

AN EPIDEMIC ZOOXANTHELLAE EXPULSION DURING 1983 IN THE LOWER FLORIDA KEYS CORAL REEFS : HYPERTHERMIC ETIOLOGY

UNE EXPULSION EPIDEMIQUE DE ZOOXANTHELLES EN 1983 DANS LES RECIFS CORALLIENS DU SUD DE LA FLORIDE : ETIOLOGIE HYPERTHERMIQUE

W. C. JAAP

Bureau of Marine Research, Florida Department of Natural Resources
100-8th Avenue, S.E., Saint Petersburg, FLORIDA 33701, U.S.A.

ABSTRACT

Extensive reef coral zooxanthellae expulsion occurred from Key Largo to Dry Tortugas, Florida, during September 1983. Coral bleaching was intensive between Pelican Shoal and Sand Key Reef off Key West. Coral discoloration extended to depths exceeding 14 m but was especially severe in shallow (1-2 m) spur and groove habitats. Approximately 75-95% of all *Millepora complanata* and *Palythoa caribaeorum* were bone white, but most colonies remained viable. Affected *M. complanata* (bladed fire coral) retained the ability to inflict pain from dactylozooid nematocysts. Some individuals (5 to 10%) had fine algal growth indicating death on all or parts of their skeletons. Although 15 species of cnidarians, principally Scleractinia, were affected, some species (*Madracis mirabilis*, *Porites porites*, *Montastraea cavernosa*, *Dendrogyra cylindrus*) appeared to be immune. A quantitative sample at Eastern Sambo Reef on 6 October documented 11 species and 209 colonies; *M. complanata* comprised 32.5% of all colonies. Transmission electronmicrographs did not reveal epidemic pathogenic organisms in affected coral tissues. Warm, calm weather prior to the expulsion was conducive to elevated seawater temperature. A seawater thermograph deployed off Marquesas Key recorded temperatures of 32.3°C during the period.

A seven month post-event survey revealed that most hermatypic organisms had recovered normal color. Survival of hermatypic cnidarians was high. Twenty quadrats sampled during and seven months after the event were compared using classification analysis (Czekanowski's quantitative coefficient); mean similarity value among all quadrats was 0.69, and 12 of 20 quadrats had similarity values > 0.70. Values obtained using this technique in similar habitats generally ranged from .4 to .9 annually. The event is an example of a disturbance of intermediate frequency and magnitude controlling shallow reef communities.

RESUME

Des expulsions massives de zooxanthelles de coraux ont eu lieu de Key Largo à Dry Tortugas en Floride en Septembre 1983. Le blanchiment des coraux a été intensif entre Pelican Shoal et le récif de Sand Key au large de Key West. Le blanchiment des coraux s'est étendu à des profondeurs excédant 14 m mais a été particulièrement sévère en eau peu profonde dans la zone éperons-sillons (1-2m). Environ 75 à 95% de tous les *Millepora complanata* et *Palythoa caribaeorum* ont été blanchis mais la plupart des colonies restent viables. Les *M. complanata* affectés (les lames de coraux de feu) gardent la capacité d'infliger des brûlures à partir des nématocystes. Quelques individus (5-10%) arborent un fin recouvrement algal indiquant la mort de tout ou une partie de leur squelette. Bien que 15 espèces de Cnidaïres, principalement des Scléractiniaïres, aient été affectées, quelques autres (*Madracis mirabilis*, *Porites porites*, *Montastraea cavernosa*, *Dendrogyra cylindrus*) apparaissent sauvées. Un échantillon quantitatif à Eastern Sambo du 6 Octobre, révèle 11 espèces et 209 colonies. *M. complanata* compose 32.5% de toutes les colonies. La microscopie électronique à transmission ne révèle pas d'organisme pathogène dans les tissus altérés des coraux. La chaleur et le temps calme précédant l'expulsion des zooxanthelles a provoqué une élévation de la température des eaux. Un thermographe installé à Marquesas Key a révélé des températures de 32.3°C au cours de cette période.

Une étude réalisée 7 mois après l'événement a révélé que la plupart des organismes hermatypiques avaient retrouvé une couleur normale. La survie des Cnidaïres hermatypiques est élevée. 20 quadrats pendant et 7 mois après l'événement ont été comparés et analysés (coefficient quantitatif de Czekanowski). La valeur moyenne de similarité parmi tous les quadrats est de 0.69 et 12 des 20 quadrats ont des valeurs de similarité > 0.70. Les valeurs obtenues en utilisant cette technique dans des habitats similaires s'étendent en général de 0.4 à 0.9 annuellement. L'événement observé est un exemple de perturbation de fréquence et de grandeur intermédiaire contrôlant les communautés récifales peu profondes.

INTRODUCTION

A major zooxanthellae expulsion occurred in Florida Keys coral reefs during early September 1983. Such events occur infrequently in Florida reef communities (Vaughan 1911; Mayer 1914; Shinn 1966; Jaap 1979) and other Caribbean areas (Goreau 1964; Glynn 1968). Although a great number of zooxanthellae expulsions were reported from tropical areas during 1982-1983, these were related to radical climate and oceanographic changes caused by a severe El Niño event (Glynn 1983; 1984a; 1984b; Coffroth et al. 1984; Lasker et al. 1984). Coral mortality was significant in the Gulf of Panama; Galapagos Islands; Moorea, French Polynesia; Nukunonu Atoll, Tokelau Islands; Paulau, Pari, Seribu, and Karimunjawa Islands, Indonesia (Glynn 1984a; 1984b).

METHODS

A fixed wing single engine aircraft was used to survey reefs from Big Pine Key to Dry Tortugas following reports of coral discoloration. Visual observations supplemented by photography evaluated the geographic range of the phenomenon. Reef surveys were conducted in Key Largo National Marine Sanctuary (KLNMS) and off Key West using snorkel and scuba; observations were recorded on waterproof paper and documented with photography.

Samples of normal and blanched cnidarians (*Palythoa caribaeorum*, *Millepora complanata*, *Madracis mirabilis*, and *Acropora palmata*) were collected for histological studies. Specimens were preserved in Zenker's formalin fixative; histological techniques followed Yevich and Barszcz (1977). Other specimens of the same species were fixed in a glutaraldehyde, paraformaldehyde, and sodium cacodylate solution for transmission electron microscope (TEM) examination.

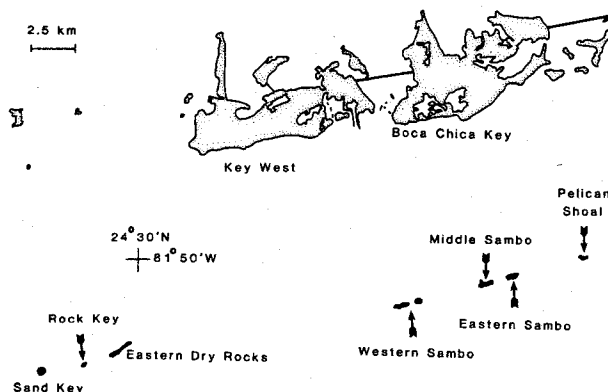


Figure 1. Area of severe zooxanthellae expulsion south of Key West, Florida.

A site at Eastern Sambo Reef selected for evaluation of community dynamics was located approximately 8 km S. of Boca Chica Key (Figure 1). The sampling site was located on a spur in 3 to 4 m depths. Sampling used reference stakes driven into the reef frame and secured with hydraulic cement. A metric fiberglass tape measure was extended 20 m between the stakes. A 1-m² quadrat was centered on the tape at each

meter for censusing the Cnidaria within the quadrat. Quadrat maps were drawn (following Weinburg 1981) on 6 October 1983 and 9 May 1984. A Nikonos camera with 15 mm lens and 400 ISO color print film mounted on a unipod apparatus (Done 1983) was used to photograph the transect. Data were tabularized by date and analyzed for species abundance, frequency of occurrence, percent abundance, density (mean and standard deviation per square meter), diversity (H') evenness (J'), and biological index (McCloskey 1970). Species area curves, classification, and ordination, all based upon species abundance, were processed with the SPARCR and ORDANA benthic analysis computer programs (Bloom et al. 1977); 4th root data transformation (Field et al. 1982) was performed before classification analysis. Czekanowski's quantitative coefficient (also known as Bray-Curtis) (Bloom 1981) with group average sorting was used to generate dendograms. Interstation linkages were plotted from coefficient values. Environmental data were received from the Key West weather station, U.S. Geological Survey Fisher Island Station, and the University of Miami.

DESCRIPTION OF THE PHENOMENON

Coral bleaching in Florida occurred from off Elliott Key to Dry Tortugas, a distance of about 222 km. Impact was most severe off Key West: Pelican Shoals, Eastern, Middle, and Western Sambo, Eastern Dry Rocks, Rock Key, and Sand Key Reefs (Figure 1). Blanched coral was first reported on 3-4 September by divers, boaters, and fishermen from Key West.

Aerial surveys from 152 - 305 m altitude revealed that shallow spurs and reef flats were an abnormal white color. This was true for all reefs between and including Pelican Shoal and Sand Key. There were reports of blanched coral from Looe Key Reef and Dry Tortugas, but this could not be seen from the air.

Diving inspections disclosed that this zooxanthellae expulsion was significantly greater than the 1973 expulsion in the same area (Jaap 1979). From a distance, spurs looked like snow-draped ridges (Figure 2).



Figure 2. Blanched *Millepora complanata* in the spur and groove habitat, 1-2 m, Eastern Sambo Reef, 20 September 1983.

Close examination revealed that bladed fire coral (*Millepora complanata*) and golden sea mat (*Palythoa caribaeorum*), were bone white. Few individuals of either species exhibited normal golden-yellow color; many were blanched from base to tip. However, most blanched organisms were alive; *M. complanata* induced pain to forearm and wrist when touched, and *Palythoa* polyps were expanded and capable of retracting tentacles when stimulated.

Three degrees of zooxanthellae expulsion were observed. (1) Paling. The entire coralla was uniformly lighter than normal in color but not white. This was most frequently observed in *Montastraea annularis*, *Siderastrea siderea*, *Colpophyllia natans*, and *Meandrina meandrites* in the fore-reef area. (2) White spotting. Some portions of the coralla retained normal color, while other portions were contrastingly stark white (Figure 3). This was observed in a number of species but most frequently in *Acropora palmata* and *M. annularis*. (3) Total blanching. Complete loss of color was most frequently seen in the shallow spur and groove habitat. Species expressing this degree of discoloration were principally *M. complanata*, *P. caribaeorum* and some specimens of the octocoral, *Briareum asbestinum*.



Figure 3. Spotty blanching condition in *Agaricia agaricites*, Sand Key Reef, 6 m, 5 October 1983.

Sixteen species of Cnidaria expelled zooxanthellae and six species appeared to be unaffected (Table 1).

Table 1. Cnidarians affected and unaffected during the 1983 Florida zooxanthellae expulsion.

I. Blanched species	
<i>Palythoa caribaeorum</i>	<i>Millepora alcicornis</i>
<i>Meandrina meandrites</i>	<i>Millepora complanata</i>
<i>Briareum asbestinum</i>	<i>Siderastrea siderea</i>
<i>Montastraea annularis</i>	<i>Madracis decactis</i>
<i>Agaricia agaricites</i>	<i>Colpophyllia natans</i>
<i>Acropora palmata</i>	<i>Diploria strigosa</i>
<i>Acropora cervicornis</i>	<i>Diploria clivosa</i>
<i>Diploria labyrinthiformis</i>	<i>Porites astreoides</i>

II. Species not discolored

<i>Ricordea florida</i>	<i>Eusmilia fastigiata</i>
<i>Madracis mirabilis</i>	<i>Porites porites</i>
<i>Montastraea cavernosa</i>	<i>Dendrogya cylindrus</i>

Surveys revealed blanched cnidarians to depths of 12 m, those at greatest depths usually occurring in pale or spotted conditions.

Millepora complanata at shallow reef areas in the Sambo group (Figure 1) exhibited >95% incidence of blanching. At Rock Key, Eastern Dry Rocks, and Sand Key Reefs, the incidence was reduced to about 75%. Mortality of *M. complanata* populations was estimated at 5 - 15% based on immediate blue-green algal colonization of the coralla.

Examinations at KLNMS revealed significantly less impact than that seen in the Key West area. Pale or spotted discoloration was commonly observed, but total discoloration was rare.

Histological examination of blanched and normally colored *M. complanata* indicated total loss of *Symbiodinium microadriaticum* (the endosymbiont alga) in blanched samples. Blanched specimens also contained abundant mucoid-polysaccharide material in the cytoplasm. Examination of normally colored *M. complanata* with TEM at 14,000 to 20,000 magnification revealed typically healthy complements of zooxanthellae (Figure 4), but blanched coral tissues contained degenerate *S. microadriaticum* (reduced or no chloroplasts, lack of lipids, and ruptured membranes) (Figure 5). Abnormal mitochondria and unidentified structures were observed in coral tissue of several blanched specimens. No pathogenic microorganisms were detected; however, fungal mycelium was observed in *M. complanata* and *Madracis mirabilis* tissues.

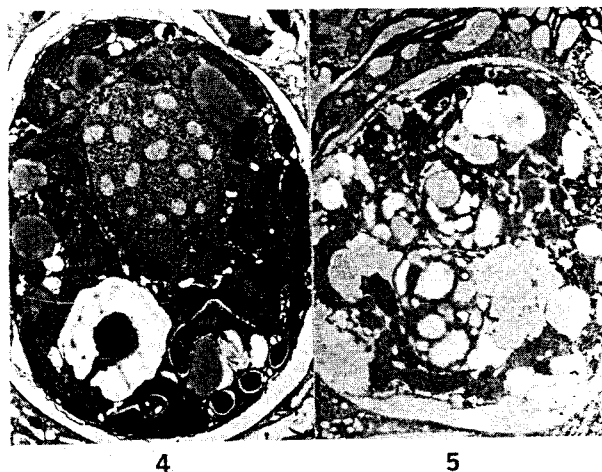


Figure 4. Zooxanthella (*Symbiodinium microadriaticum*) from normally pigmented *M. complanata*, 20,200 magnification, Sand Key Reef, 1-2 m, 6 October 1983.

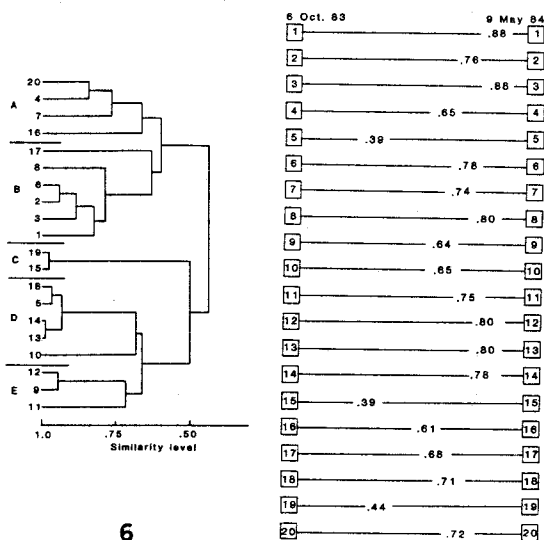
Figure 5. Degenerate zooxanthella from blanched *M. complanata*, 20,200 magnification, Eastern Sambo Reef, 1-2 m, 6 October 1983.

Observations conducted during May 1984 disclosed near total return of normal color to corals throughout the reef tract. Mass mortality had not occurred.

COMMUNITY STRUCTURE

Species area curves documented sufficient sample size to quantitatively assess community structure. *Millepora complanata*, *A. agaricites*, *P. astreoides*, and *P. caribaeorum* dominated the community, comprising 93.3% of the assemblage in October 1983. In May 1984, major changes had occurred in the abundance of dominant organisms. There was an increase of 155 colonies. The number of species increased by one, and colony density increased from 10.45 to 18.15/m². *Millepora complanata* increased from 68 to 162 colonies. Both diversity and evenness (H' and J') decreased.

Homogeneity was high among the 20 quadrats sampled in October 1983. Site group linkage documented 43 cases of similarity greater than 0.65, 19 cases greater than .80, and 10 cases greater than 0.90. A classification dendrogram (Figure 6) defined five site groups. However, further evaluation disclosed only four groups actually characterized by differences in dominant species. *Porites astreoides* dominated site group A; *A. agaricites* and *P. astreoides* dominated group B; *M. complanata* was the only species in group C, and, in association with several other species, dominated group D; and *P. caribaeorum* was the prominent species in group E.



6

7

Figure 6. Dendrogram of 20 quadrats, Eastern Sambo Reef, 6 October 1983, computed with Czekanowski's quantitative coefficient, 4th root data transformation, of species abundance with group average sorting; quadrat numbers to left of clusters. A = quadrats dominated by *P. astreoides*; B = quadrats dominated by *P. astreoides* or *A. agaricites*; C, D = quadrats dominated by *M. complanata* or *M. complanata* in association with other species; E = quadrats with *P. caribaeorum* dominating.

Figure 7. Temporal similarity of 20 quadrats sampled 6 October 1983 and 9 May 1983 as indicated by Czekanowski's quantitative coefficient. Transect numbers within squares; coefficient values derived from species abundance and 4th root transformation.

Classification comparison of the 20 quadrats between October 1983 and May 1984 disclosed a mean similarity value of 0.69±0.14 (Figure 7). Only three quadrats exhibited radical change, expressing similarity values of 0.39 (2 cases) and 0.44. Inspection of species abundances in these quadrats showed there had been significant changes between October and May. For example, the initial assemblage in one quadrat was comprised of 5 *M. complanata* and 3 *P. caribaeorum*. Seven months later, that quadrat contained 11 *M. complanata*, 10 *A. agaricites*, 2 *P. astreoides* and 3 *P. caribaeorum*. These changes were due to recruitment by larval settlement and fragmentation propagation. Differential mortality also contributed to the increase of discrete *M. complanata* colonies.

ENVIRONMENTAL CONDITIONS AND ETIOLOGY

Air and seawater temperatures were above normal compared to historical data; wind velocity was below normal (Table 2).

Table 2. Environmental parameters for Key West and Sand Key for September.

Parameter	Observed	Historical norms*
Air temperature (°C)		
Range	27.2-30.3	25.9-30.1
Mean	28.5	27.9
Wind speed (km/hr)		
Range	0-33	0-61
Mean	13.8	16.1
Seawater temperature (°C)		
Range	29.0-32.3(M;HC)	28.7-31.2
Mean	30.5(M), 31.6(HC)	30.3

*Historical sources: Climate (U.S. Dept. of Commerce 1982b), Seawater, 1879-1907 (Vaughan 1918). M: Marquesas thermograph; HC Hen and Chickens thermograph.

Hourly mean air temperature from 25 August until 10 September at Key West ranged from 27.2±1.2°C (+1 Std. dev.) at 05:00 to 30.3±0.7°C at 14:00. Wind velocities ranged from 0 to 33 km/hr with a mean of 13.8±3.5 km/hr. Several days of relatively calm wind were noted, the mean velocity on 29 August was 7.1±4.7 km/hr. Wind direction was SE and ESE during most of the period. Cloud cover averaged about 66% and was variable. Daily rainfall ranged from 0 to 36 mm but averaged only 5 mm/day (meteorological information summarized from Key West weather station data). There are no seawater temperature data from the Pelican Shoal - Sand Key area for August and September 1983, but seawater temperatures from Florida Bay, Big Pine Channel were approximately 33°C during late August and early September (B. Causey, personal communication). A thermograph deployed at Marquesas Key, 31 km west of Sand Key, in 1.5 m depth recorded hourly temperatures ranging from 29.0 to 32.3°C from 7 September through 18 September; mean value was 30.5±0.7°C. A thermograph deployed at Hen and Chickens Reef, 6.1 m, 143 km NE of Sand Key, off Plantation Key recorded temperatures of 31.4 to 32.2°C between

31 August and 14 September. Low tides occurred at Sand Key between 12:00 and 17:00 from 25 to 28 August and 3 to 10 September. (U.S. Dept. of Commerce 1982a). Predicted tidal heights for these low tides were datum to 18 cm above datum. High tides for the same two periods were predicted at 30 to 33 cm above datum.

The zooxanthellae expulsion in the Florida Keys during 1983 was most probably the result of elevated temperature. Other environmental parameters contributed directly or indirectly to heating of the water column. Clear sky, low tides at or near midday, and low wind velocities probably all contributed to the event. Doldrum conditions that existed during the period are not unusual during late summer. The water was near calm with very slight swells during the surveys. A local fisherman commented that there had been "dirty water" along the reefs for several weeks during late August (P. Horton, personal communication). Ultraviolet radiation may have added to the stress during midday low tides (Jokiel 1980).

The depth of occurrence (to >12 m) of the blanching is possibly explained by density sinking of heated surface waters. During doldrum periods, evaporation creates hypersaline surface layers which maintain their integrity and slowly sink. Some mixing with cooler subsurface waters occurs, but pockets of hot hypersaline water can reach the bottom and make contact with cnidarians and other benthos. This water probably has other unfavorable characteristics, i.e., low oxygen saturation, high chlorinity, and reduced pH. The spotty expression of zooxanthellae expulsion may be explained by prolonged contact of hyperthermal-hypersaline water with portions of cnidarian colonies. In shallower waters, it is probable that corals were bathed in a more uniform mass of hyperthermic water.

Localization of the zooxanthellae expulsion in the lower Keys is consistent with the hydrodynamics, geography, meteorology, and thermodynamics of the region. Vaughan (1918) reported that summer (June-September) seawater temperatures were elevated at Sand Key compared to Dry Tortugas, Carysfort Light, or Fowey Rocks. The east-west axis of the lower Keys reef tract accommodates heating of the water column there; winds and seas during summer are normally from the ESE, a path parallel to the reef tract axis. In the upper Keys, the reef tract axis is N - S, hence winds and seas are orthogonal to the reefs, affording greater water exchange across the reefs.

Scleractinia accommodate poorly to slowly elevating seawater temperature (Mayer 1914). Mayer reported that *A. palmata*, *A. muricata* (= *prolifera* and/or *cervicornis*), *Agaricia* sp., *M. annularis*, *M. cavernosa* (listed as genus *Orbicella*), *P. astreoides*, *D. clivosa*, and *S. siderea* suffered physiological stresses between 31.8 and 36.4°C. Death occurred at temperatures exceeding 35.8°C (Mayer 1914). Maximum temperature reported from the lower Keys during August-September 1983 was 33°C. During low tides on calm days, temperatures may have exceeded 33°C. Natural localized hyperthermic conditions as high as 38°C have been reported from shallow Florida reef flats (Mayer 1914).

Shallow-water coral reef communities are polytrophic. Carbon photosynthetically fixed by zooxanthellae is translocated to animal tissues

(Muscantine and Porter 1977). Reef cnidarians also obtain carbon heterotrophically from zooplankton, from feeding on other benthos, and from dissolved and particulate organics. In shallow water, the autotrophic energy source is a major contribution to resident cnidarian populations. Some coral species receive the majority of daily carbon requirements via phototrophism (Muscantine et al. 1981; Davies 1984; Porter 1984). Calcification, reproduction, and maintenance are affected when the carbon budget is radically changed. Expulsion of zooxanthellae alters the trophic balance, requiring affected organisms to rely to a greater extent on heterotrophic resources.

Expelled zooxanthellae can be consumed by filter-feeding organisms (Frankboner and Reid 1981). Recovery of zooxanthellae following an expulsion is reported to take 6-15 weeks (Goreau 1964; Jaap 1979), during which surviving *S. microadriaticum* undergo division to reestablish symbiont populations within host cnidarians. Additional zooxanthellae may be secondarily obtained via zooplankton prey (Fitt and Trench 1981; Fitt 1984) and from detrital material (Steele 1975). Connell (1973; 1978) proposed that disturbances of intermediate magnitude and frequency were responsible for maintaining high species diversity in shallow-water coral reef communities. In Florida, the shallow spur and groove habitat supports low diversity coral communities (Jaap 1983; 1984). Disturbance is of a magnitude and/or frequency that does not enhance high diversity. During the present event, overall species diversity decreased (although at least temporary increases were noted in a few quadrats). Dominance of the most abundant, and presumably most tolerant, organisms increased.

The source of alternative nutrition for affected cnidarians on the shallow reefs is unknown. Is there sufficient energy stored to compensate for zooxanthellae loss? Do degenerating zooxanthellae create an organic soup that can be utilized by the blanched cnidarians? Are physiological processes reduced or shut down to compensate for lost energy? Reef ecologists should focus attention on these questions to better understand the significance of zooxanthellae expulsions.

ACKNOWLEDGEMENTS

Appreciation is expressed to John Halas and Billy Causey (FDNR, Bureau of Environmental Land Management) for assistance with field surveys and for providing Florida Bay seawater temperature data (Causey). Lt. Fred Klohn (FDNR Marine Patrol) piloted the aircraft during the aerial surveys. Peter Horton, a Key West citizen provided a boat for transportation to the reefs off Key West for field observations. Marine Patrol officers Florian Lamey, David Lewis, and Ron Hull supported field logistics during later surveys. Ruth Reese and Earnest Truby (FDNR Bureau of Marine Research) prepared histological and TEM material, respectively. J. Harold Hudson (U.S. Geological Survey, Fisher Island Station) provided Marquesas Key thermograph data. Tom Lee (University of Miami) provided Hen and Chickens reef temperature information. The Key West weather station provided meteorological data. William Lyons and Karen Steidinger provided editorial criticism.

REFERENCES

- Bloom, S. 1981. Similarity indices in community studies: potential pitfalls. Mar. Ecol. Prog. Ser. 5:125-128.
- Bloom, S., S. Santos and J. Field. 1977. A package of computer programs for benthic community analysis. Bull. Mar. Sci. 27(3): 577-580.
- Coffroth, M.A., E.C. Peters and H.R. Lasker. 1984. Zooxanthellae expulsion among Caribbean reef coelenterates in Panama. pp. 23, 24 in Proc. Advances in reef science. Atlantic Reef Committee and Int. Soc. for Reef Studies, University of Miami, Miami, Fla.
- Connell, J.H. 1973. Population ecology of reef building corals. Pp. 205-245 in O. Jones and R. Endean eds. Biology and Geology of Coral Reefs (Vol. 2) Academic Press, New York.
- _____. 1978. Diversity in tropical rain forests and coral reefs. Science (Wash. D.C.): 199: 1302-1310.
- Davies, P.S. 1984. The role of zooxanthellae in the nutritional energy requirements of Pocillopora eydouxi. Coral Reefs 2(4) 175-180.
- Done, T. 1983. Photogrammetry in coral ecology: a technique for the study of change in coral communities. In Vol. 2, pp. 315-320 Proc. 4th Int Coral Reef Symp., Manila.
- Fankboner, P. and R. Reid. 1981. Mass expulsion of zooxanthellae by heat stressed reef corals a source of food for giant clams Tridacna gigas. Experientia (Basel) 37(3): 251-252.
- Field, J., K. Clarke and M. Warwick. 1982. A practical strategy for analysing multi-species distribution patterns. Mar. Ecol. Prog. Ser. 8: 37-52.
- Fitt, W.K. 1984. The role of chemo-sensory behavior of Symbiodinium microadriaticum: intermediate hosts and host behavior in the infection of coelenterates and mollusks with zooxanthellae. Mar. Biol. (Berl.) 81(1): 9-18.
- Fitt, W.K. and R.K. Trench. 1981. Spawning, development and acquisition of zooxanthellae Symbiodinium microadriaticum by Tridacna squamosa (Mollusca Bivalvia) Biol. Bull. (Woods Hole) 161(2) 213-235.
- Glynn, P.W. 1968. Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposure in Puerto Rico. Mar. Biol. (Berl.) 1(3): 226-243.
- _____. 1983. Widespread coral bleaching and death in Panama (1983). Reef Encounter 1: 4.
- _____. 1984a. Widespread coral mortality and the 1982-83 El Nino warming event. Environ. Conserv. 11(2): 133-146.
- _____. 1984b. Coral reefs and recent disturbances cause for concern? pp. 41, 42, in Proc. Advances in Reef Science. Atlantic Reef Committee, and Int. Soc. for Reef Studies, University of Miami, Miami, Fla.
- Goreau, T.F. 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science (Wash., D.C.) 145(3630): 383-386.
- Jaap, W. 1979. Observations on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys, USA. Bull. Mar. Sci. 29(3): 414-422.
- _____. 1983. Community structure of stony corals (Scleractinia and Milleporina) in southeast Florida reef communities. p. 31 in Colloque Annuel Biologie et geologie des Recifs Coralliens. University of Nice, Juan les Pins, France.
- _____. 1984. Community structure of stony corals, Looe Key National Marine Sanctuary. pp. 57, 58 in Proc. Advances in Reef Science. Atlantic Reef Committee and Int. Soc. for Reef Studies, University of Miami, Miami, Fla.
- Jokiel, P.L. 1980. Solar ultraviolet radiation and coral reef epifauna. Science (Wash. D.C.) 207: 1069-1071.
- Lasker, H.R., E.C. Peters, and M.A. Coffroth. 1984. Bleaching of reef coelenterates in the San Blas Islands, Panama. Coral Reefs 3(4):183-190.
- Mayer, A.G. 1914. The effects of temperature upon tropical marine animals. Carnegie Inst. Wash. Publ. Dept. Mar. Biol., Pap. Tortugas Lab. 6(183): 3-24.
- McCloskey, L.R. 1970. The Dynamics of the Community Associated with a Marine Scleractinian Coral. Int. Rev. Gesamten Hydrobiol. 55(1): 13-81.
- Muscantine, L. and J. Porter. 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454-460.
- Muscantine, L., L. McCloskey and R. Marian. 1981. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. Limnol. Oceanogr. 26(4): 601-611.
- Porter, J.W. 1984. Photo adaptation by reef corals to increasing depth. pp. 97-98 in Proc. Advances in Reef Science. Atlantic Reef Committee and Int. Soc. for Reef Studies, University of Miami, Miami, Fla.
- Shinn, E.A. 1966. Coral growth-rate an environmental indicator. J. Paleontol. 40(2): 233-240.
- Steele, D. 1975. Stages in the life history of a symbiotic zooxanthella in pellets extruded by its host Aiptasia tagetes (Duch. and Mich.) (Coelenterata Anthozoa). Biol. Bull. (Woods Hole) 149: 590-600.
- U.S. Dept. of Commerce. 1982a. Tide tables high and low predictions 1983 east coast of North and South America, including Greenland. Washington D.C. 285 pp.
- _____. 1982b. Local climatological data Annual Summary with comparative data, Key West, Florida. Natl. Climatic Data Center, Asheville, North Carolina 13 pp.
- Vaughan, T.W. 1911. Recent Madreporaria of southern Florida. Carnegie Inst. Wash. Year Book 8: 135-144.
- _____. 1918. The temperature of the Florida coral reef tract. Carnegie Inst. Wash. Publ. 213: 321-339.
- Weinberg, S. 1981. A comparison of coral reef survey methods. Bijdr. Dierk. D. 51(2): 199-218.
- Yevich, P.P., and C.A. Barszcz. 1977. Preparation of aquatic animals for histopathological examination. U.S. Environ. Prot. Agency. Cincinnati, Ohio. 20 pp.