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COMMUNITY DYNAMICS OF STONY CORALS (MILLEPORINA AND SCLERACTINIA) AT KEY LARGO NATIONAL MARINE SANCTUARY, FLORIDA, DURING 1981-1986.

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ABSTRACT

Four reefs were sampled annually from 1981 through 1986 in Key Largo National Marine Sanctuary (KLNMS), a coral reef area that is used intensively for snorkeling, diving, and fishing by local residents and tourists. The dynamics at one site, Molassses Reef, is reported. The site was located on a spur with buttresses of Montastraea annularis and thickets of Acropora palmata. Seventeen to 19 species and 266 to 355 colonies were counted annually. Acropora cervicornis, A. palmata, M. annularis, and Millepora alcicornis constituted 66% to 90% of all colonies. Incidence of Acropora cervicornis declined 96% between 1981 and 1986. Acropora palmata varied from 2.3 to 5.4 colonies/m^2, and M. annularis varied from 0.9 to 2.3/m^2. We assessed changes in numbers of colonies from twenty-five 1-meter^2 quadrats using Czekanowski similarity coefficients. Similarity of quadrats between years ranged from 0 to 1 with 56% to 88% of the values > 0.50, 16% to 68% > 0.70, and 4% to 20% > 0.90. The greatest difference in similarity occurred after two hurricanes in the fall of 1985.

INTRODUCTION

Key Largo National Marine Sanctuary (KLNMS) is the seaward extension of John Pennekamp Coral Reef State Park (JPCRSP). The sanctuary is located east of Key Largo, Florida, USA, approximately 80 km south of metropolitan Miami (Figure 1). The sanctuary is 45 km long, with an area of 259 km^2, and depth ranges from < 1 to 99 m. The marine ecosystem seaward of Key Largo is a mosaic of red mangrove fringe (Rhizophora mangle), rocky hardgrounds, carbonate sediments, seagrasses (Thalassia testudinum and Syringodium filiforme), and coral reef communities (Marszalek 1981, Jaap 1984).

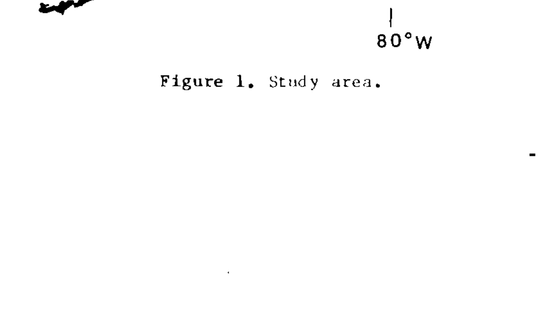

Figure 1. Study area.

Sanctuary resources are used intensely by southern Florida residents and tourists visiting the Florida Keys. Fishing includes recreational and commercial harvest of finfish and the spiny lobster (Panulirus argus). Snorkling is popular on shallow reefs (Grecian Rocks, Key Largo Dry Rocks, and White Bank Dry Rocks), and scuba diving staged from private craft and larger commercial tour boats is popular at Molasses, French, Elbow, and Carysfort Reefs. Glass-bottom boat tours, popular among non-swimmers, operate principally around Molasses and French Reefs. Research and educational programs also are important activities in KLNMS.

These reefs may be the most visited in the world; each year more than 500,000 people enter JPCRSP, the major landside point of departure to KLNMS. This census does not include visitors who enter KLNMS in private boats or from charter operations that originate outside JPCRSP. Annual economic benefit derived from reef resources in the sanctuary is estimated at 1.6 billion dollars (Mattson and DeFoor 1985).

Intense use of the sanctuary is harming its biota. Physical damage to corals is caused by anchor deployment (Halas 1985), boat grounding, diver-related disturbance, and fishing lines, hooks, lobster pots, and buoys that come in contact with reefs (Jaap 1984).

Contamination by pesticides, herbicides, trace metals, and other high risk chemicals poses a threat to KLNMS. South Florida urban and agricultural drainage discharges show evidence of trace metal and pesticide contamination of water, sediments, and organisms (Manker 1975, Skinner and Jaap 1986, Simmons and Love 1987). The dramatic population increase in southeast Florida threatens the coastal ecosystem with nutrient enrichment and loss of natural filtration and organic uptake as the mangrove and seagrass communities are degraded and destroyed. A combination of nutrient excess, diminished water transparency, phosphate inhibition of calcification, biotic replacement, and increased bioerosion threaten the vitality of coral reef communities (Simkiss 1964, Weiss and Goddard 1977, Smith et al. 1981, Hallock and Schlager 1986).

The KLNMS is managed by the National Oceanic and Atmospheric Administration (NOAA), Sanctuary Program Office. We define management as the maintenance and enhancement of desirable resource characteristics. In order to manage these reef resources, an information base including knowledge of the current state of the resources, the rate of change, and the etiology of change is required (Dahl 1981, Kelleher 1981). The resources are worthy of stewardship for economic, recreational, and ecological reasons (Harris and Williams 1975, Bradbury and Reichelt 1981, Mattson and DeFoor 1985). Additionally, the reefs form a living breakwater to hurricane- and storm-agitated seas and contribute sediments from the breakdown of carbonate skeletons and shells.

Reef development seaward of Key Largo began during the Holocene transgression, about 5 - 7 x 10^3 BP (Shinn et al. 1977, 1981). Two distinct reef types are found in KLNMS: inshore patch reefs and offshore bank reefs. Patch reefs range in size from 20 to 400 m, are irregular in outline, and usually occur in depths < 10 m. Dominant corals include the star coral Montastraea annularis, the brain corals Copophyllia natans and Diploria strigosa, and the starlet coral Siderastrea siderea.

Offshore bank reefs are conspicuous because of their physiographic-faunal zonation, a sequence of habitats or communities correlated to depth and associated physical factors (light, temperature, and wave environment). This sequence (back reef, reef flat, spur and groove, fore reef, and drowned reef outcrops) is similar at many Florida and Caribbean reefs. Bank reefs may be 1 km long and several hundred meters wide from the reef flat to the deep terminus. Principal framework corals in the bank reefs are elkhorn coral, Acropora palmata, the star coral Montastraea annularis, and the brain coral Colpophyllia natans.

Scleractinian corals are essential reef builders (Wells 1957, Stoddart 1969, Yonge, 1973). Their zooxanthellae are also the principal coral reef primary producers (Lewis 1977, Gladfelter 1985, Kinsey 1985). Reef Scleractinia are massive and relatively stable; consequently, results of repetitive quantitative censuses are not influenced greatly by movement except in cases of major storms or shipwrecks (Woodley et al. 1981, Jaap 1984).

Earlier studies of coral populations in KLNMS were not quantitative, or the sample size was insufficient to establish cause and effect relationships (Antonius 1974, Voss 1983). White and Porter (1985) and Dustan and Halas (1987) provide information on the nature of coral community dynamics at Carysfort Reef in KLNMS. To enhance the information base on reef coral dynamics in KLNMS, we instituted an annual survey of four of the more heavily used reefs.

METHODS

FIELD DATA ACQUISITION

Monitoring stations were established at Carysfort, Elbow, French, and Molasses Reefs during July and August 1981 and August 1982 (Figure 1). Reefs were sampled annually (summer or early fall) through 1986. Halas chose the site at each reef as representative of the habitat in the particular depth where the site was situated. Sites were in areas with high diver visitation and some recreational fishing. Each site was mapped using a compass and a fiberglass tape measure to establish bearings and distances to prominent reference features. Endpoints of sampling transects were marked with 0.9 m long, 19 mm diameter copper-clad survey markers that were driven into the reef framework and secured with hydraulic cement (Halas 1985). The tape measure was extended between the marking stakes, and a one m^2 frame of 19 mm diameter PVC pipe was centered on specific meter increments along the tape. For example, if meter six was sampled, the quadrat frame was centered at meter six and extended from 5.5 to 6.5 m on the tape. Quadrat numbers were selected randomly before initial sampling at each site. All stony corals (Milleporina and Scleractinia) within the quadrat perimeter were inventoried by transcription mapping (Weinberg 1981); grid paper was used to map the location of each stony coral colony in reference to the quadrat frame. Acropora cervicornis usually was treated as thickets or clumps rather than as individual branches. For brevity, we report herein only the results for Molasses Reef, except for the pooled reef classification analysis.

SITE DESCRIPTION

Molasses Reef is located at the southeastern corner of KLNMS. The monitoring site was established on a spur in 5 to 6 m depths in a habitat similar to Van Duyl's (1985) A. palmata-head coral community. Two transects with 25 quadrats were sampled at Molasses reef.

DATA ANALYSIS

Annual estimates were obtained of species abundance, percent abundance (abundance of a species divided by the sum of all species abundances), frequency of occurrence (percentage value determined by dividing the number of quadrats in which a species occurred by the total number of quadrats sampled at a site), and density of species and colonies (the number occurring in a m^2, with means and standard deviations).

Bloom (1981) compared several similarity indices and concluded that Czekanowski's quantitative coefficient was robust, being influenced by neither dominant nor rare species. We calculated Czekanowski's similarity annually across reefs and across quadrats. Classification was computed with the "ORDANA" benthic analysis computer program (Bloom et al. 1977); species abundance data were transformed to 4th root before computation (Field et al. 1982). Group average sorting (Boesch 1977) was used to develop dendrogram linkage. The significance of change within and across years was evaluated by grouping quadrats by dominate species in the first year (1981) and using the non-parametric Kurskal-Wallis variance of ranks test (Zar 1974) with the hypothesis that quadrats exhibited stability (no change).

RESULTS

Seventeen to 19 species and 212 to 355 colonies were inventoried on Molasses Reef annually during the six years (Table 1). Acropora cervicornis, A. palmata, Montastraea annularis, and Millepora alcicornis constituted 65.7 to 89.6% of the assemblage. After 1981, A. cervicornis exhibited

Table 1. Abundance (A) and percent abundance of coral colonies at Molasses Reef.

Species	1981 A	1981 %	1982 A	1982 %	1983 A	1983 %	1984 A	1984 %	1985 A	1985 %	1986 A	1986 %
Acropora cervicornis	125	38.5	78	22.0	25	7.5	27	8.8	9	3.4	5	2.4
Acropora palmata	108	33.2	96	27.0	135	40.3	130	42.4	129	48.5	79	37.3
Montastraea annularis	38	11.7	46	13.0	22	6.6	56	18.2	44	16.5	43	20.3
Millepora alcicornis	20	6.2	58	16.3	38	11.3	26	8.5	35	13.2	22	10.4
Siderastrea siderea	6	1.9	10	2.8	12	3.6	8	2.6	11	4.1	10	4.7
Millepora complanata	5	1.5	7	2.0	2	0.6	5	1.6	3	1.1	5	2.4
Agaricia agaricites	4	1.2	33	9.3	70	20.9	38	12.4	18	6.8	24	11.3
Montastraea cavernosa	3	0.9	4	1.1	4	1.2	2	0.7	1	0.4	3	1.4
Madracis mirabilis	3	0.9									2	0.9
Porites astreoides	2	0.6	4	1.1	6	1.8	2	0.7	1	0.4	3	1.4
Favia fragum	2	0.6	2	0.6	2	0.6	3	1.0	1	0.4	1	0.5
Diploria labyrinthiformis	2	0.6	2	0.6	2	0.6	1	0.3	2	0.8	2	0.9
Mycetophyllia lamarckiana	2	0.6	4	1.1	3	0.9	1	0.3	6	2.3	4	1.9
Colpophyllia natans	2	0.6	2	0.6	3	0.9	2	0.7	2	0.8	1	0.5
Dichocoenia stokesii	1	0.3	1	0.3							1	0.5
Meandrina meandrites	1	0.3	1	0.3	1	0.3	1	0.3	1	0.4	1	0.5
Mycetophyllia aliciae	1	0.3										
Mycetophyllia ferox			3	0.9	2	0.6	2	0.7				
Porites porites			2	0.6	4	1.2	1	0.3	1	0.4	4	1.9
Dichocoenia stellaris			1	0.3	1	0.3	1	0.3	1	0.4		
Eusmilia fastigiata			1	0.3	3	0.9	1	0.3	1	0.4	2	0.9
Totals												
Species		17		19		18		18		17		18
Colonies		325		355		335		307		266		212

Table 2. Percent frequency of occurrence and mean density (colonies/m²) of corals at Molasses Reef.

Species	1981 f	1981 density $\bar{x}$	1981 density s	1982 f	1982 density $\bar{x}$	1982 density s	1983 f	1983 density $\bar{x}$	1983 density s	1984 f	1984 density $\bar{x}$	1984 density s	1985 f	1985 density $\bar{x}$	1985 density s	1986 f	1986 density $\bar{x}$	1986 density s
A. cervicornis	68	5.0	6.3	56	3.1	4.3	32	1.0	2.4	40	1.1	1.7	20	0.4	1.0	12	0.2	0.7
A. palmata	88	4.3	3.2	76	3.8	4.1	92	5.4	4.1	80	5.2	4.6	84	5.2	4.1	56	3.2	4.1
M. annularis	36	1.5	4.1	44	1.8	5.6	36	0.9	1.7	36	2.2	6.1	40	1.8	2.9	44	1.7	3.5
M. alcicornis	48	0.8	1.0	68	2.3	4.4	60	1.5	1.7	48	1.0	1.4	52	1.4	1.9	48	0.9	1.3
S. siderea	16	0.2	0.7	32	0.4	0.7	32	0.5	0.9	24	0.3	0.6	28	0.4	1.0	28	0.4	0.9
M. complanata	16	0.2	0.5	12	0.3	0.8	08	0.1	0.3	08	0.2	0.3	08	0.1	0.4	08	0.2	0.3
A. agaricites	12	0.2	0.5	56	1.3	2.5	72	2.8	3.3	60	1.5	1.7	44	0.7	1.1	52	1.0	1.3
M. cavernosa	08	0.1	0.4	08	0.2	0.6	16	0.2	0.4	08	0.4	0.3	04	0.0	0.2	12	0.1	0.3
M. mirabilis	04	0.1	0.6													08	0.1	0.3
P. astreoides	08	0.1	0.3	12	0.2	0.5	20	0.2	0.5	08	0.1	0.3	04	0.0	0.2	08	0.1	0.4
F. fragum	04	0.1	0.4	08	0.1	0.3	08	0.1	0.3	08	0.1	0.4	04	0.0	0.2	04	0.0	0.2
D. labyrinthiformis	08	0.1	0.3	08	0.1	0.3	08	0.1	0.3	04	0.0	0.2	08	0.1	0.3	08	0.1	0.3
M. lamarckiana	08	0.1	0.3	12	0.2	0.5	12	0.1	0.3	04	0.0	0.2	12	0.2	0.7	08	0.2	0.6
C. natans	04	0.1	0.4	04	0.1	0.4	12	0.1	0.4	04	0.1	0.4	04	0.1	0.4	04	0.0	0.2
D. stokesii	04	0.0	0.2	04	0.0	0.2										04	0.0	0.2
M. meandrites	04	0.0	0.2	04	0.0	0.2	04	0.0	0.2	04	0.0	0.2	04	0.0	0.2	04	0.0	0.2
M. aliciae	04	0.0	0.2															
M. ferox				08	0.1	0.4	08	0.1	0.3	08	0.1	0.3						
P. porites				08	0.1	0.3	08	0.2	0.6	04	0.0	0.2	04	0.0	0.2	08	0.2	0.5
D. stellaris				04	0.0	0.2	04	0.0	0.2	04	0.0	0.2	04	0.0	0.2			
E. fastigiata				04	0.0	0.2	12	0.1	0.3	04	0.0	0.2	04	0.0	0.2	08	0.1	0.3
Summation density (N=25 quadrats)																		
Species/m²		3.4±1.6			4.7±1.6			4.2±1.8			3.6±1.6			3.3±1.5			3.3±1.8	
Colonies/m²		13.0±3.4			14.2±11			12.8±5.8			12.3±7.2			10.6±4.1			8.5±6.2	

f: species frequency of occurrence; number of quadrats in which a species occurred divided by total number of quadrats sampled, expressed as percentage.
$\bar{x}$: mean number of colonies per square meter.
s: standard deviation

Table 3. Reef temporal similarity values between years, 1981-1986, based on Czekanowski quantitative coefficient and 4th root data transformation (0 = no similarity; 1.00 = total similarity)

	Molasses Reef					
Quadrat number	81-82	82-83	83-84	84-85	85-86	81-86
1	.40	.74	.74	.50	.67	.35
2	.70	.56	.87	.74	.30	.26
3	.73	.70	.48	.50	.84	.60
4	.79	.96	.87	.80	.76	.70
5	.63	.71	.76	.85	.77	.62
6	.74	.83	.92	.81	.72	.32
7	.86	.71	1.00	.60	.26	.47
8	.67	.82	.78	.69	.69	.22
9	.21	.43	.86	.47	0	.24
10	.88	.81	.93	.65	.35	.30
11	.89	.81	.76	.74	.71	.59
12	.76	.78	.79	.74	.71	.36
13	.84	.75	.88	.84	.79	.51
14	.76	.47	.84	.44	.60	.60
15	.86	.73	.70	.79	.91	.64
16	.97	.52	.38	.66	.46	.30
17	.59	.77	.76	.71	.79	.51
18	.78	.49	.99	.97	0	0
19	0	0	.92	1.00	.90	.98
20	0	0	.77	.98	1.00	.92
21	.79	.73	.67	.87	.91	.89
22	.78	.58	.31	.54	.80	.60
23	.84	.76	.87	.94	.60	.47
24	.73	.88	.74	.66	.86	.74
25	.60	.68	.85	.87	.63	.56

	Percent of similarity values greater than .50, .70, and .90					
	81-82	82-83	83-84	84-85	85-86	81-86
>.50	88%	80%	88%	88%	76%	56%
>.70	68%	60%	84%	60%	56%	16%
>.90	8%	4%	20%	16%	16%	8%

	Pooled Reef Similarity			
Time period	Carysfort	Elbow	French	Molasses
1981-1982	.80	.70	---	.83
1982-1983	.82	.83	.88	.92
1983-1984	.83	.84	.96	.93
1984-1985	.85	.76	.97	.92
1985-1986	.88	.81	.89	.89
1981-1986	.72	.77	.69	.86

a marked decrease in abundance, declining from 38.5% to < 3% in 1986 (Table 1). Percent abundance of Agaricia agaricites increased from 1.2% in 1981 to 20.9% in 1983 but decreased to 11.3% in 1986. Percent abundance of Acropora palmata varied from 33.2 to 48.5% of the colonies (Table 1), and its frequency of occurrence was highest of all species (Table 2). Colony density ranged from 3.2 to 5.4 for A. palmata and 0.9 to 2.2 for Montastraea annularis (Table 2).

Similarity of quadrats at Molasses Reef was relatively high (Table 3), with the highest similarities generally occurring between 1983-84 and the lowest similarities occurring between 1985-86. There was a trend of decreasing quadrat similarity between years, but there was no trend in pooled quadrat similarity.

To illustrate the dynamics of change, we randomly selected quadrats 5 and 11. Acropora palmata was the most abundant species at quadrat 5, and one to four other species occurred with A. palmata during the six year period (Table 4). Abundance of Montastraea annularis at quadrat 11 was relatively constant; all other species except Agaricia agaricites recruited to the area after the first census or disappeared and then reappeared later (Table 4).

Decrease in abundance of Acropora cervicornis during the study (Table 1) was a significant 96%. Other frequently occurring species exhibited non-trend patterns of fluctuating abundance between years.

Table 4. Species abundance at quadrats 5 and 11, Molasses Reef, 1981-1986.

Species	Quadrat 5						Quadrat 11					
	81	82	83	84	85	86	81	82	83	84	85	86
A. palmata	8	10	12	9	12	10	2	2	4		2	
M. annularis	1	1	1	1	1	2	4	4	3	3	3	3
M. alcicornis		1	1	1	1	1			1			
A. agaricites		1		2			2	3	5	3	3	1
S. siderea						1		1	1	1	1	1
A. cervicornis		1							1	1		1
M. lamarckiana			1									
F. fragum										1		
E. fastigiata						1						

Pooled quadrat data documented strong clustering within reef sites (Figure 2). Molasses Reef pooled intrasite similarity values ranged from 0.83 to 0.93 (Table 3). The Elbow Reef site was linked to other reef sites at a 0.30 similarity level; this reflected dominance of A. palmata and relatively low species diversity compared to the other sites. Carysfort Reef was linked to French and Molasses Reefs at a 0.55 similarity level; Carysfort site was dominated by M. annularis. French and Molasses Reefs were most similar, with co-dominant species (A. palmata and M. annularis). Molasses and French Reef sites were linked at a 0.76 similarity level. French and Molasses Reefs were most stable between years, and Elbow Reef was the least stable during the six years.

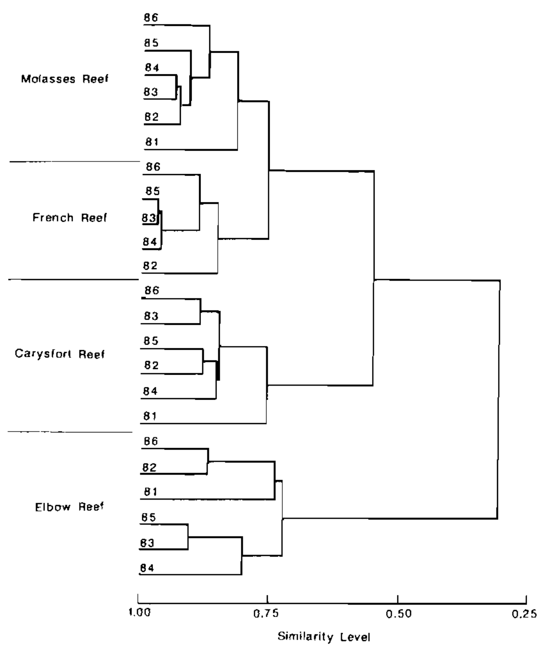

Figure 2. Similarities of sampling sites, KLNMS, 1981-1986.

DISCUSSION

The faunal composition of coral reef communities is largely dependent upon the magnitude and frequency of disturbance (Connell 1978, 1979, Hughes and Jackson 1985). Disturbances create open patches that become available for recruitment of new organisms. Both physical (climatic) and biological (disease) disturbances are relatively common at Florida reefs. These disturbances create alternative states and may or may not influence the ultimate carrying capacity of the habitat (Connell 1978). Human activity in recent times also has influenced reef communities in Florida. Coral species composition of these reefs often is determined by surviving individual colonies that extend into open patches and contribute larvae or fragments following the disturbance. Existing colonies often influence the micro-habitat (shade, water movement, planktonic food availability) and thus survival of recruits.

Similarity values derived from pooled quadrat data demonstrate that classification analysis is sufficiently sensitive to detect influences of different species at each reef. The pattern of individual reef sites clustering together was faithfully maintained in all years (Figure 2). The pooled values implied about 20% annual change. Individual quadrat similarity values were considerably more variable, reflecting differential influence of disturbance forces on resident species.

During the study, we observed disturbance to the reef communities from hurricanes, hyperthermia, epidemic disease, and human interference, undoubtedly affecting each quadrat and reef site differently. At Molasses Reef, the most dramatic changes occurred in nine quadrats where A. cervicornis was abundant in 1981 but virtually disappeared during subsequent years (Table 1). There were 125 clusters and individual branches of A. cervicornis in 1981, 78 in 1982 (38% loss), and 25 in 1983 (68% loss); by 1986, there were only 5 small branches (96% loss compared to 1981). Acropora cervicornis also declined at other reef sites. A Caribbean pandemic disease has been suspected as the cause of severe mortality in this species during recent years (Bak and Criens 1981, Van Duyl 1982, Knowlton et al. in press), killing more than 90% of the A. cervicornis populations during 1981-1982 in Curaçao and Bonaire. We suspect that the same disease infected staghorn corals off Key Largo.

A 1981-1982 winter storm dislodged, upended, and fragmented a large Acropora palmata colony near the sampling site. The fragments lodged in several quadrats. Hurricanes Kate and Elena fragmented and distributed small pieces of A. palmata throughout the study site during the fall of 1985.

Disease virtually eradicated Diadema antillarum, a major invertebrate herbivore, from Florida Keys reefs in late summer 1983 (Lessios, et al. 1984a, 1984b, Bauer and Agerter 1987). Diadema plays an important role in the creation of space for settlement of coral larvae. The echinoid rasps the algae, which is the major competitor for space in the coral reef habitat (Sammarco 1980). A general trend of increased algal cover was noted at the sites after 1983.

A zooxanthellae expulsion during late summer 1983 resulted in some bleaching of corals but no mortality (Jaap 1985).

Disturbances caused by humans at the Molasses Reef site included the breaking of corals by divers and anchors, and the chronic entanglement of fishing tackle in the reef. We found hooks, monofilament lines, wire leaders, lead sinkers, and lures embedded in or wrapped around corals. There was evidence of wounds caused by the fishing activity.

Considering the intense nature of perturbation, the resiliency of these reef communities is remarkable.

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REFERENCES

Antonius, A. 1974. Final report of the coral reef group of the Florida Keys project for the project year 1973. Harbor Branch Foundation, Ft. Pierce, Fla. 193 pp.

Bak, R.P.M. & Criens, S.R. 1981. Survival after fragmentation of colonies of Madracis mirabilis, Acropora palmata, and A. cervicornis (Scleractinia) and the subsequent impact of a coral disease. **Proc. 4th Int. Coral Reef Symp., Manila** 2:221-227.

Bauer, J.C. & Agerter, C.J. 1987. Isolation of bacteria pathogenic for the sea urchin Diadema antillarum (Echinodermata: Echinoidea). **Bull. Mar. Sci.** 40(1):161-165.

Bloom, S.A. 1981. Similarity indices in community studies: potential pitfalls. **Mar. Ecol. Prog. Ser.** 5:125-128.

Bloom, S.A., Santos, S.L. & Field, J.G. 1977. A package of computer programs for benthic community analyses. **Bull. Mar. Sci.** 27(3):577-580.

Boesch, D.F. 1977. Application of numerical classification in ecological investigations of water pollution. **Ecological Research Series**, U.S. Environmental Protection Agency 600/3-77-033, 114 pp.

Bradbury, R.H. & Reichelt, R. 1981. The reef and man: rationalizing management through ecological theory. **Proc. 4th Int. Coral Reef Symp., Manila** 1:219-223.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. **Science** 199 (4335):1302-1310.

Connell, J.H. 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. In: **Population dynamics**, Anderson, R.M., Turner, B.D., & Taylor, L.R. (eds.), Blackwell Scientific Publications, Oxford, pp. 141-163.

Dahl, A.L. 1981. Monitoring coral reefs for urban impact. **Bull. Mar. Sci.** 31(3):544-551.

Dustan, P. & Halas, J.C. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. **Coral Reefs** 6(2):91-106.

Field, J., Clarke, K. & Warwick, R. 1982. A practical strategy for analyzing multispecies distribution patterns. **Mar. Ecol. Prog. Ser.** 8:37-52.

Gladfelter, E.H. 1985. Metabolism, calcification, and carbon production. II. Organism-level studies. **Proc. 5th Int. Coral Reef Congr., Tahiti** 4:527-539.

Halas, J.C. 1985. A unique mooring system for reef management in the Key Largo National Marine Sanctuary. **Proc. 5th Int. Coral Reef Congr., Tahiti** 4:237-242.

Hallock, P. & Schlager, W. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. **Palios** 1:389-398.

Harris, J.A. & Williams, D.G. 1975. The ecological basis for natural resource management. **Proc. Ecol. Soc. Aust.** 9:192-203.

Hughes, T.P. & Jackson, J.B.C. 1985. Population dynamics and life histories of foliaceous corals. **Ecol. Monogr.** 55(2):141-166.

Jaap, W.C. 1984. **The ecology of the south Florida coral reefs: a community profile.** U.S. Fish Wildl. Serv. FWS/OBS-82/08. 138 pp.

Jaap, W.C. 1985. An epidemic zooxanthellae expulsion during 1983 in the lower Florida Keys coral reefs: hyperthermic etiology. **Proc. 5th Int. Coral Reef Congr., Tahiti** 6:142-148.

Kelleher, G.G. 1981. Research needs for coral reef management planning. **Proc. 4th Int. Coral Reef Symp., Manila** 1:231-241.

Kinsey, D.W. 1985. Metabolism, calcification, and carbon production. I. System level studies. **Proc. 5th Int. Coral Reef Congr., Tahiti** 4:505-526.

Knowlton, N., Lang, J.C. & Keller, B.D. in press. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Submitted to Ecol. **Monogr.**

Lessios, H., Robertson, D. & Cubit, J. 1984A. Spread of Diadema mass mortality through the Caribbean. Science 226:335-337.

Lessios, H., Cubit, J. Robertson, D., Shulman, M., Parker, M., Garrity, S. & Levings, S. 1984B. Mass mortality of Diadema antillarum on the Caribbean coast of Panama. **Coral Reefs** 4:173-182.

Lewis, J.B. 1977. Processes of organic production on coral reefs. **Biol. Rev.** 52:305-347.

Manker, J.P. 1975. Distribution of mercury, lead, cobalt, zinc, and chromium in suspended particles and bottom sediments - upper Florida Keys, Florida Bay, and Biscayne Bay. Ph.D. dissertation, Rice University, Houston, Texas. 114 pp.

Marszalek, D.S. 1981. Florida reef tract marine habitat and ecosystem (map series). Published in cooperation with the Florida Dept. of Natural Resources, U.S. Dept. of the Interior Bureau of Land Management, and the Univ. of Miami.

Mattson, J.S. & DeFoor, J.A., III. 1985. Natural resource damages: restitution as a mechanism to slow destruction of Florida's natural resources. J. **of Land Use and Environ. Law** 1(3):295-319.

Sammarco, P.W. 1980. Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. **J. Exp. Mar. Biol. Ecol.** 45:245-272.

Scheer, G. 1967. Uber die Methodik der Untersuchung von Korallenriffen. **Morph. Okol. Tiere** 60:105-114.

Shinn, E.A., Hudson, J.H., Halley, R.B., & Lidtz, B. 1977. Topographical control and accumulation rate of some Holocene coral reefs: south Florida and Dry Tortugas. **Proc. 3rd Int. Coral Reef Symp., Miami** 2:1-7.

Shinn, E.A., Hudson, J.H., Halley, R.B., and Lidz, B. 1981. Spurs and grooves revisited: construction versus erosion. **Proc. 4th Int. Coral Reef Symp., Manila** 1:475-484.

Simkiss, K. 1964. Phosphates as crystal poisons of calcification. **Biol. Rev.** 39:487-505.

Simmons, G.M., Jr. & Love, G.F. 1987. Water quality of newly discovered submarine ground water discharge into a deep coral reef habitat. National Oceanic and Atmospheric Administration. **Symp. Ser. for Undersea Res.** 2:155-163.

Skinner, R.H. & Jaap, W.C. 1986. Trace metals and pesticides in sediments and organisms in John Pennekamp Coral Reef State Park and Key Largo National Marine Sanctuary. Report to the Coastal Zone Management Office, National Oceanic and Atmospheric Administration, Washington, D.C. 40 pp.

Smith, S.V., Kimmerer, W.J., Laws, E.A., Brock, R. E., & Walsh, T.W. 1981. Kaneohe Bay sewage diversion experiment. Perspectives on ecosystem responses to nutritional perturbation. **Pac. Sci.** 35:279-395.

Stoddart, D.R. 1969. Ecology and morphology of recent coral reefs. **Biol. Rev.** 44:433-498.

Van Duyl, F.C. 1982. Distribution of Acropora palmata and Acropora cervicornis along the leeward coasts of Curaçao and Bonaire. Annual meeting Int. Soc. for Reef Studies, Leiden. Abst.

Van Duyl, F.C. 1985. Atlas of the living reefs of Curaçao and Bonaire (Netherlands Antilles) **Utig. Natuurwet. Studiekring. Suriname Ned. Antillen** 117:1-79.

Voss, G.L. 1983. An environmental assessment of the Key Largo National Marine Sanctuary. Report to the Marine Sanctuary Program Office, National Oceanic and Atmospheric Administration, Washington, D.C. 384 pp.

Weinberg, S. 1981. A comparison of coral reef survey methods. **Bijdr Dierk De** 51(2):199-218.

Weiss, M.P. & Goddard, D.A. 1977. Man's impact on coastal reefs - an example from Venezuela. **Am. Assn. Petrol. Geol. Stud. in Geol.** 4:111-124.

Wells, J.W. 1957. Coral reefs. In: **Treatise on Marine Ecology and Paleoecology. Vol. I. Ecology,** J. Hedgepeth (ed.), Geol. Soc. Am. Mem. 67, New York, pp. 609-631.

White, M.W. & Porter, J.W. 1985. The establishment of two permanent photographic transects in Looe Key and Key Largo National Marine Sanctuaries (Florida Keys). **Proc. 5th Int. Coral Reef Symp., Tahiti.** 6:531-537.

Woodley, J., & 19 others. 1981. Hurricane Allen's impact on Jamaican coral reefs. **Science** 214 (4522):749-755.

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

Zar, J.H. 1974. **Biostatistical analysis.** Prentice-Hall, Inc. Englewood Cliffs, N.J., 620 pp.