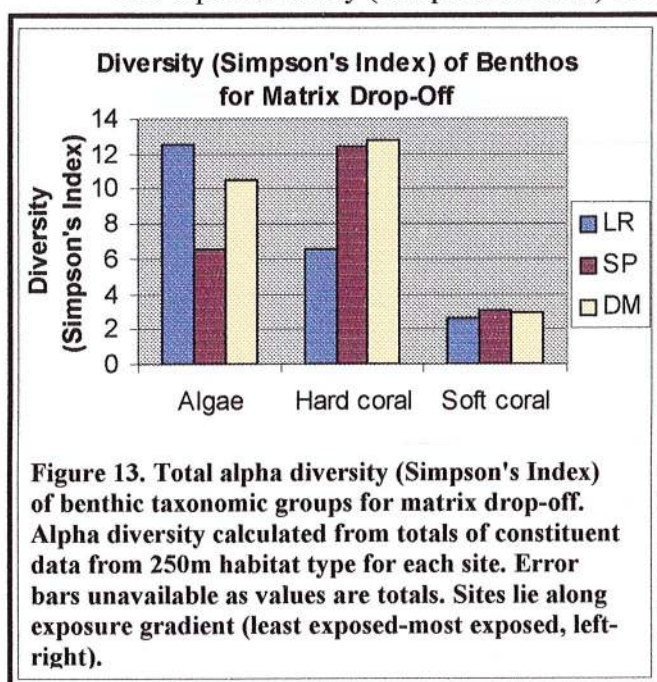
One-way analyses of variance for benthic cover show no significant differences between algal cover ($F_{2,17}=1.44$, $p>0.05$), but show significant differences between sites for hard and soft coral cover ($F_{2,17}=1.44$, $p>0.05$, and $F_{2,17}=104.17$ $p<0.001$ respectively). The benthic cover and species richness for hard coral follow trends that are expected by the intermediate disturbance hypothesis: Deadmans has the highest



species richness and an intermediate hard coral cover, the latter result being insignificant.

Diversity of Benthos for Matrix Drop-off

The alpha diversity (Simpson's Index) of hard coral increase along the



exposure gradient (see fig. 13), but a one-way analysis of variance shows the differences between sites for hard coral diversity to be insignificant ($F_{2,17}=2.54$, $p>0.05$).

Spurs and Grooves

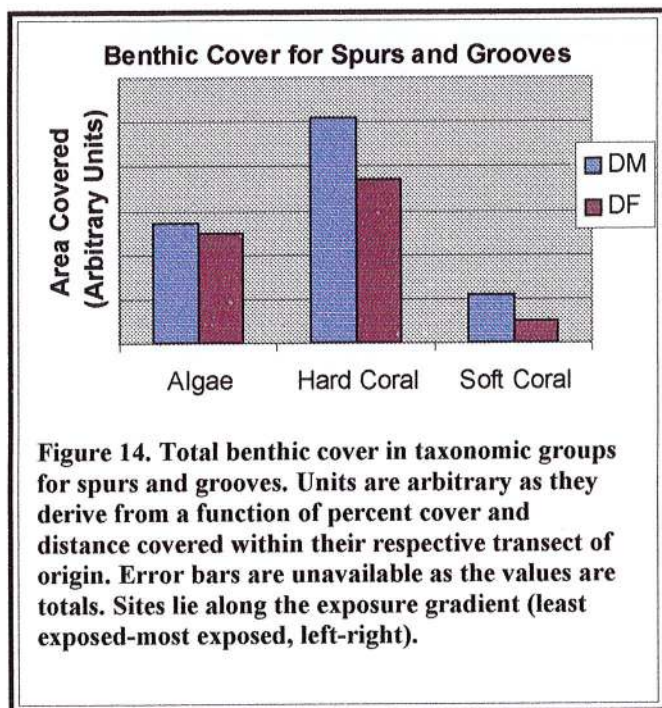
Spurs and grooves are characterised by large elevations of coral and algae running parallel in a seaward direction separated by surge channels. Only two sites had sufficient data for 250m habitat types of spurs and grooves. These were the most exposed sites on the windward side of the atoll, Deadmans and Dog Flea.

Benthic Species Richness for Spurs and Grooves

The species richness of the benthos does not differ significantly in any of the benthic taxonomic groups (1 tailed Student's t-test: algae, $p>0.05$; hard coral $p>0.05$; soft coral $p>0.05$).

Benthos Cover for Spurs and Grooves

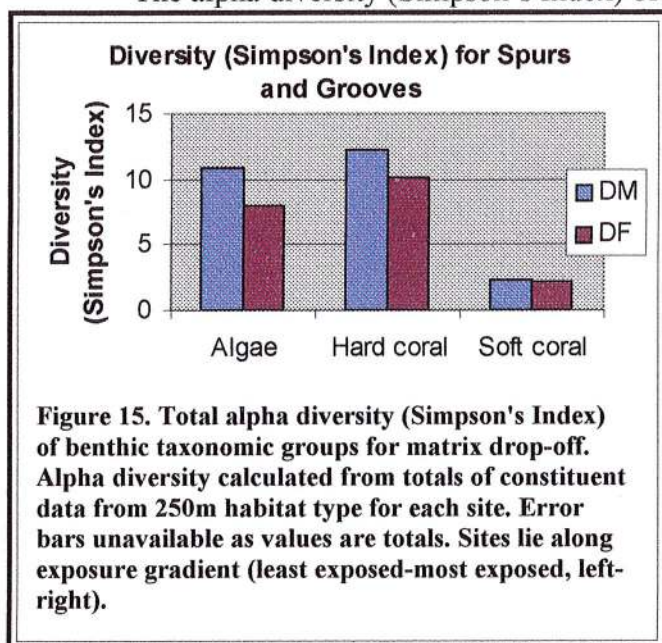
A Student's t-test for hard coral cover shows the differences between sites to



be significant ($p<0.05$). Due to the increased exposure at Dog Flea it is expected that there be less hard coral cover. This is shown in fig. 14. There is, however, no significant difference between sites for algal or soft coral cover (Student's t-test: algae $p>0.05$; soft coral $p>0.05$).

Diversity of Benthos for Spurs and Grooves

The alpha diversity (Simpson's Index) of benthic species is highest for all



taxonomic groups at Deadmans,

the less exposed site (see fig.15).

Student's t-tests show these trends

to be significant only for hard coral

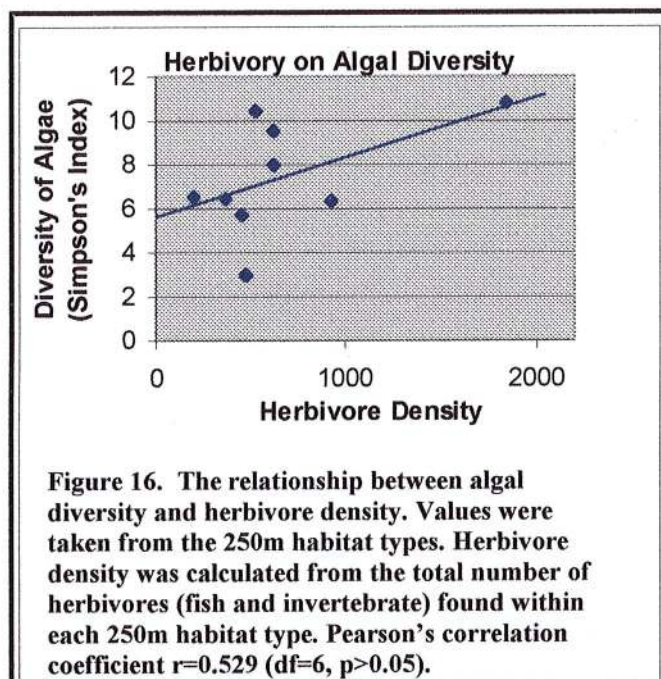
(algae $p > 0.05$; hard coral, $p < 0.05$;

soft coral $p > 0.05$).

BENTHOS AND ANIMAL ASSEMBLAGES

Herbivory on Algal Diversity

The number of all species of herbivores, fish and invertebrates, were taken for

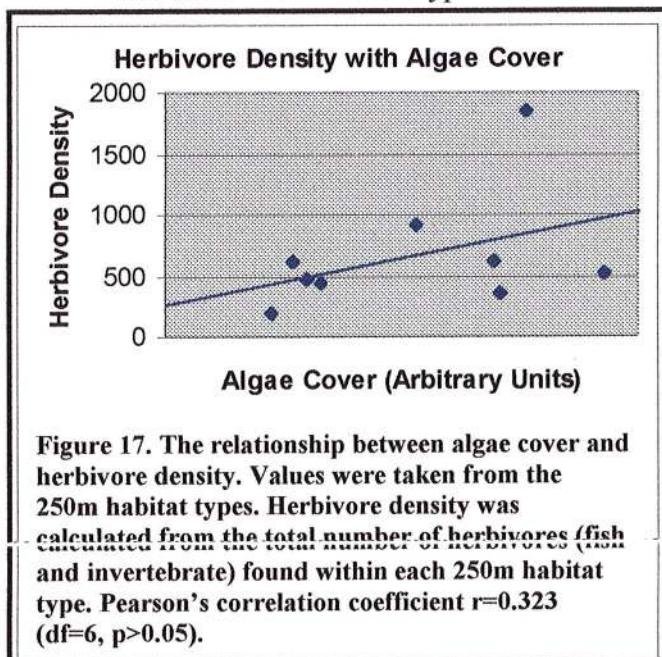


each 250m habitat type at each site. This gives a qualitative measure of herbivory, a biotic disturbance to algae, which was used to calculate a Pearson's correlation coefficient between herbivory and algal diversity (Simpson's Index). The result was $r=0.529$ ($df=6$, $p>0.05$).

The relationship is shown diagrammatically in fig. 16. This correlation is not significant.

Algal Cover on Herbivore Density

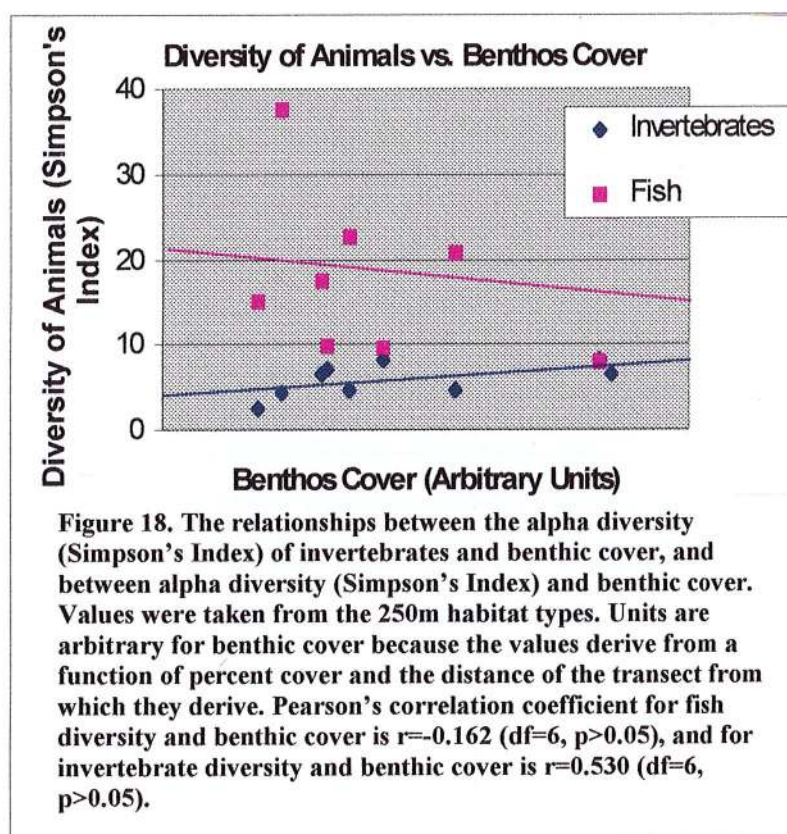
The same 250m habitat types used for the herbivory – algal diversity



regression were used to investigate a relationship between the benthos and the species it supports. A Pearson's correlation coefficient between herbivore density and algal cover was calculated. The result was $r=0.323$ ($p>0.05$), not a significant correlation, illustrated in fig. 17.

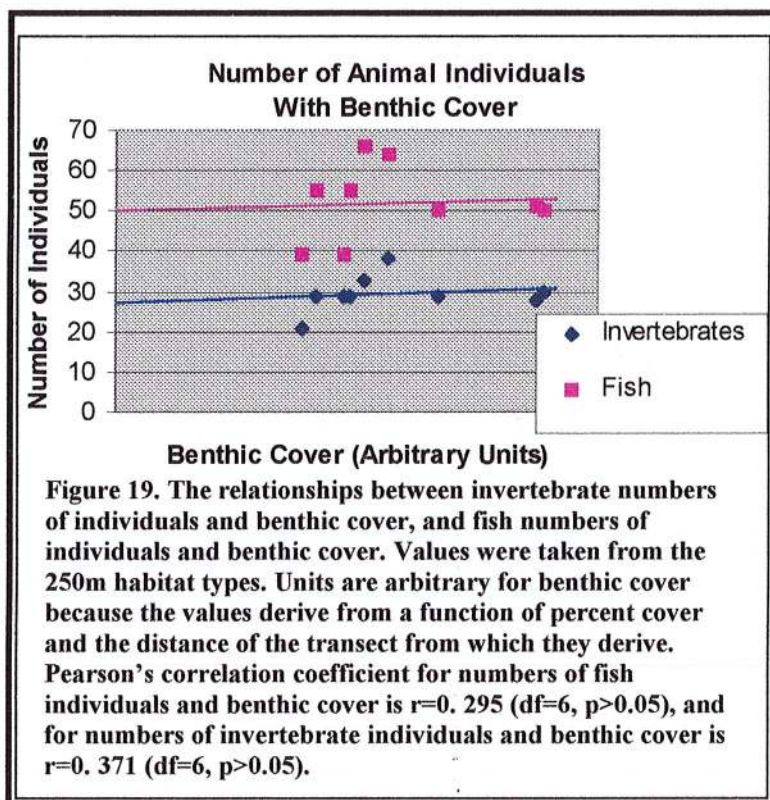
Diversity of Animals and Benthos Cover

A Pearson's correlation coefficient was calculated for the diversity of invertebrates and benthic cover, and for the diversity of invertebrates and benthic cover. The fish diversity-benthic cover was $r = -0.162$ ($p > 0.05$) and the invertebrate diversity-benthos cover was $r = 0.37$ ($p > 0.05$). Both weak positive correlations are not significant. The relationship between these variables is illustrated in fig.18.



Animal Density and Benthos Cover

Pearson's correlation coefficients were also calculated for numbers of fish individuals with benthos cover, and number of invertebrate individuals and benthos cover. For fish individuals-benthos cover $r = 0.295$ ($p > 0.05$), and for invertebrate individuals-benthos cover $r = 0.397$ ($p > 0.05$). Neither of these correlations is significant (see fig.19).



DISCUSSION

INTERPRETATION OF RESULTS

According to the intermediate disturbance hypothesis (Connell, 1978), the diversity of coral should be highest at intermediate levels of disturbance, and the coral cover will be intermediate at this level of disturbance compared to less disturbed sites with higher cover and more disturbed sites with less cover. Only hard coral will be discussed in the context of wind driven disturbance, as the results for soft coral and algae are largely insignificant and disturbances processes acting on algae derive mainly from herbivory.

Sites in their entirety

Hard coral species richness decreases along the exposure gradient, whereas the alpha diversity of hard coral increases to a maximum at Deadmans (the 2nd most exposed site), then decreases at the most exposed site, Dog Flea. These two sets of results are not conflicting because the alpha diversity is a more comprehensive measure of diversity than species richness, incorporating the factor of evenness. The results for hard coral alpha diversity are consistent with the intermediate disturbance hypothesis (Connell, 1978): hard coral diversity increases at both high and low exposure and is maximal at an intermediately exposed site (Deadmans). This suggests that exposure to wind is a variable that affects hard coral diversity. In order to support the intermediate disturbance hypothesis the coral cover must be intermediate at the site of highest diversity, but the results indicate no significant differences between sites for hard coral cover.

Use of all the transects at each site and comparing species richness is not likely to support the intermediate disturbance hypothesis because of the differences between sites in their habitat constituents. For example, a site which has more sand

habitat than another is likely to show a limited species richness, because areas of sand are characteristically low in species. This may explain why the results for each site in their entirety show no patterns explained by the hypothesis. This is true for species richness and alpha diversity (Simpson's Index). The most useful test of the intermediate disturbance hypothesis is the comparison of hard coral diversity and cover in the 250m habitat types.

Habitat Types

Sand and Coral Matrix

Alpha diversity of hard coral for sand and coral matrix habitats follow a similar trend to that of the diversity of sites in their entirety (albeit more loosely), and is therefore in accordance with the intermediate disturbance hypothesis. The hard coral cover however does not follow the expected trend: coral cover is highest, and therefore not intermediate, at sites where hard coral diversity is highest.

Matrix Drop-off

Hard coral cover increases with increased exposure. If wind exposure acts as a disturbance then the opposite of this relationship is expected. The relationship between hard coral diversity and hard coral cover cannot be seen as the hard coral diversity of each site is not significantly different.

Spurs and Grooves

Hard coral cover is higher at the less exposed site, Deadmans (only Deadmans and Dog Flea have spurs and grooves habitats), which is expected. Hard coral diversity is also highest at the less exposed site. Both the diversity of hard coral and coral cover show trends in accordance with the intermediate disturbance hypothesis.

Comparing Habitat Types

There may seem to be some discrepancy between habitat types. Hard coral diversity is highest at Deadmans in the sand and coral matrix and spurs and grooves habitat types, but there is no significant difference between sites for matrix drop-off habitats. This may be due to the factor of depth. Wind generated disturbance not only acts on a gradient around the atoll, but also along a gradient with depth. Wind generated disturbance decreases with depth. There is a 200-fold decrease in wave force from the surface to a depth of 30m (Roberts *et al.*, 1975). The sand and coral matrix is the most shallow habitat and is therefore subjected to greatest wind generated disturbance. Data for matrix drop-off and spurs and grooves are from similar depth ranges (18-30m). Matrix drop-off data is not available for Dog Flea, the most exposed site, and at the less exposed sites wind generated disturbance does not appear to be intense enough at this depth range to exert a significant structuring force on the hard coral diversity. Data for spurs and grooves are only available for the two most exposed sites, Deadmans and Dog Flea. The most exposed site, Dog Flea, may be significantly structured by wind generated disturbance even at depth, giving rise to significantly different hard coral diversities at both sites. The disturbance regime at Dog Flea is beyond “intermediate” *in sensu* Connell(1978), whereas Deadmans’ is closer to “intermediate”, resulting in a higher hard coral diversity and greater cover at the less exposed site. The results from the spurs and grooves are the only that are in accordance with the intermediate hypothesis in terms of hard coral diversity and cover.

ALTERNATIVE HYPOTHESIS FOR THE PATTERNS OF HARD CORAL DIVERSITY OBSERVED

All corals need some water movement in order to survive (Hubbard, 1974; Jokiel, 1978; Stoddart, 1969). At sites low on the exposure gradient certain hard coral species will be able to grow more than others under a limited water motion regime. These corals will have a competitive advantage and diversity will be low (as is seen). At higher water motion regimes this competitive advantage is lost, and diversity will be higher as will coral cover (as is seen for sand and coral matrix hard coral results). At sites with very high water motion regimes the water motion will act as a disturbance which reduces coral cover, and will reduce diversity if the overall disturbance regime is beyond “intermediate” *in sensu* Connell(1978). This model would fit the results from this study, but other studies contradict this model. Low water movement promotes diversity as it reduces competitive exclusion by reducing growth rates of all corals (Huston, 1985).

Benthos and Animal Assemblages

There are no significant correlations between the composition of the benthos and the animal assemblages they support. The availability of a resource (algal food for herbivores, or shelter in coral for most demersal animals) does not seem to affect the density of animals dependent on the resource. This may be due to the limited data available, but it may also be due to the processes that structure coral reef animal assemblages (see Fish Assemblages, below).

Algal Diversity and Herbivory

Herbivory is a disturbance acting upon algae in coral reef ecosystems. If the overall disturbance regime to which the algae is subjected is intermediate, then,

according to the intermediate disturbance hypothesis, algal diversity should be maximal. The disturbance caused by herbivores is never likely to be high (beyond “intermediate” *in sensu* Connell, 1978) as the benthos supports fish below its carrying capacity (see discussion below on coral reef fish assemblages). Therefore, a trend of increasing algal diversity is expected with increasing herbivore density. Only a very weak positive non-significant correlation can be seen from this study.

Damselfish (Pomacentridae) “gardening” has been noted to promote algal diversity (Hixon and Brostoff, 1983). The damselfish “gardens” are very small and perhaps the scale of the study overshadows processes acting on a smaller scale. Only certain areas are intensively “gardened” and territorially guarded by fish. Other herbivores graze on a larger scale, thus the intensity of their grazing in any one area is low. It is perhaps only in these damselfish “gardens” that disturbance is intense enough to promote algal diversity through compensatory mortality, although other herbivores have been noted to increase algal diversity (Paine and Vadas, 1969).

Fish Assemblages

The majority of coral reef fish have a pelagic larval stage to their life cycles before settlement on the reef for the largely demersal adult stage of their lives (Sale, 1978). Mortality approaches 100% in the larvae (Sale, 1980) primarily from predation (Doherty *et al.*, 1985). This accounts for the very high fecundities of coral reef fish with egg production of 10,000 to 1,000,000 per female (Sale, 1980). Before the 1970’s it was generally accepted that these larvae were planktonic, passively drifting on currents and it was left to chance whether they drifted onto a reef and complete the demersal, adult stage of their life cycles. It was also believed that the population ecology of coral reef fish assemblages was driven by resource-limitation and

competition. These views can no longer be held as true. The larval stages of these fish have great control and sensory awareness over the direction in which they travel and have to be regarded as nekton rather than plankton (Pain, 1997). Coral reef fish assemblages are structured not by competition, but by the stochastic survival of sparse larval recruits that hold the fish populations well below their carrying capacity. The age-class structure of the fish assemblages changes little following recruitment, and so it is the processes occurring within the pelagic larval stage of coral reef fish that largely determine the structure of adult populations.

Resource-Limitation or Recruit-limitation (in Fish Assemblages)

Before the 1980's, the huge quantities of larvae produced by the highly fecund coral reef fishes were believed to produce an excess of recruits that could be supported by coral reef resources (MacArthur, 1972). Post-settlement processes of intra and interspecific competition for limited resources were believed to determine the structure of the fish assemblages (Sale, 1980). This belief has been dismissed through experimental investigation. If a surplus of recruits existed then removal of fish from a reef would result in rapid recolonization, but results show that recolonization is slow and that recruitment is similar on empty reefs to that of control reefs (Sale, 1980). Similarly, if a surplus existed and reefs were at their carrying capacities then the removal of food source or of shelter specific to some fish would result in their populations decreasing. Work from Robertson *et al.* (1981) revealed that this did not happen, and that there was sufficient habitat to support 50% more herbivorous pomacentrids (damselfish) without reducing fish growth rates or reproductive success. Natural disturbance events such as El Nino or *Acanthaster planci* infestations reduce live coral cover and increase algae cover for many years following, but the increase in algal food for herbivorous fish is not met by a matched

increase in fish (Wellington & Victor, 1985; Williams, 1985). This lack of increase in fish is due to the limited recruits available. Most experimental work has shown that coral reef fish do not reach the carrying capacity of their habitats due to this lack of recruits and this supports non-equilibrial models for these fish assemblages (Williams, 1980; Doherty, 1982). The results of this study support this non-equilibrial model, as there is no correlation between algae cover and herbivore density, nor is there a correlation between benthic cover and total fish density. Algae cover represents a food resource to herbivores, and total benthic cover represents resource of shelter and food. The lack of correlation indicates that the fish assemblages are not resource limited. The benthos, therefore, is supporting fish below its carrying capacity, in turn indicating that fish assemblages are recruit limited.

Reasons For Recruit Limitation (in Coral Reef Fish Assemblages)

Recruits are limiting as the larval pelagic stage of coral reef fish results in mortalities of close to 100% (Sale, 1980). Studies have revealed that most of this mortality is due to predation (Doherty *et al.*, 1985). Predation pressures are higher closer to the reef and the closer to the reef the fewer larvae are found. This may be adaptive, or it may simply be that concentrations of larvae close by the reef are lower as they have been predated (Shulman, 1985). The longer the larvae is at the time of settlement the lower its chances of post-settlement predation. It may then seem advantageous to spend a long period as a pelagic so as to be as large as is viable on available food resources before recruitment. However, there appears to be no general trend in large recruits and long pelagic stages. This may be due to the fact that the longer the pelagic existence the greater the chances of predation (Doherty & Williams, 1988). Some fish occupy “nursery” habitats before recruitment to the reef.

These “nurseries” are seagrass beds (Bell *et al.*, 1987), mangroves (Lindeman, 1989), tide pools (Randall, 1961), estuaries, and algal beds (Bellwood & Choat, 1989) and are sanctuaries where planktivorous animals and, thus predation, are reduced. Here the larvae are able to grow into juveniles before returning to settle on the reef. Reefs that do not have these nursery habitats in close proximity are expected to suffer a reduced rate of recruitment (Shulman, 1985). Other fish, such as *Halichoeres bivittatus*, bury themselves in the sand whilst still larvae and emerge once developed into juveniles and then move to the reef (Victor, 1983).

Recruitment Structures Adult Fish Assemblages

The age-class structure of coral reef fish assemblages is highly variable and this is a reflection of the variability in yearly recruitment (Russell *et al.*, 1974). This is a particularly prominent feature on small isolated reefs such as lagoonal patch reefs where rare species are often represented only in one year-class (Williams & Sale, 1981). There is a great consistency within age-classes from one year to the next (Doherty & Williams, 1988). This consistency is maintained from the time of settlement and it is recruitment that is primarily responsible for this structure (Doherty & Sale, 1988). Actual numbers of fish are likely to be reduced, by predation or disease, as the fish progress through adulthood, but this reduction will be randomly distributed throughout all species. Competition does not play a significant role in the structure of coral reef fish assemblages and therefore resources are not limited. This may explain why this study shows no correlation between benthic resources (algae as food, and coral as shelter) and fish density.

MEASURING DISTURBANCE

There are many forms of disturbance to which coral reefs are subjected and these operate over a wide range of spatial and temporal scales (see table 3).

Table 3. Patterns of disturbance on Caribbean coral reefs at different spatial and temporal scales (Jackson, 1991).

Process	Spatial extent	Duration	Frequency
Predation	1-10cm	Minutes-days	Weeks-months
Damselfish Gardening	1m	Days-weeks	Months-years
Coral collapse (bioerosion)	1m	Days-weeks	Months-years
Bleaching or disease of individual corals	1m	Days-weeks	Months-years
Storms	1-100km	Days	Weeks-years
Hurricanes	10-1000km	Days	Months-decades
Mass bleaching	10-1000km	Weeks-months	Years-decades
Epidemic disease	10-1000km	Years	Decades-centuries
Sea-level or temperature change	Global	10,000-100,000 Years	10,000-100,000 Years

Comprehensive measures of disturbance on coral reefs are extremely difficult to make. This is because an effective method would have to account for all forms of disturbance described in table 3, for their relative intensities, and account for events that may have occurred years previously. Aronson and Precht (1995) used a measure of topographic complexity as a correlate to the amount of disturbance a particular area of reef is subjected to. This is a very easy way of quantifying disturbance as it can be measured *in situ* with a length of chain. By using this method they concluded that intermediate disturbance promotes diversity on coral reefs. The use of topographic complexity as a measure of disturbance is, however, questionable. At high levels of disturbance, biotic and abiotic, there will be little topographic complexity because the reef is not able to grow sufficiently under such a high disturbance regime. At low levels of disturbance topographic complexity will be high as the dominant species (in their study sites), *Agaricia tenuifolia*, a foliose scleractinian coral, is able to become well established and cover a high proportion of the benthos. *A. tenuifolia* is

topographically complex compared to the massive corals, but is more fragile and is thus more readily damaged by disturbance. Aronson and Precht therefore claim that topographic complexity can be used as what they describe as “an integrated measure of disturbance”. This is superficially a very simple, efficient and comprehensive measure of the disturbance regime to which a reef is, and has been, subjected.

However, topographic complexity is a measure of the stage of succession reached by that part of the reef, not a measure of disturbance. It can only be used as a measure of disturbance if the intermediate disturbance hypothesis is true, and therefore cannot be used as a variable to test it. Used in such a fashion, their research is bound to support the intermediate disturbance hypothesis: at early stages of succession diversity is low, and at climax community diversity is low, and most diversity occurs during the intermediate stages of succession. This is what they have shown, but not that disturbance is influencing this.

The variable of disturbance reflected in the exposure gradient chosen around Turneffe atoll is limited in its usefulness. It is not quantifiable. It does not account for historical disturbance events other than any that are wind generated, but is efficient and valid, due to the predominant north-westerly winds (Aronson and Precht, 1995, and personal observations). The use of herbivore density as a biotic disturbance acting upon algae is also efficient and valid. Unlike the exposure gradient, it is quantifiable. Unfortunately, age class data for fish were not recorded due to the impracticalities of such an undertaking for the scale of the areas studied. Age class data along with a knowledge of the intensity of herbivory of each species at each age class would have allowed the measure of biotic disturbance upon algae to be more accurate. In the absence of such knowledge herbivore density is valid. A comprehensive measure of diversity appears to be impossible on coral reefs.

CONCLUSION

The results indicate that the intermediate disturbance hypothesis does not explain the patterns of diversity found around Turneffe Atoll. There is only one habitat type for which hard coral diversity and cover are in accordance with the hypothesis. This habitat type (spurs and grooves) is only represented in two sites, and without other sites along the exposure gradient, it is possible that conclusions drawn are wrong. The use of a wind-exposure gradient, albeit valid, is not a comprehensive measure of disturbance. Whatever the reasons for the patterns of hard coral diversity at the sites around the atoll, high levels of diversity are largely due to an increase in evenness and not due to increase in species richness.

The results support a model of recruit-limited fish and invertebrate assemblages. The effects of herbivory seem not to promote algal diversity on the landscape scale

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APPENDIX

ONE-WAY ANALYSIS OF VARIANCE TABLES

Species richness of sites in their entirety:

Algae					
SOURCE	DF	SS	MS	F	p
FACTOR	3	118.7	39.6	1.04	0.381
ERROR	77	2863.6	38.2		
TOTAL	80	2982.3			

Hard Coral					
SOURCE	DF	SS	MS	F	p
FACTOR	3	490.6	163.5	3.29	0.025
ERROR	77	3632.7	49.8		
TOTAL	80	4123.3			

Soft Coral					
SOURCE	DF	SS	MS	F	p
FACTOR	3	3.48	1.16	0.86	0.466
ERROR	77	98.60	1.35		
TOTAL	80	102.08			

Benthic Cover for sites in their entirety

Algae					
SOURCE	DF	SS	MS	F	p
FACTOR	3	196383	65461	0.41	0.747
ERROR	77	11838834	159984		
TOTAL	80	12035217			

Hard Coral					
SOURCE	DF	SS	MS	F	p
FACTOR	3	830016	276672	2.71	0.051
ERROR	77	7449632	102050		
TOTAL	80	8279648			

Soft Coral					
SOURCE	DF	SS	MS	F	p
FACTOR	3	223751	74584	4.18	0.009
ERROR	77	98.60	1.35		
TOTAL	80	102.08			

Diversity of Benthos for sites in their entirety

Algae					
SOURCE	DF	SS	MS	F	p
FACTOR	3	130.94	42.65	6.14	0.001
ERROR	77	490.66	7.11		
TOTAL	80	621.60			

Hard Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	151.32	50.44	5.22	0.003
ERROR	77	705.37	9.66		
TOTAL	80	856.69			

Soft Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	3.312	1.104	1.61	0.195
ERROR	77	19.415	0.686		
TOTAL	80	52.727			

Benthic species richness of sand and coral matrix:

Algae

SOURCE	DF	SS	MS	F	p
FACTOR	3	118.7	39.6	1.04	0.381
ERROR	77	2863.6	38.2		
TOTAL	80	2982.3			

Hard Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	490.6	163.5	3.29	0.025
ERROR	77	3632.7	49.8		
TOTAL	80	4123.3			

Soft Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	3.48	1.16	0.86	0.466
ERROR	77	98.60	1.35		
TOTAL	80	102.08			

Benthic Cover for sand and coral matrix

Algae

SOURCE	DF	SS	MS	F	p
FACTOR	3	40730	13577	1.93	0.133
ERROR	65	456087	7017		
TOTAL	68	496817			

Hard Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	121729	40576	4.12	0.010
ERROR	65	640550	9855		
TOTAL	68	762279			

Soft Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	8221	2740	3.77	0.015
ERROR	65	47933			
TOTAL	68	56154			

Diversity of sand and coral matrix

Hard coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	263.7	87.9	7.90	0.000 (<0.001)
ERROR	65	678.9	11.1		
TOTAL	68	942.6			

Soft Coral

SOURCE	DF	SS	MS	F	p
FACTOR	3	3.312	1.104	1.61	0.195
ERROR	77	19.415	0.686		
TOTAL	80	52.727			

Benthic species richness of matrix drop-off:

Algae

SOURCE	DF	SS	MS	F	p
FACTOR	2	0.13	0.07	0.01	0.991
ERROR	16	118.50	7.41		
TOTAL	18	118.63			

Hard Coral

SOURCE	DF	SS	MS	F	p
FACTOR	2	163.3	81.7	2.54	0.111
ERROR	16	515.4	32.2		
TOTAL	18	678.7			

Benthic Cover for matrix drop-off

Algae

SOURCE	DF	SS	MS	F	p
FACTOR	2	18837	94.19	1.44	0.264
ERROR	17	111199	6541		
TOTAL	19	130036			

Hard Coral

SOURCE	DF	SS	MS	F	p
FACTOR	2	18837	94.19	1.44	0.264
ERROR	17	111199	6541		
TOTAL	19	130036			

Soft Coral

SOURCE	DF	SS	MS	F	p
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FACTOR	2	2981731	1490866	104.17	0.000(<0.001)
ERROR	17	47933	14312		
TOTAL	19	56154			

Diversity of matrix drop-off benthos

Hard Coral

SOURCE	DF	SS	MS	F	p
FACTOR	2	163.3	81.7	2.54	0.111
ERROR	16	515.4	32.2		
TOTAL	18	678.7			

Data is available on request on Microsoft Excel spreadsheet. The quantity of data was too great to put in the Appendix.

If data are required contact:

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