

Thermal Tolerance in Tropical versus Subtropical Pacific Reef Corals¹

STEPHEN L. COLES,² PAUL L. JOKIEL,³ AND CLARK R. LEWIS⁴

ABSTRACT: Upper lethal temperature tolerances of reef corals in Hawaii and at Enewetak, Marshall Islands, were determined in the field and under controlled laboratory conditions. Enewetak corals survived *in situ* temperatures of nearly 34° C, whereas 32° C was lethal to Hawaiian corals for similar short-term exposures. Laboratory determinations indicate that the upper thermal limits of Hawaiian corals are approximately 2° C less than congeners from the tropical Pacific. Differences in coral thermal tolerances correspond to differences in the ambient temperature patterns between geographic areas.

REEF CORALS are generally considered to be stenothermic (Mayer 1914, Vaughan and Wells 1943, Wells 1957), with relatively fixed upper and lower lethal temperature limits (Mayer 1918). Yet some corals have been reported to survive temperature extremes in nature well beyond the limits established by classical experiments (Gardiner 1903, Wood-Jones 1910, Yonge and Nicholls 1931, Orr and Moorhouse 1933, Motoda 1940, Kinsman 1964, MacIntyre and Pilkey 1969). Sufficient data exist (Mayer 1918; Edmondson 1928; Jokiel et al., in press) to suggest geographic differences in coral thermal tolerance, although preliminary studies, both classical (Mayer 1918) and recent (Jones and Randall 1973), have not confirmed this possibility. Unfortunately, comparison of existing data is difficult because of incomplete information concerning the temperature environments of corals under natural conditions and because of differences in experimental techniques applied by different researchers.

The purpose of the present investigation was twofold: to measure the intensity and duration of maximum natural temperature elevations among living corals on tropical and subtropical reefs, and to compare upper thermal limits of tropical and subtropical corals under identical experimental conditions.

METHODS

Studies were conducted at Enewetak (Eniwetok) Atoll, Marshall Islands, and Kaneohe Bay, Oahu, Hawaii. Seven stations were established at Enewetak among living corals in the shallow waters off Igurin (Glenn) Island. Four of these stations were located on the leeward ocean reef flat, and the remaining three on the lagoon side of the island. Continuously recording thermographs and maximum-minimum thermometers recorded temperature among the corals at each station between 29 August and 3 September 1974. Mortality and condition of corals at each station were observed and compared with temperature conditions that had occurred during the observation period.

Upper lethal temperatures of Enewetak and Hawaiian corals were experimentally determined in 16-liter plastic aquaria flushed with continuous flows of temperature-regulated seawater. Temperatures were maintained with quartz-glass resistance heaters regulated by proportional controllers and by adjustments of the flow rates. Temperature in each aquaria

¹ Hawaii Institute of Marine Biology contribution no. 483. This study was partially funded by U.S. Environmental Protection Agency grant R800906, Atomic Energy Commission contract AT(26-1)-628 to the Mid-Pacific Marine Laboratory, and by the Hawaiian Electric Company, Inc. Manuscript received 25 April 1975.

² Hawaiian Electric Company, Inc., Environmental Department, Post Office Box 2750, Honolulu, Hawaii 96803.

³ University of Hawaii, Hawaii Institute of Marine Biology, Post Office Box 1346, Kaneohe, Hawaii 96744.

⁴ University of Hawaii, Hawaii Institute of Marine Biology, Post Office Box 1346, Kaneohe, Hawaii 96744.

was monitored continuously with a scanning thermistor tele-thermometer and recorder. Residence time of water within the containers was very short (4–8 minutes), dissolved oxygen was maintained at near saturation by constant aeration, and a natural daylight regime was used. Therefore, detrimental effect of factors other than heat stress were minimized. The same apparatus and procedures were used in experiments conducted by the same investigators within a few weeks of each other at the two locations, thereby reducing any chance of differences between Enewetak and Hawaiian results due to experimental procedure.

Two thermal stress experiments were conducted at each location. In the first, corals were collected and allowed to acclimate overnight at ambient temperature in the aquaria. Temperatures were then raised at a rate of 2° C/hr until desired test temperatures were reached. The specified temperatures were then held to the end of the experiment. In the second experiment, corals were collected and acclimated as before. The temperature was then raised to 34° C within 10–20 minutes, held for 3 hours, and then lowered again to ambient. At Enewetak, this stress cycle was repeated six times, with 6-hour ambient holding periods intervening between cycles. In Hawaii, extensive damage to the corals occurred on the first cycle, so only two 34° C cycles were imposed, separated by 14 hours at ambient.

RESULTS AND DISCUSSION

Monthly mean seawater temperatures at Enewetak are 2°–5° C higher than Hawaii throughout the year (Figure 1). This study was conducted in late summer, when ambient temperatures at both locations were maximal. Tidal range at Enewetak was high during the period of field measurements, with low tide occurring near midday. These factors, together with calm, sunny weather, produced extreme temperature elevations on the shallow reef flats. Enewetak ambient open-ocean water temperature at the time of the survey was approximately 29.5° C.

The reef flat coral fauna and zonation were very similar to those reported for Bikini Atoll

(Wells 1954). *Acropora* (*A. delicatula* and *A. palmerae*) was dominant, and *Pocillopora*, as well as microatolls of *Porites*, were common. *Leptastrea*, *Millepora*, and *Heliopora* were also present. *Pocillopora*, *Porites*, and *Millepora* were found at the three lagoon stations, but *Acropora* was conspicuously absent.

At the most shoreward reef-flat station, which represented the boundary of coral growth, water circulation was cut off during midday low tides. The temperature here exceeded 34° C for 1–2 hours at low tide, killing many corals. Inside of this station, where no corals occurred, temperatures above 36° C were measured. At the other ocean reef-flat stations, the temperature generally held at 31°–32° C for a several hour period at low tide, with occasional short-term increases to as much as 34° C. Minimum water temperature reached 27° C during periods of low tide at night. Minimum and maximum temperature extremes measured during this study were as much as 2° C greater than those measured previously by Wells (1951) in equivalent zones during the month of June at Arno Atoll, Marshall Islands, and variation was also greater. On one occasion a midday storm decreased the temperature to a low of 25.5° C which, after the storm, rose to 32° within 1 hour.

The death of coral along the inner margin of the coral zone on the reef flat suggests that we observed near-lethal natural conditions of temperature on the reef. Because most of the corals that died were not exposed to air at low tide, we attributed their death to prolonged exposure at 34° C. Also, much of the coral on the ocean reef that was subjected to brief exposures to 34° C lost zooxanthellar pigment, indicating severe thermal stress (Yonge and Nicholls 1931, Jokiel and Coles 1974). Branches of *Acropora* that extended above the minimum low tide level were probably damaged more by dessication (Mayer 1918, Edmondson 1928) than by high temperature. The air temperature during midday low tide was substantially lower (28.5° C) than the water temperature (32° C).

Temperature variations on the lagoon reefs, which did not uncover at low tide, were more moderate, but longer periods of temperature elevation occurred. At one lagoon station a

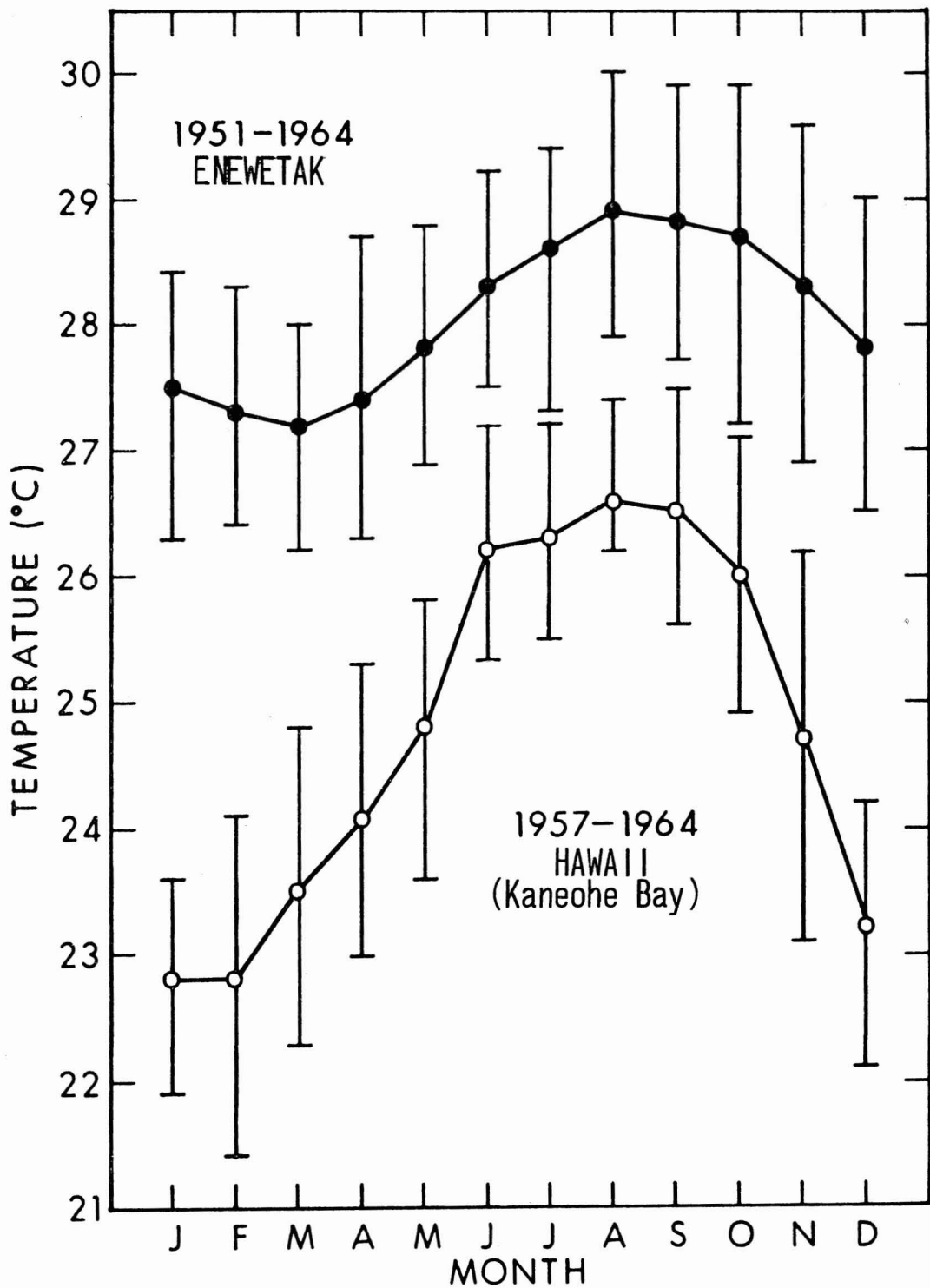


FIGURE 1. Monthly mean surface water temperatures for Kaneohe Bay, Oahu, and Enewetak Atoll, Marshall Islands (U.S. Coast and Geodetic Survey 1965). Upper and lower limits represent monthly mean maxima and minima.

temperature of 32° C held for nearly 6 hours on 31 August. On other days, temperatures ranged to 30°–31° C during midday maxima for up to 8 hours. No damage to corals occurred at the lagoon stations.

Similar *in situ* thermograph studies on a Hawaiian reef subjected to thermal enrichment from a power generating station (Jokiel and Coles 1974, Coles 1975) have shown that prolonged exposure to temperatures above 30° C is sublethal to common Hawaiian corals and that temperatures above 32° C are lethal. In contrast, such extremes were tolerated by similar Enewetak species. In Hawaii, the highest natural water temperature that we have measured over several summers among living corals on the shallow and protected Coconut Island reef flat of Kaneohe Bay was approximately 30° C during clear, calm summer periods of midday spring low tides. Several hours of exposure to this temperature did not kill corals. On two occasions, Maragos (1972) observed temperatures of 32° C on the shallow Kaneohe Bay barrier reef that appeared to be lethal to Hawaiian corals (*Fungia scutaria* and *Pocillopora meandrina*). Exposures to naturally occurring temperatures of 32° C did not harm corals at Enewetak.

Because other detrimental factors (low dissolved oxygen, altered salinity, etc.) often co-occur with high natural temperatures in the field, the *in situ* observations are not conclusive, this fact necessitating use of controlled laboratory experiments.

Results (Table 1) verify that Enewetak corals can withstand substantially higher absolute temperatures than can their Hawaiian congeners. A mean temperature of 32.4° C killed most Hawaiian species tested, with 31.3° C being clearly detrimental, producing substantial loss of zooxanthellae and some tissue damage and coral mortality. The same temperatures at Enewetak for similar exposure periods produced little or no damage. Corals at 31.6° C remained pigmented and were often observed to have expanded polyps. Slight damage was noted at 32.7° C, suggesting that this temperature approaches a critical value. Mortality was nearly complete at 35° C, although one *Porites lutea* survived this treatment.

Results from the thermal shock experiment

showed an even greater difference in the ability of corals from the two areas to withstand thermal stress. At Enewetak, all species tested survived six cycles of 34° C exposure. *Pocillopora elegans* and *Acropora formosa* showed slight tissue damage by the end of the experiment, while *Porites lutea* and *Acropora hyacinthes* were undamaged. By contrast, one cycle to 34° C in Hawaii killed *P. meandrina* and damaged *Pocillopora damicornis*, *Porites lobata*, and *Montipora verrucosa*. A second cycle killed one to two specimens of each of these species. *Fungia scutaria* was moderately affected, with one specimen losing pigmentation.

These results indicate that in both subtropical and tropical environments large populations of corals are exposed to temperatures precariously close (within 1° to 2° C) to their upper lethal limit during the summer months. High temperature alone can account for the exclusion of corals from some shallow inshore areas. Mean summer ambient water temperature at Enewetak is approximately 2° C higher than it is in Hawaii (Figure 1), and a corresponding difference of about 2° C was observed between the two locations for upper lethal temperature, upper sublethal temperature, and maximum reef flat temperature among living corals. At both locations, increases of +2° C above annual maxima appear to produce sublethal effects, while an increase of +4 to +5° C is lethal to most coral species.

The primary purpose of this research was to reexamine Mayer's (1918) conclusion that subtropical species of corals do not differ from tropical species in upper thermal tolerance. Mayer did not base his conclusion on data from the same species. Therefore, for purposes of this study it was important to use common, shallow-water species which occurred where *in situ* temperature data were taken at each location, even though different species were present at the two locations. It is possible, however, for one to evaluate the species effect using our data along with data taken from the classical literature. Upper lethal limits for the widely distributed coral *Pocillopora* are available from a number of geographic localities. The taxonomy of this genus is confused, and it has been suggested that *Pocillopora damicornis*, *danae*, *verrucosa*, *meandrina*, *elegans*, *brevicornis*, *lobilifera*,

TABLE 1

SURVIVAL OF CORAL SPECIMENS TO TEMPERATURE ELEVATIONS AT ENEWETAK AND HAWAII

Temperature (°C)*	ENEWETAK											
	29.1			31.6			32.7			35.6		
	96			93			60			10		
Exposure Time (hrs)	N	I	D	N	I	D	N	I	D	N	I	D
Condition†												
<i>Pocillopora elegans</i>	3			3			2	1				3
<i>Acropora hyacinthes</i>	2	1		2	1		2	1				3
<i>Acropora formosa</i>	3			1			2	1				1
<i>Porites lutea</i>	1	1		3			3				1	1
<i>Fungia scutaria</i>	1			1			1	1				1
Totals	10	2	0	10	1	0	10	4	0	0	1	9

Temperature (°C)*	HAWAII								
	27.1			31.3			32.4		
	96			95			50		
Exposure Time (hrs)	N	I	D	N	I	D	N	I	D
Condition†									
<i>Pocillopora meandrina</i>	3				1	2			3
<i>Pocillopora damicornis</i>	3			1	2			1	2
<i>Montipora verrucosa</i>	3				3				3
<i>Porites lobata</i>	3				3				3
<i>Fungia scutaria</i>	3			3				2	1
Totals	15	0	0	4	9	2	0	3	12

NOTE: Numbers in body of table represent individual colonies.

* Standard errors of mean temperatures are less than 0.1° C based on hourly samplings.

† N, normal pigmentation and good condition; I, intermediate condition with loss of pigmentation and/or tissue; D, death.

and others probably are part of a continuous series that might represent a single species (Vaughan 1907: 100; 1918: 78; Crossland 1952: 109). Figure 2 shows all available data on the upper temperature tolerance of three species of *Pocillopora* from Hawaii and from tropical areas in the Pacific Ocean. Survival time for both Hawaiian and tropical *Pocillopora* shows a highly significant ($P < 0.01$) decreasing exponential relationship with temperature. Analysis of covariance indicates no significant difference between the slopes of the two regression lines ($P < 0.50$; $F = 0.039$, $df = 1, 12$) but a highly significant ($P < 0.01$; $F = 58.97$, $df = 1, 13$) difference between their ele-

vations. The 2° difference in temperature tolerance between Hawaiian and tropical corals indicated by the present study is substantiated throughout the temperature range for these combined data.

This analysis indicates that the natural temperature environment at a geographic location is far more important than taxonomic distinctions based on minor structural differences in determining coral temperature tolerance. Although *Pocillopora damicornis* appears to be slightly more tolerant of elevated temperatures than are *P. meandrina* in Hawaii or *P. elegans* in the tropics, it does follow the same temperature-survival time relationship.

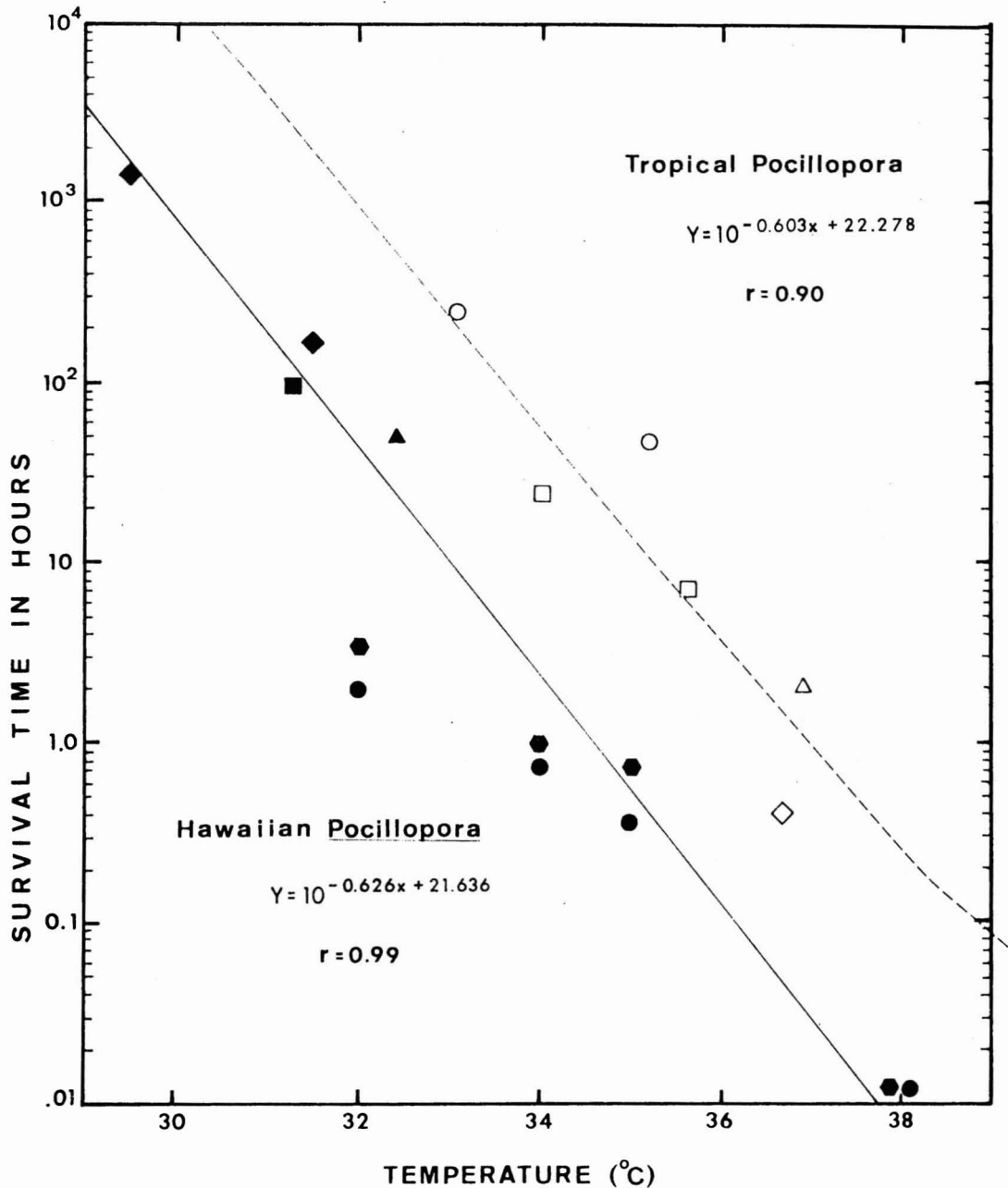


FIGURE 2. Semilogarithmic plot of temperature versus survival time, in hours, for Hawaiian and tropical Pacific *Pocillopora*. The data have been taken from six sources, as follows. 1. Edmondson 1928, Hawaii: solid circle, *Pocillopora meandrina*; solid hexagram, *P. cespitosa* (sny. *P. damicornis*). 2. Mayer 1918, Great Barrier Reef, Australia: open triangle, *P. bulbosa* (sny. *P. damicornis*). 3. Mayor 1924, American Samoa: open diamond, *P. damicornis*. 4. Jones and Randall 1973, Guam: open circle, *P. damicornis*. 5. Jokiel et al., in press, Hawaii: solid diamond, *P. damicornis*. 6. Present study: Enewetak, open square, *P. elegans*; Hawaii, solid triangle, *P. damicornis*; Hawaii, solid square, *P. meandrina*.

The regression calculated for Hawaiian *Pocillopora* excludes the Edmondson (1928) data at 32° C. Edmondson's experiments were conducted in closed containers in which accumulated toxic metabolites probably biased experiments lasting 1 or more hours. Such artifacts were eliminated by use of an open system in the present and other recent studies (Jokiel et al., in press).

Tropical *P. damicornis* is clearly more thermally tolerant than is its subtropical Hawaiian counterpart.

These results contradict the classical concept (Mayer 1918) that a fixed physiological boundary determines coral upper lethal temperature limits, and that corals from different geographic locations subjected to different temperature regimes have the same upper thermal limit. Studies on the effect of temperature on calcification (Clausen 1972) and carbon fixation (Coles 1973) in the same species of Enewetak and Hawaiian corals have shown physiological differences in corals from the two regions. These studies provide insight into possible mechanisms responsible for the observed differences in lethal limit.

It may be assumed that the predecessors of Hawaiian corals, being derived from the tropical Indo-Pacific fauna (Ekman 1953), were originally resistant to high temperature stress. However, water temperatures in Hawaii seldom naturally exceed 30°, but do undergo larger annual fluctuations at a lower temperature range than in the tropics. The process which has enabled establishment of reef corals in Hawaiian waters has apparently reduced the capability of many species to withstand temperatures above 30° C. It remains to be demonstrated whether the observed differences in thermal tolerance at the two locations result from selective processes acting on many generations, or whether temperature resistance in corals can be changed by physiological acclimatization to gradual increases in temperature over long time periods.

LITERATURE CITED

- CLAUSEN, C. 1972. Factors affecting calcification processes in the hermatypic corals *Pocillopora damicornis* and *Porites compressa*. Ph.D. Thesis. Loma Linda University, Loma Linda, California. 95 pp.
- COLES, S. L. 1973. Some effects of temperature and related physical factors on Hawaiian reef corals. Ph.D. Thesis. University of Hawaii, Honolulu. 133 pp.
- . 1975. A comparison of effects of elevated temperature versus temperature fluctuations on reef corals at Kahe Point, Oahu. Pac. Sci. 29(1): 15–18.
- CROSSLAND, C. 1952. Madreporaria, Hydrocorallinae, Heliopora, and Tubipora. Great Barrier Reef Expedition 6: 86–257. British Museum (Natural History).
- EDMONDSON, C. H. 1928. The ecology of an Hawaiian coral reef. Bull. Bernice Bishop Mus. 45. 64 pp.
- EKMAN, S. 1953. Zoogeography of the sea. Sidgwick & Jackson, London. 417 pp.
- GARDINER, J. S. 1903. The fauna and geography of the Maldive and Laccadive Archipelagoes. Vol. 1. At the University Press, Cambridge. 471 pp.
- JOKIEL, P. L., S. L. COLES, E. B. GUINTEHER, G. S. KEY, S. V. SMITH, and S. J. TOWNSELY. In press. Effects of thermal loading on the Hawaiian nearshore marine biota. U.S. Environmental Protection Agency, final report of project no. 18050 DDN.
- JOKIEL, P. L., and S. L. COLES. 1974. Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. Pac. Sci. 28(1): 1–18.
- JONES, R. S., and R. H. RANDALL. 1973. A study of biological impact caused by natural and man-induced changes on a tropical reef. Univ. Guam Mar. Lab., Tech Rep. 7. 184 pp.
- KINSMAN, D. J. J. 1964. Reef coral tolerance of high temperatures and salinities. Nature 202: 1280–1282.
- MACINTYRE, I. G., and O. H. PILKEY. 1969. Tropical reef corals: tolerance of low temperatures on the North Carolina continental shelf. Science 166: 374–375.
- MARAGOS, J. E. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. Thesis. University of Hawaii, Honolulu. 290 pp.
- MAYER, A. G. 1914. The effects of temperature on tropical marine animals. Carnegie Inst. Washington Publ. 183: 3–24.
- . 1918. Ecology of the Murray Island coral reef. Carnegie Inst. Washington Publ. 213: 3–48.
- MAYOR, A. G. 1924. Structure and ecology of Samoan reefs. Carnegie Inst. Washington Publ. 340: 1–25.
- MOTODA, S. 1940. The environment and the life of massive coral, *Goniastrea aspera* Verrill inhabiting the reef flat in Palao. Palao Trop. Biol. Sta. Stud. 2: 61–104.

- ORR, A. P., and F. W. MOORHOUSE. 1933. Variations in physical and chemical conditions on and near Low Isles Reef. *Sci. Rep. Great Barrier Reef Exped.* 2(4): 87-98.
- U.S. COAST AND GEODETIC SURVEY. 1965. Publ. no. 31-3 (revised). U.S. Government Printing Office, Washington, D.C.
- VAUGHAN, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. *U.S. Nat. Mus., Bull.* 59. ix+427 pp.
- . 1918. Some shoal-water corals from Murray Island, Cocos-Keeling Islands and Fanning Island. Pages 51-234 *in* Carnegie Inst. Washington Publ. 213.
- VAUGHAN, T. W., and J. W. WELLS. 1943. Revision of the suborders, families and genera of the Scleractinia. *Geol. Soc. Am., Spec. Pap.* 44. 363 pp.
- WELLS, J. W. 1951. The coral reefs of Arno Atoll. *Atoll Res. Bull.* 9: 1-13.
- . 1954. Recent corals of the Marshall Islands. *U.S. Geol. Surv., Prof. Pap.* 260-I: 385-486.
- . 1957. Coral reefs. Pages 609-632 *in* J. W. Hedgepeth, ed. *Treatise on marine ecology and paleoecology*. Vol. 1. *Geol. Soc. Am., Mem.* 67. 1296 pp.
- WOOD-JONES, F. 1910. *Corals and atolls*. Lovell Reeve & Co., London. 392 pp.
- YONGE, C. M., and A. G. NICHOLLS. 1931. Studies on the physiology of corals. IV. The structure, distribution and physiology of zooxanthellae. *Sci. Rep. Great Barrier Reef Exped.* 1(6): 135-176.