OBSERVATIONS ON ZOOXANTHELLAE EXPULSION AT MIDDLE SAMBO REEF, FLORIDA KEYS

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ABSTRACT

Large-scale discoloration of Middle Sambo reef, 7.8 km from Boca Chica Key, Monroe County, Florida, was investigated on September 26, 1973. Discoloration of organisms was generally confined to the reef flat. The hydrozoan coral *Millepora complanata* displayed greatest discoloration. Some *Acropora palmata*, *Montastraea annularis*, and *Palythoa* sp. colonies were mildly discolored. Corals were still viable.

Calm weather, high ambient temperatures, and low tides at midday are believed to have caused water temperature elevation sufficient to produce thermal stress, thereby causing expulsion of endosymbiotic algae, *Gymnodinium microadriaticum*, with consequent discoloration of cnidarian hosts. Most organisms regained normal color within 6 weeks. Reports of similar coral discoloration incidents are reviewed. Short periods of thermal stress appear to have little lasting effect on shallow reef cnidarian communities.

On September 25, 1973, an officer of the Florida Marine Patrol reported discolored and bleached corals at Middle Sambo reef, a fringing bank reef, 24°29.4′N, 81°40.5′W, or about 7.8 km (4.2 nmi) from the south shore of Boca Chica Key in Monroe County (Fig. 1). I was sent by the Florida Department of Natural Resources Marine Research Laboratory (FDNRMRL) to investigate and conduct a snorkeling and scuba reconnaissance of the reef on September 26 and 27. The shallow flat has poor coral development due to exposure to environmental extremes; heavy seas break over it during storms and portions are emergent during some spring tides. Depth of the flat is less than 1 m (2 ft; National Ocean Survey [NOS] chart, 854, 1972). Conspicuous benthic organisms inhabiting the reef flat include: *Padina* sp., *Halimeda* sp., Corallinaceae, *Millepora complanata* (Lamarck, 1816) [fire coral], *Millepora* sp. (encrusting form), small stunted colonies of *Gorgonia ventalina* Linné, 1758 [sea fan], *Acropora palmata* (Lamarck, 1816) [elkhorn coral], *Favia fragum* (Esper, 1795) [star coral], *Montastraea annularis* (Ellis and Solander, 1786) [common star coral], and *Palythoa* sp.

Observations revealed random occurrence of mottled discoloration among hermatypic organisms inhabiting the reef flat; however, deeper regions of the reef, the spur and groove tract, and the area farther seaward displayed little evidence of discoloration. *Millepora complanata* showed the greatest incidence of discoloration; terminal fronds were colorless white, while basal portions of the same colonies displayed typical coloration (Fig. 2). *Acropora palmata* (Fig. 3), *Montastraea annularis*, and *Palythoa* sp. were affected but not as severely. The affected corals were visually inspected and appeared viable. *Acropora palmata* polyps were extended and undulating; upon tactile stimulation, they retracted into their calices. Nematocysts from dactylzooids of *Millepora* spp. inflicted pain to my forearm and wrist areas. Goreau (1964) noted similar pain-inducing qualities for discolored *Millepora* in Jamaica. Pain infliction by discolored *Millepora* colonies may indicate that they still possess functional feeding and defensive mechanisms despite the loss of zooxanthellae.

Cause of discoloration was expulsion of zooxanthellae, the endosymbiotic algae found in tissues of hermatypic reef organisms (Yonge and Nicholls, 1931). Zooxanthellae found within endodermic epithelium of Scleractinia and Milleporina

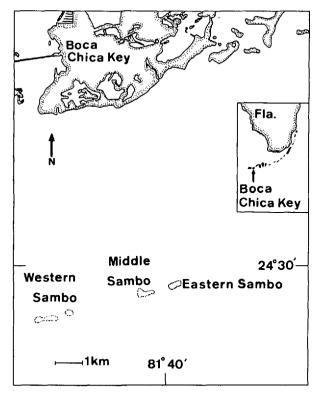


Figure 1. Location of Middle Sambo reef, NOS chart 1251, 1973.

are suspected to be *Gymnodinium microadriaticum* (Freudenthal) Taylor, 1971 (Dinophyceae). Dense concentrations of zooxanthellae are responsible for much of the color characteristics of scleractinian and milleporinian reef corals.

Natural factors causing reef coral discolorations, damage, or death include waves generated by hurricanes or cyclones, and salinity alteration from heavy rainfalls that often accompany tropical storms (the runoff frequently carries silt and debris from the adjacent land masses). Hurricane Flora deposited 550 mm of rain on Port Royal, Jamaica, in October, 1963, causing massive zooxanthellae expulsion among hermatypic organisms inhabiting shallow reefs (Goreau, 1964).

Thermal elevation of shallow reefs and tidal emergence also adversely affect shallow reef biota. Vaughan (1911) reported bleached heads of Orbicella (=Montastraea) annularis caused by tidal emergence at Dry Tortugas, Florida. Colonies of Orbicella, Eusmilia fastigiata (Pallas, 1766), Diploria clivosa (Ellis and Solander, 1786), and Manicina areolata (Linné, 1758) were killed by the exposure. In a subsequent incident, waters surrounding Bird Key, Dry Tortugas, were heated by several days of calm wind conditions resulting in mortalities among Octopus, Fissurella, and other mollusks, Diadema, and fishes; corals were injured (Mayer, 1918). Yonge and Nicholls (1931) reported expulsion of zooxanthellae from Favia and Goniastrea at Low Isles reef, Australia, due to natural thermal stress. They also reported expulsion due to laboratory induced stresses of heat, starvation, altered salinity, and total deprivation of light. Acropora cervicornis (Lamarck, 1816) transplanted inshore at Key Largo, Florida, during growth studies suffered zooxanthellae expulsion during late summer, but the symbionts were regenerated

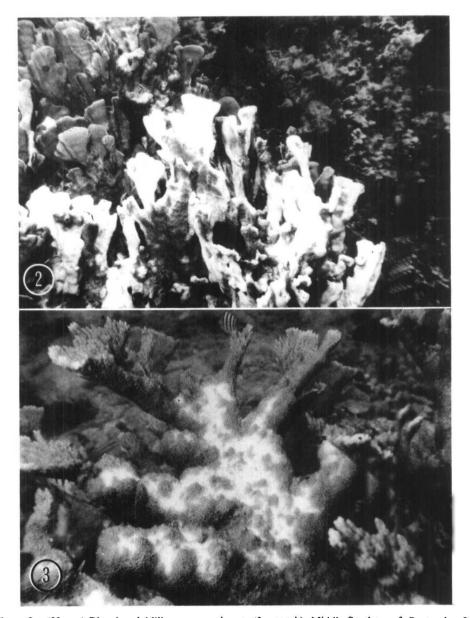


Figure 2. (Upper) Discolored *Millepora complanata* (Lamarck), Middle Sambo reef, September 26, 1973.

Figure 3. (Lower) Discolored *Acropora palmata* (Lamarck), Middle Sambo reef, September 26, 1973.

when cooler water temperatures returned (Shinn, 1966). Glynn (1968) reported massive mortalities among *Palythoa* and certain echinoids (*Tripneustes*, *Lytechinus*, and *Brissus*) at Caracoles reef flat, Puerto Rico, coincident with low tides at or near midday. Later observations revealed mortalities among corals of *Porites furcata* Lamarck, 1816 communities on the shallow reefs near Magueyes Island, Puerto Rico (Glynn, 1973). Loya (1972) reported scleractinian deaths on a reef flat in the Gulf of Eilat when synergistic meterological and astronomical

factors caused emergence of the reef flat during the heat of the day. Jokiel and Coles (1974), Coles (1975), Purkerson (1973), and Jones et al. (1976) reported thermal addition from power plant cooling water discharge caused zooxanthellae expulsion and mortality among corals (in order cited, Kahe, Hawaii, [first two]; Card Sound, Florida; and Tanguisson, Guam.

Conversely, seasonal loss of zooxanthellae in *Oculina* sp. and *Solenastrea hyades* (Dana, 1846) caused by reduced temperature in North Carolina has been noted by J. M. Wells (personal communication). In vitro thermal tolerance studies on *Pocillopora damicornis* (Linné), *Montipora verrucosa* (Lamarck) and *Porites compressa* Dana from Hawaii and Eniwetok indicate these species will expel their zooxanthellae at temperature below 21°C (Coles, 1973). Hudson et al. (1976) postulated that chilled water and other undetermined factors caused the death of reef corals at Hen and Chickens patch reef, 3.4 km (1.8 nmi) off Plantation Key, Florida.

The reported expulsion mechanism is concentration of zooxanthellae in the absorptive region of the mesenterial filaments; rejection occurs via the coelenteron; in some cases, algae cells are ejected in wafts of mucus (Yonge and Nicholls, 1931; Coles, 1973).

Expulsion of zooxanthellae is thought to be caused by the same factors influencing coral tissue metabolism. Yonge and Nicholls (1931) state that lowered metabolism of the host caused by stress reduces the available supply of nutrients (primarily nitrites, nitrates, phosphates, sulfates, and CO₂) for algal symbionts. Mayer (1918), commenting on the toxic effect of heat on stony corals, felt that carbonic acid accumulation and pH alteration in tissues caused the mortality. Heat exposure increases viscosity of cellular protoplasm (Gunter, 1957). Coles (1973) noted temperature increases resulted in increased coral-zooxanthellae respiration, gross zooxanthellae photosynthetic production and reduction in gross production/respiration ratios in Hawaiian species of P. damicornis, M. verrucosa, and P. compressa. The ratio reduction was interpreted to indicate that some metabolic wastes were not being utilized in the photosynthetic process by the zooxanthellae. Muscatine (1971) offered several hypotheses regarding possible triggering mechanisms of zooxanthellae expulsion. He suggested that a decrease in space caused by atrophied host tissues during heat-salinity stresses may stimulate rejection of symbionts or that stressed coral tissues may limit availability of nutrients thus starving zooxanthellae. Yonge (1963) and Taylor (1973) suggested that nitrogen and phosphorus are the limiting factors governing zooxanthellae growth. Host tissues may secrete a specific substance or substances inhibiting the physiology of zooxanthellae, or to carry this somehwat further, the substance or substances may alter the zooxanthellae environment such that it becomes intolerable.

Stress-inducing conditions at Middle Sambo are believed to be the synergistic effect of low tides at or near midday coincident with calm wind conditions during the warmest time of year. The Key West area experiences a mixture of semi-diurnal and daily tides (U.S. Department of Commerce, 1972a). Tidal ranges at Middle Sambo are similar to those at Key West, 0.4 m (1.3 ft) and 0.5 m (1.8 ft) during spring tides; low tide occurs about 50 min and high tide about 62 min earlier than at Key West (S. Berkman, personal communication). Spring tide occurred September 12 and the autumnal equinox fell on September 23 (U.S. Department of Commerce, 1972a). Daylight tides at Key West, 17 to 24 September, are depicted in Figure 4.

There was a change in pattern from midday high tides to midday low tides from 17 to 22 September (Fig. 4); water level was below the mean low water reference

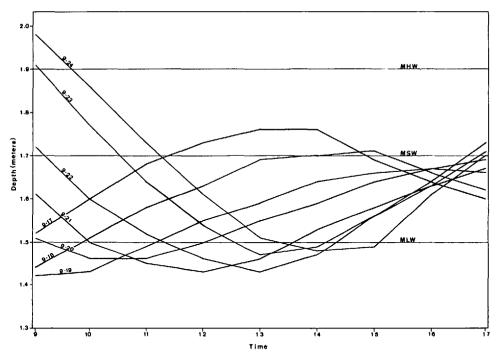


Figure 4. Tidal heights, 0900 to 1700 h, Key West, Florida, September 17 to 24, 1973. MHW: mean high water, MSW: mean standard water, MLW: mean low water. Source: NOS, NOAA.

mark (1.5 m) 50 to 67% of the midday period (1100 h to 1400 h) from 19 to 24 September. Tidal range is moderated by the equinox (Fairbridge, 1966); range was minimal, 0.23 m (9 in) on September 19 and 20. Lowest water levels (1.43 m) occurred at 1000 h (September 19), 1200 h (September 21), and 1300 h (September 22). Although the above data were reported from the Key West recording station located in the harbor area, a similar tidal range (with a time difference of one hour earlier) would not appreciably alter the tidal pattern at Middle Sambo.

Peak solar radiation is reported to occur from 0900 h to 1500 h in Florida and Jamaica (Barnes and Taylor, 1973). Hanson and Poindexter (1972) reported on several aspects of solar radiation near Pacific and Elbow reefs off Key Largo, Florida, during winter and spring of 1971. They found transmittance was greatest at solar noon; albedo was greater in early morning and late afternoon. Peak solar energy on the water surface occurred from 1000 h to 1400 h; most of the energy was expended in warming the water column.

United States Coast Pilot (U.S. Department of Commerce, 1972b) reports that mean surface water temperature for Key West is 29.7°C, prevailing winds are ESE, averaging 16.7 km/h, and a 66% potential for cloudless skies exists in September. Meterological data provided by the National Climatic Center (NOAA) for the Key West weather station (located 11.5 km, 310° from the affected reef) show air temperatures ranged from 25.0 to 31.6°C from 0900 h September 19, through 1700 h September 24, 1973. Maximum air temperature occurred at 1400 h on September 20 (Fig. 5). Wind direction was variable; hourly vectors for the same time period show ENE to ESE (67.6 to 112.5°) winds dominated 32.7% of the time. Wind has an important cooling effect on shallow reef flats and low velocities ranging from 0 to 25.9 km/h (mean = 11.3 km/h) prevailed at the time.

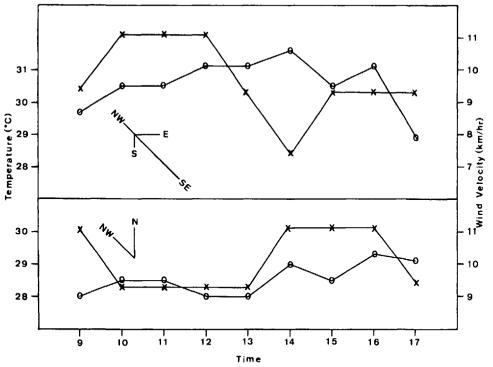


Figure 5. Air temperatures (O), wind velocities (X), and wind directions, 0900 to 1700 h, September 19 (bottom) and 20 (top), 1973. Source: National Climatic Center, Key West, weather station.

Glynn (1973) noted a rapid rise in seawater temperature during periods of low wind velocity. Mean Key West wind velocity from 19 to 24 September 1973 was 5.4 km/h less than the average value given in the U.S. Coast Pilot. Depression of midday air temperature noted for the time in question was partially the result of rain squalls.

I revisited Middle Sambo reef November 6, 1973, 6 weeks after the first observations. Most affected organisms had recovered their natural coloration; only Millepora complanata displayed minor symptoms of discoloration. Goreau (1964) noted Millepora required more than 14.5 weeks to regain its normal color; most other hermatypic organisms regained their normal complement of zooxanthellae in 6 to 10 weeks. Yonge and Nicholls (1931) reported 10.5 weeks for three species of Favia and one Goniastrea to regain their zooxanthellae after expulsion due to natural thermal stress.

Scleractinian reef corals are reported to flourish in temperatures of 25 to 29°C (Wells, 1956, 1957; Stoddart, 1969); however, under unusual conditions, some are reported to survive 40°C (Kinsman, 1964). Upper thermal limits were laboratory-determined for 18 species of Florida scleractinian corals (Mayer, 1914). Tolerance ranges for individual species were variable; Acropora palmata had a lethal temperature of 35.8°C; polyp movement ceased at 34.7°C. In a later study, Mayer (1918) reported Acropora muricata (=palmata?) succumbed to heat stress at 34.7°C. Coles (1973) determined the minimum thermal limits for M. verrucosa to be 18 to 19°C, and the maximum 31 to 32°C, with optimum growth and other optimum physiological vital signs occurring at 27 to 28°C. Shinn (1966) reported zooxanthellae expulsion from A. cervicornis at or near 33.8°C at Key Largo in

September. Wells (in Kinsman, 1964) believed 32°C was the maximum temperature tolerable for *Acropora*.

Water temperature of the Florida reef tract is warmest during August and September (Vaughan, 1918; Shinn, 1966; computerized summary of available oceanographic data in one degree square 41 within modified Canadian square 1110, National Ocean Data Center, NOAA, 1974). Vaughan (1918) summarized seawater temperature data for Florida reef tract lighthouses from 1879 to 1899; at Sand Key, 20.7 km west of Middle Sambo, September temperatures (averaged for 10-day periods) ranged from 28.7 to 31.4°C with a mean of 30.0°C. Smith et al. (1950) reported monthly seawater temperatures ranging from 24.35 to 29.8°C between July, 1945 and June, 1946 at Pacific Reef off Old Rhodes Key. During 1961, maximum temperature at Margot Fish Shoal, off Elliot Key, was 30.5°C (Jones, 1963).

The ecological repercussion of zooxanthellae expulsion would be a decrease in calcification rates of the corals. Zooxanthellae are able to affect the rate of skeletogenesis of hermatypic reef corals (Goreau, 1959; Goreau and Goreau, 1959, 1960a, 1960b; Pearse and Muscatine, 1971; Vandermeulen et al. 1972; and Muscatine, 1973). Light-enhanced calcification is directly photosynthesis-dependent (Vandermeulen et al. 1972). In situ calcium uptake experiments on *Manicina areolata* with and without zooxanthellae show that the rate of calcium uptake by colonies possessing zooxanthellae was 19 times greater than colonies void of zooxanthellae (Goreau and Goreau, 1959). In vitro experiments indicated calcification is inhibited by thermal stress (Coles, 1973; Jones et al. 1976). In *A. cervicornis* transplanted by Shinn (1966) growth rate (i.e. calcification) ceased when zooxanthellae were expelled, but resumed growth when zooxanthellae were regained.

When zooxanthellae are regained in 6 to 10 weeks, the effect on coral growth is probably minimal. Sublethal effects were noted for *Pocillopora meandrina* Dana exposed to 31+°C; most specimens returned to normal during lower ambient temperatures (Coles, 1975). However, in cases of chronic zooxanthellae loss, growth was inhibited. Other facets of the biology of the organisms were probably also affected. Yonge and Nicholls (1931) reported colonies lacking zooxanthellae were less able to remove sediment from their tissues than those having the algal symbionts. In cases where thermal addition from power plant discharge was continuous, mortalities occurred among stony corals near the discharge area due to the long term exposure (Jokiel and Coles, 1974; Coles, 1975; Jones et al. 1976).

Meterological and tidal information and other reports of zooxanthellae expulsion indicate that the most probable cause of expulsion at Middle Sambo was solar-thermal elevation of water covering the shallow reef flat. I subsequently observed some evidence of zooxanthellae expulsion at Sand Key during August, 1974. Such occasional reactions are probably not uncommon during late summer, when conditions are optimal for causing heat stress, but they are evidently of short duration with little long-lasting effect upon the reef cnidarian communities.

SUMMARY

On September 26, 1973, observations conducted on the shallow reef flat at Middle Sambo, near Key West, revealed varying degrees of discoloration among hermatypic reef organisms. Scleractinian reef corals, *Acropora palmata* (elk horn coral) and *Montastraea annularis* (common star coral), and the brachycnemian zooantharian *Palythoa* sp. displayed moderate discoloration; the hydrozoan fire coral *Millepora complanata*, exhibited a high degree of discoloration.

Affected organisms were viable, despite loss of dinoflagellate symbionts, Gymnodinium microadriaticum; polyps reacted upon tactile stimulation and Millepora dactylzooids discharged nematocysts. Observations 6 weeks later revealed almost complete recovery except for Millepora complanata.

Meterological and tidal data indicate the synergistic effect of low tides during midday from 19 to 24 September and high air temperature with variable low wind velocity produced elevated seawater temperature on the shallow reef flat, causing hermatypic organisms to expel zooxanthellae.

Such phenomena probably occur infrequently on shallow Florida Keys reefs, with little lasting effect.

NOTE ADDED IN PROOF: Gymnodinium adriaticum was recently transferred to Zooxanthella by Loeblich and Shirley (J. Mar. Biol. Ass. U.K., 59: 195).

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LITERATURE CITED

- Barnes, D. J., and D. L. Taylor. 1973. In situ studies of calcification and photosynthetic carbon fixation in the coral *Montastrea annularis*. Helgol. wiss. Meeresunters. 24: 78-81.
- Coles, S. L. 1973. Some effects of temperature and related physical factors on Hawaiian reef corals. Ph.D. dissertation. University of Hawaii, Honolulu, Hawaii. 133 pp.
- 1975. A comparison of effects of elevated temperature versus temperature fluctuations on reef corals at Kahe Point Oahu. Pac. Sci. 29: 15-18.
- Fairbridge, R. W. 1966. The encyclopedia of oceanography. Van Nostrand Reinhold Co., New York. 1,021 pp.
- Glynn, P. W. 1968. Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposure in Puerto Rico. Mar. Biol. (N.Y.) 1: 226-243.
- ——. 1973. Ecology of a Caribbean coral reef. The *Porites* reef—flat biotope: I. Meteorology and hydrography. Mar. Biol. (N.Y.) 20: 297–318.
- Goreau, T. F. 1959. The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. Biol. Bull. (Woods Hole) 116: 59-75.
- —. 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science (Wash. D.C.) 145(3630): 383-386.
- -, and N. I. Goreau. 1959. The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. Biol. Bull. (Woods Hole) 117: 239-250.
- ----. 1960a. The physiology of skeleton formation in corals. III. Calcification rate as a function of colony weight and total nitrogen content in the reef coral *Manicina areolata* (Linnaeus). Biol. Bull. (Woods Hole) 118: 419-429.
- ——. 1960b. The physiology of skeleton formation in corals. IV. On isotopic equilibrium exchanges of calcium between corallum and environment in living and dead reef-building corals. Biol. Bull. (Woods Hole) 119: 417–427.
- Gunter, G. 1957. Temperature. Pages 159-184 in J. Hedgepeth, Ed. Treatise on Marine Ecology and Paleoecology. Vol. I. Ecology. Geol. Soc. Am. Mem. 67. New York Lithographic Corp., New York.

- Hanson, K. J., and M. F. Poindexter. 1972. The solar irradiance environment of Florida coastal water during FLARE. NOAA Tech. Mem. ERL AOML 16: 32 pp.
- Hudson, H. J., E. A. Shinn, R. B. Halley, and B. Lidz. 1976. Sclerochronology: a tool for interpreting past environments. Geology (Boulder) 4: 361-364.
- Jokiel, P., and S. Coles. 1974. Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. Pac. Sci. 28: 1-18.
- Jones, J. A. 1963. Ecological studies of the southeastern Florida patch reefs. Part I. Diurnal and seasonal changes in the environment, Bull. Mar. Sci. Gulf Caribb. 13: 283-307.
- Jones, R. S., R. Randall, and M. Wilder. 1976. Biological impact caused by changes on a tropical reef. EPA 6001 3-76-027. Washington, D.C. 209 pp.
- Kinsman, D. 1964. Reef coral tolerance of high temperatures and salinities. Nature (Paris) 202(4939): 1280-1282
- Loya, Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. (N.Y.) 13: 100-123.
- Mayer, A. G. 1914. The effects of temperature upon tropical marine animals. Carnegie Inst. Washington Publ. Pap. Tortugas Lab. 6(183): 3-24.
- ——. 1918. Toxic effects due to high temperature. Carnegie Inst. Washington Publ. XII: 175-178. Muscatine, L. 1971. Endosymbiosis of algae and coelenterates. Pages 179-191 in H. M. Lenhoff, L. Muscatine, and L. V. Davis, eds. Experimental Coelenterate Biology. University of Hawaii Press. Honolulu. Hawaii.
- ——. 1973. Nutrition of corals. Pages 77-115 in O. A. Jones and R. Endean, eds. Biology and Geology of Coral Reefs, Vol. II. Biology 1. Academic Press, Inc., New York.
- National Oceanic and Atmospheric Administration. 1974. Unpublished computerized oceanographic data. National Oceanographic Data Center, Rockville, Md.
- Pearse, V., and L. Muscatine. 1971. Role of symbiotic algae (zooxanthellae) in coral calcification. Biol. Bull. (Woods Hole) 141: 350-363.
- Purkerson, L. 1973. Thermal pollution in lower Biscayne Bay, Florida. Unpublished report presented at the Thermal Ecology Symposium, May 3-5, 1973. Augusta, Georgia.
- Shinn, E. A. 1966. Coral growth rate, an environmental indicator. J. Paleontol. 40: 233-240.
- Smith, F. G. W., R. H. Williams, and C. C. Davis. 1950. An ecological survey of the subtropical inshore waters adjacent to Miami. Ecology 31(1): 119-146.
- Stoddart, D. R. 1969. Ecology and morphology of recent coral reefs. Biol. Rev. (Camb.) 44: 433-498.
- Taylor, D. L. 1973. The cellular interactions of algal-invertebrate sybiosis. Pages 1-44 in F. S. Russell and C. M. Yonge, eds. Adv. Mar. Biol. XI. Academic Press, New York.
- U.S. Department of Commerce. 1972a. Tide tables high and low predictions 1973 east coast of North and South America, including Greenland. Washington, D. C. 288 pp.
- ——. 1972b. United States coast pilot 4, 10th ed.—1972. Atlantic coast, Cape Henry to Key West. Washington, D.C. 230 pp.
- Vandermeulen, J. H., D. Davis, and L. Muscatine. 1972. The effect of inhibitors of photosynthesis on zooxanthellae in corals and other invertebrates. Mar. Biol. (N.Y.) 16: 185-191.
- Vaughan, T. W. 1911. Recent Madreporaria of southern Florida. Carnegie Inst. Washington Year Book 8: 135-144.
- Wells, J. W. 1956. Scleractinia. Pages F328-443 in R. C. Moore, ed. Treatise on Invertebrate Paleontology. Pt. F. Coelenterata. Geol. Soc. Am. Univ. Kansas Press, Lawrence, Kansas. ———. 1957. Corals. Pages 1087-1104 in J. Hedgpeth, ed. Treatise on Marine Ecology and Paleo-
- ecology. Vol. 1. Ecology. Geol. Soc. Am. Mem. 67. New York Lithographic Corp., New York. Yonge, C. M. 1963. The biology of coral reefs. Pages 209–260 in F. S. Russel, ed. Advances in
- Marine Biology. I. Academic Press, New York.

 —, and A. G. Nicholls. 1931. Studies on the physiology of corals. V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. Sci. Rep. Great Barrier Reef Exped. 1928–1929 1(7): 177–211.
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