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Effects of Temperature on Photosynthesis and Respiration in Hermatypic Corals*

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Abstract

Photosynthesis and respiration rates of the reef corals *Pocillopora damicornis* (Linn.), *Montipora verrucosa* (Lamarck), *Porites compressa* Dana and *Fungia scutaria* Lamarck were measured under controlled temperatures. Results indicate that coral metabolism is closely adapted to ambient temperature conditions. Tropical corals measured at Enewetak, Marshall Islands, showed greater primary production compared to maintenance requirements at elevated temperatures than did subtropical varieties of the same species in Hawaii. Photosynthesis:respiration (P:R) ratios were significantly and negatively related with temperature between 18° and 31°C for all Hawaiian corals, whereas at Enewetak this ratio generally showed a curvilinear relationship for this temperature range. Extrapolations of P:R regressions on temperatures to a value of 2.0 (estimated as a minimum required for long-term functional autotrophy) coincide for Hawaiian specimens with published upper lethal temperatures. Extrapolation of P:R regressions for Enewetak specimens at temperatures above 25°C suggests lethal temperatures for these corals to be 2 to 5 C° higher than for Hawaiian corals, in good agreement with recent experimental findings. Interspecific differences in P:R temperature regressions for Hawaiian corals correlating with upper lethal temperature tolerances are described.

Introduction

The first obvious symptom of temperature stress acting upon reef corals is the disruption of the symbiotic association between animal tissue and intracellularly contained zooxanthellae, ending with rapid expulsion of the symbiont. (Yonge and Nicholls, 1931; Jones and Randall, 1973; Jokiel and Coles, 1974, 1977). Little is known about temperature-related metabolic changes which may precede this disruption. Direct linear relationships between metabolic processes and temperature are well established for poikilotherms, and can be assumed to apply directly to reef corals. However, the comparative effects of temperature on zooxanthellar photosynthesis versus coral-algal respiration have never been investigated. Assuming the relationship between the coral and its symbiont to be a functional one, it is probable that an

inability by the coral to maintain normal rates of production compared to respiration would be an important factor leading to destruction of the symbiotic association under thermal stress.

Although reef corals as a group are generally considered to be stenothermic (Wells, 1957), the ambient temperature regimes of different geographic areas where the same species of corals occur can differ quite distinctly. For example, mean monthly temperatures of unrestricted surface lagoon water at Enewetak (formerly Eniwetok) Atoll, Marshall Islands exceeded monthly mean surface temperatures in Kaneohe Bay, Hawaii by 2 to 5 C° (Coles et al., 1976). The Enewetak August average maximum temperature (30°C) is 9 C° higher than the Kaneohe Bay February average minimum (21°C). Moreover, in areas of restricted circulation, temperature differences between Enewetak and Hawaii are even more extreme than these values and still support rich coral growth. Such differences suggest the possibility that the corals resident in the two areas have become physiological-

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ly adapted to different temperature regimes. However, little information is available for reef corals concerning possible metabolic differences related to different temperature environments.

This study describes acute responses of photosynthetic and respiration rates to temperature change for 4 coral species in Hawaii and for 2 of these species at Enewetak. The relationship between photosynthesis:respiration ratios and temperature is compared between experimental locations and evaluated in regard to known critical temperatures for survival of reef corals.

Materials and Methods

Oxygen production under constant light and respiration in darkness by corals was measured during daylight hours in a closed system containing 800 to 900 ml of sea water. Temperatures were controlled by enclosing experimental chambers in a water jacket through which fresh water was circulated at desired temperatures. Experimental chambers and water jacket were constructed of clear Plexiglass and silicone rubber. Water within the chambers was mixed with magnetic stirrers.

The apparatus was held in a box 60 cm square x 35 cm deep, the inside of which had been painted white to promote back-reflection of light during photosynthesis experiments. Ambient light was excluded by closing the open side of the box with black plastic sheeting. Light was provided during photosynthesis measurements by two 150 W incandescent floodlights held 15 cm above coral chambers. The lights emitted considerable heat, which was reduced by a Plexiglass enclosure through which a shield of fresh water 3.5 cm thick continually circulated between the lights and the coral chambers. Light reaching corals in the chambers was measured with a Yellow Springs Instruments (YSI) Model 65 Radiometer. Incident light in the chambers was 2×10^{-2} g-cal $\text{cm}^{-2} \text{sec}^{-1}$, comparable to natural midday surface light intensities in Hawaii. Spectral distribution of radiant energy for the incandescent light was not measured, but available information (Instrumentation Specialties Co., 1972) indicates spectral quality of incandescent light to differ drastically from natural sunlight. Although use of an artificial light source precludes unequivocal extrapolation of laboratory results to natural conditions, such use insured replicability of light intensity and quality among temperature treatments.

Dissolved oxygen concentrations within the experimental chambers were continuously measured with a YSI Model 54A Oxygen Meter, which utilizes a Clark-type polarographic probe (Clark et al., 1953). The instrument was calibrated as per manufacturer's specifications before each run, using sea water saturated with air at the temperature of the chamber sea water. Results were continuously recorded with a YSI Rustrak recorder. Changes in O_2 concentrations indicated linear responses with time and were converted to mg O_2 produced or consumed by multiplying $\text{O}_2 \text{ l}^{-1}$ values by the volume in liters of sea water contained by the experimental chambers.

In the Hawaii experiments, sea water pumped from Kaneohe Bay was passed through 3 Cuno "Aqua Pure" filters to remove particulate matter. Experiments performed at Enewetak used water directly from the laboratory sea water system. Starting temperatures for experiments conducted at both Hawaii and Enewetak approximated the daytime ambient water temperatures at the time of the measurements (Hawaii = 24°C , Enewetak = 28°C). Temperatures were raised or lowered between runs by introducing sea water at the new temperature while simultaneously draining chamber water used at the previous temperature. Sufficient water to flush the chamber at least twice was passed through the system in reaching new temperatures. Temperatures of introduced water had previously been altered from ambient by storing in a freezer or by heating with a glass-enclosed resistance heater. Rates of temperature change between experiments did not exceed $0.5 \text{ }^\circ\text{C min}^{-1}$.

Temperatures of sea water within the coral chambers were measured at the beginning and end of each individual run with the YSI oxygen probe thermister. Temperature was maintained at $\pm 0.5 \text{ }^\circ\text{C}$ of listed values for all runs. The temperature sequences used were as follows: Hawaii: 24° (ambient), 21° , 18° , 24° (ambient check), 26° , 28° and 31°C ; Enewetak: 28° (ambient), 31° , 28° (ambient check), 25° , 22° and 19°C .

Experiments were performed on 3 to 4 specimens each of *Pocillopora damicornis* (Linn.), *Montipora verrucosa* (Lamarck), *Porites compressa* Dana and *Fungia scutaria* Lamarck in Hawaii, and these experiments were replicated on *Pocillopora damicornis* (4 specimens) and *M. verrucosa* (3 specimens) at Enewetak. Corals were collected from shallow (0.5 to 2.0 m) depths and transported with minimum disturbance to the laboratory. Specimens showing any indication of tissue damage were rejected from experimentation. Experimental speci-

mens were maintained in the shade in flowing sea water for 1 to 7 days until time of experiment. Experimental results showed no apparent relationships with pre-experiment holding time or time of day of experiment. Additional supplementary experiments were conducted on *Pocillopora damicornis* in Hawaii to examine effects of chamber confinement, time of day, and temperature sequence. Negligible changes in P and R occurred during alternating 30 min light and dark periods at constant temperature ($23.5^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$), for a total of 6 h. Bacterial respiration (see also Franzisket, 1970) and temperature sequence in Hawaii were also found to be negligible factors. Temperature sequence was important at Enewetak, however, where temperatures below 21°C produced considerable expulsion of zooxanthellae. The different temperature sequence at Enewetak was therefore chosen to impart as little stress from experimental manipulation as possible.

A typical experimental series proceeded as follows: after rapid transfer to an experimental chamber, corals were acclimated 0.5 to 1 h in stirred, ambient-temperature sea water. The chamber lid was then fastened, taking care to exclude air bubbles, and a volume of ambient-temperature sea water sufficient to renew the chamber twice was passed through the chamber. The oxygen production in light and respiration in dark of the coral was measured for 10 to 40 min periods; light and dark runs were alternated. All measurements were made at dissolved oxygen concentrations between 80 and 100% of saturation. Following determinations at ambient temperature, water temperature in the chamber was changed as described above, at least 15 min allowed for the coral to accommodate to the new temperature, and the runs repeated. Duplicate runs in light and dark were made at each temperature for all Hawaii specimens and at intermediate temperatures at Enewetak; measurements at upper and lower extreme temperatures at Enewetak were based on individual runs.

Results

The oxygen produced in light and measured by this method is only a partial estimate of photosynthetic production at any temperature. Actual photosynthetic rates (P) are here estimated by summing oxygen production measured in light with oxygen consumption or respiration (R) measured in darkness, assuming equivalent light and dark respiration rates. Drew (1973) has substantiated this approach by

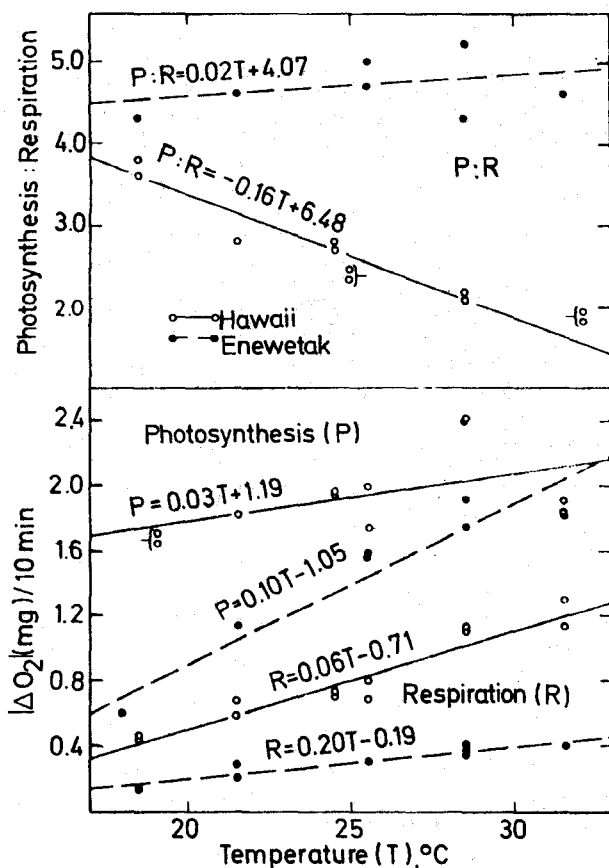


Fig. 1. *Pocillopora damicornis*. Linear regressions of respiration (R), photosynthesis (P) and P:R ratio on temperature for a Hawaiian and an Enewetak specimen. Significance levels of regression coefficients are given in Table 1

finding good agreement between production estimated by this method and carbon 14 measurements of reef coral photosynthesis under field conditions.

A comparison of results for single specimens of *Pocillopora damicornis* in Hawaii and Enewetak is shown in Fig. 1. The patterns shown are typical of results obtained at the two locations. For the Hawaiian specimen, P and R show similar positive regressions with temperature. A constant ratio between these parameters (P:R) is not maintained with increasing temperature for the Hawaiian specimen, but rather P:R decreases significantly ($P < 0.001$). By contrast, for the Enewetak specimen, the positive regression of P with temperature is substantially greater than the regression of R. Consequently, the regression of P:R shows a slightly positive, although not significant, relationship with temperature.

The regressions of P, R and the P:R ratio on temperature were calculated for

Table 1. Coefficients of linear regression of production and respiration on temperature for Hawaii and Enewetak corals. SE: standard error. ** = regression highly significant ($P < 0.01$); * = significant ($P < 0.05$); ns = P 0.10. nd: no data

Species	Production		Respiration	
	Hawaii	Enewetak	Hawaii	Enewetak
<i>Pocillopora damicornis</i>	0.059**	0.15**	0.071**	0.056**
	0.059**	0.14**	0.084**	0.039**
	0.030 ns	0.10**	0.061**	0.020**
	0.060*	0.070**	0.051**	0.018**
$\bar{x} \pm SE$	0.052 \pm 0.007	0.115 \pm 0.018	0.066 \pm 0.007	0.033 \pm 0.009
<i>Montipora verrucosa</i>	0.025**	0.033**	0.019**	0.011**
	0.040**	0.030**	0.034**	0.014**
	0.045**	0.040**	0.021**	0.024*
	0.052**			
$\bar{x} \pm SE$	0.040 \pm 0.006	0.034 \pm 0.003	0.025 \pm 0.003	0.016 \pm 0.004
<i>Porites compressa</i>	0.070**	nd	0.055**	nd
	0.070*		0.055**	
	0.070**		0.051**	
	0.039**		0.046**	
$\bar{x} \pm SE$	0.062 \pm 0.008		0.052 \pm 0.002	
<i>Fungia scutaria</i>	0.052**	nd	0.034**	nd
	0.030*		0.019**	
	0.034**		0.029**	
$\bar{x} \pm SE$	0.038 \pm 0.007		0.027 \pm 0.004	

each specimen. Highly significant positive regressions ($P < 0.01$) of R on temperature were found for all specimens (Table 1). All but one specimen similarly showed significant or highly significant positive regressions of P on temperature, and the regression for this specimen approached significance ($P < 0.10$).

Assuming regression coefficients interrelating changes in oxygen flux with changes in temperature to be independent of differences among the altitudes of the regression lines, the P and R regression coefficients for different specimens can be statistically compared. Means and standard errors of means of regression coefficients are given in Table 1. Mean R coefficients were not significantly different from mean P coefficients for all 4 species in Hawaii; however, for the 2 species examined at Enewetak, highly significant differences between mean values of P and R coefficients were found (two-tailed t tests, $P < 0.01$). The individual values of P coefficients for Enewetak *Pocillopora damicornis* and *Montipora verrucosa* ranged from 1.6 to 5.0 times R coefficients for the same specimens (Table 1), indicating an adaptation of the Enewetak corals toward greater autotrophic capability at the generally warmer water temperatures of

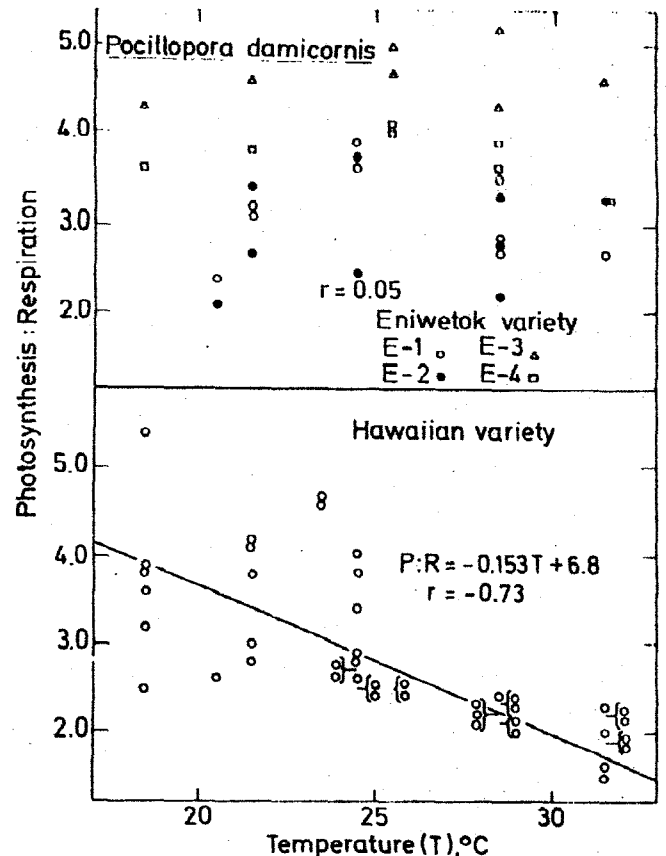


Fig. 2. *Pocillopora damicornis*. Temperature-P:R ratio relationships for Hawaiian and Enewetak corals. Specimens measured at Enewetak are designated by different symbols to enable determination of individual trends. Linear regression coefficient for lumped Enewetak results is not significant ($P < 0.50$). Linear regression and correlation coefficient (r) of lumped results for Hawaiian specimens are highly significant ($P < 0.001$)

this location. Furthermore, comparing coefficients of the same parameter between the two areas, the mean P coefficient for *P. damicornis* at Enewetak was significantly greater than the mean P coefficient of Hawaiian specimens, whereas the mean R coefficient of Enewetak *P. damicornis* was significantly less than found for this species in Hawaii (two-tailed t tests, $P < 0.05$). However, no significant differences were found between P or R coefficients for Hawaiian versus Enewetak *M. verrucosa*.

The P:R ratio is a dimensionless number which provides an estimate of the degree to which algal production of organic material exceeds plant plus animal consumption. This parameter is potentially useful because it normalizes biomass and size differences among specimens and allows comparisons independent of also-

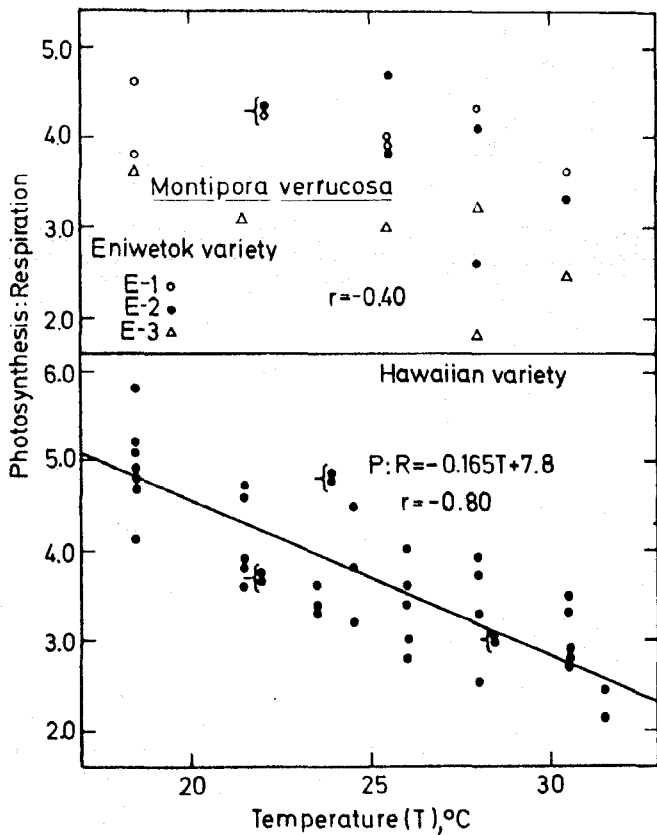


Fig. 3. *Montipora verrucosa*. Temperature-P:R ratio relationships for Hawaiian and Eniwetak corals. Linear regression coefficient for lumped Eniwetak results is not significant ($P < 0.10$). Linear regression and correlation coefficients (r) of lumped results for Hawaiian specimens are highly significant ($P < 0.001$)

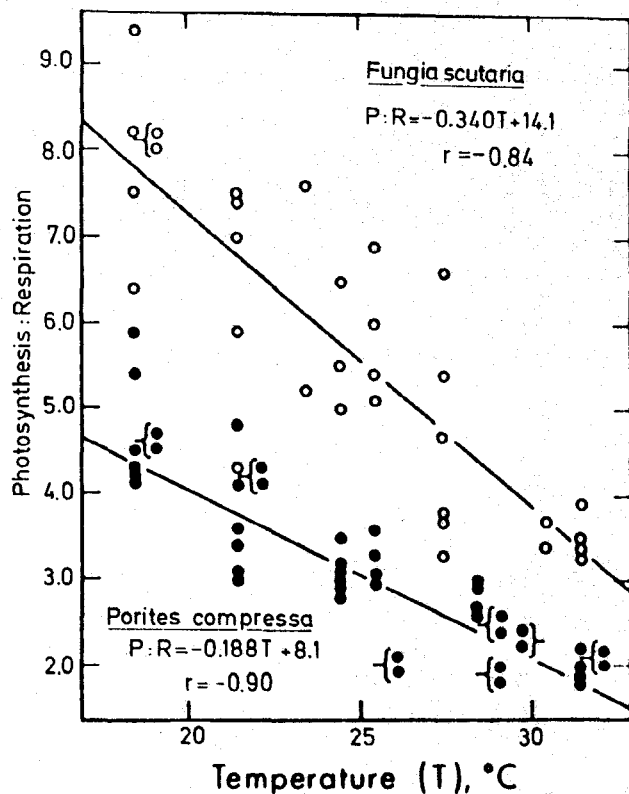


Fig. 4. *Porites compressa* and *Fungia scutaria*. Temperature-P:R ratio relationships for Hawaiian corals. Linear regression and correlation coefficients are highly significant ($P < 0.001$) for both species

lute levels of metabolic activity, assuming that P and R are similarly size-related. Figs. 2, 3, and 4 indicate highly significant negative relationships between temperature and the P:R ratio for the 4 species measured in Hawaii. By contrast, no consistent pattern was found for the 2 species tested at Eniwetak. Individual specimens of *Pocillopora damicornis* showed curvilinear relationships between P:R and temperature, with an inflection point at approximately 25°C (Fig. 2). P:R ratios were relatively constant for *Montipora verrucosa* between 18° and 25°C and decreasing above 25°C (Fig. 3).

Table 2 reports P:R values for Hawaiian specimens in yet another manner. Ninety-five percent confidence limits are calculated for the regression coefficients and for the estimated average

Table 2. 95% confidence limits on regression coefficients of photosynthesis:respiration (P:R) on temperature and of estimated P:R values at 30°C for Hawaiian hermatypic corals

Species	Regression coefficient			P:R at 30°C		
	\bar{x}	Upper	Lower	\bar{x}	Upper	Lower
<i>Pocillopora damicornis</i>	-0.153	-0.109	-0.197	2.21	2.40	2.02
<i>Montipora verrucosa</i>	-0.165	-0.125	-0.205	2.85	3.02	2.68
<i>Porites compressa</i>	-0.188	-0.144	-0.232	2.15	2.34	1.96
<i>Fungia scutaria</i>	-0.340	-0.258	-0.422	3.89	4.25	3.53

P:R at 30°C (Sokal and Rohlf, 1969; p. 435). The negative regression coefficient for *Fungia scutaria* is significantly steeper than the coefficients for the other species, indicating that P:R values for this species are more strongly affected by temperature changes. However, *F. scutaria* is still the most productive coral in terms of its own energy needs throughout the measured temperature range. Its P:R value at 30°C is significantly greater than the value for *Montipora verrucosa*, which itself shows a significantly greater value than either *Porites compressa* or *Pocillopora damicornis*.

Discussion

Decreases in the P:R ratio with acute increases in temperature similar to those shown in this study have been demonstrated for the red macroalgae *Chondrus crispus* and *Gigartina stellata* (Mathieson and Burns, 1971) and the anemone *Anthopleura elegantissima* (P. Leviten and J. Kanwisher, unpublished ms); and similar effects have long been noted for terrestrial plants (Blackman, 1905). These comparable results for such phylogenetically disjunct autotrophic organisms suggest that continuous elevations in temperature above normal ambient levels result in reduced autotrophic ability until adaptive processes occur, the organisms succumb, or as in the case of corals, the host loses its photosynthetic symbionts.

Most previous studies of coral oxygen production and respiration at constant ambient temperatures (Yonge et al., 1932; Kawaguti, 1937; Goreau, 1956; Kanwisher and Wainwright, 1967; Roffman, 1968; Franzisket, 1969; Johannes et al., 1972; McCloskey, personal communication) have indicated the coral-algal association to be autotrophic in shallow water, with photosynthetic production by the algae well exceeding respiration of algae and coral. A P:R ratio of less than 1 when extrapolated over 24 h would indicate that the coral-algal association produces less organic material than it consumes. If daytime and nighttime respiration equal one another, and if the P values reported here approximate a day-time average, then a day-time 12 h P:R ratio of less than 2 indicates net consumption of organic materials. Extrapolation of P:R regression lines for all Hawaiian specimens yields P:R values of 2 at about 33°C (mean = 33.4, standard error = 0.88), near the upper lethal temperature limit that has been indicated for Hawaiian corals (Edmondson, 1928; Jokiel and Coles, 1974, 1977; Coles, 1975; Coles

et al., 1976). Assuming this close agreement to be more than coincidence, it does not explain why the ratio shows no significant relationship with temperature for the two species of corals examined at Enewetak.

This discrepancy may be resolved by recognizing that the lower experimental temperatures used were well below normal Enewetak water temperatures, but nearly coincided with the lower extreme temperatures that occur in Hawaii. During 1951-1964, surface water temperatures at Enewetak never fell below 26°C, whereas winter surface temperatures in Hawaii sometimes approached 21.0°C (Coles et al., 1976). The lower experimental temperatures were therefore more likely to impair photosynthesis at Enewetak. At experimental temperatures greater than 25.0°C, a negative linear relationship between P:R and temperature is indicated for both species at Enewetak. The regression lines which were calculated using these data yielded a P:R value of 2 at 38.8°C for *Pocillopora damicornis* ($r = -0.38$, $P < 0.20$), and at 35.4°C for *Montipora verrucosa* ($r = -0.49$, $P < 0.20$). Although these negative correlations were not significant, the regressions suggest that lethal temperatures for Enewetak specimens should be 2 to 5°C higher than for Hawaiian corals.

The difference in upper lethal temperature suggested by these results has been verified experimentally and by field observations. Upper lethal temperatures of 34°C to 35°C were found for 5 species of coral at Enewetak, compared to lethal temperatures of 31°C to 32°C, for Hawaiian congeners (Coles et al., 1976). Moreover, Clausen and Roth (1975) have determined the dominant temperature optimum for skeletal deposition of *Pocillopora damicornis* to be 4°C higher in Enewetak than in Hawaii. These results indicate that tropical and subtropical corals are rigorously adapted to their ambient water-temperature conditions. The classical concept that temperature-related physiological processes in corals are independent of natural selection (Mayer, 1918) is, therefore, in need of re-evaluation.

More detailed inspection of the 30°C P:R differences among the 4 species tested in Hawaii (Table 2) indicates relationships with their interspecific differences in temperature sensitivity. Despite its significantly greater decrease in P:R with increasing temperature, *Fungia scutaria* showed significantly greater absolute P:R values at all temperatures than any other species examined. Long-term mortality experiments (Coles et al., 1976; Jokiel and Coles,

1977) have shown *F. scutaria* to have a higher lethal temperature than the other three species tested in Hawaii. The P:R data imply that *Montipora verrucosa*, which showed 30°C P:R values in Hawaii intermediate between the values of *F. scutaria* and *Pocillopora damicornis*, may initially be more tolerant of increased temperature than *P. damicornis*. This interpretation has also been substantiated by mortality experiments (Jokiel and Coles, 1977).

Pocillopora meandrina, a close relative of *P. damicornis*, was observed to be the coral most sensitive to heated effluent discharged from the electrical generating station at Kahe Point, Oahu, Hawaii (Jokiel and Coles, 1974). No experimental data are available to compare P:R temperature effects between the two *Pocillopora* species. However, Edmondson (1928) and Coles et al. (1976) found *P. meandrina* to be the more temperature-sensitive species. *P. damicornis* is common to the reef flat, where it encounters considerable diurnal and annual temperature variations, while *P. meandrina* occurs almost entirely along open coastlines in water of relatively moderate temperatures.

Porites compressa is the coral species most abundant in Kaneohe Bay, and is one of the corals most responsible for calcification in embayed waters throughout Hawaii (Maragos, 1972). Determinations of long-term thermal tolerance of this species have not been conducted. However, the P:R data from the present experiments give some idea of the comparative sensitivity of *P. compressa* to thermal stress. Confidence limits on P:R ratios at 30°C for *P. compressa* are nearly identical to those of *Pocillopora damicornis*, suggesting that *Porites compressa* is at least as sensitive to long-term thermal stress as is *Pocillopora damicornis*. Observations of thermal stress effects at the Kahe thermal outfall (Jokiel and Coles, 1974) suggest that *Porites compressa* is less temperature-tolerant than its closest common local relative, *P. lobata*, but considerably more resistant than *Pocillopora meandrina*.

The above comparisons indicate that short-term studies of oxygen production and consumption may be useful for predicting the relative longer-term sensitivities of other species of reef corals and other autotrophic organisms or symbiotic associations. Lethal temperature limits of reef corals appear to occur at physiologically significant and predictable temperatures. Moreover, the trends with temperature determined in the present study are consistent with previous studies of coelenterate metabolism.

Respiration increases approximating Q₁₀'s of 2.0 have been reported for various coelenterates (Vernon, 1895; McClendon, 1917; Lenhoff and Loomis, 1957; Sassaman and Mangum, 1970; Mangum et al., 1972). Adaptive differences in the respiration rates of geographically separate populations of *Aurelia aurita* were determined by Mayer (1914), and acclimation capacity to elevated temperatures by coelenterates has been demonstrated with respiration measurements for the anemone *Metridium senile* (Sassaman and Mangum, 1970), and for various scyphozoans, including *A. aurita* (Mangum et al., 1972). The present study is the first to indicate adaptive differences in the photosynthesis and respiration of reef corals related to their thermal histories and geographic locations. It remains to be demonstrated for corals whether these metabolic characteristics are sufficiently labile to be altered by experimental acclimation.

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