LONG-TERM RECOVERY PROCESS OF A CORAL COMMUNITY AFTER A CATASTROPHIC DISTURBANCE

Mitchell W. Colgan

UNIVERSITY OF GUAM MARINE LABORATORY

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ABSTRACT

The 1968-1969 outbreak of Acanthaster planci at Tanguisson Reef, Guam, caused a catastrophic mortality of corals. The subsequent recovery was examined from data collected in 1970, 1971, 1974, 1980 and 1981. Four categories of survivors were found: 1) corals in turbulent shallow water habitats, 2) corals which were not the preferred food of Acanthaster, 3) living patches of partially eaten colonies and 4) small colonies located in cryptic interstices. Nonrandom recruitment of corals was the primary factor in determining the eventual distribution of adult colonies. Zones were established through the settlement of juvenile corals and were further differentiated by the positive correlation between the abundance of adult and juvenile conspecifics. The contagious distribution pattern developed as a result of the strong associations between adults and juveniles within localized areas. The feeding preferences of Acanthaster were determined and an analysis of coral community structure showed a shift from predominance of nonpreferred prey in the early years after the Acanthaster disturbance to a prevalence of preferred prey species as the recovery of the coral community progressed. The recovery of the coral community was facilitated by the presence of patches of surviving corals as well as the continued structural integrity of the reef.

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INTRODUCTION

As human populations increase and cultures shift to more modern technology and large-scale economic development, the presumably delicate natural ecosystems become subject to more severe environmental stresses. Because of this, economic development and land-management must be done with careful prior planning. For proper prior assessment of the impact of human activities, we must have a knowledge of the ability of tropical biological communities to respond to perturbations.

Different points of view exist concerning the ability of coral communities to recover from disturbances (Connell 1978). In one school of thought, coral reefs are viewed as highly organized stable ecosystems with their populations in equilibrium (Grassle 1973). Another school views coral reef communities as being in a state of nonequilibrium resulting from frequent disturbances (Connell 1978).

The stable equilibrium school believes that the environmental predictability of the tropics enables the development of stable communities through specialization which eases competitive pressures (Diamond 1975). Competition between corals is reduced by finely dividing resources along a nutritional gradient between autotrophy and heterotrophy (Porter 1976). Disturbances per se are not important in overall community structure, though on a small scale, disturbances may provide space for opportunistic species (Grassle 1973). Major disturbances are rare and recovery from them requires a long successional process (Endean 1973, 1974, 1977) so the effects of these disturbances are long felt within the community (Ricklefs 1973:767). Diversity is highest at the culmination of succession, and the climax community is generally constant in time and space.

In the late 1960s and early 1970s, outbreaks of a coral predator, _Acanthaster planci_, were recorded throughout the Pacific (Potts 1980; Pearson 1981). Such large scale disturbances within stable coral communities generated considerable concerns (Chesher 1969a, b; Endean 1973, 1974), since it was thought that the magnitude of the damage was unprecedented and that the reef would be unable to adjust to the change. It was predicted that recovery would take decades or longer (Endean 1973, 1974; Endean and Stablum 1975; Goreau et al. 1972), and even the possiblity of extinction of the entire scleractinian order was raised (Chesher 1969a).

The furor which resulted over _Acanthaster_ focused a great deal of attention on coral reefs and on the role that disturbances play in the coral reef ecosystem (Connell 1978). Disturbances are viewed as being any type of space-clearing activities, be they biological or physical. Disturbances to sessile communities renew space, a potentially limiting resource, and prevent the monopolization of an area by one or a few species. In addition to outbreaks of _Acanthaster_, disturbances to the coral community have been low tides (Glynn 1976; Loya 1976), typhoons (Glynn et al. 1964; Perkins and Enos 1968; Stoddart 1974; Randall and Eldredge 1977), earthquakes (Stoddart 1972), slumping (Goreau and Goreau 1973), lava flows (Grigg and Maragos 1974), chilling (Shinn 1972), bioerosion (Connell 1973; Pang 1973; Scoffin and Garrett 1974; Highsmith 1981), suffocation by blue-green algae (Randall 1973a), overgrowth by sponges (*Terpios* sp. [Bryan 1973]) and the movement of tunicates (Birkeland et al. 1981). A variety of species prey upon reef-building corals, e.g., the seastar *Culcita novaeguineae* (Goreau et al. 1972), the urchins *Diadema* (Bak and Engel 1979) and *Eucidaris* (Glynn et al. 1979), fishes (Glynn et al. 1972; Glynn 1973; Randall 1974; Neudecker 1979; Wellington ms), molluscs (Glynn et al. 1972), and a polychaete worm, *Hermodice carunculata* (Glynn et al. 1972; Shinn 1976). These numerous disturbances would lead to a relatively unpredictable and less stable environment than previously thought. Disturbances are also considered to be important in the structuring of other communities: rocky intertidal (Paine 1966, 1971, 1979; Dayton 1971; Levin and Paine 1974; Sousa 1979a, b; Paine and Levin 1981; and others), forests (Horn 1975; Whitmore 1974; Connell 1978; Garwood et al. 1979), and the deep-sea communities (Dayton and Hessler 1972).

A swarm of *Acanthaster* invaded Tanguisson Reef in the summer of 1968 and by the winter of 1969 they were gone. During their presence, the coral community experienced a major impact. Species richness, coral density and cover were sharply reduced (Randall 1973a). The purpose of this study was to gain an understanding of community development by examining the recovery of this coral community. The rate of recovery was informative regarding the ability of coral communities to accomodate major disturbances. Knowledge of changes in the coral community is useful in understanding the establishment of zones. A long term perspective of recovery can be obtained by combining the data from current work (1980-1981) with data collected in 1970 (Randall 1973a), 1971 (Randall 1973b) and 1974 (Jones et al. 1976).

STUDY SITE

Tanguisson Reef was selected as the study site in 1980-1981 because previous work was conducted there concerning the effects of the Acanthaster outbreak in 1968-1969. Randall documented the early stages of coral community recovery at Tanguisson Reef in 1970, 1971 and 1974 (Randall 1973a, b; Jones et al. 1976). His published work and his wealth of unpublished data made Tanguisson Reef an ideal location for a long term examination of the development of a coral reef community.

Tanguisson Reef is located on the northwestern coast of Guam's limestone plateau (Fig. 1) and is situated along a narrow coastal terrace at the base of a steep cliff. Waters surrounding the reef were free of terrestrial sediments and were very clear. Rough surf was common and hampered much of the research activity.

Seven physiographic zones are distinguished at Tanguisson Reef (Jones et al. 1976). From shore, a narrow pitted and pinnacled limestone intertidal zone borders a submerged reef flat platform. A poorly developed convex algal ridge at the reef margin is cut by numerous surge channels. The reef front is between 1 m and 6 m deep and 50 to 70 m wide. A series of buttresses and channels gives a high and variable relief. Channels are irregularly spaced and range in depth from 1 m to 3 m. Fine sediments seldom accumulate in this zone, but coarse sand, rubble, and boulders veneer the channel floors in places. Room-and-pillar construction is found in the upper portion of the zone;

Figure 1. Location of the study area.

this is typical of an actively growing reef (Emery et al. 1954). A sharp decline in the reef front slope and the absence of the buttress and channel system delineate the end of the reef front and the start of the submarine terrace.

The submarine terrace slopes gently downward from 6 m to a depth of 16 m. The terrace ranges from 40 m to 110 m in width. A few knolls and pinnacles dot its surface but, in general, the relief is less than on the reef front or the submarine terrace. Numerous shallow, irregular channels cut across the terrace. Sand and gravel-sized sediments form thin deposits at places along the channel floors.

An abrupt increase in the reef slope marks the beginning of the seaward slope. The seaward slope dips downward from 16 m to 33 m and has an average width of 60 m. Topographic relief is less than on the reef front, but the surface appears to be more irregular. Many channels slice its surface. Fine sediments are abundant, accumulating in basins and on channel floors. Eventually, these sediments are transported to the second submarine terrace.

Three zones are of particular interest (i.e., reef front, submarine terrace, and seaward slope) since the greatest effects of Acanthaster predation are found in these areas.

METHODS

In 1970, three transect areas were delineated perpendicular to the shore, to a depth of 33 m (Randall 1973a). Along the transects, sampling stations were designated at 10 m intervals. At each station, two replicate 1-m^2 quadrats were used to sample the coral. For each coral, two linear measurements across the length and width of a coral were recorded and the growth form was noted. The linear measurements were converted to area estimates by the formula, $A = (\sqrt{lw/2})^2\pi$. From these data, the following statistics were calculated: coral density (colonies/m^2), percent live cover, and species frequency. Also, size class and growth form distributions were obtained. This quadrat method was used to survey the reef in 1970, 1971 and 1974.

The 1980-1981 study combined two sampling techniques (the point-quarter technique [Cottam et al. 1953] and counts of coral in quadrats) to resurvey the reef along Randall's previous transect areas. In 1980, only the point-quarter method was used, in place of the quadrat method. This change in technique was initiated as a time saving measure after the results from the two methods were shown not to be significantly different (Colgan in press). Other authors have also used the point-quarter sampling method on a coral reef in lieu of quadrat methods (Loya 1979).

For the point-quarter method, sampling stations were established every two meters along the transect from the start of the reef front to a depth of 36 m. At each station, four quadrants were defined and the distance to the center of the nearest coral in each sector was measured. Two linear measurements were taken for each coral and the growth form was noted. The area of each coral was calculated using the same formula as used in the previous studies. From these data, the following were calculated for each species:

$$\text{Total density of all species} = \frac{\text{Unit area}}{\text{(Mean point-to-point distance)}}$$

$$\text{Relative density} = \frac{\text{Individuals of a species}}{\text{Total number of colonies of all species}} \times 100$$

$$\text{Density} = \frac{\text{Relative density of a species}}{100} \times \text{Total density of all species}$$

Percent cover = Density of species x Average area of each species

$$\text{Relative percent cover} = \frac{\text{Percent cover a species}}{\text{Total percent cover for all species}} \times 100$$

$$\text{Frequency of occurrence} = \frac{\text{Number of points at which a species occurs}}{\text{Total number of points sampled}}$$

$$\text{Relative frequency of occurrence} = \frac{\text{Frequency value for a species}}{\text{Total of frequency values for all species}} \times 100$$

Importance value = Relative values for percent cover + Density + Frequency

In 1981, a quadrat-count method similar to that used by Randall was employed to survey the reef. For 1981, distinctions were made between adults (diameter $\geq$ 5 cm) and juveniles (diameter $\leq$ 4 cm), but specific measurements were not taken. Resurveying with quadrats was necessary because the point-quarter method did not produce enough data to answer the new questions raised concerning the nature of coral recruitment and reef zonation. The data collected using quadrats were used in all recruitment, density, diversity, distribution, and species frequency calculations. Species diversity indices were calculated using the Shannon-Wiener species index ($\log_2$) for the number of colonies: space occupied by other than living corals was not included as a category for the index because this was the method used for calculating the index in other coral reef surveys (Grigg and Maragos 1974; Glynn 1976; Loya 1976).

Raw data from studies in previous years were made available and much of it was reanalyzed. New information concerning the distribution of juvenile and adult corals, species diversity, population density, recruitment patterns, and community succession are presented here for the first time. The species listed in the previous studies by Randall have been updated to be consistent with current nomenclature. Several species have been synonymized, reducing the species richness values previously reported. In 1974, raw data for each replicate were lumped into one sample. Unfortunately, this led to replicates in other years being lumped. Thus, all density values are expressed as colonies per 2-m^2. In addition, some raw data from 1970 were lost, causing the reductions in sample sizes for that year noted on many tables. These reduced samples were used to generate statistics for zones but were not subjected to parametric analysis.

To determine if Acanthaster have preferred prey, a survey was conducted on Guam at Fafai Beach and Piti Bay where A. planci were actively feeding. A ¼-m^2 quadrat criss-crossed with 8 lines forming 16 intersecting points was used to survey the area. Over 500 samples were taken. The genus of each coral found below a point was recorded and its condition noted. From these data, the availability of a prey category and the level of predation were determined for each genus sampled.

RESULTS

Zonation

In previous studies at Tanguisson Reef, a tacit assumption was made that the biological zones corresponded to the physiographical zones (Randall 1973a, b; Jones et al. 1976; Colgan in press). This assumption was validated by an examination of a matrix of Jaccard similarity coefficients (Sokal and Sneath 1963) of the species present within zones and years which revealed that the species compositions were more similar within physiographic zones than between zones, regardless of years (Table 1). A dendrogram constructed from the similarity indices illustrates three distinct clusters (reef front, submarine terrace, and seaward slope) with only the 1970 seaward slope outside the major clusters (Fig. 2). The coral community zones were also analyzed by a hypergeometric distribution to determine the probability that the species composition from the zones in the same year and in different years were derived from the same species pool (methods in Kropp and Birkeland in press).

With one exception, there were no significant differences found within zones, only between zones (Table 2). The 1970 seaward slope community was significantly different from the communities of all other zones and years, but by 1971 the seaward slope community had obtained a species composition typical of the seaward slope in later years. A random recruitment pattern would have been evidenced by strong interzone similarities since recruits would have tended to be

Table 1. Jaccard similarity indices of coral species composition between zones and years. RF = Reef front, ST = Submarine terrace, SS = Seaward slope.

RF 70	---											
ST 70	.427	---										
SS 70	.192	.254	---									
RF 71	.750	.408	.208	---								
ST 71	.512	.606	.333	.524	---							
SS 71	.298	.493	.390	.371	.592	---						
RF 74	.760	.413	.222	.808	.541	.376	---					
ST 74	.543	.538	.282	.527	.785	.568	.574	---				
SS 74	.365	.398	.333	.352	.516	.683	.358	.580	---			
RF 81	.697	.482	.242	.678	.589	.445	.784	.637	.440	---		
ST 81	.473	.430	.217	.473	.610	.491	.461	.780	.561	.603	---	
SS 81	.288	.325	.234	.288	.408	.509	.310	.476	.676	.385	.515	---
	RF 70	ST 70	SS 70	RF 71	ST 71	SS 71	RF 74	ST 74	SS 74	RF 81	ST 81	SS 81

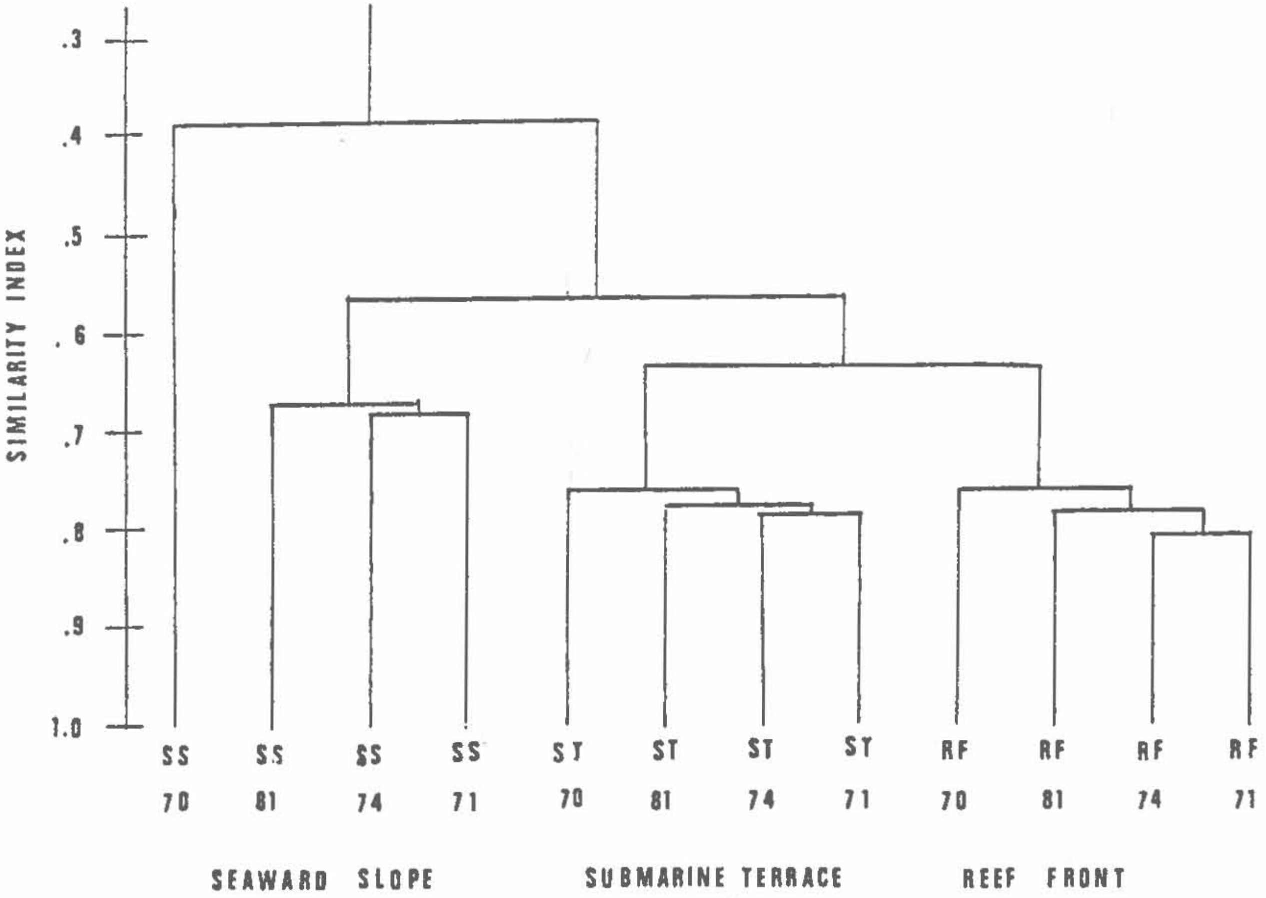

Figure 2. Dendrogram constructed from similarity indices (Table 1).

Table 2. The probability that coral species from different zones and years are members of the same species pool. The probabilities were calculated using the hypergeometric distribution. Levels of significance of differences are indicated as follows: *≤.05, **≤.01, ***≤.001. RF = Reef front, ST = Submarine terrace, SS = Seaward slope.

RF 70	---											
ST 70	***	---										
SS 70	***	***	---									
RF 71	.278	***	***	---								
ST 71	***	.188	**	**	---							
SS 71	***	**	*	***	*	---						
RF 74	.337	***	***	.547	**	***	---					
ST 74	***	.55	**	**	1	*	**	---				
SS 74	***	**	**	***	**	.367	***	**	---			
RF 81	.708	*	***	.488	*	***	1	*	***	---		
ST 81	**	.44	***	**	.62	*	***	.79	**	**	---	
SS 81	***	***	**	***	***	.151	***	***	.251	***	***	---
	RF 70	ST 70	SS 70	RF 71	ST 71	SS 71	RF 74	ST 74	SS 74	RF 81	ST 81	SS 81

distributed evenly across all zones, especially during the earlier years. The zonation found for all species and years would seem to be the result of nonrandom recruitment processes.

The distributional patterns of 49 species were examined to determine if species tended to be found in significantly greater abundances in certain zones. In 1970, 62.79% of the species tested showed strong association with certain zones (Table 3). The magnitude of the distribution indices increased significantly with time, as the number of colonies increased (Friedman's test, $X^2_{[3]} = 39.398$***). The cause of the increases in distinct distributional patterns of coral species among zones was that by 1981, 87.5% of the species showed strong associations with particular zones.

Species Composition

The biological zones of the reef front, submarine terrace, and seaward slope at Tanguisson Reef are not as visually distinct as those described for atolls (Wells 1954) or for islands of the Caribbean (Goreau 1959), since one or a few species are not predominant in a zone. Instead, each zone has a characteristic assemblage of species. This absence of a single predominant species was reflected in the high species evenness values for all zones (Table 4). There was no case in which a single species contributed more than 25% of the total number of colonies and usually the most abundant species represented less than 20% (Appendix 1).

From 1970 to 1980, the species composition of the community of each zone had changed from predominance by nonpreferred prey of *Acanthaster* to predominance of preferred prey species. An assessment

Table 3. Distribution indices (X^2-value) for each of 49 coral species for 1970, 1971, 1974 and 1981. The expected values assumed random settlement and was adjusted for the unequal sampling in each zone. The Friedman's method for randomized blocks was used to determine if there was a trend in the distributional pattern with time. A bar indicates that less than three individuals were sampled. The occurrence of a species in a zone is considered to be other than random if $X^2 \geq 5.991$.

	Years (a)			
Species (b)	1970	1971	1974	1981
Psammocora nierstraszi	6.250	0.133	1.269	1.225
Psammocora sp. 1	---	5.807	8.054	21.543
Stylophora mordax	6.088	2.739	4.798	1.651
Pocillopora elegans	27.624	58.520	3.139	15.122
Pocillopora eydouxi	---	1.232	3.373	4.532
Pocillopora setcheli	63.33	46.836	161.609	193.022
Pocillopora verrucosa	13,840	9.361	2.067	24.455
Acropora humilis	3.257	1.531	8.091	24.901
Acropora irregularis	7.797	4.413	6.911	5.216
Acropora nasuta	8.901	33.218	42.318	50.731
Acropora surculosra	6.708	16.010	6.639	213.747
Acropora tenuis	---	.684	2.584	10.625
Acropora wardi	4.037	13.850	5.944	20.644
Acropora spp. 1	63.330	62.416	66.597	78.003
Astreopora gracilis	1.540	6.871	2.561	43.445
Astreopora myriophthalma	2.650	7.002	20.090	82.018
Montipora cf. *M. caliculata*	0.024	4.449	8.155	23.436
Montipora conicula	2.960	11.166	2.986	4.962
Montipora elschneri	8.385	6.344	24.725	61.430
Montipora foveolata	2.364	---	7.800	51.092
Montipora hoffmeisteri	---	1.294	12.155	55.422
Montipora monasteriata	2.960	5.807	16.115	6.616
Montipora verrilli	17.929	42.984	55.483	46.206
Montipora verrucosa	---	6.871	5.155	37.754
Pavona spp. 2	41.987	36.004	16.928	5.444
Porites lichen	---	19.967	5.029	16.155
Porites lobata	8.561	38.219	74.580	103.514
Porites lutea	1.873	5.145	34.642	175.559
Porites (S.) iwayamaensis	11.166	30.534	20.360	10.107
Favia favus	8.125	60.025	48.992	167.195
Favia pallida	1.237	2.642	3.816	62.009
Favia stelligera	39.038	29.922	58.130	56.172
Favites russelli	.024	4.065	10.890	20.379
Goniastrea edwardsi	8.700	1.770	4.186	49.412
Goniastrea pectinata	9.261	26.980	25.342	36.847
Goniastrea retiformis	114.007	221.880	176.538	109.327
Platygyra deadalea	4.534	0.75	0.688	3.251
Platygyra pini	3.257	2.837	1.711	17.206
Leptoria phrygia	39.688	31.646	27.223	56.573
Montastrea curta	17.173	29.332	50.561	19.638

Table 3 Continued.

	Years (a)			
Species	1970	1971	1974	1981
Leptastrea purpurea	12.674	63.778	5.646	46.264
Leptastrea transversa	10.943	50.386	194.794	204.743
Cyphastrea spp. 3	3.722	6.866	18.511	99.564
Galaxea fascicularis	118.297	163.303	237.476	168.999
Acanthastrea echinata	26.056	8.206	31.158	4.914
Lobophyllia spp. 4	0.261	5.851	0.225	3.725
Echinophyllia aspera	2.650	10.987	12.734	7.957
Millepora platyphylla	15.093	7.892	33.501	---
Millepora tuberosa	7.990	11.269	16.540	24.319
ΣR_{ij}	88	111	131	160

$$\chi^2_{[3]} = \frac{12(88^2 + 111^2 + 131^2 + 160^2)}{4(49)\ (4+1)} - 3(49)\ (4+1)$$

$$= 34.398^{***}$$

---

1. *Acropora cerealis* and *Acropora variabilis* were combined.
2. *Pavona varians* and *Pavona* sp. 1 were combined.
3. *Cyphastrea chalcidicum*, *Cyphastrea microphthalma* and *Cyphastrea serailia* were combined.
4. *Lobophyllia corymbosa* and *Lobophyllia costata* were combined.

Table 4. Species evenness values $(-\Sigma p_i \log_2 p_i)/\log_2 n$ for zones and years.

	1970	1971	1974	1981
Reef front	.832	.801	.800	.784
Submarine terrace	.909	.824	.772	.812
Seaward slope	.876	.830	.782	.824

of the feeding preferences of Acanthaster showed that Montipora and Acropora were significantly preferred over all other genera (Table 5). Preferred species were drastically reduced in size and number at Tanguisson following the 1968-1969 outbreak of Acanthaster. In 1971, nonpreferred species were relatively more common in all reef zones, with their relative importance greatest on the submarine terrace and seaward slope where Acanthaster concentrated its feeding efforts (Table 6). Subsequently, through recruitment and fast growth, preferred species reestablished themselves. In 1980, preferred species were predominant on two zones, the reef front and submarine terrace. Since 1974 there was a decline in the importance of nonpreferred species on the seaward slope (Table 6). A detailed breakdown of the changes in the species distribution is found in Appendix 1.

Juvenile Corals and Recruitment

The distribution and abundance of juvenile (diameter $\leq$ 4 cm) corals (Bak and Engle 1979) were examined from data collected from 177 2-m^2 quadrats. The examinations covered the years 1970, 1971, 1974 and 1981 which included a sample of 4091 juvenile corals.

Since 1970, the juvenile coral density changed significantly in all three zones (Table 7). The density of juveniles reached a peak in 1974 (reef front - 7.75/m^2, submarine terrace - 12.30/m^2, and seaward slope - 12.70/m^2). These mean densities were lower than those recorded in the Caribbean (17/m^2, Bak and Engle 1979) and in the Great Barrier Reef (15/m^2, Connell 1973). After 1974, there were significant declines in the densities of juveniles in two zones (reef front, t_{37} = 2.35*; submarine terrace, t_{40} = 5.21***).

Table 5. Generic level discrimination of feeding preferences of *Acanthaster*. The expected values for chi-square assumed that the corals were being preyed upon in the same proportion as was available. Preferred prey were preyed upon in significantly greater numbers than expected. Nonpreferred prey were preyed upon in significantly fewer numbers than expected. Neutral prey were preyed upon in approximately the same numbers as was available. Electivity indices (E) were calculated from the formula, $E = (r_i - p_i)/(r_i + p_i)$, r_i equals the proportion in the diet and p_i equals the proportion available (Glynn 1976). The data from two study sites on Guam were combined.

	X^2	Electivity Index	n
Preferred Prey			
Montipora	162.099***	+ .232	840
Acropora	73.726***	+ .292	206
Nonpreferred Prey			
Porites	100.476***	- .945	202
Pocillopora	76.547***	- .604	256
Porites (Synarea)	65.848***	-1.000	126
Leptastrea	17.408***	- .447	90
Stylophora	10.617***	- .524	46
Millepora	9.473***	- .464	47
Favia	7.620**	- .769	22
Goniastrea	4.978*	-1.000	12
Neutral Prey			
Pavona	1.042ns	- .247	19
Astreopora	1.006ns	+ .107	44
Alveopora	.156ns	- .133	15

Table 6. Coral community indices (CCI) as indicators of change in the species composition with time. CCI = Σ(importance value x *Acanthaster* feeding preference rating). *Acanthaster* prey preference rating: +1 preferred species, -1 nonpreferred, 0 all other (see Table 5). Importance value = Σ(relative frequency + relative density + relative percent cover). The index values range from -300 (all nonpreferred species) to +300 (all preferred species).

	1971	1974	1980
Reef front	-32.09	-46.90	+43.71
Submarine terrace	-70.03	-39.97	+73.37
Seaward slope	-173.42	-107.51	-74.97

Table 7. Density of juvenile (diameter ≤4 cm) coral colonies per 2-m^2, $\overline{Y}$ ± 95% confidence intervals (n), calculated for zones and years. A two-way anova with 18 replicates was used to analyze the data for 1971, 1974 and 1981. A random number table was used to discard replicates in excess of 18 for the two-way anova.

	1970	1971	1974	1981
Reef front	10.7 ± 4.05(16)	13.5 ± 4.94(19)	15.5 ± 7.63(19)	6.4 ± 1.52(20)
Submarine terrace	15.8 ± 3.33(7)	19.8 ± 3.68(20)	24.6 ± 4.48(21)	10.7 ± 2.72(21)
Seaward slope	9.0 ± 4.74(8)	18.6 ± 2.87(20)	25.4 ± 4.67(19)	24.3 ± 3.51(18)

Source of variation	df	MS
Subgroups	8	842.77
years (a)	2	593.38***
zones (b)	2	1947.27***
Interaction (AXB)	4	415.22***
Within subgroups	153	70.85
TOTAL	161	

Significant differences in density were found between zones and between years (Table 7). The submarine terrace and seaward slope were most affected by Acanthaster and had the greatest number of juveniles.

Although juvenile coral density reached its highest level in 1974, it was in 1970 and 1971 that the greatest proportion of the coral population was made up of juveniles (Table 8). Juveniles were the major contributors to the population on the seaward slope until 1974. In 1981, juvenile corals accounted for 20% of the coral population (Table 8). This decrease in percentage of juveniles was significant for years, with the highest percentages in each zone falling in 1970 (Friedman's test, $X^2_{[3]} = 9^*$). A significant stratification between zones was also evident (Friedman's test, $X^2_{[2]} = 8^*$) with the seaward slope consistently having the highest percentage of juveniles in its coral population. There was a noticeable change in the orientation of juvenile corals with depth. In shallow water (less than 8 m deep) juveniles corals were found on vertical surfaces or within cryptic spaces. At depths greater than 18 m, juvenile corals were usually on horizontal surfaces.

Juvenile corals that were found within a 2-m^2 quadrat without conspecific adults were defined as independent juveniles. These juveniles were pioneers, settling in areas where their adults were not found in close proximity. After the swarm of Acanthaster left Tanguisson Reef, few adult-sized corals remained. The reestablishment of the coral community came about through the initial settlement of independent juveniles. In 1970, on the two zones most affected by Acanthaster (submarine terrace and seaward slope), independent juveniles contributed over 75% of the juvenile coral population

Table 8. Percent of corals that were juveniles (diameter ≤ 4 cm) in the samples for zones and years. Two Friedman's randomized block tests were used to analyze the data between years and between zones.

	Years				
Zones	1970	1971	1974	1981	ΣR_{ij}
Reef front	36.55	32.53	32.09	12.96	4
Submarine terrace	67.56	62.66	49.90	17.20	8
Seaward slope	88.88	73.10	59.07	27.74	12
ΣR_{ij}	12	9	6	3	

Years

$$X^2 = \frac{12(12^2 + 9^2 + 6^2 + 3^2)}{4(3)\ (4+1)} - 3(3)\ (4+1)$$

$$= 9*$$

Zones

$$X^2 = \frac{12(12^2 + 8^2 + 4^2)}{3(4)\ (3+1)} - 3(4)\ (3+1)$$

$$= 8*$$

(Table 9). Subsequently, the percentage of independent juveniles significantly declined in all zones (Friedman's test, $X^2_{[3]} = 9^*$). This decline was negatively correlated with the rise in the adult coral population in each zone (Spearman rank correlation, $r_s = -.979^{***}$).

The density of independent juveniles was highest on the submarine terrace and seaward slope throughout the study; it significantly declined with time for all zones (Table 10).

Juvenile corals showed an association with specific zones by either settlement or survival. The distribution patterns of 37 species for 1971, 1974 and 1981 were examined using a chi-square test as an index of distribution (significant association is recognized when $X^2 \geq 5.991$, cf. Table 11). In 1971, 1974 and 1980, 63.64%, 65.71% and 75.00%, respectively, of the species examined showed association with specific zones. Thirty species with more than sixteen juveniles censused in any one year were examined with a chi-square goodness-of-fit test; 28 species exhibited a significant preference for specific zones (indicated by an asterisk in Table 11). The two species not associated with specific zones were *Acropora humilis* and *Stylophora mordax*. There were no changes in the general distribution of juveniles over time (Friedman's test, $X^2_{[3]} = .055$ns).

Juveniles not only showed zone-specific recruitment, but, by 1974, they were also found in greatest number in the same zones in which adults of their species were most abundant. The pattern of juveniles settling in the same zones as their adults developed during the course of community recovery. In 1971, 39% of the 23 species tested had both the adults and juveniles abundant in the same zones. By 1981, juveniles of 87% of the 23 species were associated with their adults

Table 9. The percentages of independent juvenile (diameter $\leq$ 4 cm) coral colonies (i.e., without a conspecific adult in a 2-m^2 quadrat) in a sample of juveniles, calculated for zones and years. Two Friedman's randomized block tests were used to analyze the data between years and between zones.

	1970	1971	1974	1981	ΣR_{ij}
Reef front	36.26	28.89	22.58	6.06	4
Submarine terrace	76.11	53.83	34.47	20.74	9
Seaward slope	100.00	55.81	42.52	12.35	11
ΣR_{ij}	12	9	6	3	

$$X^2 = \frac{12(12^2 + 9^2 + 6^2 + 3^2)}{4(4)\ (4+1)} - 3(3)\ (4+1)$$

$$= 9^*$$

$$X^2 = \frac{12(11^2 + 9^2 + 4^2)}{3(4)\ (3+1)} - 3(4)\ (3+1)$$

$$= 6.5^*$$

Table 10. The number of juvenile (diameter ≤4 cm) coral colonies that were found independent of adult conspecifics (diameter ≥5 cm) in 2-m^2 quadrats, $\bar{Y}$ ± 95% confidence interval (n), calculated for zones and years. A two-way anova with 18 replicates as used to analyze the data for 1971, 1974 and 1981. A random number was used to discard replicates in excess of 18 for the two-way anova.

	1970	1971	1974	1981
Reef front	3.9 ± 2.07(16)	3.9 ± 1.60(19)	3.5 ± 1.27(19)	0.4 ± .39(20)
Submarine terrace	12.0 ± 3.43(7)	10.7 ± 2.67(20)	9.2 ± 2.15(21)	2.2 ± .74(21)
Seaward slope	9.0 ± 4.74(8)	10.4 ± 2.64(20)	10.8 ± 2.23(19)	3.0 ± 1.06(18)

Source of variation	df	MS
Subgroups	8	313.83
years (a)	2	698.19***
zones (b)	2	474.86***
Interaction (AXB)	4	41.13*
Within subgroups	153	15.49
TOTAL	161	

Table 11. Juvenile (diameters $\leq$4 cm) coral zonal settlement distribution indices (X^2) for 37 species and 22 genera. The expected values assumed random settlement and was adjusted for unequal sampling in each zone. The Friedman's method for randomized blocks was used to analyze the species data with 2 or more entries. Association with certain zones was recognized when $X^2 \leq 5.991$. Goodness-of-fit test for $n \geq 16$, significance level ns >.05, * $\leq$ .05, ** $\leq$ .01, *** $\leq$ .001.

	1971 X^2	1974 X^2	1981 X^2
Psammocora	3.597	4.905	3.400
Psammocora nierstraszi	.343	1.194	
Psammocora sp. 1	5.139	2.600	2.413
Stylophora mordax	2.225	1.142	1.445ns
Pocillopora	12.202	4.070	9.012
Pocillopora elegans	17.704	7.856*	4.713
Pocillopora setchelli	17.704	73.850***	33.219***
Pocillopora verucosa	1.800	3.342	28.738***
Acropora	4.002	.436	3.092
Acropora humilis	1.696	6.141***	4.299ns
Acropora surculosa		5.469	19.011***
Acropora tenuis	8.321	2.794	5.785
Acropora wardi		5.469	3.707
Astreopora	9.642	9.689	33.469
Astreopora myriophthalma	4.326	9.689**	17.744***
Montipora	67.743	39.913	32.622
Montipora elschneri	7.515	4.127	18.470***
Montipora foveolate		7.914	13.324
Montipora hoffmeisteri		.071	9.112**
Montipora verrilli	36.680***	30.617***	8.824*
Pavona	31.661	6.830	.099
Pavona spp. +	20.819***	6.182*	.334
Leptoseris		8.902	
Goniopora		1.563	
Porites	36.539	95.280	146.377
Porites lichen	2.535	3.899	2.413
Porites lobuta	30.262***	49.942***	49.998***
Porites lutea	7.562	32.268***	96.051
Porites (S.) iwayamaensis	10.277		1.859
Favia	3.988	21.021	37.864
Favia favus	39.510***	32.396***	31.719***
Favia pallida	7.130*	15.637***	17.768***
Favia stelligera	15.184***	12.229**	2.843
Favites	6.284	5.886	19.304
Favites russelli	7.130*	3.553NS	19.304***
Goniastrea	11.780	8.378	22.355
Goniastrea edwardsi	4.112	1.470	23.297***
Goniastrea pectinata	19.565***	22.173***	11.987
Goniastrea retiformis	48.504***	41.265***	10.023

Table 11 Continued.

	1971 X^2	1974 X^2	1981 X^2
Platygyra	6.656	6.958	.447
Platygyra pini	7.778*	6.958*	
Leptoria phrygia	6.344*		
Montatrea curta	13.850	10.534	
Leptastrea purpurea	42.804***	2.571	7.563
Leptastrea transversa	33.090***	103.149***	40.874***
Cyphastrea spp. ++	2.391	18.204***	32.308***
Galaxea fascicularis	2.843ns	1.102	23.324***
Acanthastrea echinata	.843	16.230***	.385
Lobophyllia spp. +++	2.225		
Echinophyllia aspera	.052	9.594***	
Millepora	1.44	3.796	7.173
Millepora tuberosa	1.645	4.795	7.173
ΣR_{ij}	72	73	71

$$X^2 = \frac{12(72^2 + 73^2 + 71^2)}{36(3)\ (3+1)} - 3(36)\ (3+1)$$

$$= .055\text{ns}$$

\+ *Pavona varians* and *Pavona* sp. 1 were combined.

++ *Cyphastrea chalcidicum*, *Cyphastrea microphthalma* and *Cyphastrea serailia* were combined.

+++ *Lobophyllia corymbose* and *Lobophyllia costata* were combined.

(Table 12). This was a significant change in the general distribution pattern (Cochran's Q = 13.9***).

Once adults became established, there was an increased likelihood of additional juveniles settling in their vicinity, as indicated by a significant positive relationship between the abundance of adults and their juveniles. In 1970, two zones (reef front and submarine terrace) showed significant correlations between the abundances of adult and juvenile conspecifics (Table 13) and, by 1971, all zones showed a similar relationship ($p \leq .001$). The correlations became significantly stronger within zones with time as shown by tests of homogeneity.

It has been suggested that juveniles disperse away from their adults rather than to them (Connell 1973). This concept was tested for 34 species in 1971, 1974 and 1981 with a coefficient of association (Krebs 1972:383) between adults and juveniles in the same 2-m^2 quadrat. In 1971, 50% of the species showed significant positive associations (Table 14). There was a significant increase in the affinities between adults and juveniles with time (Friedman's test, $X^2_{[2]} = 31.824$***), and by 1981, 79% of the species showed significant positive adult-juvenile associations. Positive associations would tend to produce clumped rather than random or even distributions. An examination of 150 distribution patterns within zones of 44 species in 1971, 1974 and 1981 showed clumped distributions in 87.3% of the cases (coefficient of dispersion, $S/\overline{Y} \geq 1.50$, $n \geq 10$ colonies per zone). Of the 19 cases of random distribution, 89.5% were from the suborder Astrocoeniina of which 33.3% were members of the family Pocilloporidae.

Table 12. Patterns of the abundance of juvenile (diameter ≤ 4 cm) coral settlement by zones as indicated by their proximity to the zone in which the adults (diameter ≥ 5 cm) of their species were most abundant. 0 = same zone, 1 = different zone. Cochran's Q-test was used to analyze the change in the settlement patterns for 23 species of corals.

	1971	1974	1981	Σ
Psammocora nierstraszi	1	1	1	3
Pocillopora elegans	0	1	0	1
Pocillopora setchelli	0	0	0	0
Acropora spp.[1]	0	0	0	0
Montipora elschneri	1	0	0	1
Montipora verrilli	1	0	0	1
Pavona spp.[2]	0	1	1	2
Porites lichen	1	0	0	1
Porites lobata	1	0	0	1
Porites lutea	1	0	0	1
Favia favus	0	0	0	0
Favia pallida	1	1	0	2
Favia stelligera	1	0	0	1
Favites russilli	1	0	0	1
Goniastrea edwardsi	1	0	0	1
Goniastrea pectinata	0	0	0	0
Goniastrea retiformis	0	0	0	0
Platygyra pini	1	1	0	2
Leptastrea purpurea	1	0	0	1
Leptastrea transversa	1	0	0	1
Cyphastrea spp.[3]	0	0	0	0
Acanthastrea echinata	0	0	0	0
Millopora tuberosa	1	1	1	3
	14	6	3	23

$$Q = \frac{(3-1)[(3\times 241)-23^2]}{(3\times 23)-41}$$

$$= 13.9^{***}$$

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[1] *Acropora cerealis* and *Acropora variabilis* were combined.

[2] *Pavona varians* and *Pavona* sp. 1 were combined.

[3] *Cyphastrea chalcidicum*, *Cyphastrea microphthalma* and *Cyphastrea seraila* were combined.

Table 13. Correlation coefficients with 95% confidence limits between adult (diameter ≥ 5 cm) and juvenile (diameter ≤ 4 cm) abundances within zones and years. A test of homogeneity of the correlation coefficients within zones was used for analysis. Significance levels: ns >.05, * ≤ .05, ** ≤ .01, and *** ≤ .001.

	1970	1971	1974	1981
Reef front	r=.615*** (53) L= .406 L=.762	r=.653*** (60) L=.475 L=.786	r=.497*** (62) L=.278 L=.667	r=.918***(66) L=.867 L=.950
Submarine terrace	r=.403* (35) L= .066 L=.657	r=.746*** (50) L=.604 L=.843	r=.921*** (63) L=.879 L=.952	r=.950*** (74) L=.920 L=.969
Seaward slope	r=-.189ns (20) L=-.603 L=.305	r=.532*** (57) L=.322 L=.682	r=.913*** (60) L=.857 L=.948	r=.862*** (73) L=.786 L=.912

Reef front X^2 = 47.740***

Submarine terrace X^2 = 55.589***

Seaward slope X^2 = 55.190***

Table 14. Association coefficient (V) between juvenile corals (diameter ≤ 4 cm) and adult corals (diameter ≥ 5 cm) calculated for 34 species for 1971, 1974 and 1981. The coefficient ranges from -1 to +1 with 0 indicating independence. A 2X2 contingency test was used to determine the probability of an association [$p(X^2)$]. The significance levels are indicated as follows: NS >.05, * ≤ .05, ** ≤ .01, and *** ≤ .001. The Friedman's method for randomized blocks was used to determine if there was a significant change in the coefficient of association with time. A bar indicates an absence of either adults or juveniles in the sample.

	Years (a)					
	1971		1974		1981	
Species (b)	V	$p(X^2)$	V	$p(X^2)$	V	$p(X^2)$
Psammocora nierstraszi	.502	**	.244	NS	.680	***
Psammocora sp. 1	-.070	NS	-.035	NS	.534	***
Stylophora mordax	---	---	.195	NS	.026	NS
Pocillopora elegans	.628	***	.250	NS	.411	**
Pocillopora setchelli	.413	**	.557	***	.740	***
Pocillopora verrucosa	.134	NS	.556	**	.644	***
Acropora humilis	-.062	NS	.151	NS	.224	NS
Acropora nasuta	.332	NS	.101	NS	.483	**
Acropora surculosa	.442	**	-.099	NS	.540	***
Astreopora myriophthalma	.153	NS	.329	*	.508	***
Montipora elschneri	.300	NS	.101	NS	.435	**
Montipora foveolata	---	---	.131	NS	.455	**
Montipora hoffmeisteri	-.053	NS	.151	NS	.505	***
Montipora verrilli	.440	**	.267	NS	.456	**
Montipora verrucosa	-.051	NS	-.056	NS	.282	NS
Pavona spp. +	.687	***	.319	NS	.575	***
Porites lichen	.116	NS	.319	NS	.318	NS
Porites lobata	.427	**	.489	***	.785	***
Porites lutea	.165	NS	.323	*	.500	***
Porites (S.) iwayamaensis	.371	**	.438	**	.349	*

Table 14 Continued.

	Years (a)					
	1971		1974		1981	
Species (b)	V	$p(X^2)$	V	$p(X^2)$	V	$p(X^2)$
Favia favus	.165	NS	.323	*	.599	***
Favia pallida	.094	NS	-.001	NS	.465	***
Favia stelligera	.461	**	.437	**	.294	NS
Favites russelli	.260	*	.811	***	.581	***
Goniastrea edwardsi	.348	**	.343	*	.531	***
Goniastrea pectinata	.448	**	.090	NS	.521	***
Goniastrea retiformis	.6645	***	.681	***	.497	***
Platygyra pini	.276	NS	.106	NS	.359	NS
Leptoria phrygia	.276	NS	.165	NS	.391	*
Leptastrea purpurea	.589	***	.484	**	.291	NS
Leptastrea transversa	.518	***	.668	***	.658	***
Cyphastrea spp. ++	.245	NS	.257	NS	.644	***
Galaxea fascicularis	.371	**	.438	**	.689	***
Millepora tuberosa	.348	*	.539	***	.384	**
ΣR_{ij}	55		60		89	

$$X^2 = \frac{12(55^2 + 60^2 + 89^2)}{3(34)\ (3+1)} - 3(34)\ (3+1)$$

$$= 31.824^{***}$$

\+ *Pavona varians* and *Pavona* sp. 1 were combined.

++ *Cyphastrea chalcidicum*, *Cyphastrea microphthalma* and *Cyphastrea serailia* were combined.

Based on the strong associations between adults and juveniles, there should be positive correlations between the numbers of adults and the numbers of juveniles in 2-m^2 quadrats. A negative correlation might indicate competition between adults and juveniles. In 1970 and 1971, no significant correlations were discovered because of the scarcity of adults. In 1974 and 1981, two zones exhibited a significant positive correlation, which suggests that the presence of adults increased the probability of settlement of juveniles (Table 15).

Diversity

Predation by Acanthaster reduced the coral species richness and diversity. After the swarm of Acanthaster left Tanguisson, only 84 species were recognized. This was a reduction of 47 species from 131 species prior to the predation (Randall 1973c). Species richness rose quickly, and, by 1974, 115 species were found on Tanguisson Reef. This rise was a result of emergence of once cryptic patches and the recruitment from neighboring areas and refuges. In 1981, 154 species were identified at Tanguisson Reef (Appendix 1).

In 1970, the mean number of species found within a quadrat was also depressed: the reef front had 5.4 species/m^2, the submarine terrace had 4.9 species/m^2, and the seaward slope had 2 species/m^2. In the years to follow, there were significant increases in the species richness per quadrat (Table 16) as independent juvenile corals dispersed into new areas. In 1981, there were significant differences between zones, with the largest number of species per quadrat found on the seaward slope.

Table 15. Correlation coefficients between the number of adults (diameter ≥ 5 cm) and the number of juveniles (diameter ≤ 4 cm) in 2-m^2 quadrats within zones and years. The correlation coefficients within zones were analyzed by a test of homogeneity. Significance levels: ns $> .05$, * $\leq .05$.

	1970	1971	1974	1981
Reef front	-.230ns (16)	-.046ns (19)	.539* (19)	.522* (20)
Submarine terrace	.296ns (7)	.119ns (20)	-.330ns (21)	.536* (21)
Seaward slope	-.352ns (8)	.217ns (20)	.506* (19)	.341ns(18)

Reef front X^2 = 7.333ns

Submarine terrace X^2 = 8.097*

Seaward slope X^2 = 3.435ns

Table 16. The number of species per 2-m^2 quadrat, $\bar{Y}$ ± 95% confidence interval (n), for zones and years. A two-way anova with 18 replicates was used to analyze the data for 1971, 1974 and 1981. A random number table was used to reduce replicates in excess of 18 for the two-way anova.

	1970	1971	1974	1981
Reef front	10.8 ± 2.01(6)	13.3 ± 2.34(19)	15.0 ± 2.547(19)	14.9 ± 2.49(20)
Submarine terrace	9.7 ± 1.75(7)	12.7 ± 1.67(20)	17.9 ± 1.56(21)	21.7 ± 2.18(21)
Seaward slope	4.1 ± 1.89(8)	12.1 ± 1.74(20)	16.0 ± 1.74(19)	26.3 ± 1.97(18)

Source of variation	df	MS
Subgroups	8	387.79
years (a)	2	949.45***
zones (b)	2	181.52***
Interaction (AXB)	4	210.10***
Within groups	153	20.69
TOTAL	161	

Shannon-Wiener species diversity indices (Pielou 1975) were calculated within zones in two ways: the mean diversity per 2-m^2 quadrat and the total diversity of the entire zone. The total diversity of the zones was rather high after the disturbance in 1970 (reef front - 4.87, submarine terrace - 4.81, and seaward slope - 4.04). This was surprising since in two zones (submarine terrace and seaward slope) less than 1% of the space was occupied by live corals. The high diversity values were attributed to new recruits and to the presence of numerous small remnant pieces of coral that survived predation. The diversity of the reef front had not changed significantly since 1970 (Table 17). The diversity of the submarine terrace had fluctuated around the value of 4.8, and there was a significant difference between 1974 and 1981 (.4025* > MSD, Games and Howell method [Sokal and Rohlf 1981]). The coral species diversity on the seaward slope in 1970 was significantly lower than in the other years and the coral diversity of the seaward slope in 1974 was significantly less than in 1980.

The mean diversity values illustrated slightly different patterns. The reef front, least affected by Acanthaster, showed no significant differences in diversities over time (Table 18). The other two zones exhibited significant changes in diversities (Table 18). The seaward slope in 1981 had the highest mean diversity, and it was significantly different from all other zones and years, except for the 1981 submarine terrace (Table 19). In general, since 1970 there have been significant increases in the mean coral diversities of the reef since 1970 (Friedman's test, $X^2_{[3]} = 9^*$).

Table 17. Total Shannon-Wiener species diversity indices ($-\Sigma p_i \log_2 p_i$) ± standard error (n) for zones and years, the values corrected for bias. The values and standard errors were calculated according to methods given in Poole (1974:392).

	1970	1971	1974	1981
Reef front	4.8708 ± .071(632)	4.7174 ± .0684(789)	4.7149 ± .0598(919)	4.7080 ± .0604(987)
Submarine terrace	4.8111 ± .0769(320)	4.8190 ± .0693(632)	4.5943 ± .0637(1035)	4.9968 ± .0455(1306)
Seaward slope	4.0401 ± .112(159)	4.7905 ± .0961(521)	4.5467 ± .0671(817)	5.0957 ± .043(1576)

Table 18. Mean Shannon-Wiener species diversity indices ($-\Sigma p_i \log_2 p_i$) per 2-m^2 quadrat for zones and years, $\bar{Y} \pm$ standard error (n), the values corrected for bias. Two Friedman's randomized block tests were used to analyze the data between years and between zones.

	1970	1971	1974	1981	ΣR_{ij}
Reef front	2.585 ± .897(16)	2.889 ± .470(19)	2.982 ± .848(19)	3.143 ± .480(20)	5
Submarine terrace	2.670 ± .420(7)	3.028 ± .450(20)	3.384 ± .330(21)	3.781 ± .363(21)	11
Seaward slope	1.489 ± .649(8)	2.963 ± .518(20)	3.310 ± .406(19)	4.053 ± .313(18)	8
ΣR_{ij}	3	6	9	12	

Years

$$\chi^2 = \frac{12(3^2 + 6^2 + 9^2 + 12^2)}{4(3)\ (4+1)} - 3(3)\ (4+1)$$

$$= 9^*$$

Zones

$$\chi^2 = \frac{12(5^2 + 11^2 + 8^2)}{3(4)\ (3+1)} - 3(4)\ (3+1)$$

$$= 4.5\text{ns}$$

Table 19. Unplanned comparisons among pairs of mean diversity indices for zones and years using the Games and Howell method. The differences $Y_i - Y_j$ are given below the diagonal and the corresponding MSD_{ij} values at 0.05 level of significance are given above. Differences > MSD_{ij} are indicated with an asterisk.

	RF 70	RF 71	RF 74	RF 80	ST 70	ST 71	ST 74	ST 81	SS 70	SS 71	SS 74	SS 81
RF 70	0	1.293	1.430	1.290	1.428	1.277	1.240	1.252	1.690	1.392	1.262	1.243
RF 71	.304	0	1.134	.761	1.096	.738	.649	.669	1.479	.791	.713	.653
RF 74	.397	.093	0	1.132	1.305	1.116	1.078	1.070	1.597	1.540	1.099	1.060
RF 81	.558	.254	.161	0	1.991	.736	.646	.667	1.478	.789	.711	.651
ST 70	.085	.219	.312	.473	0	1.074	1.076	1.061	1.567	1.103	1.074	1.081
ST 71	.443	.139	.046	.115	.358	0	.619	.640	1.500	.767	.686	.624
ST 74	.799	.495	.402	.241	.714	.356*	0	.500	1.486	.682	.589	.516
ST 81	1.196	.892	.799	.638	1.111*	.753*	.397	0	1.500	.701	.661	.541
SS 70	1.096	1.40	1.493*	1.654	1.181	1.539*	1.895*	2.292*	0	1.500	1.480	1.489
SS 71	.108	.074	.019	.180	.293	.065	.421	.818	1.474	0	.743	.686
SS 74	.725	.421	.328	.167	.640	.282	.074	.471	1.821*	.347	0	.594
SS 81	1.468*	1.644*	1.071*	.910*	1.383*	1.025*	.669*	.272	2.564*	1.090*	.743*	0

Growth Forms

After corals in the reef community were preyed upon by Acanthaster, the living corals that remained were either complete colonies which the Acanthaster had by-passed or were remnant patches of partially eaten colonies. Often corals in the latter category, along with recruits, initially had an encrusting form. These early encrusters became the source for expansion and recolonization, and they accounted for 68% of the corals encountered in 1970. In 1971, the number of encrusting forms rose to 74% which coincided with a rise in coral recruitment. After 1971, encrusting forms declined, resulting from growth form differentiation of ephemeral encrusting recruits and the generation of remnant patches which caused a rise in other species specific growth forms (i.e., massive, corymbose, etc., cf. Table 20). This change from two dimensional to three dimensional growth form increased the topographic complexity of the reef. This was seen in all reef zones and was reflected in increases in growth form diversity values (i.e., 1.10 to 1.98 on the seaward slope, cf. Table 20). However, when comparing the three zones, the trends of increasing heterogeneity and complexity were seen to a lesser extent on the submarine terrace, because of the abundance of perpetual encrusters (i.e., Montipora spp. and Leptastrea spp.).

Size Distribution, Coral Coverage and Density

In 1970, the size distribution was skewed towards smaller corals (Table 21). This clumped distribution of the size classes of all corals was reflected initially in low evenness values of .19 for size-classes on the submarine terrace and .20 for the size-classes on

Table 20. Distribution of corals by growth forms from 1970 to 1980 and growth form diversity ($H' = -\Sigma p_i \log_2 p_i$). Data from all transects are combined and expressed in relative values.

	REEF FRONT				SUBMARINE TERRACE				SEAWARD SLOPE			
	70	71	74	80	70	71	74	80	70	71	74	80
MASSIVE	20.25	15.46	32.35	30.77	21.81	6.96	32.08	15.92	8.75	19.75	46.39	37.50
ENCRUSTING	59.49	62.23	26.36	30.22	78.13	84.34	58.16	66.55	80.75	80.04	39.05	41.30
FOLIACEOUS	0	0	0	0	0	0	.19	.20	3.11	1.54	.86	1.90
FLABELLATE	1.11	.89	1.85	1.37	.31	1.74	0	.59	0	0	0	.27
CORYMBOSE	4.59	6.34	7.08	18.41	0	.63	3.00	8.20	0	.38	2.82	10.33
CESPITOSE	12.66	13.56	31.37	17.86	1.56	4.59	5.70	7.40	4.97	3.84	6.48	3.53
ARBORESCENT	1.27	1.52	.76	.27	0	0	.10	0	0	.38	6.61	0
PHACELOID	.63	0	.22	.55	.31	.95	.39	0	1.24	.19	.12	.27
COLUMNAR	0	0	0	.55	.31	.79	.39	.78	.62	1.92	2.93	2.46
SOLITARY	0	0	0	0	.31	0	0	.39	.62	.96	.61	2.46
Total number of colonies	632	789	918	364	320	632	1035	512	161	521	817	368
H'	1.69	1.64	2.00	2.14	.86	.95	1.46	1.64	1.10	1.13	1.73	1.98

Table 21. Distribution of corals by size class (diameter in cm) from 1970 to 1980. Data from all transects are combined and expressed in relative values, with size class evenness value ($J' = -\Sigma p_i \log_2 p_i / \log_2 n$).

	REEF FRONT				SUBMARINE TERRACE				SEAWARD SLOPE			
Size Class (cm)	70	71	74	80	70	71	74	80	70	71	74	80
0 - 5	49.68	41.32	41.94	15.93	85.94	71.36	61.84	16.41	83.85	82.15	69.65	32.60
6 - 10	31.65	40.18	38.78	25.82	13.44	23.10	26.09	22.66	15.53	14.78	23.62	33.42
11 - 15	9.34	9.76	9.15	21.98	.63	4.59	6.76	17.18	0	2.69	4.41	17.12
16 - 20	2.85	3.80	4.58	11.26	0	.47	2.80	15.63	.62	.19	2.08	7.07
21 - 25	2.06	1.65	2.18	6.87	0	.32	1.55	8.01	0	.19	0	4.35
26 - 30	1.74	1.77	1.53	4.94	0	.16	.68	5.66	0	0	.12	3.30
31 - 35	.32	.51	.76	4.40	0	0	.19	6.84	0	0	.12	1.36
36 - 40	.95	.13	.22	1.92	0	0	0	1.76	0	0	0	0.82
41 - 45	.79	.38	.33	2.50	0	0	0	2.73	0	0	0	0
46 - up	.63	.51	.54	4.39	0	0	.10	2.73	0	0	0	0
Total number of colonies	632	789	918	364	320	632	1035	512	161	521	817	368
J'	.57	.57	.58	.87	.19	.34	.45	.88	.20	.25	.36	.68

the seaward slope. Both of these zones had been devastated by Acanthaster which reduced the live coral cover to less than 1%. By 1980, there had been an increase in the size class evenness values in each zone: reef front - .57 to .87, submarine terrace - .19 to .88, seaward slope - .20 to .68. The relatively high initial evenness values of the reef front zone reflected the presence of a refuge area resulting from water turbulence within the zone where Acanthaster planci did not venture in large numbers.

The study of the nearby reef in Tumon Bay (Randall 1973c) was used to estimate the living coral surface coverage for Tanguisson Reef prior to the 1968 predation by Acanthaster: reef front - 49%, submarine terrace - 59%, seaward slope - 50% (Randall 1973a). The surface coverage was reduced to 21%, 0.9% and 0.5%, respectively, on Tanguisson Reef after the disturbance (Table 22). In 1980, the zones exhibited the following coverage: reef front - 43%, submarine terrace - 66%, seaward slope - 36%. The increase in percent cover was positively correlated with the increase in the average coral size (r = .928***). No correlation was found between density and cover (r = .424ns). The rapid increases in coverage on the submarine terrace was partially the result of predominance of fast growing encrusting Montipora. The other two zones have been slower to recover than the submarine terrace. However, if current trends are maintained, by 1984 both zones will have reached the prior levels at Tumon Bay. In Jones et al. (1976), Randall projected slower recovery times: reef front, 24 years; submarine terrace, 21 years; seaward slope, 35 years. This overestimation of recovery times was based on linear extrapolation from early recovery

Table 22. Percent live coral cover for zones and years. Two Friedman's randomized block tests were used to analyze for differences between years and between zones.

	1970	1971	1974	1981	ΣR_{ij}
Reef front	20.9	21.9	24.8	43.7	11
Submarine terrace	0.9	4.0	12.0	65.9	9
Seaward slope	0.5	2.1	6.3	36.2	4
ΣR_{ij}	3	6	9	12	

Years

$$X^2 = \frac{12(3^2 + 6^2 + 9^2 + 12^2)}{4(3)\ (4+1)} - 3(4)\ (4+1)$$

$$= 9^*$$

Zones

$$X^2 = \frac{12(4^2 + 9^2 + 11^2)}{4(3)\ (3+1)} - 3(4)\ (3+1)$$

$$= 6.5^*$$

data which did not take into account the disproportionate increase in surface area coverage with the increase in diameter of the coral.

The density of coral colonies has risen significantly in all zones since 1970 (Table 23). This increase in density corresponded with the settlement of juvenile corals. In 1981, the highest density was found on the seaward slope which had the lowest percent coral cover and the smallest corals.

Table 23. Density of coral colonies per 2 m^2, $\overline{Y}$ ± 95% confidence interval (n), calculated for zones and years. A two-way anova with 18 replicates was used to analyze the data. A random number table was used to discard replicates in excess of 18 for the two-way anova.

	1970	1971	1974	1981
Reef front	33.3 ± 5.78(19)	41.5 ± 9.76(19)	48.3 ±15.01(19)	49.4 ± 9.12(20)
Submarine terrace	16.0 ± 3.76(20)	31.6 ± 5.24(20)	49.3 ± 4.94(21)	62.2 ± 8.18(21)
Seaward slope	7.9 ± 2.37(20)	26.1 ± 3.58(20)	43.0 ± 3.58(20)	87.6 ± 6.65(18)

Source of variation	df	MS
Subgroups	11	8228.14
years (a)	3	22393.00***
zones (b)	2	168.88ns
Interaction (AXB)	6	3832.13***
Within subgroups	204	290.00
TOTAL	215	

DISCUSSION

By all measurements, the coral community at Tanguisson Reef experienced "catastrophic" effects (as defined in Harper 1977; Paine 1979) from predation by Acanthaster . The large swarm of Acanthaster left few corals alive. Four categories of survivors were found after the event: 1) corals in turbulent shallow water habitats, 2) corals which were not the preferred food of Acanthaster, 3) living patches of partially eaten coral colonies, and 4) small colonies located in cryptic interstices.

Most of the corals living in shallow areas less than 2 m in depth on the reef front were not preyed upon. Acanthaster apparently does not venture into heavily wave-assaulted areas (Laxton 1974) since they lose their hold and are tossed around by water turbulence and surge (Birkeland and Randall 1979).

Below the refuges of turbulence, there were scattered patches of nonpreferred corals by-passed by Acanthaster. Patches of nonpreferred prey have been observed in Hawaii (Branham et al. 1971), on the Great Barrier Reef (Endean 1973), on Saipan (Goreau et al. 1972), in the Eastern Pacific (Glynn 1976) and in American Samoa (Birkeland and Randall 1979). The nonpreferred prey fell into two categories: coral species which Acanthaster usually does not eat (e.g., Millepora, Porites, P. (Synaraea), etc., [Table 6]) and species which would be eaten (Pocillopora and Stylophora) were they not protected by crustacean symbionts (Glynn 1976). As Acanthaster approach the protected colony, the symbionts move to the branch tips, and repulse the predators by pinching at their tube feet and spines (Glynn 1976, 1980). The behavior of these symbionts indirectly protects adjacent colonies resulting in the survival of a halo of living corals around the defended colony (pers. obs.).

Both preferred and nonpreferred prey often survived as partially eaten colonies. These remnant patches represented a good sample of the previous community and were capable of reproduction and regrowth. Colonies expanded from these patches and reveneered dead surfaces (Fishelson 1973; Glynn 1974; Colgan in press).

The last category of survivors was found in cryptic interstices of the reef where Acanthaster could not reach. Typical of these corals are Stylocoeniella armada and Pavona sp. 1 which survived in relatively high numbers. In 1970, small cryptic corals contributed 10.76% of the sample, on the seaward slope while in 1981 cryptic corals made up only .69% of the community.

The presence of numerous small patches of survivors contributed to the high diversity and species richness values in all zones following predation by the swarm of Acanthaster, but in submarine terrace and seaward slope these small patches accounted for less than 1% of surface cover. The surviving corals enabled a degree of local recovery, thus allowing for the rapid recovery from the large scale disturbance (Connell and Slatyer 1977).

The recovery of the Tanguisson Reef community following the predation was achieved by recruitment and regrowth. Recruitment has been continuous since the swarm of Acanthaster left the area and accounted for the rise in density and species richness in all zones.

Likewise, the density of juvenile corals also increased with the greatest number being found in 1974. This peak in the density of juveniles did not coincide with the time when space was most abundant. It has often been stated that space is the most important limiting factor in sessile communities (Connell 1961; Paine 1966; Dayton 1971; Connell 1978). However, in 1970 and 1971, settlement of juvenile corals was limited by the number of recruits. A similar situation of limited recruitment resulting from nonspacial restraints has been seen in settling plate data (Birkeland et al. in press). At Tanguisson Reef, it was only after an adult population was established that the density of juveniles increased. The presence of adults has aided in the rapid recovery of other disturbed reef communities (Endean and Stablum 1973; Loya 1976; Pearson 1981).

Recovery was initially slow because the adult population was sparse and clustered into small patches. With time, the adult population increased and recovery was accelerated. The recovery process can be viewed as a positive feed-back system with the establishment of adults facilitating increased recruitment, which in turn establishes more adults. When a major portion of space becomes occupied by adult colonies, the proportion of recruits decreases.

The reestablishment of adult colonies came about through regrowth and dispersion. The settlement of "independent" juveniles which survived away from conspecific adults was important. Most of the juvenile corals in 1970 and 1971 were of this category. The development of these pioneer juveniles established adults in places away from the immediate areas of surviving patches. With a growing and widely dispersed adult population, there was a decline in "independent" juveniles. Early in the community development, the juveniles of most species dispersed away from adults. In 1981, the reverse was true. There were statistically significant associations between the presence of adult and juvenile conspecifics within local areas. The affinity of juveniles to adults resulted in a contagious settlement pattern (Lewis 1974; Dana 1976). By 1981, the distribution of coral species was increasingly clumped within zones. The reef underwent a shift within zones from random distribution to clumped distribution.

In 1981, adult and juvenile conspecifics were abundant in the same zone and the various coral species were associated with certain zones. During the early stages of recovery, adults were found inhabiting zones that were different from the ones with which their juveniles were associated. Within areas affected by <u>Acanthaster</u>, the numbers of adults were reduced and adults were commonly found in zones with which they were not significantly associated in 1981. Recruitment reestablished the adults in zones in which they were typically found. This caused a shift in coral distribution. Juvenile corals did not show a similar shift in distribution, indicating that zonation was the outcome of zone-specific recruitment.

The species assemblages within zones resulted from nonrandom recruitment and survival of juveniles. The response of larvae to physical factors such as light, substrate (Yonge 1973), water motion (Jokiel 1978) and other factors may ultimately determine their distribution. Also, selective predation by fish may have limited the distribution of a few species (Neudecker 1979; Wellington ms.). Coral community structure within zones does not appear to be influenced by interspecific coral aggression (Lang 1971, 1973).

The strong positive correlation between adult and juvenile abundances further differentiated the zones of the reef. The correlation had increased significantly with time as the species that normally inhabited the zone reestablished themselves. In 1981, the position of the most abundant species was reinforced through disproportionate recruitment (Connell 1973; Grigg and Maragos 1974; Loya 1976). Without additional disturbances to reverse this trend, the reef could be expected to become increasingly stratified with a few top competitors dominating. On atolls, where disturbance levels are less than on high islands such as Guam (Birkeland and Randall 1979), zones are highly stratified with a few abundant species (Wells 1954). It would seem that the striking zones on atolls have developed in the absence of major disturbances which enable a few species to dominate a zone.

Twelve years after the disturbance, species richness and diversity were still on the increase, resulting in high values for all zones. Connell (1978) discussed six hypotheses which could explain the high diversity seen on coral reefs. At Tanguisson Reef, the hypotheses of intermediate disturbances and compensatory mortality appear to be most applicable.

On a coral reef, compensatory mortality occurs when predation or disturbance disproportionately affect the species which occupy the most space. Acanthaster does have a feeding preference (Table 5). In 1971, as the result of the feeding activity of Acanthaster, nonpreferred species were the predominant corals in all zones. Their predominance was short-lived and by 1980, preferred prey had become more important with regards to frequency, density and cover (Table 6) because of a greater rate of recruitment and faster growth. The predation on these fast-growing, preferred species resulted in a form of compensatory mortality. On other reefs where preferred species were rare, predation by Acanthaster benefited the corals holding the most space (Branham et al. 1971; Glynn 1976).

The intermediate disturbance theory (Connell 1978) applies to smaller random disturbances which constantly affect a reef. These disturbances prevent local competitive elimination of species (Paine 1966; Dayton 1971; Connell 1978; Levin 1976; Sousa 1979a, b) and this maintains species in the community and produces a high species diversity (Sousa 1979a).

At Tanguisson, the agents of these smaller disturbances include storms (Randall and Eldredge 1977), an encrusting sponge, Terpios (Bryan 1973), a blue-green alga, probably Anacystis dimidiata (Randall 1973a), small outbreaks of Acanthaster (Colgan in press), and fish predation (Neudecker 1979). Often, the distributions of these disturbances were random and their intensities varied, causing unequal successional setbacks in the affected patches (Paine and Levin 1981).

In 1981, the landscape of the reef was a mosaic of unsynchronized successional patches (Levin and Paine 1974, Paine and Levin 1981). The mosaic quality of the reef added to the overall species diversity and heterogeneity of the reef.

CONCLUSION

Within a period of twelve years, measurements of species diversity, percent cover, growth form diversity, size class evenness and species richness at Tanguisson Reef approached or exceeded values at a comparable reef area prior to the outbreak. This rapid recovery from a natural disturbance indicates a greater resilience in the coral community than was once believed. However, this resilience is contingent upon the particular type of disturbance encountered. Every perturbation creates a locally unique patch (Levin 1976) because of the inherent variations in the size and intensity of a disturbance. These variables, along with the nature of the surrounding environment, directly control the course of the recovery upon an available surface.

At Tanguisson, the structural integrity of the reef framework was maintained. The stable substrate provided a surface for settlement and the complex structure offered a refuge for some recruits (Birkeland 1977). However, perturbations that destroy the structural characteristics or alter the quality of the environment require longer recovery times than those observed at Tanguisson Reef. An example can be found in man-made disturbances such as dredging. Dredging and increased sedimentation may cause massive coral mortality and may drastically alter the environment as well as the reef structure (Johannes 1975). The resulting unstable surface provides an unsuitable substrate for recruitment, and, even after dredging is halted, the resuspension of sediment delays the start of recovery (Johannes 1975). More than thirty years after the completion of the dredging operation the effects of the disturbance may still be profound (Dodge and Vaisnys 1977). Coral reef communities are surprisingly resilient to natural catastrophic disturbances, but they may not show the same resilience after man-made disturbances.

LITERATURE CITED

Bak, R. P. M., and M. S. Engel. 1979. Distribution and abundance of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol. 54:341-352.

Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc. 3rd Int. Coral Reef Symp. 1:15-21.

Birkeland, C., L. Cheng, and R. A. Lewin. 1981. Motility of didemnid ascidian colonies. Bull. Mar. Sci. 31(1):170-173.

Birkeland, C., and R. H. Randall. 1979. Report on the Acanthaster planci (Alamea) studies on Tutuila, American Samoa. Report submitted to Office of Marine Resources, Government of American Samoa. 53p.

Birkeland, C., D. Rowley, and R. H. Randall. in press. Coral recruitment patterns at Guam. Proc. 4th Int. Coral Reef Symp.

Branham, J. M., S. A. Reed, J. H. Bailey, and J. Caperon. 1971. Coral-eating sea stars Acanthaster planci in Hawaii. Science 172: 1155-1157.

Bryan, P. 1973. Growth rate, toxicity and distribution of the encrusting sponge Terpios sp. (Hadromerida:Suberitidae) in Guam, Mariana Islands. Micronesica 9(2):237-242.

Chesher, R. H. 1969a. Destruction of Pacific coral by Acanthaster planci. Science 165:280-283.

______________. 1969b. Acanthaster planci, impact of Pacific coral reefs. Final report to U.S. Dept. Interior Westinghouse Research Laboratories. 151p.

Colgan, M. W. in press. Succession and recovery on the coral reef after predation by Acanthaster planci (L.). Proc. 4th Int. Coral Reef Symp.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42:710-723.

______________. 1973. Population ecology of reef-building corals. *In* O. A. Jones and R. Endean (eds.). Biology and Geology of Coral Reefs. Vol. 2, Biol. 1. Academic Press, New York, pp.205-245.

______________. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-1144.

Cottam, G., J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology 34:741-756.

Dana, T. F. 1976. Reef-coral dispersion patterns and environmental variables on a Caribbean coral reef. Bull. Mar. Sci. 26(1):1-13.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Res. 19:199-208.

Diamond, J. M. 1975. Assembly of species communities. *In* M. L. Cody and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, pp. 342-444.

Dodge, R. E., and J. R. Vaisnys. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. J. Mar. Res. 35(4):715-730.

Emery, K. O., I. Tracey Jr., and H. S. Ludd. 1954. Geology of Bikini and nearby atolls: Part 1, Geology. U.S.G.S. professional paper 260-A. 265p.

Endean, R. 1973. Population explosion of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. *In* O. A. Jones and R. Endean (eds.). Biology and Geology of Coral Reefs. Vol. 2, Biol. 1. Academic Press, New York, pp.389-438.

______________. 1974. *Acanthaster planci* on the Great Barrier Reef. Proc. 2nd Int. Coral Reef Symp. 1:563-576.

______________. 1977. *Acanthaster planci* infestation of the Great Barrier Reef. Proc. 3rd Int. Coral Reef Symp. 1:185-191.

Endean, R., and W. Stablum. 1975. The apparent extent of the recovery of reefs of Australia's Great Barrier Reef devastated by the crown-of-thorns starfish. Atoll Res. Bull. 168:1-26.

Fishelson, L. 1973. Ecological and biological phenomena influencing coral-species composition on the reef table at Eilat (Gulf of Aqaba, Red Sea). Mar. Biol. 19:183-196.

Garwood, N. C., D. P. Janos, and N. Brokaw. 1979. Earthquake-caused landslides: a major disturbance to tropical forest. Science 205: 997-999.

Glynn, P. W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. *In* O. A. Jones and R. Endean (eds.). Biology and Geology of Coral Reefs. Vol. 2, Biol. 1. Academic Press, New York, pp.271-324.

_____________. 1974. Rolling stones among the scleractinia: Mobile coralliths in the Gulf of Panama. Proc. 2nd Int. Coral Reef Symp. 2:183-197.

_____________. 1976. Some physical and biological determinants of coral community structure in the Eastern Pacific. Ecol. Monogr. 46(4):431-456.

_____________. 1980. Defense by symbiotic crustacea of host corals elicited by chemical cues from predator. Oeologia (Berl.) 47: 287-290.

Glynn, P. W., L. R. Almodovar, and J. G. Gonzalez. 1964. Effects of Hurricane Edith on marine life in La Parguera, Puerto Rico. Carib. J. Sci. 4(2&3):335-345.

Glynn, P. W., R. H. Stewart, and J. E. McCosker. 1972. Pacific coral reefs of Panama: structure, distribution and predators. Geol. Rundsch. 61:483-519.

Glynn, P. W., G. M. Wellington, and C. Birkeland. 1979. Coral reef growth in the Galapagos: limitation by sea urchins. Science 203: 47-49.

Goreau, T. F. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology 40:67-90.

Goreau, T. F., and N. I. Goreau. 1973. The ecology of Jamaican coral reefs. II. Geomorphology, zonation and sedimentary phases. Bull. Mar. Sci. 23(2):399-464.

Goreau, T. F., J. C. Lang, E. A. Graham, and P. D. Goreau. 1972. Structure and ecology of the Saipan reefs in relationship to predation of *Acanthaster planci* (Linnaeus). Bull. Mar. Sci. 22(1):113-152.

Grassle, J. F. 1973. Variety in coral reef communities. In O. A. Jones and R. Endean (eds.). Biology and Geology of Coral Reefs. Vol. 2, Biol. 1. Academic Press, New York, pp.247-270.

Grigg, R. W., and J. E. Maragos. 1974. Recolonization of hermatypic coral on submerged lava flows in Hawaii. Ecology 55:387-395.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London. 892p.

Highsmith, R. C. 1981. Coral bioerosion: damage relative to skeletal density. Am. Nat. 117(2):193-198.

Horn, H. S. 1975. Markovian processes of forest succession. In M. L. Cody and J. M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, pp. 196-211.

Johannes, R. E. 1975. Pollution and degradation of coral reef communities. In E. J. Fergusonwood and R. E. Johannes (eds.). Tropical Marine Pollution. Elsevier Sceintific Publ., Amsterdam, pp.13-51.

Jokiel, P. L. 1978. Effects of water motion on reef corals. J. Exp. Mar. Biol. Ecol. 35:87-97.

Jones, R. S., R. H. Randall, and M. J. Wilder. 1976. Biological impact caused by changes on a tropical reef. U.S. Environmental Protection Publ. EPA-600/3-76-027. 208p.

Krebs, C. J. 1972. Ecology: the experimental analysis of distribution and abundances. Harper & Row, Publ., New York. viii+694p.

Kropp, R. K., and C. Birkeland. in press. Comparison of crustacean associates of Pocillopora verrucosa from a high island and an atoll. Proc. 4th Int. Coral Reef Symp.

Lang, J. C. 1971. Interspecific aggression by scleractinian corals. 1. The rediscovery of Scolymia cubensis (Milne Edwards & Haime). Bull. Mar. Sci. 21:952-959.

______________. 1973. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. Bull. Mar. Sci. 23(2):260-279.

Laxton, J. H. 1974. Aspects of the ecology of the coral-eating starfish Acanthaster planci. J. linn. Soc. Biol. 6:19-45.

Levin, S. A. 1976. Population dynamic models in heterogeneous environments. Ann. Rev. Ecol. Syst. 7:287-310.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proc. Nat. Acad. Sci. USA 71(7):2744-2747.

Lewis, J. B. 1974. Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. Proc. 2nd Int. Coral Reef Symp. 2:201-206.

Loya, Y. 1976. Recolonization of Red Sea coral affected by natural catastrophes and man-made perturbation. Ecology 57:278-289.

____________. 1979. Plotless and transect method. In D. R. Stoddard and R. E. Johannes (eds.). Coral Reef: Research Methods. UNESCO, Paris, pp.197-218.

Neudecker, S. 1979. Effects of grazing and browsing fish on the zonation of corals in Guam. Ecology 60(4):666-672.

Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.

____________. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecol. 52:1096-1106.

____________. 1979. Disaster, catastrophe and local persistence of the sea plan Postelsia palmaeformis. Science 205:685-687.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbances and the dynamics of pattern. Ecol. Monogr. 51(2):145-179.

Pang, R. K. 1973. The ecology of some Jamaican excavating sponges. Bull. Mar. Sci. 23(2):227-243.

Pearson, R. G. 1981. Recovery and recolonization of coral reefs. Mar. Ecol. Prog. Ser. 4:105-122.

Perkins, R. D., and P. Enos. 1968. Hurricane Betsy in the Florida-Bahama area: geologic effects and comparison with Hurricane Donna. J. Geol. 75:710-717.

Pielou, E. C. 1975. Ecological Diversity. Wiley-Interscience Publ., New York. vii+165p.

Poole, R. W. 1974. An Introduction to Quantitative Ecology. McGraw-Hill Co., New York. x+532p.

Porter, J. W. 1976. Autotrophy, heterotrophy and resource partitioning in Caribbean reef-building corals. Am. Nat. 110:731-742.

Potts, D. C. 1980. Crown-of-thorns starfish: man-induced pest or natural phenomenon? In R. K. Kitching and R. E. Jones (eds.). The Ecology of Pests. CSIRO Publ. Serv., Canberra, pp.55-89.

Randall, J. E. 1974. The effect of fishes on coral reefs. Proc. 2nd Int. Coral Reef Symp. 1:166-169.

Randall, R. H. 1973a. Distribution of corals after *Acanthaster planci* (L.) infestation at Tanguisson Point, Guam. Micronesica 9(2):213-222.

______________. 1973b. Coral reef recovery following extensive damage by the "crown-of-thorns" starfish, *Acanthaster planci* (L.). *In* T. Tokioka and S. Nishimura (eds.). Proc. 2nd Int. Symp. on Cnidaria, Publ. Seto Mar. Biol. Lab. 20:462-489.

______________. 1973c. Reef physiography and distribution of corals at Tumon Bay, Guam, before crown-of-thorns starfish *Acanthaster planci* (L.) predation. Micronesica 9(1):119-158.

Randall, R. H., and L. G. Eldredge. 1977. Effect of typhoon Pamela on the coral reefs of Guam. Proc. 3rd Int. Coral Reef Symp. 2:525-531.

Ricklefs, R. E. 1973. Ecology. Chiron Press, Newton. 705p.

Scoffin, T. P., and P. Garrett. 1974. Processes in the formation and preservation of internal structure in Bermuda patch reefs. Proc. 2nd Int. Coral Reef Symp. 2:429-449.

Shinn, E. A. 1972. Coral reef recovery in Florida and the Persian Gulf. Environmental Conservation Department, Shell-Oil Company, Houston, Texas. 9p.

______________. 1976. Coral reef recovery in Florida and the Persian Gulf. Environ. Geol. 1:241-254.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., San Francisco. xi+859p.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco. 359p.

Sousa, W. P. 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60(6):1125-1239.

______________. 1979b. Experimental investigation of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49(3):227-254.

Stoddart, R. D. 1972. Catastrophic damage to the coral community by earthquakes. Nature 239:51-52.

______________. 1974. Post-hurricane changes on the British Honduras reefs: re-survey of 1972. Proc. 2nd Int. Symp. on Coral Reefs 2:473-483.

Wellington, G. M. ms. Coral community development in the Gulf of Panama: control and facilitation by resident reef-fishes.

Wells, J. W. 1954. Recent corals of the Marshall Islands. U.S.G.S. professional paper 260-I:385-486.

Whitmore, T. C. 1974. Change with time and the role of cyclones in tropical rain forests on Kolombangara, Solomon Islands. Commonwealth Forestry Institute Paper No. 46.

Yonge, C. M. 1973. The nature of reef-building (hermatypic) corals. Bull. Mar. Sci. 23:1-15.

Appendix 1. Zonal distribution of coral species with their relative frequencies for the years 1970, 1971, 1974 and 1981. The numbers represent the percent of the total number of individual colonies counted within each zone within each year. A "+" denotes that a species was observed within a zone but not in the samples. The zones are designated as follows: RF = Reef front, ST = Submarine terrace, and SS = Seaward slope.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
ASTROCOENIIDAE												
Stylocoeniella armada (Ehrenberg)	1.26	1.25	6.33	1.39	1.16	1.54	.54	.77	.86	.51	1.45	.44
THAMNASTERIIDAE												
Psammocora digitata Milne-Edwards & Haime	.32								+	+		+
Psammocora nierstraszi van der Horst	1.58	.94		.76	.63	.77	.33	.77	.98	.30	.46	.44
Psammocora sp. 1					.47	1.34		.58	1.35		1.99	1.21
Psammocora sp. 2			3.16	.38	.63	.19		.10		+	.61	+
POCILLOPORIDAE												
Stylophora mordax (Dana)	1.27	1.56		.63	.63		.44	.68		2.63	1.99	.95
Seriatopora aculeata Quelch												+
Seriatopora hystrix Dana						.19			+			.13
Pocillopora ankeli Scheer & Pillai											.08	
Pocillopora danae Verrill							.33			+		
Pocillopora elegans Dana	2.37			4.06			1.96	3.00	2.33	1.01	2.60	.70
Pocillopora eydouxi Milne-Edwards & Haime	.32			.38		.38	.22	+	.61	.10	.61	.51
Pocillopora ligulata Dana	+			.13			+			+		
Pocillopora setchelli Hoffmeisteri	5.06			3.30			8.16			10.23		
Pocillopora verrucosa (Ellis & Solander)	.16	3.75	.63	.25	2.37	2.88	.11	.29	.73	.71	.38	1.71
ACROPORIDAE												
Isopora palifera (Lamarck)									+			+
Acropora abrotanoides (Lamarck)										+	+	

Appendix 1 Continued.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
Acropora cerealis (Dana)	1.42			.63			+			1.52		
Acropora delicatula (Brook)									.37		.46	.06
Acropora diversa (Brook)									.12		.69	.19
Acropora granulosa (Milne-Edwards & Haime)									.73			.44
Acropora humilis (Dana)	.79		1.90	.63	.16	.58	.62	1.45	.86	1.01	1.68	2.66
Acropora irregularis (Brook)	1.11			.51			.65	.10		.41	.61	
Acropora monticulosa (Bruggemann)	.16			.25			.65			.81		
Acropora nasuta (Dana)	.95			2.41			2.29			2.84		
Acropora ocellata (Klunzinger)	+			.25			3.37			.10		
Acropora quelchi (Brook)											.15	.38
Acropora rambleri (Bassett-Smith)						.38		.10	1.96		+	1.14
Acropora smithi (Brook)	.48			.63			+			.61		
Acropora squarrosa (Ehrenberg)	.63			.25			+			.10	+	
Acropora surculosa (Dana)	1.11	.63		1.65	.32		.76	.87		14.79	1.61	
Acropora tenuis (Dana)		+	+		.32	.19		.10	.49	.10	.69	.89
Acropora valida (Dana)	.32			+			.11			.41		
Acropora variabilis (Klunzinger)	3.64			3.68			3.48			2.74		
Acropora wardi Verrill	.95	1.56		1.14			.22	.68		1.93	.38	
Acropora sp. 1	.16			1.01	.47		.33	+		.10	+	
Acropora sp. 2									.24			+
Astreopora eliptica Yabe & Sugiyama											+	+
Astreopora gracilis Bernard	.16	.94				.96		.29	+		1.07	2.28
Astreopora listeri Bernard								+			+	+
Astreopora myriophthalma (Lamarck)		.94			1.27	1.73		1.93	3.18	.10	2.83	4.76
Montipora acanthella Bernard												.82
Montipora cf. *M. caliculata* (Dana)	.95	1.88	4.43	2.28	3.01	1.34	.76	1.55	.37	.51	1.68	+
Montipora colei Wells										.81	.08	
Montipora conicula Wells	.48			1.52	.63		.44	.48		.30	.69	.06
Montipora cf. *M. ehrenbergii* Verrill	.16	3.13		.13	1.11	.19	.44	1.64		1.26	.38	
Montipora elschneri Vaughan	1.27	.63		1.14	1.27		3.16	1.74	.12	5.17	7.50	.57

Appendix 1 Continued.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
Montipora floweri Wells											+	
Montipora foveolata (Dana)	.63	1.25		+	.16	.19	.22	1.55	1.56	+	2.68	3.24
Montipora hoffmeisteri Wells	.16			.13	.63	.19	.66	2.22	.86	.91	6.28	2.28
Montipora monasteriata (Forskal)	.48			.76	.16			1.16	.12	1.01	.61	
Montipora planiuscula (Dana)												.13
Montipora venosa Ehrenberg											.69	
Montipora verrilli Vaughan	5.22	3.13	7.59	5.32	9.65	.77	6.64	8.88	1.59	2.74	6.89	1.58
Montipora verrucosa (Lamarck)						.96		.48	.98		2.37	2.47
Montipora sp. 1 (papillate)	1.27	.94		.63	4.43	.19	1.63	1.06	.12	.71	.23	.32
Montipora sp. 2 (tuberculate)							.65	.10		.61	.77	1.14
Montipora sp. 3 (tuberculate)	.79			1.01	1.11		.76	.19		.10	.77	
Montipora sp. 4 (papillate)				.76			.33	.29		.41	.15	
Montipora sp. 5 (foveolate)				.13			.44			+		
Montipora sp. 6 (glabrous)								1.06	.24		.31	.13
Montipora sp. 7 (foveolate)											.08	.19
Montipora sp. 8 (tuberculate)										.71	1.23	.25
Montipora sp. 9 (papillate)												.82
Montipora sp. 10 (ramose)												+
AGARICIDAE												
Pavona duerdeni Vaughan	1.58	2.50		.25	.32		.22	+		.30	+	
Pavona explanulata Lamarck					.32			+			+	
Pavona maldivensis (Gardiner)	.16			.25	.16	.19	.33	+	+	+	.15	.06
Pavona varians Verrill	2.06	12.19		2.92	7.12	.38	3.05	2.61	.61	+	+	.63
Pavona venosa (Ehrenberg)									.37			+
Pavona sp. 1	+	+	+	+	+	+	+	+	+	1.01	1.99	.51
Pavona sp. 2	.63		1.90	+	1.74	.19	.22	.19		1.11	+	
Gardineroseris planulata (Dana)					.32	1.54		.19	.12	.30	.15	
Leptoseris cf. *L. explanata* Yabe & Sugiyama												+

Appendix 1 Continued.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
Leptoseris hawaiiensis Vaughan									.12			+
Leptoseris incrustans (Quelch)			1.90			.19			.61			.25
Leptoseris mycetoseroides Wells						.19			+			+
Leptoseris sp. 1												+
Pachyseris speciosa (Dana)			+			+			+			+
SIDERASTREIDAE												
Coscinaraea columna (Dana)									+			+
FUNGIIDAE												
Cycloseris costulata Ortmann		.63				.77			+		.08	.19
Cycloseris hexagonalis Milne-Edwards & Haime			1.99									+
Diaseris fragilis Alcock												+
Fungia concinna Verrill												+
Fungia fungites (Linneaus)										+	+	.13
Fungia paumotuensis Stutchbury												+
Fungia repanda Dana												+
Fungia scutaria (Lamarck)						.19			.61	+	+	.44
Herpolitha limax (Esper)												.13
Sandolitha robusta (Quelch)												.06
PORITIDAE												
Goniopora arbuscula Umbgrove						.96		.10	.49	.30	.31	+
Goniopora columna Dana		1.31	1.27		.63			.10				
Goniopora sp. 1					.15			+	.12		+	
Porites australiensis Vaughan	.48	1.56			1.74	4.03		+	.37	.30	+	.06
Porites lichen Dana				.63	.63	1.34	.22	1.16	.89	.30	1.07	1.46
Porites lobata Dana	.63	3.13		.50	7.59	9.21	.33	5.80	11.87	+	4.98	6.35
Porites lutea Milne-Edwards & Haime	1.42	5.31	10.76	1.01	3.32	3.45	1.63	7.54	7.83	1.11	3.60	9.52

Appendix 1 Continued.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
Porites murrayensis Vaughan											.23	.19
Porites superfusa Gardiner	1.58		.63	.89			.54			.61		
Porites viridis Gardiner									.24			+
Porites sp. 1 (Columnar)											+	.57
Porites (S.) *horizontalata* Hoffmeisteri			.63						+			+
Porites (*S.*) *iwayamaensis* Eguchi		1.25	7.59		.63	4.22		.29	2.08	.61	1.07	1.40
Porites (*S.*) *vaughani* Crossland			.63			3.45			2.82	.30		1.21
Stylaraea punctata Klunzinger										+		
Alveopora sp. 1		+			+			.19		.30	1.53	1.02
FAVIIDAE												
Favia favus (Forskal)		1.88		.25	.63	7.68	.11	3.00	7.22	+	1.23	6.28
Favia matthai Vaughan	.63			.38			.54			1.72		
Favia pallida (Dana)	2.85	5.63	7.59	1.21	2.37	3.65	1.96	2.71	4.41	.20	2.76	4.00
Favia rotumana (Gardiner)		.63		.25	.15			.10	.61		+	.25
Favia stelligera (Dana)	6.17	6.25		4.56	6.33	.38	6.53	3.19	.24	4.96	.61	+
Favia sp. 1												.13
Favites abdita (Ellis & Solander)							+			+		
Favites flexuosa (Dana)		.63	.63	.13	.95	.19	+	.29	.12	.10	.15	+
Favites russelli (Wells)	.95	1.88	3.16	1.14	3.32	2.69	.65	2.42	1.35	.71	1.53	2.16
Oulophyllia crispa (Lamarck)				.13					.24		.15	.13
Goniastrea edwardsi Chevalier	.95	3.44		.51	1.58	1.34	.76	1.74	1.10	+	1.61	2.79
Goniastrea pectinata (Ehrenberg)		2.50	.63		.47	3.65		.10	2.08		+	1.14
Goniastrea retiformis (Lamarck)	10.92	2.50		16.10	.95		10.0	.58		6.08	.08	
Platygyra daedalea (Ellis & Solander)	.95	.94		.13	.16	.19	.11	.19	+	.81	.54	.06
Platygyra pini Chevalier	.79	.94		.89	.95	2.49	1.20	.68	1.71	+	.23	.82
Leptoria phrygia (Ellis & Solander)	5.69	4.38		3.93	1.74		2.50	.77		3.14	+	
Hydnophora microconos (Lamarck)	.16				.47		.22	.19	+	.30	.08	+
Hydnophora tenella Quelch												+

Appendix 1 Continued.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
Montastrea curta (Dana)	1.58			2.15			3.05	.19	+	1.26	+	+
Montastrea magnistellata Chevalier											.15	.06
Plesiastrea versipora (Lamarck)											+	
Diploastrea heliopora (Lamarck)			+		.16	.38		+	.12		+	.25
Leptastrea bottae (Dana)									.12		+	
Leptastrea purpurea (Dana)		1.25	8.23		.16	6.53	.88	.97	.12	+	.31	1.78
Leptastrea transversa Klunzinger	.79	5.00	15.82	1.90	13.96	14.20	.88	24.44	20.07	.61	16.92	13.20
Cyphastrea chalcidicum (Forskal)												.57
Cyphastrea microphthalma (Lamarck)	.16			.76	1.11	2.11	.44	1.45	4.41	.30	.77	3.11
Cyphastrea serailia (Forskal)	.64		1.27			1.15	.33	.10	+	+	.15	.57
Echinopora lamellosa (Esper)	.32		1.90		.16	.19		+	+	.10	.07	.13
OCULINIDAE												
Galaxea fascicularis (Linneaus)	15.21	5.94	5.70	16.73	2.37	2.69	16.76	.87	2.45	13.48	.69	1.21
MERULINIDAE												
Merulina ampliata (Ellis & Solander)						.19			.12			.06
Scapophyllia cylindrica (Milne-Edwards & Haime)											+	
MUSSIDAE												
Scolymia cf. *S. australis* (Milne-Edwards & Haime)											+	
Acanthastrea echinata (Dana)	3.80	2.81		1.39	.32	.38	2.83	.87	+	.91	1.07	1.27
Lobophyllia corymbosa (Forskal)			2.53		.47		.11	.10		+	.15	
Lobophyllia costata (Dana)	.63	.63			.47	.19	.11	.29	.24	.10	.23	+
PECTINIIDAE												
Echinophyllia aspera (Ellis & Solander)			.19	.25	.47	2.49	.22	.87	2.44	+	.23	.51
Mycedium elephantotus (Pallai)						.58			.12			+

Appendix 1 Continued.

	1970			1971			1974			1981		
	RF	ST	SS	RF	ST	SS	RF	ST	SS	RF	ST	SS
CARYOPHYLLIIDAE												
<u>Euphyllia</u> <u>glabrescens</u> (Chamisso & Eysenhardt)								+			.08	
<u>Plerogyra</u> <u>sinuosa</u> (Dana)												+
DENDROPHYLLIIDAE												
<u>Turbinaria</u> <u>stellulata</u> (Lamarck)											+	
MILLEPORIDAE												
<u>Millepora</u> <u>dichotoma</u> Forskal	.16						.11	+		+	+	
<u>Millepora</u> <u>platyphylla</u> Hemprich & Ehrenberg	1.42			1.01	1.72		1.185	+	+	.20	+	+
<u>Millepora</u> <u>tuberosa</u> Boschma	.79	3.13		1.52	3.80	.96	1.09	2.51	.49	.20	2.60	1.14
STYLASTERIDAE												
<u>Stylaster</u> <u>profundiporus</u> Broch										+	+	+
<u>Distichopora</u> <u>gracilis</u> Dana					.47					+	+	+
TUBIPORIDAE												
<u>Tubipora</u> <u>musica</u> Linnaeus											+	
HELIOPORIDAE												
<u>Heliopora</u> <u>coerulea</u> (Pallas)		.31				.38		+	.24	+	.08	.13
Total number of species observed	63	44	30	63	62	59	69	79	79	88	99	107
Total number of species sampled	60	41	26	60	60	57	62	63	60	66	73	73
Total number of colonies sampled	632	320	159	789	632	521	919	1035	817	987	1306	1576
Total area samples (m^2).	38	40	40	38	40	40	38	42	38	40	42	36