Pacific Science (1982), vol. 36, no. 1


# Some Effects of Light on Coral Growth[1]

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ABSTRACT: The rate of coral growth under varied light regimes was tested using $^{45}Ca$ uptake while temperature was held constant. *Pocillopora damicornis* and *Acropora formosa*, respectively, were used in Hawaii and Enewetak under natural and artificial light conditions. Light intensity and spectral distribution patterns were determined for all experiments.

*Pocillopora damicornis* was tested under different natural light conditions and total darkness. Light enhances calcification within limits. Calcification was shown to have a negative regression with light at 380 nm when that light was partitioned from visible light (400–800 nm), thus indicating longwave ultraviolet inhibition.

*Acropora formosa* held for 6 hr of pretreatment under natural light conditions during the day or in the dark at night calcifies faster during the day than at night. This testing, which was conducted for 20 min under either dark or light conditions, did not show a statistically significant difference between dark or light testing conditions.

This same species was pretreated for 4 hr with dark, low light, and high light intensities at the same time of the day; then the samples were immediately tested for calcification rate for 20 min under dark conditions. Those pretreated under high light calcified faster than those pretreated under low or dark conditions, indicating a light-dependent lag effect.

DROWNED REEFS (Macintyre 1972, Matthews et al. 1974) testify to the deleterious effects of increasing depth on coral growth. Hermatypic corals and the reefs they form are primarily shallow-water phenomena. Their restriction to shallow water presumably results primarily from a light requirement due to the presence of a symbiotic alga (zooxanthellae) in the coral tissue.

Numerous studies have linked light, photosynthesis, zooxanthellae, and calcification, although exact relationships and the mechanisms involved are not yet fully understood. Photosynthetic inhibitors also inhibit calcification (Chalker and Taylor 1975, Vandermeulen, Davis, and Muscatine 1972). Calcification rates are greater in light than in dark (Goreau 1959). Rates may be directly related to light intensities (Chalker and Taylor 1975, Maragos 1972), although the exact relation can probably be modified or obscured by (1) endogenous diurnal rhythmicities (Chalker 1977, Vandermeulen and Muscatine 1975); (2) a delayed calcification response to light conditions (Barnes and Crossland 1978, Roth 1974); (3) saturating and inhibiting light intensities (Barnes and Taylor 1973); (4) adaptation to environmental light conditions (Barnes and Taylor 1973, Falkowski and Dubinsky 1981, Wethey

[1] This research was supported by National Oceanic and Atmospheric Administration grants 04-4-158-26 and 04-3-158-54, National Science Foundation grant GB-24816 to the Scripps Institution of Oceanography for the Symbios project of the Alpha Helix, National Institutes of Health grant RR-00276 to the Scientific Computation Facility of Loma Linda University, and grants from the Geoscience Research Institute. Manuscript accepted 21 November 1981.

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and Porter 1976*a*, *b*); and (5) other environmental parameters. Evidence supports an inverse relation between natural light intensities and pigment/zooxanthellae concentrations (Coles and Jokiel 1978, Maragos 1972) and a positive relation between natural light intensities (depth gradient) and ultraviolet radiation absorbance by zooxanthellae or coral pigment (Maragos 1972), suggesting light controls on both pigment quantity and quality. Interestingly, no definite relation between pigment/zooxanthellae concentration and calcification rate has been demonstrated (Goreau 1963, Maragos 1972). The effect of spectral quality on calcification is not known.

Our research (Experiment 1) tested for the effects of light intensity, spectral quality, and pigment quantity and quality on calcification rate in the coral *Pocillopora damicornis* incubated under natural light conditions. Experiment 2 (with *Acropora formosa*) tested for diurnal rhythmicities in calcification rate (with light effects controlled). Experiment 3 (also on *A. formosa*) tested for delayed calcification response to light conditions.

## MATERIALS AND METHODS

### *Experiment 1*

To test the effect of the quantity and quality of natural light on coral calcification rate, incubations in $^{45}Ca$-enriched seawater were done at different depths and under different cloud conditions. Colonies of *Pocillopora damicornis* were collected from a depth of 6–11 m in Kaneohe Bay, Oahu, Hawaii, from 3 to 8 hr before their incubation. They were brought to the laboratory, and 3–4-cm compound branches were cut from the colonies and mounted upright in plastic racks so that each rack had one branch from each of four colonies. Specimens were kept immersed in seawater except for brief (1–2 sec) periods of air exposure (e.g., during transfers). Prior to the incubation these coral racks were kept at a 1–2-m depth in the lagoon east of the Hawaii Institute of Marine Biology, where the experiments were done.

During an incubation the racks were placed in containers constructed of type II uvt (ultraviolet-transmitting) Plexiglas. This plastic (in the thickness used) transmits about 90 percent of visible light and ultraviolet radiation down to 375 nm wavelength; at about 320 nm, 50 percent of the ultraviolet radiation is transmitted; and very little is transmitted at 275 nm. While measuring light in the sea, this kind of plastic was placed on the spectroradiometer diffuser to give a spectrum similar to that received by the coral being tested, thus taking into account any effects of solarization on the plastic. The containers held 500 ml of natural seawater which had 50 μCi or less of $^{45}Ca$ with a specific activity of 8–12 mCi $mg^{-1}$ $CaCl_2$. To avoid contact between incubation seawater and surrounding seawater, these containers were placed in a housing (Figure 1) also constructed of type II uvt Plexiglas. The housing could hold two containers and could be accessed from below to permit rapid transfer of the coral racks to start or stop an incubation.

All incubations were for 15 min and occurred between 10:45 and 15:18 (to minimize circadian effects). All incubations (except two done in complete darkness) were under natural light conditions. During an experiment the housing was mounted in the lagoon so that there were 5, 40, 110, or 250 cm of seawater above the coral. During the 15-min incubation the downward irradiance at the depth of the coral was monitored with an ISCO spectroradiometer model SR. Measurements were made from five to seven times at each of seven wavelengths (380, 450, 550, 650, 750, 850, and 950 nm) during the course of the incubation (Figure 2). Light intensity is reported in watts per square meter ($W\ m^{-2}$). Both depth of incubation and (particularly) cloud cover affected the natural light intensity during the incubations. Representative curves of downward irradiance are given in Figure 2.

Before the incubation proper the coral was acclimated for at least 15 min under the light conditions of the incubation. If necessary, the temperature was gradually adjusted to 27°C during this acclimation and main-

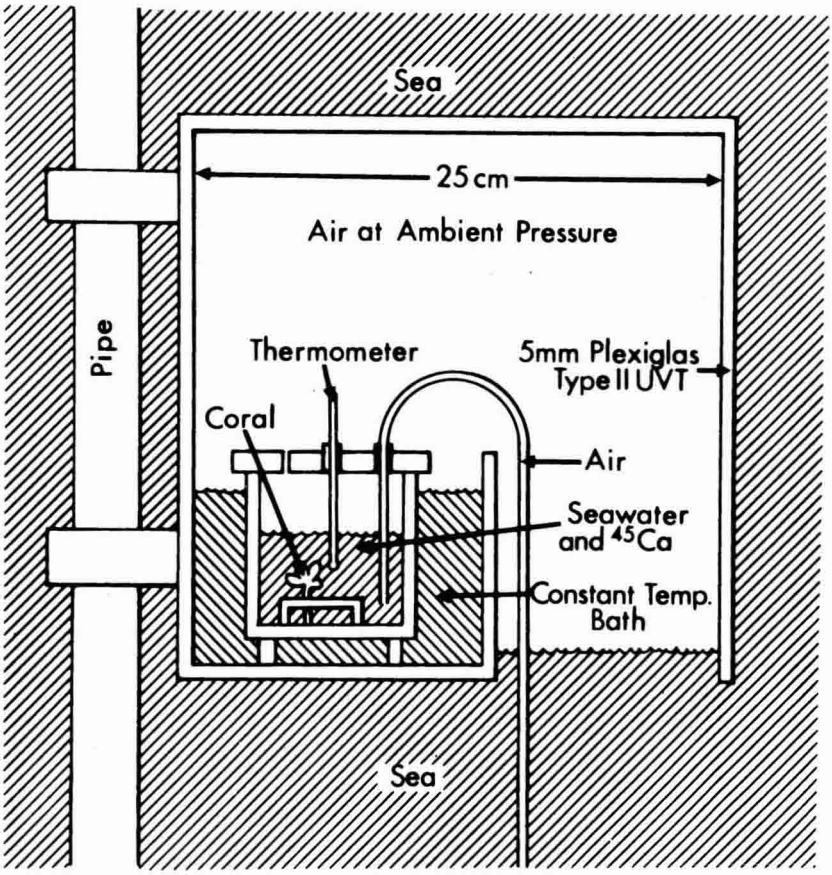


FIGURE 1. Experimental setup for testing rate of calcification under natural light.

tained at 27°C (usually ± 0.2°C) by adding warm or cool water to a water bath around the incubation containers. Air was bubbled into the containers to circulate the seawater and maintain $CO_2$ concentration. Incubations were started by placing a coral rack in seawater with $^{45}Ca$. They were stopped by placing the rack in chilled (5°C) seawater. At incubation termination the racks were taken immediately to the laboratory and four tips approximately 5 mm in length were cut from each branch for a total of sixteen tips per container (one branch from each of four colonies).

For pigment extraction, each tip was placed in 3 ml of chilled acetone that had been kept over granular anhydrous sodium carbonate. Extraction proceeded for about 30 hr in the dark. Pigment quantity was measured with a Beckman DB-G grating spectrophotometer. Absorbance was measured at 434 nm (primary peak) and 662 nm (secondary peak). No measurable amount of $^{45}Ca$ was taken up by the acetone during this extraction process.

Following pigment extraction, tips were dried and their length and diameter measured. Tissue was removed using 1 ml of 1 *N* NaOH heated in a boiling water bath for 7 min followed by six water rinses. The cleaned tips were dissolved in 0.5 ml 3 *N* HCl and aliquots taken for $^{45}Ca$ assay.

*Experiment 2*

To separate diurnal (e.g., an endogenous rhythm) effects from light effects, the coral *Acropora formosa* was incubated in $^{45}Ca$-

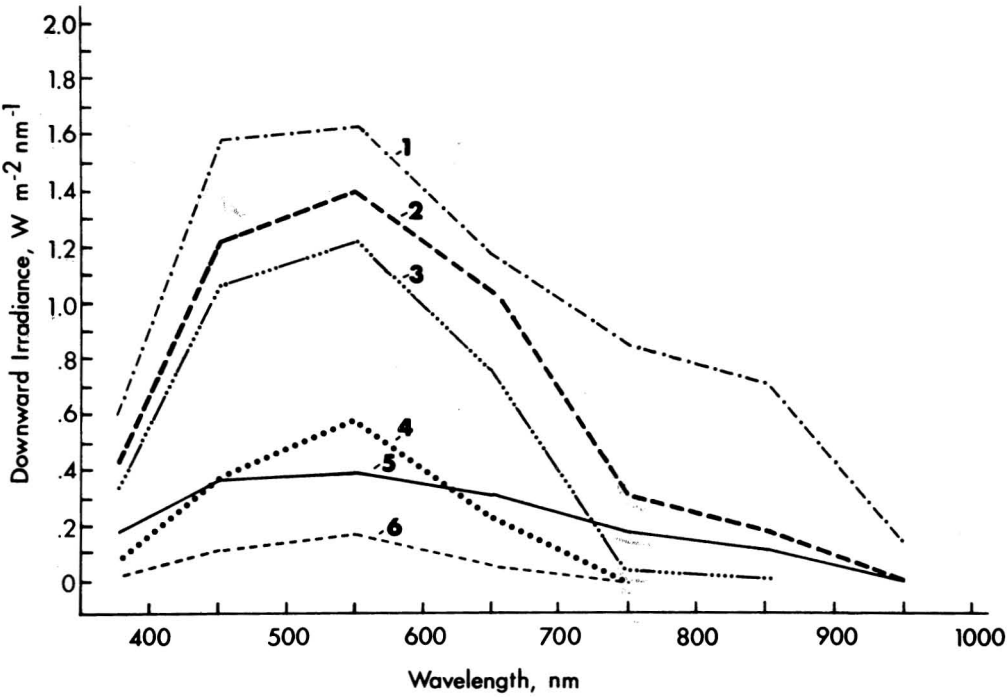


FIGURE 2. Samples of the spectral distribution of downward irradiance of light in the sea for the natural light experiments, Coconut Island, Oahu, Hawaii. Cloud cover and water turbidity were more important than depth in determining intensity. Line 1, 5-cm depth, mostly clear sky; line 2, 40-cm depth, scattered clouds; line 3, 110-cm depth, scattered clouds; line 4, 250-cm depth, partly cloudy; line 5, 5-cm depth, overcast and some rain; line 6, 250-cm depth, overcast. Lines 4 and 5 represent spectral distributions for points *a* and *b*, respectively, of Figure 4.

enriched seawater under four sets of test conditions: night/dark, night/light, day/dark, and day/light. Two replicate incubations (each replication with twelve coral branch tips) were performed under each condition. *Acropora formosa* branch tips about 4 cm in length were collected at 0–2-m depth in Enewetak Atoll (Marshall Islands) lagoon. They were mounted upright in plastic racks and then left in the ocean under natural light (day or night) for about 6 hr—until just prior to the incubation. All incubations were for 20 min and occurred between 14:13 and 15:19 (day incubations) and 02:09 and 03:04 (night incubations). (Sunrise and sunset times were about 07:35 and 19:15, respectively.)

During an incubation the coral racks were placed in containers with opaque neutral gray sides and a transparent top constructed of type II uvt Plexiglas. They each held 700 ml of natural seawater containing 50 μCi or less of $^{45}Ca$ with a specific activity of 8–12 mCi mg$^{-1}$ $CaCl_2$. Air was bubbled into the containers to circulate the seawater and maintain $CO_2$ concentration. Temperature was maintained at 28°C (usually within ± 0.2°C).

Upon recovery from the ocean and just prior to the incubation proper the corals were acclimated for 20 min to all incubation conditions except light. Acclimation light conditions were natural light (day incubations) and total darkness (night incubations). If necessary, the temperature was gradually adjusted to 28°C. The incubation proper was started by placing the coral in a container with $^{45}Ca$-enriched seawater. Incubations were in both total darkness (night/dark and day/dark) and artifical light (night/light and day/light). The artificial light was a cool-beam 300-W incandescent flood lamp in a white

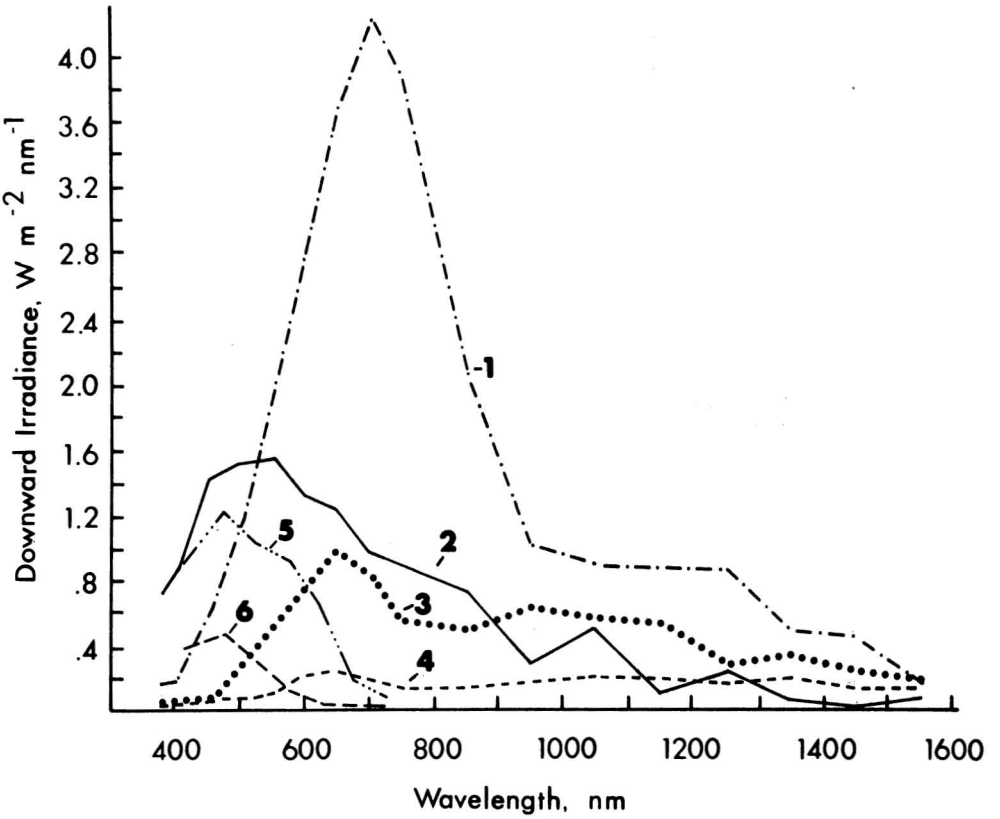


FIGURE 3. Spectral distribution of downward irradiance of artificial light sources and some natural environments (given for comparison). 1, high-intensity light used for Experiment 3; 2, noon sun at sea level, clear sky, Freeport, Bahamas, 9 April 1973; 3, light used for incubation of Experiment 2; 4, low-intensity light used for Experiment 3; 5, Enewetak Lagoon, 1.3 m below sea level, clear sky at noon, 4 June 1971; 6, Enewetak Lagoon, 21 m below sea level, clear sky at noon, 4 June 1971.

chamber. The spectral distribution of the downward irradiance is given as line 3 in Figure 3.

The incubation was terminated by immersing the coral in chilled 0.25 *N* NaOH. Tips 15 mm long were cut from each branch and treated twice (7 min each) in 1 *N* NaOH in a boiling water bath with shaking between treatments, followed by three washes in 0.01 *N* NaOH. Tips were dried at 105°C and $^{45}$Ca content assayed.

*Experiment 3*

To test for a delayed response of calcification to light and a qualitative light intensity effect on calcification, *Acropora formosa* branches were pretreated in darkness and in low- and high-intensity light for 4 hr prior to a dark incubation in $^{45}$Ca-enriched seawater. Except for differences noted, methods used were similar to those in Experiment 2. Incubation containers were clear (type II uvt Plexiglas) on all sides, containing 1000 ml seawater, and held nine coral branches during incubation.

*Acropora formosa* branches were collected on the evening previous to the incubation, mounted upright in racks, and left in the ocean. They were recovered before daylight and brought to the laboratory for a 4-hr pretreatment of darkness, low light intensity, or high light intensity. (Figure 3 gives light spectral intensities.) Seawater was changed twice during the pretreatment.

Incubations were begun by transferring the coral to $^{45}Ca$-enriched seawater. All incubations were in the dark for 20 min between 11:00 and 11:30. Six replicates (with nine branches each) were done on different days for each pretreatment condition (a total of fifty-four branches for each condition). To clean all tissue from the skeleton adequately, it was necessary in the postincubation processing of tips from six of the incubations to have an additional treatment in 1 *N* NaOH in a boiling water bath for 4 min. This added treatment was equally distributed between pretreatment conditions.

*Calcium-45 Assay and Conversion to Calcium Carbonate Units*

In all experiments replicate samples of the $^{45}Ca$-enriched incubation seawater were taken and $^{45}Ca$ content determined from liquid scintillation counting (LSC). In Experiment 1, $^{45}Ca$ incorporation into the coral tips was also measured with LSC. Counts were performed for 100 min or 100,000 counts, whichever came first—usually the latter.

In Experiments 2 and 3, $^{45}Ca$ incorporation was determined on intact (undissolved) tips with a Geiger–Müller (G–M) tube. Counts were done to about 4000. (The G–M tube was much more readily accessible than was LSC and permitted more immediate monitoring of experimental results.) The relative efficiency of the G–M tube compared with LSC was determined and corrected for in the G–M tube results.

Both LSC and G–M tube results were corrected for background, decay, and differences in the length of incubation. From the ratio of $^{45}Ca$ to natural Ca concentration in the incubation seawater, results were converted to micrograms $CaCO_3$ per hour per tip. In Experiment 1, the Ca concentration for seawater from each incubation was determined with a Perkin–Elmer 303 atomic absorption spectrophotometer. For Experiments 2 and 3 natural $^{40}Ca$ concentration was considered to be 400 mg liter$^{-1}$.

*Inorganic Uptake of Calcium-45*

Our tests were designed for relative comparisons of different treatments. Inorganic exchange and adsorption of $^{45}Ca$ onto the coral skeleton is assumed to be the same for comparable treatments (however, see Barnes and Crossland 1977).

Inorganic uptake of $^{45}Ca$ should be considered when estimating absolute growth rates (Table 1), but it is difficult to separate from organically induced growth. Maximum figures for inorganic exchange and/or adsorption may be represented by the lowest rates of $^{45}Ca$ uptake in living tips (Table 1). These lowest rates may represent a state of no growth. Since this is not known, the real values may be lower. Passive transfer of $^{45}Ca$ in dead coral would most likely not be the same as for live coral.

Tests on $^{45}Ca$ uptake in tips killed in hot or cold seawater usually gave comparable or higher results than the minimum found in living tips. Calcium-45 uptake in *Acropora formosa* tips killed in this way did not show a significant relationship to time even when tested for several hours, thus suggesting an adsorption phenomenon.

*Measurement of Light Intensity*

Light intensity is reported as the downward irradiance at the position of the corals in an experiment. This is only a relative estimate of the intensity of radiant energy actually impinging on the coral, since scatter and other factors affect the ratio of downward irradiance to upward and lateral irradiance. Measurement was done using an ISCO spectroradiometer model SR which is sensitive to long-wavelength ultraviolet, visible, and infrared radiation (380–1550 nm). The half-bandwidth of detection of this instrument varies from 15 to 30 nm. The flat Teflon light-collecting diffuser of this instrument is slightly recessed in its frame, and it probably is not an exact cosine collector (Smith 1969), but is satisfactory for this study. Measurements were made at several wavelengths (usually 6–12) along the spectrum. Point values were integrated for total light intensity. The raw data from the instru-

TABLE 1

Comparison of Calcification Rates of *Acropora formosa* and *Pocillopora damicornis*

| | Coefficients of Variation | | Surface Area of Tips Used* ($mm^2$) | | Rates Observed ($\mu g\ CaCO_3\ tip^{-1}\ hr^{-1}$; $n = 5$) | | Maximum Linear Growth† ($\mu m\ hr^{-1}$) |
|---|---|---|---|---|---|---|---|
| | Sample Size | Mean (%) | Sample Size | Mean ± SE | Slowest, Mean ± SE | Fastest, Mean ± SE | |
| *Acropora formosa* | 8 experiments, with 12 samples each; 18 experiments, with 9 samples each | 34.21 | 18 | 299.02 ± 8.43 | 28.51 ± 1.46 | 199.04 ± 11.99 | 12.0 |
| *Pocillopora damicornis* | 18 experiments, with 16 samples each | 100.75 | 16 | 33.93 ± 1.70 | 0.1512 ± 0.0153 | 19.103 ± 0.8363 | 5.4 |

*Surface area estimate is a theoretical smooth surface at the tips of the corallites.
†Estimate based on mean of fastest rate.

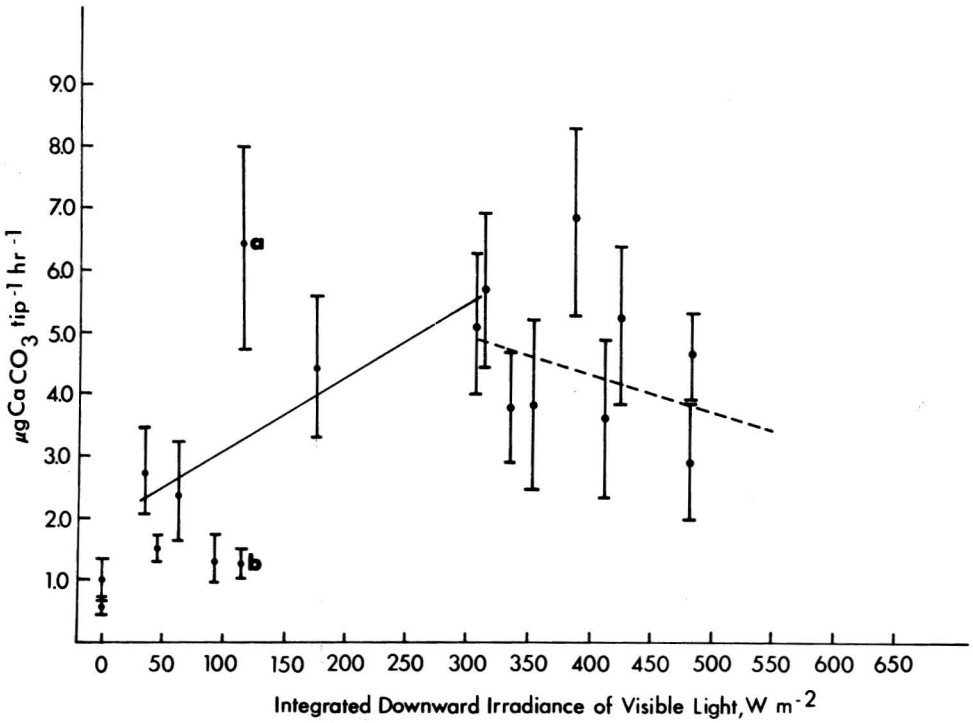


FIGURE 4. *Pocillopora damicornis*. Rate of calcification under natural light spectrum. Confidence limits represent ±1 SE. Two samples at left at zero light intensity tested in total darkness. See Figure 2 for light spectrum for points *a* and *b*.

ment were corrected for calibration based on a standard lamp, stray light, and when used underwater for an immersion factor as discussed below.

For measuring light in the sea, the spectroradiometer was placed in a Plexiglas housing provided with external controls. To eliminate errors from refraction as light entered the Plexiglas housing, the Teflon diffuser was placed outside the housing, with seawater present on both sides of the diffuser and a light pipe conducting the diffused light to the spectroradiometer. Wetting the Teflon diffuser significantly reduced diffusion. Immersion on the underside of the diffuser was corrected for by recalibration of the instrument in its housing with water between the diffuser and the housing. The immersion effect on the outside was corrected by using essentially the same method employed by Smith (1969). Correction to a theoretical wet but "no water thickness" condition was obtained by noting attenuation of various wavelengths as a column of water was decreased at seven different levels from a depth of 30 to 3 cm over the diffuser under a parallel light beam. A least-squares slope was obtained and extrapolated to zero to give the correction needed for the immersion effect on the outside of the diffuser. Corrections varied from 14.3 to 24.1 percent, according to wavelength.

## RESULTS

### *Experiment 1*

Figure 4 shows the relationship obtained between visible light intensity and calcification rate. The large variability makes interpretation difficult. The relationship appears to be nonlinear, with a suggestion of light saturation or inhibition at the higher intensities.

TABLE 2

*Pocillopora damicornis*: SIMPLE CORRELATION COEFFICIENTS BETWEEN THE NATURAL LOG OF THE CALCIFICATION RATE AND LIGHT AT VARIOUS WAVELENGTHS

| WAVELENGTH OF LIGHT (nm) | CORRELATION COEFFICIENT |
|---|---|
| 380 | 0.114* |
| 450 | 0.174† |
| 550 | 0.206† |
| 650 | 0.132* |
| 750 | 0.046 |

NOTE: Coefficients are based on 256 samples.
*Significant at the 0.05 probability level.
†Significant at the 0.01 probability level.

Statistical analysis of the data included a correlation analysis with change in wavelength, an analysis of variance test, and a multiple regression analysis with stepwise inclusion of various factors. The latter two tests involve duplication of some important factors. Because equal variances is an assumption of these analyses, all data were first converted to natural logarithms of the calcification rate to help equalize the variances. Table 2 gives simple correlation coefficients between the natural logarithm of the calcification rate and light at various wavelengths. Positive and statistically significant values occur at most wavelengths, probably primarily reflecting the general effect of increasing light intensity on calcification rate.

The results of the analysis of variance test using a general linear model are given in Table 3. As would be expected, a significant difference exists between colonies. A significant positive relationship exists between tip size (diameter) and calcification rate and between total visible light and calcification rate. A significant negative relationship exists between radiation at 380 nm (ultraviolet) and calcification rate. Pigment concentration had no significant effect on calcification rate.

Table 4 gives the results of the multiple regression analysis. These results basically agree with the analysis of variance test of Table 3. The sequence employed in the multiple regression test represents a conservative analysis for the effect of total visible light. We suspect a confounding of the colony effect (i.e., differences between colonies) with the light effect, since some colonies were all used on dark days while others were used only on bright days.

The negative relationship between light at 380 nm and calcification rate observed in this analysis suggests ultraviolet inhibition. This uv effect is best illustrated by comparing points *a* and *b* in Figure 4. Point *a* has the highest ratio of visible light/light at 380 nm (see line 4, Figure 2) of any incubation, whereas point *b* has the lowest such ratio (see line 5, Figure 2).

### *Experiment 2*

The results of Experiment 2 are given in Table 5. A two-way analysis of variance test showed a highly significant ($p < 0.01$) difference between day and night results with light and dark incubations combined. No significant difference was shown between light and dark, assuming the replicates to be different. However, if the replicates are assumed to be the same (no significant difference between replicates was shown with the analysis of variance test), then a significant ($p < 0.025$) difference between the light and dark incubations did occur.

### *Experiment 3*

The results of Experiment 3 are given in Table 6. A one-way analysis of variance test with Duncan's multiple-range test indicates a highly significant difference between dark or low-intensity light and high-intensity light preincubation treatments. The effect of high-intensity light thus appears to be carried over into the dark incubation period. No significant difference was shown between the complete darkness and low-intensity preincubation treatments.

### *Comparisons between* Acropora formosa *and* Pocillopora damicornis

Calcification rates obtained for *Acropora formosa* showed less variability than those

TABLE 3

*Pocillopora damicornis*: ANALYSIS OF VARIANCE TEST BETWEEN THE NATURAL LOG OF THE CALCIFICATION RATE ($\mu g\ CaCO_3\ hr^{-1}$) AND VARIOUS INDEPENDENT VARIABLES ADJUSTED FOR THE OTHER INDEPENDENT VARIABLES

| INDEPENDENT VARIABLES | PARTIAL REGRESSION COEFFICIENT | *F* VALUE | SIGNIFICANCE OF *F* |
|---|---|---|---|
| Colony factor | — | 9.25 | 0.000 |
| Diameter (mm) | 1.616 | 41.68 | 0.000 |
| Light at 380 nm ($\mu W\ cm^{-2}$) | −0.103 | 8.40 | 0.004 |
| Total visible light ($\mu W\ cm^{-2}$) | 0.005 | 6.18 | 0.014 |
| Pigment per surface area (absorbance $mm^{-2}$) | −0.046 | 1.12 | 0.291 |

TABLE 4

*Pocillopora damicornis*: MULTIPLE REGRESSION ANALYSIS WITH A STEPWISE INCLUSION OF VARIOUS FACTORS COMPARED TO THE NATURAL LOG OF THE CALCIFICATION RATE

| FACTOR | PARTIAL REGRESSION COEFFICIENT | *F* VALUE FOR PARTIAL REGRESSION COEFFICIENT | CUMULATIVE MULTIPLE CORRELATION COEFFICIENT |
|---|---|---|---|
| Colony (due to confounding, the effect of colony may include the effects of some of the factors listed below) | — | — | 0.670† |
| Diameter of tips | 1.57 | 41.00† | 0.732† |
| Length of tips | 0.176 | 6.10* | 0.739† |
| Total visible light | 0.00477 | 6.63* | 0.742† |
| Light at 380 nm | −0.106 | 9.16† | 0.754† |

NOTE: Coefficients are based on 256 samples.
*Significant at the 0.05 level.
†Significant at the 0.01 level.

for *Pocillopora damicornis* (Table 1). In *P. damicornis*, some tips may calcify 20–30 times faster than others within a single experimental group of sixteen. In *A. formosa*, with groups of nine to twelve tips, the factors are around 2–4, even though in this group the decay of the $^{45}Ca$ present was determined using a lower total count (see Materials and Methods section), which would tend to increase variability.

Table 1 gives data on a theoretical value for surface area of samples for comparing calcification rates with other species. The table also includes data on the fastest rates of calcification observed in the experiments reported herein and a conversion to linear growth based on the mean weight of a sample of the cylindrical shaft (not the tip) of the species studied. Potential growth rates may be higher, since in preliminary experiments we have been able, at least on a temporary basis, to nearly double rates in *Acropora formosa* either by raising the temperature 5° C or by adding carbonate ion.

## DISCUSSION

### *Light Intensity*

The positive relationship obtained in Experiment 1 between light intensity and calcification rate in *Pocillopora damicornis* is expected. Numerous studies have related light

TABLE 5

*Acropora formosa*: TESTS OF $CaCO_3$ INCORPORATION DURING THE DAY AND NIGHT UNDER LIGHT AND DARK CONDITIONS

| PRETEST CONDITIONS (7 hr) | TEST CONDITIONS (20 min) LIGHT* | DARK | MEANS | SIGNIFICANCE FOR PRETEST CONDITIONS |
|---|---|---|---|---|
| Day and natural light | 86.74 | 63.23 | 80.89 | $p < 0.01$ |
| | 92.84 | 80.74 | | |
| Night and dark | 49.90 | 45.11 | 52.09 | |
| | 54.75 | 58.59 | | |
| Means for test conditions | 71.06 | 61.89 | | |
| Significance for test conditions | Not significant† | | | |

NOTE: Values in μg $CaCO_3$ $tip^{-1}$ $hr^{-1}$. Initial figures represent the average of twelve tips in one experiment. Statistical significance is based on two-way analysis of variance.

*See Figure 3 for spectral distribution of light used.

†See text.

TABLE 6

*Acropora formosa:* LAG AND DARK, LOW-INTENSITY LIGHT, AND HIGH-INTENSITY LIGHT TESTS

| PRETEST CONDITIONS | MEAN RATE OF CALCIFICATION (μg $CaCO_3$ $tip^{-1}$ $h^{-1}$) ± 1 SE | SIGNIFICANCE* |
|---|---|---|
| Dark | 90.93 ± 5.68 | $p < 0.01$ |
| Low-intensity light | 87.70 ± 4.61 | |
| High-intensity light | 112.55 ± 5.64 | |

NOTE: Each mean represents a total of fifty-four tips (nine in each of six replicate experiments). Pretest conditions maintained for 4 hr. See Figure 3 for spectral distribution of light used for pretest condition. All samples tested in the dark for 20 min immediately following pretest treatment. Test of significance based on one-way analysis of variance and Duncan's multiple-range test.

*Lines bracket nonsignificant differences.

to calcification rate, although much evidence indicates this may not be a direct or simple relationship. Kawaguti and Sakumoto (1948) and Goreau (1959) demonstrated that corals in the light calcified more rapidly than those in the dark. Goreau and Goreau (1959) showed a crude relationship between calcification rate and light intensity in a field setting, and Chalker and Taylor (1975) demonstrated direct proportionality between (subsaturating) light intensities and calcification rate in *Acropora cervicornis*. Using transplant studies, Maragos (1972) demonstrated a positive intensity/growth relationship primarily in *Pocillopora damicornis* and *P. meandrina*. Growth in other species were less light-dependent. In situ studies (Barnes and Taylor 1973) showed a positive relationship between light intensity and calcification rate in *Montastrea annularis*.

### *Diurnal Rhythms*

The relationship between light intensity and rate is not always obvious, as indicated by much evidence, including our results with *Acropora formosa* in Experiments 2 and 3. From Experiment 2 it appears that time of day (diurnal effect) determines calcification rate more than the light condition (i.e., either light or dark). This could be due to (1) an endogenous rhythm in coral calcification rate and/or (2) a delayed rate response to the light condition.

Endogenous rhythms may, in part, determine coral calcification rate. Diurnal changes do, of course, occur both in zoo-

xanthellae photosynthesis and calcification rate (Barnes and Crossland 1978, Chalker 1977, Chalker and Taylor 1978, Smith and Kinsey 1978, Vandermeulen and Muscatine 1975). Yet it is not clear how independent of light changes these rhythms are. In *Acropora cervicornis* a calcification rhythm persisted for at least 1 day when the corals had been maintained (previous to a light incubation) in the dark (Chalker 1977). This agrees with our Experiment 1 results and provides strong evidence of an endogenous calcification rhythm. The occurrence of such a rhythm would indicate that light has an entraining function. Light may have such a function, but it is unlikely that entrainment is its primary function in controlling calcification rate.

*Delayed Response*

The second explanation of our Experiment 2 results is that they reflect a delayed response of calcification rate to particular light/dark conditions. Data of Barnes and Crossland (1978) suggest a 35–40-min delay between tissue incorporation of $^{14}C$ in photosynthesis and linear incorporation into the skeleton. Our incubations were for 20 min. A further delay may result in getting the photosynthetic apparatus functioning when starting from dark conditions. If this delayed response hypothesis is correct, either longer incubation periods or a period of preincubation acclimation to the incubation light conditions would significantly increase the difference between light and dark calcification rates.

Experiment 3 supports the hypothesis that there is a delayed response of calcification rate to light conditions. Despite all incubations being dark, those that had a 4-hr high-intensity preincubation treatment had a significantly greater calcification rate than those with a dark or low-intensity preincubation treatment. It is not possible from either Experiment 2 or 3 to estimate the length of the delayed response, although if the nominal differences in Experiment 2 are suggestive, the response going from light (pretest) to dark (incubation) appears slower than going from dark (pretest) to light (incubation). Such a delayed rate response might be a function of coral or zooxanthellae biochemistry. Barnes and Crossland (1978) suggest that passage of $^{14}C$ through intermediate compounds would explain its delayed appearance in the skeleton. Formation of the organic skeletal matrix might occur only under light conditions but be utilized in the dark (Muscatine 1973). Light-dependent nutrient flux may be involved (D'Elia 1977, Muscatine and D'Elia 1978). Energy transfer (via zooxanthellae) and removal (or buildup) of waste products, inhibitor substances, or limiting factors (Goreau and Goreau 1959) are time-dependent processes possibly explaining a delayed rate response. A similar delayed rate response was seen in the hydrocoral *Millepora complanata* (which also contains zooxanthellae) by Strömgren (1976), who found slightly faster growth at night following high light intensities during the day.

*Light Saturation*

Though the extremely high variability makes conclusions difficult, calcification rates obtained at high intensities in Experiment 1 suggest light saturation and possibly light inhibition at intensities above 300 W $m^{-2}$. In whole branch segments of *Acropora acuminata*, photosaturation in oxygen exchange rates also occurred at about 300 W $m^{-2}$ (Crossland and Barnes 1977). No inhibition occurred up to at least 800 W $m^{-2}$. In *A. cervicornis*, light saturation occurred at about 500 μE $m^{-2}$ $sec^{-1}$ (approximately 110 W $m^{-2}$) for photosynthesis and at about 800 μE $m^{-2}$ $sec^{-1}$ (approximately 175 W $m^{-2}$) for calcification (Chalker and Taylor 1978). Light inhibition of calcification occurred at least by 1950 μE $m^{-2}$ $sec^{-1}$ (approximately 425 W $m^{-2}$). Barnes and Taylor (1973), in a study of *Montastrea annularis* in situ, reported photoinhibition of calcification at 1500 fc (probably around 100–150 W $m^{-2}$).

Differences in saturation intensities could reflect differences in (1) species light responses; and/or (2) light acclimation history of

samples; and/or (3) spectral quality of light sources. Different saturation values for different species would not be expected. Differences in light acclimation history would not seem to explain the differences in saturation intensities found in the studies cited above; however, light adaptation history of coral colonies was found to govern the saturation light intensity for photosynthesis in *Pavona praetorta* (Wethey and Porter 1976*b*). The half-saturation light intensity for specimens collected at 10-m depths was 0.63 E $m^{-2}$ $hr^{-1}$ (approximately 38 W $m^{-2}$). At subsaturating light intensities light adaptation may produce both higher photosynthetic and higher calcification rates in deeper corals than would be expected from intensity/rate data on shallow-water corals (Barnes and Taylor 1973, Wethey and Porter 1976*a*, *b*). Our *Pocillopora damicornis* specimens were collected at depths of 6–11 m, which were deeper than the incubation depths of 0–2.5 m. Therefore (if light acclimation occurs in *P. damicornis*), the calcification response to light (both rate and saturation) we obtained might not be typical of actual light effects on coral naturally growing at shallow (0–2.5 m) depths. The rates would be inflated, whereas the saturation intensity would be low.

### *Spectral Quality*

If light sources with different spectral qualities are used, different saturation intensities may be expected if the photosynthetic/calcification mechanism of the zooxanthellae/coral complex is differentially sensitive to certain wavelengths. Since little is known about the relationship between spectral quality and calcification, exactly how spectral quality would affect changes in saturation intensities is not known. Photosynthesis often seems rather independent of the spectral quality of light—presumably because of the presence of accessory pigments that transfer energy.

Our results did suggest that certain wavelengths (e.g., 550 nm) appeared more highly correlated with calcification rate than others, but most wavelengths tested showed significant positive correlations. Since light intensity at specific wavelengths is not independent of total light intensities, these results may reflect the general intensity/rate relationship or factors related to the ratio of different wavelengths and not the value of a specific wavelength of light.

### *Light Inhibition*

Inhibition of calcification rate at high intensities could result from photooxidation or from ultraviolet (uv) inhibition. Photooxidation decreases photosynthesis, probably by decomposition of enzymes active in photosynthesis. It is known to occur in marine plankton (Steemann Nielsen 1975) and would be expected in the zooxanthellae of coral. In *Chlorella vulgaris*, Steemann Nielsen (1975:78) found inhibition by photooxidation at about $100 \times 10^{15}$ quanta $cm^{-2}$ $sec^{-1}$ (approximately 360 W $m^{-2}$).

The negative correlation of the 380-nm light (when partitioned from total light in the analysis of variance and multiple regression tests) strongly suggests uv inhibition. It seems to occur both at high light intensities and at low light intensities that have a high component of short-wavelength radiation. Growth inhibition by long uv light (310–390 nm) occurs in bacteria, fungi, protozoa, algae, higher plants, and mammalian (Hela) cells (Jagger 1972), but maximum inhibitory effects are with wavelengths shorter than 380 nm. Vollenweider (cited by Halldal 1966:48–49) found that when uv radiation (360–400 nm) comprised 0.5–1 percent of total light, photosynthesis was depressed by 50 percent. Jokiel (1980) reported dramatic harmful effects of uv radiation on unprotected organisms associated with coral. This negative uv effect probably results from its effect on the oxidative respiratory system.

Long uv radiation is, however, also known to mitigate the harmful effects of short uv radiation (Cook 1970, Rupert and Harm 1966) and to participate in photosynthesis (Steemann Nielsen 1975). The net effect of long uv radiation on coral calcification may be a balance between the negative effects of long uv radiation and the posi-

tive effects of long uv and associated visible light. The uv effect would be greatest near the surface and could presumably directly affect the coral, the zooxanthellae, or both. Irradiance transmittance (%/m) of uv radiation at 350 nm may vary from 73 to 94 percent in the open ocean (Jerlov 1976: 134).

Ultraviolet-absorbing substances are known to be associated with coral. Shibata (1969) found prominent uv absorbance in water extracts of both *Pocillopora* sp. (265 and 323 nm) and *Acropora* spp. (about 265 and 320 nm). He suggested that such substances might function either as a precursor of other pigments or as a filter for protection from uv radiation. The latter function is supported by a strong positive relationship observed between the concentration of uv-absorbing pigments in *Porites lobata* and light energy at their collection depths (Maragos 1972). Since incubation depths were less than collection depths in Experiment 1, these specimens may have had less natural uv protection than did colonies normally growing at the incubation depth. This would have caused particularly obvious uv inhibition.

### *Pigment Quantity and Quality*

Our results from Experiment 1 did not indicate a relationship between calcification rate and pigment concentration. Neither was there an obvious relationship between pigment quality (absorbance characteristics) and the spectral region (550 nm) best correlated with calcification rate. Several studies show a relationship between zooxanthellae/pigment concentration, depth, and/or light intensity (Coles and Jokiel 1978, Drew 1972, Dustan 1979, Falkowski and Dubinsky 1981, Maragos 1972). Although some evidence (Drew 1972, Maragos 1972) suggest that zooxanthellae/pigment concentration increases from shallow to moderate depths (e.g., 10 m), other evidence (Dustan 1979) suggests a general decrease with depth (though pigment per cell may increase slightly).

Little evidence supports a direct relationship between zooxanthellae/pigment concentration and calcification. Kawaguti (1937) did report a decrease in a "purple" pigment in *Acropora* with increasing depth; this was positively correlated with a decrease in coral growth. The complete absence of zooxanthellae does have a negative effect on calcification (Goreau 1959, Goreau and Goreau 1959). Nonetheless, neither Maragos (1972) nor Goreau (1963) found a relationship between pigment concentration and coral growth or calcification.

In our experiments a coincidence between pigment quality and spectral region best correlated with calcification rate may not have been observed because either (1) the high correlation only indicates that this spectral region (550 nm) is best correlated with total light intensity, or (2) the pigments that are coincident in absorbance with this spectral region are not acetone-soluble. These could be water-soluble accessory pigments that transfer energy to the chlorophyll *a*. Water-soluble pigments that have absorbance peaks near this spectral region are known (Prézelin and Haxo 1976).

### *Light, Depth, Calcification, and Drowned Reefs*

The general trend from 0 to 20 m (or more) depth is a decrease in coral growth rates (and $CaCO_3$ production) (Bak 1976, Baker and Weber 1975, Buddemeier, Maragos, and Knutson 1974, Dustan 1975, Highsmith 1979, Maragos 1972, Smith and Harrison 1977). However, most studies do not have the resolution needed at shallow depths (0–10 m) to precisely localize depth of maximum growth. The apparent dramatic photoinhibition occurring even at 9 m in *Montastrea annularis* (Barnes and Taylor 1973) seems incompatible with highest growth occurring at the surface. In the same species, growth rates at 0 m were nominally (but not significantly) less than rates at 4.5 and 9.0 m (Baker and Weber 1975). Unfortunately, our results can only suggest the possibility of photoinhibition in shallow-water corals (2.5 m or less), since corals collected at 6–11 m would not necessarily have the light response of those naturally growing at 0–2.5 m.

The occurrence of drowned reefs suggests submergence rates faster than net reef growth.

If maximum growth occurs below zero mean low water level, a depth of maximum coral growth should occur during submergence. If the reef continues to submerge faster than this maximum rate, effective growth will slow and eventually stop, forming an inactive drowned reef. The point at which this maximum growth occurs would probably be species-dependent. It would also be influenced by factors other than light and depth, such as temperature, sedimentation, surge and current action, nutrients, and salinity.

To localize this region of maximum growth for a particular species, high-resolution studies should be performed using many growth or transplant stations between 0 and 10 m. If transplant studies are used, sufficient time should be allowed for light adaptation. Because of typically high variability in coral growth, several replicates at each station would be needed. Monitoring of other environmental parameters may be needed to separate light and depth effects on growth from other variables (Maragos 1972). Such data for several of the important reef-forming corals should provide exact data on depth of maximum growth. They should also provide further information on photoinhibition of coral growth.

ACKNOWLEDGMENTS

The generous use of the facilities of Mid-Pacific Marine Laboratory, the Hawaii Institute of Marine Biology, and the National Oceanic and Atmospheric Administration Hydro-Lab are gratefully acknowledged. Philip Helfrich, R. E. Johannes, Albert E. Smith, and J. M. Wells provided valuable advice and encouragement. Lance Hodges and Jim Maragos helped in the collection and analysis of some of the data.

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